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Reproductive Strategies and Life-history Traits of the Savi's Pine Vole, *Microtus savii*

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ABSTRACT—Reproductive strategies, growth rates, survival, and their correlates with life-history traits are studied in the Savi's pine vole (*Microtus savii*) under both natural and laboratory conditions. 119 reproductive events were monitored, 50 out of which came from wild-born females and 69 came from captive-born females. Fertility rates were nearly identical in both males and females. Mean age at first parturition of females averaged 72.6 ± 12.1 days, and the mean time elapsed between the constitution of a given pair and the first partum was 31.5 ± 11.5 days. The litter size of captive-bred females (2.49 ± 0.7 ; range: 1 to 4) was nearly identical to that of the free-ranging females (2.5 ± 1.1). The newborn sex ratio did not significantly deviate from equality. Litter size was independent on season and on number of times that a given pair reproduced. Nevertheless, litter size tended to be inversely correlated with the length of the interpartum time, and was positively correlated with parental age. The size of the litter from which the mother and the father of a given litter were generated tended to be positively correlated with the litter size produced by them, but only the relationship relative to males attained statistical significance. Females first gave birth to young at an age between 65 and 99 days. Female puberty was attained at 50.2 ± 13.1 days, almost the same as male puberty ($x = 47.2 \pm 11.1$ days). Females gave birth to young on average once every 29.4 days. The interpartum time was not influenced by either female age or male age, but was shorter in spring and winter (wet seasons in the Mediterranean bioclimate) than in summer and autumn (dry seasons). Mean weight of the juveniles was negatively correlated with the litter size. The facts that litter size was constituted by a small number of young and that the mean gestation time was relatively prolonged suggest that *Microtus savii* is a K strategist within the Microtinae, whereas these rodents are well known to be usually extreme r-strategists. In general terms, our data are consistent with those coming from other fossorial voles, and suggest that fossorial voles (i) give birth to a lesser number of young per litter than above-ground active voles, and (ii) have an age at puberty delayed in comparison with that of above-ground active voles.

INTRODUCTION

Microtine rodents have been subjected to detailed research, especially in north-America and northern Europe, as far as several aspects of their life-history traits is concerned, including demography and population structure (Krebs *et al.*, 1969; Bonstra and Krebs, 1977; Ford and Pitelka, 1984; Bonstra and Boag 1987; Sandell *et al.*, 1990, 1991; Erlinge *et al.*, 1991; Guédon and Pascal 1993; Paradis *et al.*, 1993; Paradis, 1995), and reproductive biology as well (Buchalczyk, 1961; Lefevre, 1976; Schropfer, 1977; Schadler, 1978; Schadler and Butterstein, 1979; Niethammer and Krapp,

1982). However, very little is known on the correlates of litter size, primary sex-ratio, survival rates, and fecundity in the microtine species which are endemic to the Mediterranean region, as e.g. the Savi's pine vole *Microtus savii*. This lack of knowledge is a serious problem not only for our general understanding of the diversities of microtine rodent life-history traits (Tamarin and Krebs, 1969; Viitala *et al.*, 1996), but also because these species are agricultural pests in the Mediterranean region where they sometimes cause dramatic damage to several crops (Santini, 1977, 1983). Thus, any reliable control program against these rodents cannot be successfully put into practice (Santini, 1983; Caroli, unpublished data). The Savi's pine vole is a subterranean burrowing species, living in open grassy areas and in cultivations (Santini, 1983; Caroli, unpublished data). Its galleries consist of relatively rec-

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tilinear corridors, with several exits to the open. The depth of the galleries is known to vary remarkably in relation to environmental conditions (food availability, structure and permeability degree of the soil, etc), but usually it varies between 10 and 50 cm under the ground level (Santini, 1977; Caroli, unpublished data). The diet of the Savi's vole is only vegetarian, and especially Graminaceae, Leguminosae, Compositae, and Chenopodiaceae plants are eaten (Santini, 1983; Salvioni, 1986; Caroli, unpublished data).

