The biology of the Levant vole, *Microtus guentheri* in Israel

II. The reproduction and growth in captivity

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Abstract

The reproductive biology of the Levant vole *(Microtus guentheri)* was investigated in captivity. About 200 adults and 1800 pups were kept in the breeding colony of the Wildlife Research Center of Tel Aviv University for 3 years (1977–1979). Colony records, vaginal smears, dissections and daily weighing of the pups contributed to the understanding of the reproductive potential and the postnatal development of this rodent. Levant voles breed seasonally – with maximum birth occurring in March. Pregnancy lasts for 21 days. A post-partum oestrus and a post-lactational oestrus with high fertility are common. These results indicate a high reproductive ability assuring rapid recycling at the population level. It was also found that the 5–6 pup litter is the most stimulating factor in the milk yield of the female, as judged by the high body weight per pup attained at weaning by this litter size.

Introduction

Relatively little work has been done on the Levant vole, *Microtus guentheri* either in the field or in capitivity. Bodenheimer (1949) had a breeding colony for several years, Zondek and Sulman (1940) reported on the population dynamics and Yardeni (1951) studied their behaviour during the breeding season.

We studied the biology of reproduction and population ecology of this species in the Coastal Plain of Israel (Cohen-Shlagman et al. 1984) and complemented this study by keeping Levant voles in a self-replenishing breeding colony. Physiological traits obtained from captive animals prove to be of great importance in interpreting field data. For example, the existence of post-partum oestrus is much simpler to test in captivity, and so are litter size, growth rate, sexual maturation and certain behavioral patterns.

The aim of this work is to report the results of this laboratory study and compare them with our field data and published data on other vole species.

Material and methods

A breeding colony of voles was established in the Tel Aviv University Wildlife Research Centre (WRC). Wild voles were trapped in November–December 1976 in the Coastal Plain of Israel. They were sexed, weighed and kept singly in 30 × 35 × 22 cm or 45 × 30 × 22 cm glass terraria with an iron mesh cover. Sawdust and straw were provided as bedding. Opigal powder (5 %) was spread on the floor to prevent the development of parasites. In each terrarium a 15 cm diameter flower-pot was placed as a shelter. Animals were fed on alfalfa and fresh carrots (or apples) provided once daily. The colony was kept both in an open yard and in a room with uncontrolled temperature and day-night regimes.

In January 1977 the voles were paired, and each pair was kept in 48 × 34 × 20 cm stainless steel cages with a wire mesh cover. Two flower-pots were placed in each cage; all other conditions were as mentioned above.

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The physical condition of the animals were recorded daily and the nests checked for newborn. All young voles were individually marked by toe clipping and weighed every second day. After weaning at 15–20 days of age, the young were removed from the parental cage. In addition to the monogamous pairs, we kept several cages with one male and several females, and in other cages groups of several males and females.

Vaginal smears from five paired and five unpaired females were analysed (April–July 1978). Smears were taken daily by flushing the vagina with saline from an eye-dropper. They were air dried and stained with Toluidine blue and examined microscopically. The presence of motile spermatozoa in the cauda epididymis was checked every month in 5 adult males (December 1978 to October 1979). The first appearance of spermatozoa in the cauda epididymis of young voles was examined by dissecting young males aged 30 to 100 days at 10 days intervals.

Results

Breeding in captivity

Seasonality. The distribution of births based on the analysis of colony records (birth date and litter size), is shown in Table 1. There was a major peak of births in March (36.4 %) evident in all three years of study.

The breeding season in captivity only partly overlapped the breeding season in the field (November to April; Cohen-Shlagman et al. 1984). It appears that keeping voles in captivity changed not only the time of breeding but also the fertility pattern: the third breeding season was extended and 11 births occurred both in March and October. Throughout the study period, 54 fertile pairs produced 118 litters with an average of 2.09 litters per pair ranging from 1.4 to 2.3.

Receptivity at time of pairing. An estimate of the length of first pregnancy was necessary to assess the receptivity and fertility of virgin Levant voles. The time interval between pairing and first parturition in 1977 is given in Table 2. Only 4 of the females mated and conceived immediately after pairing and gave birth – 21 to 25 days after pairing (21 days is the modal gestation length) but 17 of the females did so after 26 to 150 days following pairing. It seems, therefore, that willingness to mate increased if the nulliparous females were exposed to males for longer periods.

