Tatarida teniotis in the W-Palaearctic


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The biology of the Levant vole, Microtus guentheri in Israel

I. Population dynamics in the field

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Abstract

Investigated the population dynamics of Microtus guentheri in two places in the Southern Coastal Plain of Israel during November 1977 to September 1979. The field work was carried out once a month, during four consecutive nights placing 120 night-traps. The method of capture – marking –recapture was used with about 155 marked individuals (83 males and 72 females). Age, reproductive condition and body weight were recorded. There were two trapping peaks: December and June to September. Voles were heavier in winter than in summer but most animals lost weight in the traps. Voles were recaptured mostly within a range of 10–20 m: males showing higher attachability to their home range than females. The overall sex ratio did not differ significantly from equity. The estimated age structure of the population showed that most voles lived less than a year. The breeding season lasted from October until April. The existence of a post-partum oestrus was ascertained. The mean number of embryos was 8.8 and the largest litters were produced in February. Juvenile breeding began at an age of about 30 days. Results indicate that control measures should take place in summer such as deep ploughing of the field and field edges.

Introduction

Relatively little information has been published on Levant voles in the Mediterranean region and the Middle East (ATALLAH 1969; AHARONI 1930; BODENHEIMER 1949; BODENHEIMER and DVORETZKY 1952; HARRISON 1972; ONDRIAS 1965). The Levant vole (Microtus guentheri) as well as other voles are important agricultural pests (BODENHEIMER...
1949; Ondrias 1965). Operations to prevent damages by voles include use of pesticides, and this, in turn, causes serious damage to non-target species such as raptors (Mendelssohn 1972; Mendelssohn and Paz 1977).

The aim of this paper is to report on field work which was carried out on this species in Israel. Another part of the study was carried out on animals in captivity. The results of this second study will be reported separately.

Material and methods

The field work was carried out in Ayanot and Givat Brenner (31°50' N34°45' E) in the Southern Coastal Plain of Israel in the period November 1977 to September 1979.

In Givat Brenner the crops were maize (Zea mays) and beans (Phaseolus sp.) grown all year round while in Ayanot - wheat (Triticum dicoccoides) grew only during winter. The plants on the fringes of the fields were of sagittal plant communities: In Givat Brenner the dominant plant was Amaranthus sp. accompanied by Cynodon dactylon, Avena sterilis, Sonchus oleraceus and Cyperus cotinoides. In Ayanot the dominant plant in winter was Avena sterilis, which grew on the fringes on the field, while in the summer the area was covered by the plant community Prosopis farcata and Scolymus maculatus accompanied by Sinapis arvensis, Diplotaxis erucoides, Convolvulus arvensis, Alhagi maurorum and Ammi visnaga; and in the drainage canals on the fringes, the dominant plants were Malva nicaensis, Erodium moschatum, Inula viscosa and Echium elaterium (Weisel et al. 1975).

The area has a characteristic Mediterranean climate with mild, rainy winters and relatively hot summers. There are 40-50 rainy days a year with an average annual rainfall of 500 mm. The average minimum and the average maximum temperatures are 11°C and 27°C, respectively. Relative humidity is high, ranging from 50-80% (Rosennan 1970).

Trapping

Field work was carried out by using the method of capture – marking – release (CMR). We used 65 two-door 26 × 9 × 9 cm Sherman traps. The bait used was sunflower seeds and carrots which proved to be the most attractive bait. The bait was renewed as often as needed during the period of trapping. The traps were set monthly for periods of 4 days and nights, and were checked each morning during winter and twice daily, in the morning and afternoon, during the summer. Traps were checked twice daily in summer in

Fig. 1. The study area in Givat Brenner and pattern of trap layout
order to prevent trap mortality. In order to prevent damage to the trapped voles, insulating material (cotton wool and newspaper) were put into the traps in winter, while in the summer the traps were set in shady places whenever this was possible. Figures 1 and 2 show the location spots of the traps. The distance between these location spots was the distance between the burrows of the voles. Usually only one trap was set in each spot, but in some cases more were used according to the density of the burrows. On the whole, the layout of the traps reflected the restriction imposed by the farmers on one hand, and by the density of the burrows on the other. It was found that Howard traps were on average 5.5 times more efficient than Sherman traps.