In this paper we examine the reproductive strategy, litter size, fecundity, and growth rates, and correlated parameters in *Microtus savii* from central Italy, focusing our attention to colonies of these animals maintained for long-term under controlled laboratory conditions. In particular, a main aim of the present study is to emphasize whether general correlation between behavioural adaptations (fossorial / above-ground activity) and reproductive characteristics (puberty, litter size, etc) are found in Italian *Microtus savii*, and whether such correlation is consistent with data on other Microtinae. Moreover, we try to find some evidence on the potential relationships between reproductive biology and seasonality, as it is well known that external factors (e.g. microclimate, etc) could strongly influence the reproductive strategies of many vertebrates (e.g. see Luiselli *et al.*, 1996).

MATERIALS AND METHODS

Savi's pine voles were captured during two different trapping sessions in an apple orchard situated at approximately 600 m asl near S. Martino al Cimino (Viterbo, Latium, central Italy), and in the surrounding forest, during Spring and Autumn 1988. Four transects, composed of 10 trap-stations (spaced 10 m apart), were performed. Each trap-station consisted of two I.N.R.A. traps (see Santini, 1983), baited with oats. Each trapping session lasted five nights, and the traps were visited every morning.

The laboratory colony was maintained in indoor cages at the Department of Plant Cultivation and Defence, University of Pisa, central Italy. Voles were maintained under conditions which approximated the external ones as for photoperiod and air temperature: 16 to 31°C in summer 1988; 3 to 22°C in autumn; 4 to 18°C in winter and 11 to 25°C in spring 1989. Voles were housed in standard laboratory plexiglass mouse cages (41×25×16 cm) with inox grid lids. An upside down flower pot was provided as nest box. Every two days animals were fed with apples, bulbs, tubers, rootstocks and taproots of wild and cultivated plants, water, but above all on a plentiful supply of fresh leaves of Graminaceae and of Leguminosae.

Data on litter size and time (number of days) elapsed between two successive reproductive events (hereafter, interpartum time) were recorded for 91 litters. Weight of newborn voles was recorded on a sample of the total number of litters, totalling 105 young born over four consecutive seasons (summer: 1 July 1988–30 September; autumn: 1 October–31 December; winter: 1 January 1989–31 March; spring: 1 April–30 June 1989). The weight of newborns were recorded once every 48 hours from birth to the ninth week. Thus, the day of birth of the various voles was considered as 0 days of age. The juveniles were parted from their parents after weaning. For 30 captive-born animals (16 males and 14 females) used in the experiments we recorded their natal litter size as well as the size of the litters they generated. As these animals produced more than one litter in their life, we calculated for all analyses the mean size of the various litters.

The individuals used for assessing male and female fecundity

were paired with known breeders of the opposite sex. This procedure permitted us to correctly assess whether the eventual infertility was caused by the male or the female. Females used for puberty determination were paired with partners of known fertility as soon as the external genitalia became differentiable, i.e. at the approximate age of 40 days. This was relevant to the estimation of the age at first parturition and for the discussion of the interspecific differences at the age of puberty. Moreover, some of the above-mentioned females (n=9) were paired with males when their external genitalia were not still recognizable (ages: 28–36 days), but they produced offsprings only after at least 66 days age. The remaining sample of captive-born animals was set free in the field (S. Martino al Cimino, province of Viterbo) because, due to the high reproduction rates of these voles (see data below), it was impossible to house in the laboratory all the newborn animals. For more details on the methods employed, see Caroli (1992), and Caroli and Santini (1996).

Statistical analyses were done with a SPSS pc package (version 6.0, for Windows), with alpha set at 5%. Normality of data distribution was checked by using Kolmogorov-Smirnov test. When appropriate, data were analysed by means of parametric tests. Otherwise, non parametric statistics were employed. All means given in the text are followed by ± 1 standard deviation. Sexual size dimorphism (in body masses) was tested between seasons by using two-way ANOVAS.

Differences in litter size were assessed by Kruskal-Wallis ANOVA, while relationships between sets of variables were analysed by Spearman's rank correlation coefficient. General Linear Models (GLM) were employed to assess relationships between a dependent variable and several parameters as factors and covariates.