Post-partum fertility. The minimal time interval between successive litters may be considered as the length of pregnancy. In our Levant vole, this interval was 21 days. The time interval between successive litters in the captive vole population is shown in Table 3. It can be seen that 41.0 % of births occurred within 21 to 25 days after the previous parturition. This indicates instances of pregnancy which had arisen following mating and conception during the post-partum oestrus. Voles which did not become pregnant at the post-partum oestrus, conceived towards the end of lactation. Numerous females littered again between days 31 to 50 after the first litter when 9.8 % and 8. 2% did so on days 36–40 and 46–50, respectively. Since the modal gestation length is 21 days, these females had conceived while in oestrus before weaning their young (at 15 to 20 days); or developed a post-lactational oestrus with high fertility. The decrease in the occurrence of litters between days 26 to 30 post-partum seemed to be the result of a drop in receptivity during mid lactation (5 to 10 days post-partum). The extension of the time interval from 21 to 25 days between successive litters may be attributed to a delay in implantation in concurrently lactating females.

Succession of litters. The number of subsequent litters per pair during the reproductive seasons is shown in Table 4. Most females (92.6 %) gave birth to 1–3 litters.

Litter size. Fertility could be estimated in the Levant vole using the average size of litters throughout the years. The number of pups in a litter ranged from one to ten. The maximum number of ten pups per litter was observed in 4 voles only. The modal mean

Table 1

The incidence and number of parturitions in the breeding colony

Month	1977–1979 No. of litters	%
II	6	5.1
III	43	36.4
IV	26	22.0
V	18	15.3
VI	5	4.2
VII	5	4.2
VIII	3	2.5
IX	1	0.8
X	11	9.3
Total	118	100.0

Table 2

The time interval between pairing (in January, 1977) and first birth in 21 pairs

	Time interval (days)			
days	21–25	26–30	31–35	36–150
n	4	4	2	11
%	19.0	19.0	9.5	52.3

Table 4

The number of successive litters per pair

No. of successive litters	%	n
1	33.3	18
2	35.2	19
3	24.1	13
4	3.7	2
5	3.7	2

Table 5

Litter size in the breeding colony

Month	Mean litter size	n
II	5.8	5
III	7.0	43
IV	6.9	26
V	5.3	18
VI	5.2	5
VII	4.2	5
VIII	2.7	3
IX	3.0	1
X	4.5	11
Mean	6.1	117

Table 3

The time interval (days) between successive litters

The percentage (and number of pairs) is given for each time interval

	Time interval (days)						
	21–25	26–30	31–35	36–40	41–45	46–50	51–150
Total %	41.0 (25)	1.6 (1)	8.2 (5)	9.8 (6)	9.8 (6)	8.2 (5)	21.3 (13)

litter size in all years was 6.1 pups. The frequency of various litter sizes and means are given in Fig. 1 and Table 5.

Fertility and the time factor. The number of fertile pairs decreased with time (see Table 6). In their first year in captivity, 88 % of the breeding pairs gave birth to litters, while only about 60 % of the pairs reproduced later on.

Age at sexual maturity. Male: Motile spermatozoa were found in the cauda epididymis of all adult males examined between December to October, but none were found in males younger than 100 days. However, in one case a male aged 85 days fertilized a female. This appears to be the minimal breeding age for males.

Female: Females at weaning (n = 90) raised together with males of the same age showed delayed vaginal opening (ca. one year) when compared to females raised with sexually mature males. The youngest female in this category with an open vagina was 30 days old whereas in most females the vagina opened at 60 days of age. It appears that

pairing of juvenile females with adult males during the reproductive season may hasten the onset of puberty including an advance of vaginal opening. The minimal breeding age for females is about two months: the youngest female gave birth at 85 days of age.