Every trapped rodent was individually marked by toe clipping and was weighed on a Pesola Spring Balance to ±1 g accuracy. We also recorded reproductive conditions by examining the state of the nipples, open or closed vagina, presence of vaginal plugs and pregnancy in females and the testis size in males. Separate records were kept for each individual and each trapping locality.

In addition to the above CMR study a sample of 5 males and 5 females were collected monthly from a nearby area for laboratory examinations (dissections, vaginal smear, etc.); other voles were caught and kept alive for establishing a captive colony.

Results and discussion

The influence of trapping on captured voles

Weight change. Since the traps were set for 4 successive days, some individuals were caught night after night, and this may have influence on their physical condition and survival. The change in weight of such individuals is given in Table 1. It shows that most individuals

<table>
<thead>
<tr>
<th>% Weight change</th>
<th>n</th>
<th>1</th>
<th>11</th>
<th>36</th>
<th>20</th>
<th>82</th>
<th>35</th>
<th>15</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Of individuals recaptured</td>
<td>0.5</td>
<td>5.5</td>
<td>18.0</td>
<td>10.0</td>
<td>41.0</td>
<td>17.5</td>
<td>7.5</td>
<td></td>
</tr>
</tbody>
</table>

Table 1

The weight change (percentage of previous day weight) of voles captured on successive nights
(66 %) which were caught on successive nights lost between 1–30 % of the previous body weight, 24 % gained weight and 10 % maintained the same weight. No difference was found between males and females, and no correlation was found between initial body weight and the rate of weight decrease. Barbehenn (1955) on the contrary found that most Microtus pennsylvanicus trapped did not change their weight by more than 2 g on 2 successive nights, and only few lost 15–20 % of their initial body weight.

Survival in the traps. Out of 334 captures in this study (159 individuals) 44 died in the traps, mostly during winter: 45.2 % of all voles caught during November–February died in the traps, while only 11.8 % died in the traps during March–October.

Intraspecific interactions. It is possible that the presence of a vole in a trap will affect the chances of capturing other individuals in the same trap. Table 2 shows the catch on the second night in a trap which had captured a vole on the previous night. It indicates that there were almost equal chances for the same individual to be caught in the same trap (being male or female) or a specimen of the opposite sex, but a significantly smaller chance ($X^2 = 13.80$) that a specimen of the same sex will be caught. Similar findings were reported by Briese and Smith (1974) for a number of insectivore mammals and rodents, and by Dunaway (1968) for Reithrodontys humulis. This suggests a possible role of pheromones in sexual attraction.

**Table 2**

Consequent trapping of voles in the same trap

<table>
<thead>
<tr>
<th>Caught on day A and A+1</th>
<th>Males n</th>
<th>Females n</th>
<th>All n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Same individual</td>
<td>30 22.5</td>
<td>28 21.0</td>
<td>58 43.5</td>
</tr>
<tr>
<td>Other individual of opposite sex</td>
<td>25 18.8</td>
<td>26 19.5</td>
<td>51 38.3</td>
</tr>
<tr>
<td>Other individual of same sex</td>
<td>12 9.0</td>
<td>12 9.0</td>
<td>24 18.0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>67</strong></td>
<td><strong>66</strong></td>
<td><strong>133</strong></td>
</tr>
</tbody>
</table>

A = first day; A + 1 = second day

In some cases, when a marked adult specimen disappeared from the study area, another adult specimen of the same sex was caught in the trap which had been in the past occupied by the disappeared specimen. During August–September 1979, in 16 out of 20 cases of a disappeared individual, a male replaced a disappeared male. This suggests that the voles are fairly static and tend to live in pairs.