RESULTS

Fifty-eight specimens (twenty in spring and thirty-eight in autumn) were captured during the two trapping sessions. Concerning the habitat of capture, 53 animals were captured in open areas, and only 5 were captured in the wood. On the whole, 18 of the captured specimens were males (31%), 19 females (32.8%) and 21 juveniles (36.2%). Adult sex ratio was 0.95: 1 (χ^2 test, df=1, $P=0.81$).

Considering only adult specimens, the mean body mass was nearly the same in males (18.3 ± 2.6 g) and in non-gravid females (18.4 ± 0.9 g). However, sexual size dimorphism (in body masses) was not significantly different, and there were no significant differences in body masses of males and females between seasons (two-way ANOVA: $F_{3,30}=0.11$, $P=0.95$; sex: $F_1=0.01$, $P=0.93$; season: $F_1=0.01$, $P=0.94$).

We collected data on six females which mated in the wild (since they were already gravid at the time of capture) and were then housed in the lab. All of them gave birth within 20 day from the capture. The litter size of these females was 2.5 ± 1.1 , and ranged from 1 to 4.

On the whole, we obtained data for 119 litters, out of which 50 were obtained from wild-born females, and 69 were obtained from captive-born females.

Twenty-two males were tested for fecundity, and 21 of them (95.5%) were able to reproduce. With regard to the females, 23 (92%) out of 25 examined specimens were able to give birth to young. The difference in fertility rates between males and females was not statistically significant ($\chi^2=0.01$, df=1, $P=0.93$). The mean age at first parturition of the cap-

tive-born females ($n=15$) was 72.6 ± 12.1 days (range: 65–99 days), while the mean time elapsed between the constitution of a given pair and the first partum was 31.5 ± 11.5 days (range: 24–58 days). In thirty-eight cases we removed the male from the cage 48 hours after the female parturition. In seventeen cases (44.7%) the female gave birth to a new litter 22–24 days later.

Mean litter size of captive-bred females was 2.5 ± 0.7 ($n=119$) and ranged from 1 to 4. Thus, the litter size of captive-bred females was nearly identical to that of the free-ranging females ($P=0.8$, Kruskal-Wallis one-way ANOVA). The primary sex ratio (1.21:1, $n=106$) was not statistically biased toward a given sex ($\chi^2=0.94$, $df=1$, $P=0.33$).

Litter size was independent of season (Kruskal-Wallis one-way ANOVA: $H=3.54$, $df=3$, $P=0.31$) and on number of times that a given pair reproduced ($r_s=0.07$, $n=119$; $P=0.43$). However, the litter size slightly tended to be inversely correlated with the interpartum time, but the relationship was not statistically significant ($r_s=-0.18$, $n=89$; $P=0.09$).

Litter size was positively correlated with parental age, but only the relationship relative to males attained statistical significance (males: $r_s=0.38$, $n=60$; $P=0.003$; females: $r_s=0.19$, $n=69$; $P=0.10$). However, the general correlation of litter size to parental age was curvilinear, with litter size declining after a peak age (Fig. 1), as it is common in vole reproduction. Indeed, the breakpoints were at 225.9 days for males (curvilinear regression by quasi-Newton procedure, $r=0.843$, explained variance 71.2%), and at 217.5 days for the females ($r=0.856$, explained variance 73.2%).

The size of the litter from which the mother and the father of a given litter were generated tended to be positively correlated with the litter size produced by them, but only the relationship relative to males attained statistical significance

(males: $r_s=0.56$, $n=16$; $P=0.02$; females: $r_s=0.31$, $n=14$; $P=0.28$, see Fig. 2). Individual differences were found in the litter size of seven females which reproduced more than eight times (Kruskal-Wallis one-way ANOVA: $n=95$, $df=6$, $H=22.21$, $P<0.001$). The modal length of the gestation period fell between 20 and 24 days, and averaged 22 ± 0.8 days ($n=13$). Females first gave birth to young at an age between 65 and 99 days. Based on these ages, and subtracting the gestation period (22 days), it resulted that the female puberty was attained at an age between 43 and 77 days ($x=50.2 \pm 13.1$ days; $n=12$). Male puberty was attained at an age between 39 and 58 days ($x=47.2 \pm 11.1$ days; $n=8$). There were no statistically significant differences in age at puberty (number of days elapsed since birth) between the sexes (unpaired $t=0.53$, $df=18$, $P=0.6$).