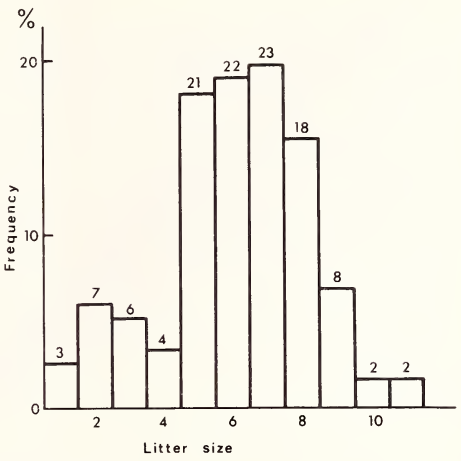

Fig. 1. Litter size frequency in the breeding colony

Vaginal smear. Microscopic examinations of the vaginal smears did not show any regular, cyclic changes in the ratio between the three cell types found in the vagina: leucocytes, nucleated epithelial cells and cornified cells. In 3 of the parturitional females examined, there was an increase in the number of epithelial and cornified cells before copulation and a decrease after impregnation. Another increase of these cells was recorded after parturition and about 10, 17 to 19 and 36 to 38 days after parturition. These results indicate that Levant voles have no apparent vaginal cycle and that vaginal smears are not reliable indices of receptivity.

Postnatal development

Microtus guentheri is a nidicolous rodent with an altricial state of development. They are born with sealed eyes covered by a thin layer of skin and closed ears attached to the head. Hairs begin to grow on the dorsal side when the pups are 4 days old, and on the ventral side on the 7th day of age. The incisors erupt on day 5. The eyes and ears open at about day 10. The toes of the forefeet begin to separate on day 7 and those of the hind feet on day 9. By day 5 they crawl out of the nest. Infant Levant voles start to eat green food on day 10 and are weaned at about day 20 post-partum.

Table 6

Age and fertility in voles of the breeding colony

Year	Mean age (years)	Total no. of pairs	No. of fertile pairs	% fertile
1977	1	24	21	88
1978	1.3	25	15	60
1979	2.0	29	18	62

Sex ratio. It was possible to determine the sex in the newborn voles during the first week of age. Females have 4 pairs of nipple sites which are conspicuous before the fur grows and covers the nipple area. Males have a dark pigmentation in the area between the anus and the penis. The overall sex ratio was 0.82 females per male ($n = 547$; $X_2 = 5.14$; $p < 0.05$). There was no difference in the sex ratio throughout the years concerned with this study.

Growth rate. The growth rate of males and females up to 45 days of age is shown in Figures 2 and 3. Growth rates were similar for both sexes (In females: $y = 1.582 + 0.626\ x$; $r = 0.978$; $n = 114$. In males: $y = 2.017 + 0.626\ x$; $r = 0.974$; $n = 116$. x = age in days; y = weight in g). Males were born on average 27 % heavier than females, and remained heavier but the weight difference later was not significant.

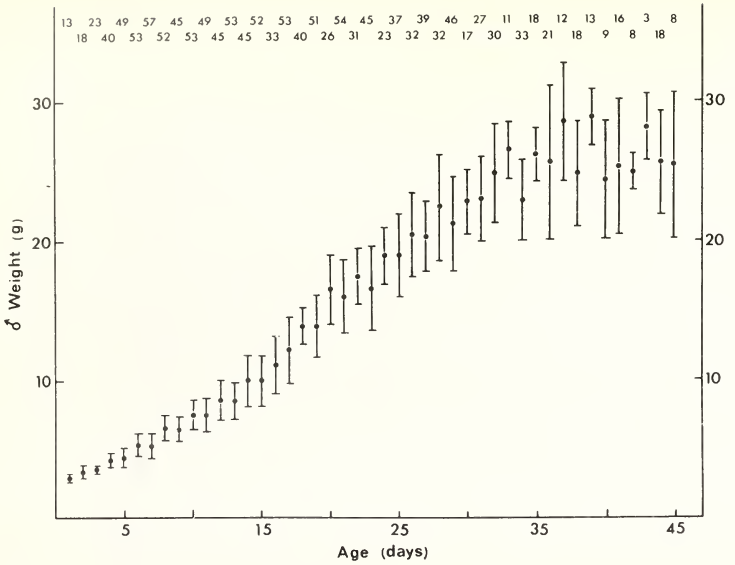

Fig. 2. Growth rate of males (means ± standard deviation). Sample sizes are given above the mean. Y = 2.107 ± 0.626x; r = 0.974; n = 116