Population dynamics

Population size. Figure 3 describes the fluctuations in the number of voles trapped in Givat Brenner and Ayanot. It also describes the estimated population size using Ford's (1964) equation that

$$P = \frac{MR_{n-1} \times N_n}{MR_n}$$

where $P$ is the estimated population size, $MR_{n-1}$ – the number of marked specimens trapped and released in month $n-1$ (including all captured specimens without those dead in the traps); $MR_n$ – the number of marked specimens released in month $n$; $N_n$ – the total number of specimens caught in month $n$.

It can be seen that the number of voles caught in Givat Brenner was very small, possibly
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Fig. 3. Trapping in the study areas: Total number trapped, newly trapped, recaptures and estimated population size according to Ford (1964)

Fig. 4. The proportion of recaptures to newly captured

because this study area was abandoned due to a series of agricultural operations which interfered with field work. The Ayanot population showed two peaks of capture, in December 1978 and July 1979 respectively. The ratio of all recaptures to new captures during each month is given in Figure 4. This figure shows that during most of the study period, most individuals caught were recaptured.

The number of captures is a function of the numbers of voles and their rate of activity. The increased activity of voles at the beginning of the breeding season in November-December (Fig. 3) is probably related to reproductive activity of this species. A comparable trend was reported for Microtus arvalis (Niethammer and Krapp 1982). The summer peak
is probably a combination of higher activity of recaptured individuals and a higher number of newly caught specimens. This higher activity may be attributed to increased food search when food conditions are deteriorating.

**Sex ratio.** The sex ratio of trapped individuals is shown in Figure 5. The overall sex ratio of wild populations did not differ significantly from 1:1; but there was a certain seasonality with a higher proportion of females in December and January and higher proportions of males in February to May. A similar trend was described in *Microtus arvalis* (Niethammer and Krapp 1982).

![Fig. 5. Sex ratio of voles trapped in Ayanot](image)

The sex ratio reflects not only the real sex ratio in the field, but also a selective trappability due to various factors such as migration rates, reproductive state etc. It is likely that the large proportion of females caught in winter is due to the higher activity above the ground during the height of the breeding season, when breeding females have higher metabolic demands than males. A higher proportion of females during the breeding season was found also in *Microtus arvalis* (Adamczewska-Andrzejewska and Nabaglo 1977). If this assumption is true, then the almost equal proportion of males to females from June to September probably reflects equal energetic demands of the two sexes. The high proportion of males caught during spring is probably due to the lower tolerance of adult males towards young males, as observed in captivity. This causes a consequently higher migration rate in males in relation to females. It is interesting to note that Krebs et al. (1976) found that a higher proportion of males existed among migrant voles that began to occupy an area which was previously cleared of voles.

**Body Weights.** Figure 6 shows the fluctuations in the median weight of trapped females and males. Both sexes showed similar fluctuations, although females are lighter than males by 2–3 g. Both sexes are heavier during winter (December–March) than the rest of the year. An increased proportion of pregnant females also contributed to the general body weight increase in winter. Since weight increase occurred in males as well, the main responsible

![Fig. 6. Median weights of voles in the study areas. For n see Fig. 3](image)
factors are probably improved food and suitable weather conditions which enable the voles to forage all day and consequently to breed. The mild winter in Israel is equivalent in climate to that of the summer of more northern areas, where voles breed and increase in weight during summer. For example *Microtus pennsylvanicus* (Inversen and Turner 1974); *Microtus oeconomus* (Tast 1972).

**Range of movement**

The range of movement of specimens which were caught more than once is given in Table 3, which shows the maximal distance between two extreme capture stations. Most voles (69 out of 94; 73%) were caught within 10 m range, and another 14 voles (15%) were caught within a range of 11-20 m. There was no correlation between body weight and range of movement, and no difference between male and female in this respect. The range of movement was larger in winter than in summer. *In winter*: 5 females (out of 11 caught several times) moved in a range of 32-93 m, 3 males (out of 6) moved 30-96 m. *In summer*: 1 female (out of 20) moved 75 m, no male was caught in a range larger than 15 m.

Table 4 shows the relationship between the number of captures of an individual (x) and the number of stations (traps) where it was caught (y). This value defined as “attachability” (z) is a measure of the “fidelity” of an individual to its home range. It can be seen that as Z values increase above one, males appear to be more attached to stations e.g. they are more stationary than females (65% and 42%, respectively).