Captive *Microtus savii* indicate that the annual cycle of reproduction was never interrupted throughout the year, despite the interpartum time was shorter in spring and winter (relatively wet seasons in central Italy) than in summer and autumn (relatively dry seasons in central Italy).

The females gave birth to young 11.8 ± 3.4 times per year ($n=7$ females observed). The mean interpartum time was 29.4 ± 13.7 days, and was not significantly influenced by both female age ($r_s=-0.04$, $n=47$; $P=0.95$) and male age ($r_s=-0.01$, $n=39$; $P=0.81$). Interpartum time was significantly affected by the reproducing pair (MANOVA: $F_{11,84}=3.48$, $P=0.001$), and, among the covariates, the only significant parameter was the season ($t=2.35$, $P=0.04$, see Fig. 3). On the contrary, no effect resulted from the litter size ($t=-0.33$, $P=0.74$) and from the order of the reproductive events of a given pair ($t=-0.53$, $P=0.60$). The interpartum time (considering also the pairs which had just a single observation, and which were excluded from MANOVA) was shorter in spring

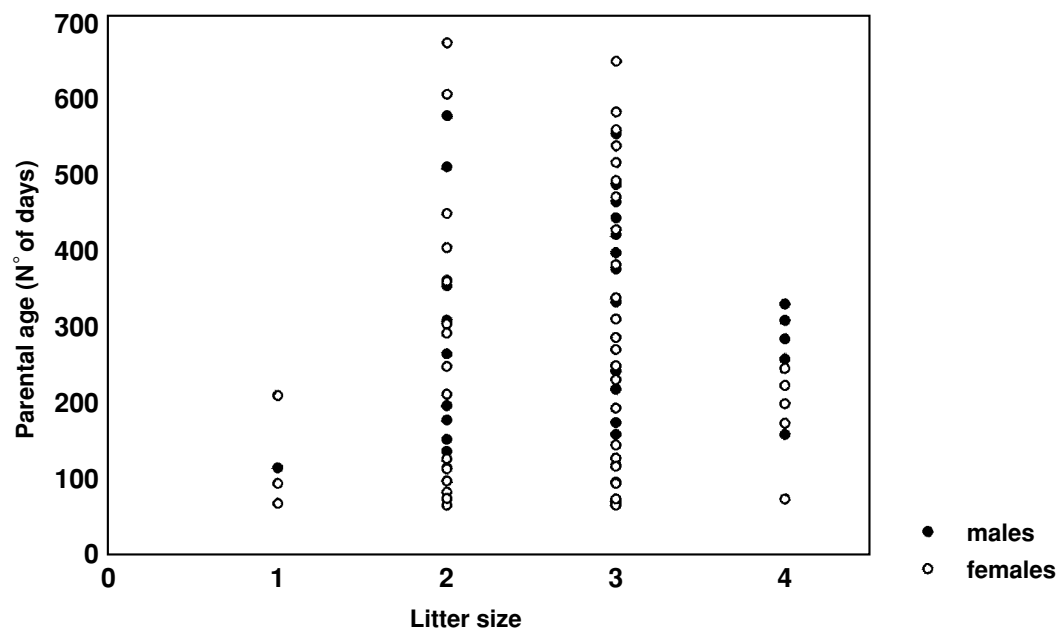


Fig. 1. Relationships between litter size and parental age. Note that only the relationship relative to males attained statistical significance (males: $r_s=0.381$, $n=60$; $P=0.003$; females: $r_s=0.196$, $n=69$; $P=0.10$).