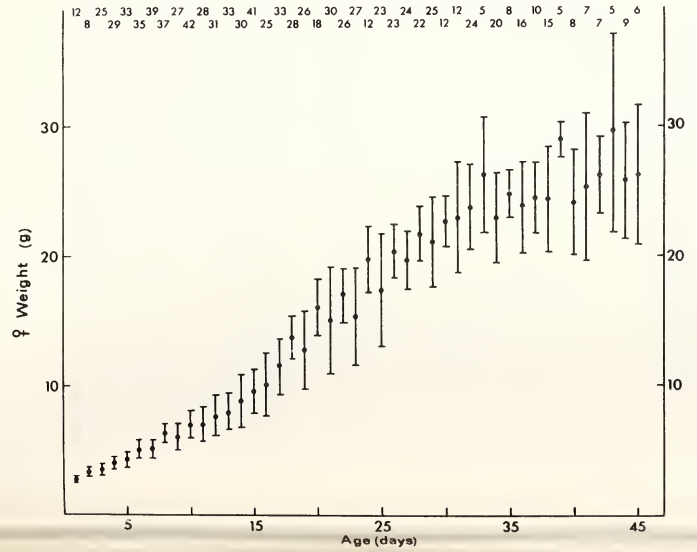

Fig. 3. Growth rate of females (means ± standard deviations). Sample sizes are given above the mean. Y = 1.582 + 0.626x; r = 0.978; n = 114

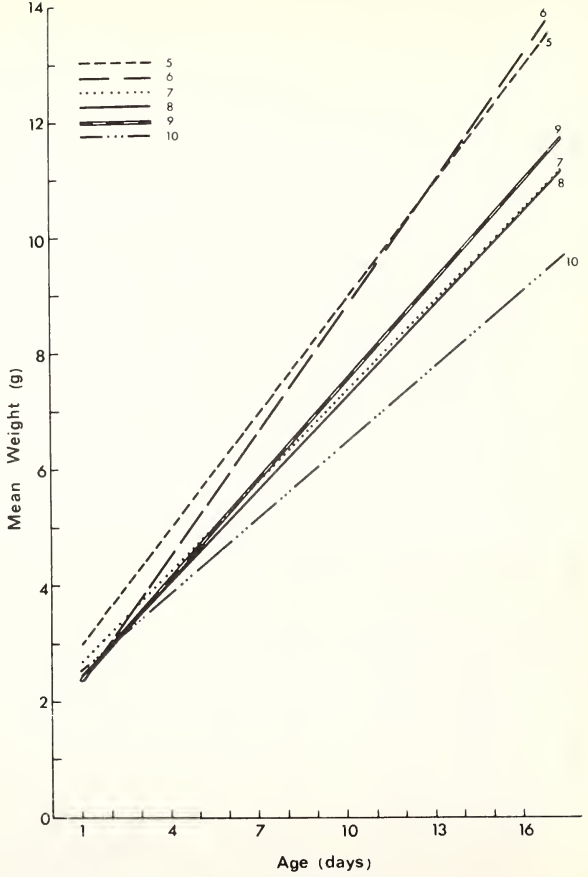

Fig. 4. The relationship between age (x), mean weight (y), and litter size. Statistical data are given in Table 7

Table 7

The relationship between age (x) and body weights (y) of voles of various litter size

Litter size	5		6		7 pups		8		9		10	
Age (days)	n	x ± S.D.	n	x ± S.D.	n	x ± S.D.	n	x ± S.D.	n	x ± S.D.	n	x ± S.D.
1	20	2.86±0.29	42	2.71±0.49	42	2.79±0.65	24	2.70±0.30	36	2.69±0.45	20	2.61±0.31
17	5	14.15±0.80	24	15.16±2.38	28	11.28±2.3	16	12.42±1.67	18	11.16±0.58	10	9.87±0.40
y =		2.35+ 0.651x		1.623+ 0.711x		2.169+ 0.516x		1.930+ 0.531x		1.749+ 0.570x		2.081+ 0.434x
r		0.988		0.983		0.983		0.979		0.988		0.989