**Activity.** Levant voles were found to be active above ground in dry weather all year round and at any time of the day, provided that ambient temperature was below 25 °C. This means that voles were active all day during most of the winter, while in summer the activity was restricted to night hours, early morning and late afternoon. In Israel, rains occur only

**Table 3**

Maximal range of movement of voles caught more than once

Specimens caught more than once in the same month (but not the same day) are included, percentages (and sample size)

<table>
<thead>
<tr>
<th>Range distance (m)</th>
<th>0-5</th>
<th>6-10</th>
<th>11-15</th>
<th>16-20</th>
<th>21-100</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>50</td>
<td>25</td>
<td>11</td>
<td>6</td>
<td>9</td>
<td>100</td>
</tr>
<tr>
<td>females</td>
<td>41</td>
<td>31</td>
<td>6</td>
<td>6</td>
<td>15</td>
<td>100</td>
</tr>
<tr>
<td>Total</td>
<td>46</td>
<td>27</td>
<td>8</td>
<td>7</td>
<td>12</td>
<td>100</td>
</tr>
</tbody>
</table>

**Table 4**

“Attachability” (z) of voles to trapping stations

Only specimens caught twice and more in an interval of at least a month are included. Attachability is defined as: number of captures (x) divided by the number of stations in which an individual was caught (y) (sample size in brackets). Note that values smaller than 1 were not considered
during winter (end of October–April) and most annuals, which are the principal food of voles, grow at that time. The suitable weather conditions for above-ground foraging, together with high food availability are probably the main factors which determine the activity pattern and the timing of breeding and the heavier body weights. A similar activity pattern was reported for Microtus arvalis. They were active mostly at night in winter and at day time in summer (Niethammer and Krapp 1982).

Age structure of the population

The estimated ages of the voles were calculated according to the following assumption: 1. The breeding season lasted from November to April, so any vole caught in November weighing more than 30 g, was considered and adult born in April of that year or before (i.e. it was aged at least 7 months). 2. The age of young specimens caught during November–May was calculated by using the growth rates of voles born in captivity (Cohen-Shlagman et al. 1984). For example, 1 month old voles weighed 20–22 g and at the end of the second month weighed up to 27 g. 3. Specimens weighing 45 g and more which were caught at the end of the breeding season (March–April) may have been born the year before or at the beginning of the breeding season. Only 6 specimens were in this category and it was assumed that they were born in November of the same year.

The estimated age structure of the population is given in Figure 7. This figure shows that most voles in the study area lived less than a year. In spite of the fact that specimens younger than 1 month form a large proportion of the population during the breeding season, they hardly appear in the figure since they were almost not caught in the traps. They presumably were not yet active above ground. We could confirm the data of Dor (1947), who examined pellets of barn owls (Tyto alba), one of the main predators of voles, and found that only 2% of the bone remains of voles belonged to the one month age group, while 33% were 2 months old and 5.4% were more than 150 days old.

Survival in the study area

The disappearance rate in the study area of 155 captured specimens is shown in Figure 8. It shows that the captured voles disappeared rapidly from the study area, and only 4 specimens (2.6%) were caught in 5 consecutive months, while 56% were captured during
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one month only. These results may suggest mortality or that the vole population is divided into two components: “Migrants” which were captured only once or twice in the same month and “residents” which were captured in several consecutive months. The proportion of resident females was slightly higher than in resident males. About half of the females (35 out of 72, 49 %) belonged to the resident population while only 33 out of 83 (40 %) of the males were residents.