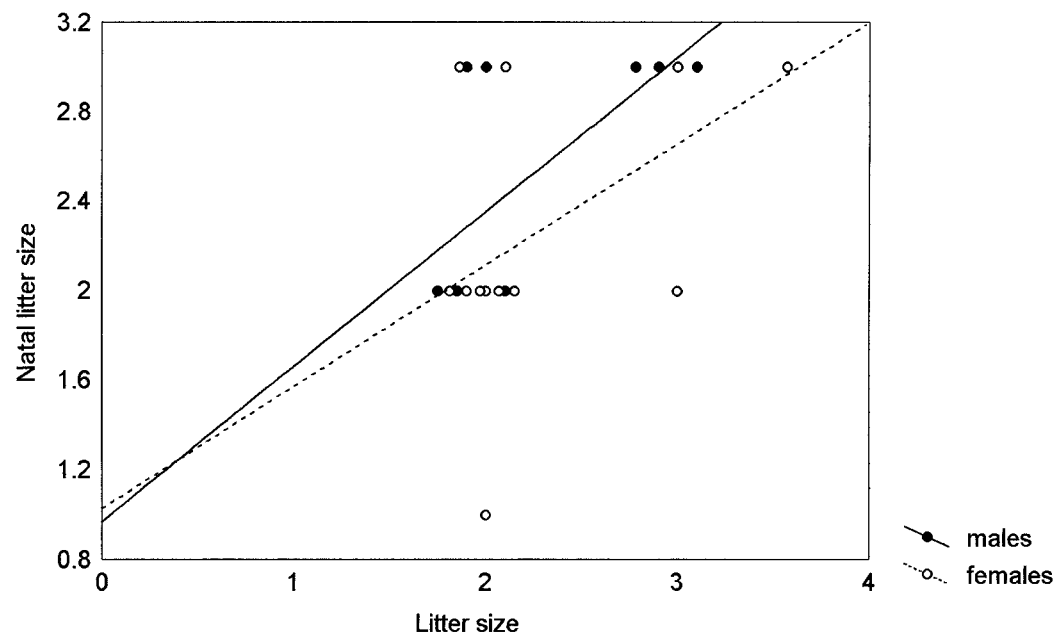


Fig. 2. Correlation between the size of the litter when the parents of a given litter were neonates (parental litter size) and the average litter size produced by them during the life (juvenile litter size). Note that only the relationship relative to males attained statistical significance.

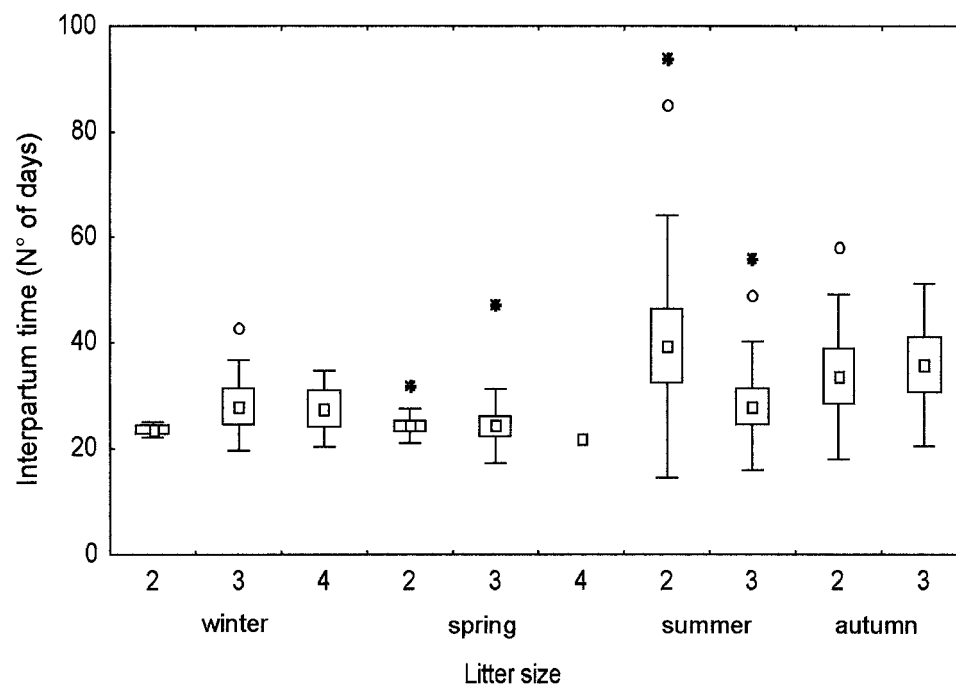


Fig. 3. Means and dispersion measures (i.e. standard deviation and standard error) of the interpartum time in the four season in *Microtus savii* maintained under laboratory conditions. For each season, the presented values are given in relation to the litter size. Symbols: small squares = means; rectangles = standard errors; horizontal segments linked by vertical lines: standard deviation; small circles and asterisks: outliers.