Table 8

Synopsis of various reproductive patterns of Levant voles in captivity

Pattern	Years 1977	1978	1979	Overall pattern
Breeding season (months)	6 (Feb.–July)	6 (Feb.–July)	8 (Mar.–Oct.)	
Mean litter size	6.8	5.6	5.5	6.1
Post-partum oestrus incidence %	67.7	42.8	4.3	41.7
Average litters per pair	2.38	1.46	2.27	2.09
% Fertile pairs	88	60	62	
Sex ratio				0.82 ♀ : 1♂
Minimal breeding age				60 days ♀ 90 days ♂

Growth rate / litter size. Until weaning (17 to 20 days post-partum), growth rates were dependent on litter size; young born in litters of 5–6 pups were heavier at weaning (maximum 15.1 g), litters of 7–9 pups were of intermediate weight (maximum 12.4 g) and pups born in litters of 10 were lightest (mean = 9.8 g), Figure 4 and Table 7.

Discussion

The breeding potential

The breeding ability of voles in our colony decreased from 1977 to 1979. This was due to the decreased proportion of breeding pairs (partly because of increased age), declining litter size, less litters per pair and a slow down of the post-partum oestrus incidence (Table 8). In 1979 the breeding season extended from 6 months to 8 months and there were two breeding peaks (March and October) instead of one. This may be an effect of captivity but other factors may also be involved.

Receptivity

The distribution of litter intervals appears to be bi-modal with a major peak of births on day 21 and minor peaks in the interval of 31–50 days. This frequency distribution can be interpreted as follows: the majority of females conceive immediately after parturition, while lactating; but a small proportion is not fertilized at this time and becomes pregnant during lactation, fertility rising apparently after the weaning of litters (17–20 days post-

partum). Similar observations and interpretations have been made on *Microtus arvalis* (Reichstein 1964); on *Microtus ochrogaster* (Richmond and Conaway 1969); on *Clethrionomys glareolus* for a laboratory colony in Sweden (Gustafsson et al. 1980); and for a laboratory colony in Oxford (Clarke and Hellwing 1983). Changes in receptivity and fertility during lactation, both high immediately post-partum, then declining and rising again at about the time of weaning are well known in other mammals such as the rabbit *Oryctolagus* sp. (Beyer and Rivault 1969); White-toothed shrew *Crocidura russula monacha* (Hellwing 1975) Mongolian gerbil *Meriones unguiculatus* (Norris and Adams 1981) etc. By contrast, receptivity and fertility are uniformly high throughout lactation in the field vole *Microtus agrestis* (Breed 1968). According to Conaway (1971) the mechanism of the post-partum oestrus increases productivity and translated to natural populations it seems to be its most important biological function in the reproductive cycle of small mammals (voles, bank voles, shrews) which have a relatively short life span. The high breeding potential of the Levant voles based on post-partum and post-lactational oestrus, is fully expressed in the good environmental conditions which prevail in the Hula Valley in Northern Israel, where voles live in irrigated alfalfa fields. Here they cause great damage to agriculture (Mendelssohn and Paz 1977).

Nulliparous females of Levant voles showed increased willingness to mate if they were exposed to males for longer periods. Similar observations have been reported for the shrew *Crocidura russula monacha* (Hellwing 1975) and for the bank vole *Clethrionomys glareolus* (Clarke and Hellwing 1983). It appears that a proportion of such females need the presence of a mature male to evoke adequate sexual behaviour or to bring about some priming of the reproductive tract (Clarke and Clulow 1973). Such captivity findings may reflect certain aspects of the social organization within the natural populations of the species concerned. The influence of social stimuli (such as the presence of males) on sexual maturation in females (vaginal opening) was noted in the Levant vole too and confirms the results obtained by Vandenbergh (1973) in mice.

Vaginal smear patterns show the Levant vole to be a species which may have no regular oestrus cycles under laboratory conditions. Similar evidence has been presented by others such as Clulow and Mallory (1970) for *Microtus pennsylvanicus;* Clarke and Kennedy (1967), Breed (1967, 1968) for *Microtus agrestis*; Richmond and Conaway (1969) in *Microtus ochrogaster* and Langford and Clulow (1979) in *Clethrionomys gapperi.* It is suggested that this phenomenon may be a general feature of the genus *Microtus* or of the Microtinae as a whole.