Interactions between voles and other species

Several animal species other than voles were accidently caught in the traps. These include toads (Bufo viridis), skinks (Eumeces schneideri), snakes (Coluber jugularis), shrews (Crocidura russula), rats (Rattus norvegicus) and jirds (Meriones tristrami) and even birds like goldfinch (Carduelis carduelis), robin (Erithacus rubecula) and bluethroat (Luscinia svecica). However only house mice (Mus musculus) were caught in large numbers. The numbers of voles and mice trapped in Ayanot is given in Figure 9. Both species showed an increase in numbers during winter 1978/9 and a decrease towards March 1979. Another population increase occurred towards the following winter but during the 1979 summer there were many more voles than mice. One can assume that the voles compete with the mice during summer when food conditions are harsher, hence the smaller population size of mice. A negative correlation between population sizes of competing rodent species has been reported by several authors (Redfield et al. 1977 for Microtus townsendii and Peromyscus maniculatus; Miller 1969 for Microtus pennsylvanicus and Microtus ochrogaster; Henttonen et al. 1977 for Microtus agrestis and Microtus oeconomus). Although mice prefer grain and voles green food, it is possible that during periods of food shortage these species compete for similar food. Another possible explanation is that in summer the voles of the study area were restricted to the edges of the field where only green food was available, the mice, on the contrary, which prefer grain, spread into the field.

Fig. 8. Rate of disappearance of voles

Fig. 9. The number of voles and mice trapped in the study area Ayanot

Reproduction

Reproductive activity and breeding season. Figure 10 shows that the percentage of females with an open vagina and females in an advanced reproductive state (pregnant or lactating) increased from October until December (open vagina) or January (pregnant and lactating)
when all captured females were in a reproductive state. In April there was a decline in reproductive activity and no pregnant females were trapped from June until October.

Reproductive activity of males was ascertained by the presence of mature spermatozoa in the cauda epididymis in specimens found dead in traps or caught for this purpose. All adult males (23) examined during October to April had motile spermatozoa.

Another indication for the start of the breeding season is the appearance of young voles. The first young, a female, was caught on 27th November 1977. It weighed 10.3 g, and by comparison to captive specimens was about 16 days old. Since pregnancy lasts 21 days, this female conceived on 20th October. The proportion of young caught in the traps in Ayanot is given in Figure 11. Most of these young weighed 25–30 g when first caught, and their estimated age (by comparison to captive ones) was about 40 days.

The evidence of these data suggests that the breeding season of the Levant voles in our study areas began by the end of October and lasted about 5 months, until April. *Microtus arvalis* in Germany has breeding season from March to October (Niethammer and Krapp 1982). It is interesting to note that *Microtus socialis*, which is widespread north of Israel up to the USSR has two breeding seasons, the first in April–June and the second in August–September (Ognev 1950).

**Pregnancy**

Female weight increased during pregnancy and decreased sharply after parturition. Only few pregnant females were caught on several successive days. In one case the weight of a pregnant female increased by 7 g (25% of the initial weight) in 2 days, and the increase in weight of 3 other females was between 33–39% within a period of 1–2 days.

The existence of post-partum oestrus was indicated by several captured females which were found to be pregnant with developed nipples and apparently nursing pups of a prior pregnancy. Other evidence for post-partum oestrus was given by a female (No. 30) that littered between the 8th and 11th December 1979, and when caught on the 12th December, had a vaginal plug, an indication of recent copulation.

**Number of embryos.** The number of embryos was estimated by dissecting captured females and by counting the number of embryos in the uterus. Mean number of embryos was 8.82
(SD = 1.29, n = 17). The smallest number of embryos (6) was found in December and the largest (11) in February. This indicates that large numbers of embryos were produced at the height of the breeding season. In Microtus arvalis (in Germany) the mean number of embryos was smaller (5.5) with a range 1–13 (Niethammer and Krapp 1982). For Microtus guentheri from Greece there is evidence for mean number of embryos of 5.6 with a range of 4 to 8 embryos (Ondrias 1965).

The mean number of placental scars was 10.73 (SD = 5.35; n = 11) and ranged between 6–19. Since placental scars in the horns of the uteri in voles may persist for 9–12 months after birth (Adamezewski-Andrezijewska 1969) during which time more than one pregnancy may occur, the large number of scars found in some females may indicate two pregnancies or more, or an embryo resorption. (Reichstein 1964).