($n=25$, $x=24.2 \pm 5.3$ days) and winter ($n=16$, $x=26.2 \pm 6.4$ days) than in summer ($n=25$, $x=33.3 \pm 19.6$ days) and autumn ($n=23$, $x=33.2 \pm 14.3$ days).

The seasonal variations of the body weight of both males and females at 5, 15, 25, 35, 45 and 55 days are presented in Fig. 4. In Table 1 the results of MANOVAs performed on the body masses (dependent variables) of the offsprings at 5, 15,

25, 35, 45 and 55 days are given. In this analysis, the factors were the various pairs and litter size, season, sex, and the number of partum were used as covariates. Based on these MANOVAs, we found statistically significant models in four of six sets of analysis, and in all cases the unique significant effect was the one attributable to the individual pair.

The mean weight of the juveniles was always negatively

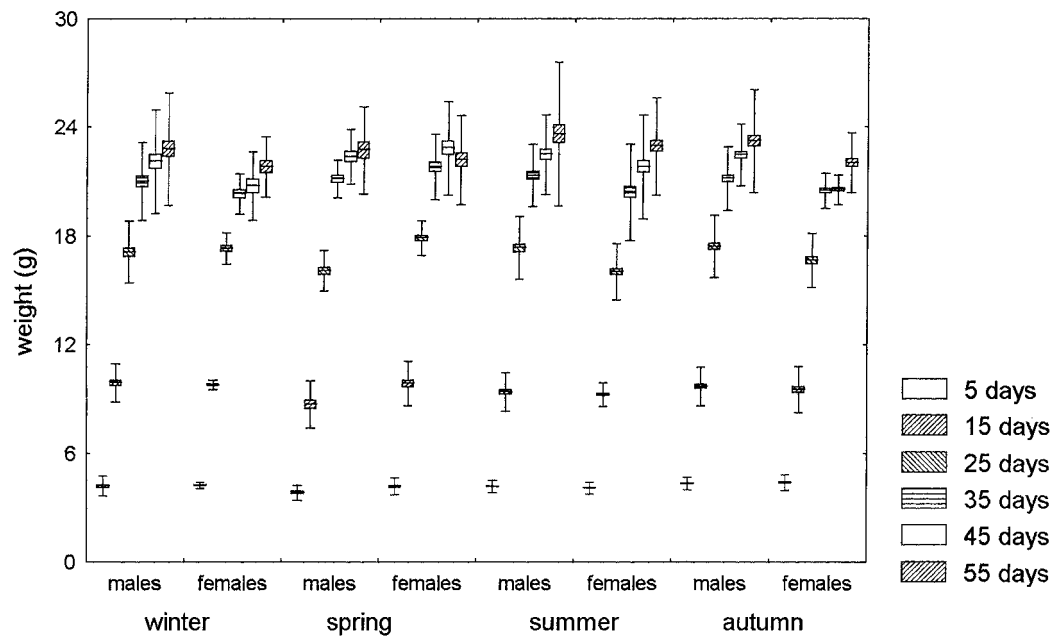


Fig. 4. Seasonal variations of the body weight of both males and females at 5, 15, 25, 35, 45 and 55 days of age.