Sexual maturation

Males. All adult males of the Levant vole examined in captivity during the breeding season had motile spermatozoa in the cauda epididymis, but none were found in males younger than 3 months. However, in the field active spermatozoa were found in males 30 days old. Lecyk (1958, 1959–1960) did not find, however, evidence for sexual activity in young *Microtus arvalis* and claimed that males born at the end of the breeding season, do not breed in the same year. Bodenheimer (1949), on the other hand, reported that sexual maturity in *Microtus guentheri* is reached at the age of 30 days. Our evidence from captivity does not support this later conclusion, but show similarity to this found for *Microtus arvalis.*

Females. Sexual maturation in *Microtus guentheri* as based on vaginal opening occurred at the age of 30 days. In *Microtus arvalis,* however, vaginal opening was observed earlier, at the age of 13 days (Frank 1956). Consequently, *Microtus arvalis* has a higher reproductive potential than *Microtus guentheri.*

Growth and litter size

A general trend of decreasing weight at weaning with increasing litter size was found in *Microtus guentheri.* Three groups could be distinguished. 1. Litters of 5–6 young with a high body weight. 2. Litters with 7–9 young of medium body weight and 3. litters of 10 young with a low body weight. A similar negative correlation between the size of the litter and weight of weaned young was reported by Reichstein (1964) for *Microtus arvalis* and by Nakatsu (1977) in *Microtus montebelli.* According to Salzmann (1963) the suckling stimulus in *Meriones shawi* may cause an increased secretion of oxytocin, which in turn increases milk production and body weight of pups. This statement cannot explain why litters of 7–8 pups in the Levant vole were heavier than litters of 10. Female Leant voles have 8 nipples and competition for nipples may also adversely affect the weight of the suckling young in large litters. This fact may explain the low body weight of the 10 pup litter. Summing up, it appears that the 5–6 pup litter is the most stimulatory factor in the milk secretion process of the Levant vole female with little or no competition for nipple attachment.

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Zusammenfassung

Die Biologie der Mittelmeer-Feldmaus, Microtus guentheri in Israel. II. Reproduktion und Wachstum in Gefangenschaft

Die Fortpflanzung der Mittelmeer-Feldmaus *(Microtus guentheri)* wurde drei Jahre lang (1977–1979) in Gefangenschaft im Wildlife Research Center der Universität Tel Aviv untersucht.

Die Dauer der Fortpflanzungsperiode, die Anzahl der Würfe, Wurfgröße und geschlechtliche Aktivität der Männchen und Weibchen wurden ermittelt. Es besteht in dieser Kolonie offenbar ein jahreszeitlich bedingter Vermehrungszyklus, der von Februar–März bis Juli oder Oktober dauert. Die meisten und größten Würfe fallen in den März.

Die Zahl der Jungen pro Wurf schwankt zwischen 1 bis 10 mit einem Durchschnitt von 6,2. Die Dauer der Trächtigkeit beträgt 21 Tage. 41.7 % der Weibchen werden bei einem nach der Geburt stattfindenden post-partum Oestrus befruchtet und brachten Würfe. Während und nach Ende der Säugezeit wurden oft Oestrus und Begattungen beobachtet (Postlaktationsoestrus). Die meisten Würfe wurden 31–50 Tage nach dem vorherigen Wurf geboren.

Die Jungen werden 17–20 Tage lang gesäugt. Das Verhältnis ♂♂ : ♀♀ ist 55 : 45. Das Wachstum ist bei Geschwistern beider Geschlechter bis zum Alter von 45 Tagen gleich. Andererseits bestehen Unterschiede im Wachstum zwischen verschiedenen Würfen, die von der Anzahl der Jungen im Wurf abhängen. Bei Würfen von 5 oder 6 Jungen hatten die Jungtiere das höchste Gewicht. Diese Tatsache beruht vielleicht darauf, daß der mit der Jungenanzahl von 1 bis 6 steigende Milchverbrauch durch erhöhte Milchproduktion ausgeglichen wird.

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