Sexual maturation

It seems that some young females begin to reproduce during the first months of life. A 19.2 g female (at an estimated age of 26 days) with an open vagina was caught on 15th January 1979 and a pregnant, 28 g (estimated age 36 days), female with 9 embryos was caught on 9th April 1979.

In most of the young males (21) born during the same breeding season no motile spermatozoa were found. Only one male, caught on 9th April weighing 22 g (estimated age about 30 days) had active spermatozoa. This young male had unusually large testes (5.5 × 8.5 mm), more than twice the size observed in other young males (2.5–3.3 × 3.5–4 mm). In Microtus arvalis a testis length of 7 mm was characteristic for sexually mature males (Reichstein 1964).

This juvenile breeding phenomenon in Microtus guentheri was reported also by Bodenheimer (1949); when 25 days old females and 30 days old males, reproduced. According to Frank (1956) females of Microtus arvalis are able to reproduce at an age of 11–13 days and small embryos were found in females with a body weight of 10 g.

Reproductive potential

Voles are known for their high reproductive potential, and Microtus guentheri is no exception. This may be demonstrated by the following record of a 56 g female (No. 28) caught on 7th December 1978: it was caught again a day later (8th December) when her weight was 42 g and her vagina bled – both indicatives of a parturition during the night. On 12th December it was caught again and showed developed nipples, evidence that she was lactating. Observations in captivity indicate that lactation in this species lasts 15–21 days (Cohen-Shlagman et al. 1984) hence the young of this litter ceased lactating on 29th December. However, the same female was caught again on 12th January, evidently

<table>
<thead>
<tr>
<th>Reproductive Patterns</th>
<th>Field</th>
<th>Captivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding season</td>
<td>October–April</td>
<td>February–October</td>
</tr>
<tr>
<td>Minimal reproductive age</td>
<td>30 days ♂</td>
<td>90 days ♂</td>
</tr>
<tr>
<td></td>
<td>36 days ♂</td>
<td>60 days ♂</td>
</tr>
<tr>
<td>Reproductive potential</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>60 pups/season</td>
<td>30 pups/season</td>
</tr>
<tr>
<td>Post-partum oestrous</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Mean litter size (or mean number of embryos)</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>1:1</td>
<td>0.82 ♀:1♂</td>
</tr>
</tbody>
</table>
lactating, which indicates that another litter was born by the end of December. When it was trapped once again on 15th January, she died in the trap and dissection showed 7 embryos. Hence, during 40 days this female was pregnant three times.

Assuming a 21 day pregnancy, a maximum 4 days interval between parturition and mating and a 5 month breeding season, a female *Microtus guentheri* may produce 7 litters a year. Since average embryo number is about 9, this female may bring forth about 60 pups during one breeding season. This reproductive potential is similar to that of *Microtus arvalis* which has a post-partum oestrus and litters 5–7 times in one breeding season (Ognev 1950). *Microtus arvalis* (Germany) shows a succession of 4 litters a year (Niet-hammer and Krapp 1982).

A comparison of some reproductive patterns of the Levant vole in the field and in captivity is given in Table 5. It can be seen that the reproductive season in captivity is more extended but the mean number of embryos and reproductive potential is higher in nature than in the laboratory.

**Agrotechnical recommendation**

Since food is scanty in summer and voles concentrate in the field edges, where food is available, control measures should take place at this time of the year and include deep ploughing of the field (including edges) and limited use of rodenticides in places only where ploughing is not feasible.

**Acknowledgements**

We are grateful to Professor H. Mendelsohn for his help and for the German translation of the summary.

**Zusammenfassung**

*Die Biologie der Mittelmeer-Feldmaus, Microtus guentheri in Israel.*

1. *Populationsdynamik im Freiland*


Die meisten Feldmäuse verloren an Gewicht, während sie in den Fallen waren, und im Winter war die Sterblichkeit in den Fallen groß. Die Aussichten für dasselbe Tier (Männchen oder Weibchen), in derselben Falle wiedergefangen zu werden, waren fast gleich, aber die Aussicht für ein Tier desselben Geschlechtes wiedergefangen zu werden, war deutlich geringer.


**References**


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