Table 1. Results of MANOVAs on the offspring body mass at 5, 15, 25, 35, 45 and 55 days. In this analysis, the factors were the various pairs, while litter size, season, sex, and the number of partum were used as covariates.

		model	factor pair	covariates			
				litter size	season	number of partum	sex
5 days	df	13, 58	9				
	F	2.05	1.89	−1,005	0.642	−0.242	0.821
	P	0.04	0.08	0.32	0.52	0.81	0.42
15 days	df	14, 70	10				
	F	2.75	3.28	−1,051	−0.916	0.224	0.055
	P	0.004	0.002	0.32	0.36	0.82	0.96
25 days	df	14, 67	10				
	F	1.13	1.15	−1,486	0.611	0.548	−1,002
	P	0.36	0.35	0.14	0.54	0.59	0.32
35 days	df	14, 72	10				
	F	1.65	1.75	0.683	0.44	0.408	−0.903
	P	0.09	0.09	0.5	0.661	0.68	0.37
45 days	df	14, 69	10				
	F	3.66	4.18	0.834	0.876	0.384	−1,844
	P	0.0002	0.001	0.41	0.38	0.7	0.07
55 days	df	14, 65	10				
	F	2.48	2.49	0.204	0.065	−0.487	−1,333
	P	0.009	0.02	0.84	0.95	0.63	0.19

correlated with the litter size, and in three stages of development this relationship was statistically significant (at 5 days: $r_s = -0.387$, $n = 31$; $P = 0.03$; at 15 days: $r_s = -0.349$, $n = 37$, $P = 0.034$; at 25 days: $P = 0.27$; at 35 days: $r_s = -0.370$, $n = 36$; $P = 0.03$; at 45 days: $P = 0.10$; at 55 days: $P = 0.19$).

130 specimens were tested to estimate the survival and mortality rates at the various ages. The number of survived specimens was checked at 20 days of age (99.2% survival),

40 days (97.7%), 50 days (95.4%), 75 days (93.1%), 100 days (89.2%), 120 days (83.8%), 240 days (73.1%), 360 days (41.5%), and 540 days (20.8%). The survival rate did not differ significantly between sexes ($\chi^2 = 0.94$, $df = 6$, $P = 0.98$).

DISCUSSION

The pattern of an uninterrupted cycle of reproduction

throughout the year in our voles mirrors the one already observed in *Microtus duodecimcostatus* from southern France, a species in which the reproductive activity of females is strongly dependent on the rainfall (Guedon and Pascal, 1993). The continued reproductive activity in our laboratory voles can also be attributable to the permanent availability of green grass in their cages, as reports in the literature suggest that young growing herbaceous plants in the diet of certain small herbivorous mammals exert a profound influence on their reproductive activity (Pinter and Negus, 1965; Birney *et al.*, 1976). However, captive-bred colonies of voles usually lack of a regular sexual cycle even under permanent food availability (Jemio, 1983).

Italian *Microtus savii* proved to be very similar to *Microtus duodecimcostatus* also in other traits of reproductive biology, including a mean litter size constituted by a low number of young compared to other microtine species (on average 2.49 versus 2.34 young per female), delayed age at puberty, relatively prolonged mean gestation time (on average 22 days versus 24 days; see Guedon and Pascal, 1993), and high survival rates of newborns. These characteristics suggest that *Microtus savii* is a K strategist within the Arvicolidae, as well as *Microtus duodecimcostatus* and *Microtus pinetorum* (Schadler, 1981, 1983; Guedon and Pascal, 1993). On the contrary, most studies of microtine rodents demonstrated that these animals are extreme r-strategists and J-shaped population growth curves are quite ubiquitous (e.g. see Kalela, 1957; Myllymaki, 1971; Viitala *et al.*, 1996). However, it should be noted that the breeding cycles of microtine rodents are generally restricted, so the Savi's pine voles' prolonged breeding seasons might be responsible to the relatively low reproductive rates shown in this study.

In general terms, review of available data suggests that fossorial voles, including *Microtus savii*, gave birth to a lesser number of young per litter than in the above-ground active Arvicolidae species (Table 2). These characteristics of the two Mediterranean voles may explain the fact no population out-

break of voles are known to occur in the Mediterranean basin (Elton, 1942). However, it has been noted that in *M. duodecimcostatus* the absence of population cycles seems to be explained also by the existence of an adaptive dispersal mechanism (Paradis, 1995).

The fact that litter size was significantly correlated with parental age is a widespread pattern in lower vertebrates—where, however, the correlation is especially evident for the maternal age (e.g. see Luiselli *et al.*, 1996), but is an uncommon pattern in mammals (Ralls, 1976; Shine, 1988). Moreover, exactly as noted in other phylogenetically unrelated vertebrates (cf. Luiselli *et al.* 1996), the size (mean weight) of the young at birth was inversely correlated with the number of young forming a litter, which clearly suggests a morphological constraint over the female to carry inadequately large embryo mass.

Interestingly, we obtained evidences suggesting that (i) the natal litter size influenced the mean litter size produced by a given individual later in the life, and (ii) the litter size of a given pair would possibly be genetically attributable more to the father than to the mother, as the size of the litter from which the mother and the father of a given litter were generated was significantly correlated only with father litter size. The reason for these patterns is intriguing but, at the moment, quite unexplicable, and further research is needed before giving any interpretation. The hypothesized genetical effects on the litter size would be better understood by designing *ad hoc* experiments by using animals of totally controlled family lines.

With regard to the minimum age of reproduction of female *Microtus savii* (nine out of twelve females which were pregnant at 42–48 days of age), it is interesting to note that our data are consistent with data available for other fossorial voles—*Microtus savii*, *Microtus duodecimcostatus*, *Microtus pinetorum* and *Microtus subterraneus*—, thus indicating that their puberty (occurring during the second month of life) is delayed in comparison with that of above-ground active voles (puberty occurring during the first month of life; see Table 2).

Table 2. Summary of the reproductive data in relation to type of behaviour in captive-bred colonies of voles. Pertinent literature sources are included

Species	Type of behaviour	Litter size		Age at puberty (days)	Literature
		Range	Mean		
<i>Microtus arvalis</i>	Above-ground active	1 to 9	5.3	21	Lefevre 1966, Martinet and Spitz 1971
<i>Microtus pennsylvanicus</i>	Above-ground active	2 to 8	5.5	25 to 38	Schadler 1978
<i>Microtus agrestis</i>	Above-ground active	2 to 8	4.7	?	Schadler 1978
<i>Microtus californicus</i>	Above-ground active	1 to 9	4.7	?	Schadler 1978
<i>Microtus montanus</i>	Above-ground active	3 to 9	6.0	?	Schadler 1978
<i>Microtus ochrogaster</i>	Above-ground active	1 to 8	3.8	40	Schadler 1978
<i>Microtus oregoni</i>	Above-ground active	1 to 6	3.8	27	Cowan and Arsenault 1954, Schadler 1978
<i>Microtus pinetorum</i>	Fossorial	1 to 6	3.1	77	Schadler 1978, Schadler and Butterstein 1979
<i>Microtus subterraneus</i>	Fossorial	1 to 5	2.7	60 to 90	Buchalczyk 1961, Wasilewski 1960
<i>Microtus subterraneus</i>	Fossorial	?	?	90	Schropfer 1977
<i>Microtus duodecimcostatus</i>	Fossorial	1 to 4	2.4	60	AA. VV. 1986
<i>Microtus multiplex</i>	Fossorial	1 to 4	2.3	?	Niethammer and Krapp 1982
<i>Microtus savii</i>	Fossorial	1 to 4	2.6	43 to 77	Present study
<i>Clethrionomys glareolus</i>	Above-ground active	?	?	32	Schadler 1978

Seasonality is important to discuss on the reproductive patterns in mammals in general (see Bronson, 1989) and especially in those species inhabiting regions characterized by strong interseasonal climatical variations, e.g. Mediterranean areas. With regards to our study case, we found that season had a little influence on most of the studied parameters, apart for the interpartum time. This relative scarce importance of the season is likely to be attributable to the general food abundance of our experiment over the whole year (see Heske et al., 1984; Bronson, 1989). However, interpartum times observed in *Microtus savii* were very similar to those observed in *Microtus pinetorum* from New York State (Schadler and Buterstein, 1979) and in *Microtus subterraneus* from Poland (Jemiolo, 1983).

In conclusion, although our study has highlighted a number of remarkable patterns, it should be noted that our data are to be considered with some caution, given the fact that the whole captive colony of voles was generated from free-ranging individuals trapped in a single locality, and there is abundant evidence from several closely-related taxa that there is much geographical and altitudinal variation in life-history traits of vole species (Viitala et al., 1996, and references therein).

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