SOCIETAS PRO FAUNA ET FLORA FENNICA


<table>
<thead>
<tr>
<th>Anzahl</th>
<th>Autor</th>
<th>Titel</th>
<th>Seitenzahl</th>
<th>Jahr</th>
</tr>
</thead>
<tbody>
<tr>
<td>60</td>
<td>Alex. Luther</td>
<td>Untersuchungen an rhabdocoelen Turbellarien. IX. Zur Kenntnis einiger Typhloplaniden. X. Über Astrotorhynchus bifidus (M'Int).</td>
<td>42</td>
<td>1950</td>
</tr>
<tr>
<td>62</td>
<td>Pontus Palmgren</td>
<td>Die Spinnenfauna Finnlands und Ostfennoskandiens. III. Xysticidae und Philodromidae.</td>
<td>43</td>
<td>1950</td>
</tr>
<tr>
<td>63</td>
<td>Sven Nordberg</td>
<td>Researches on the Bird Fauna of the Marine Zone in the Åland Archipelago.</td>
<td>62</td>
<td>1950</td>
</tr>
<tr>
<td>64</td>
<td>Floriano Papi</td>
<td>Über einige Typhloplaninen (Turbellaria neorhabdocoela).</td>
<td>20</td>
<td>1951</td>
</tr>
<tr>
<td>65</td>
<td>Einari Merikallio</td>
<td>On the Numbers of Land-Birds in Finland.</td>
<td>16</td>
<td>1951</td>
</tr>
<tr>
<td>66</td>
<td>K. O. Donner</td>
<td>The Visual Acuity of some Passerine Birds.</td>
<td>40</td>
<td>1951</td>
</tr>
<tr>
<td>67</td>
<td>Lars von Haartman</td>
<td>Der Trauerfliegenschnäpper. II. Populationsprobleme.</td>
<td>60</td>
<td>1951</td>
</tr>
<tr>
<td>68</td>
<td>Eric Fabricius</td>
<td>Zur Ethologie junger Anatiden.</td>
<td>178</td>
<td>1951</td>
</tr>
<tr>
<td>69</td>
<td>Tor G. Karling</td>
<td>Studien über Kalyptorhynchien (Turbellaria). IV. Einige Eukalyptorhynchia.</td>
<td>49</td>
<td>1952</td>
</tr>
<tr>
<td>70</td>
<td>L. Benick</td>
<td>Pilzkäfer und Käferpilze. Ökologische und statistische Untersuchungen.</td>
<td>250</td>
<td>1952</td>
</tr>
<tr>
<td>71</td>
<td>Bo-Jungar Wikgren</td>
<td>Osmotic Regulation in Some Aquatic Animals with Special Reference to the Influence of Temperature.</td>
<td>102</td>
<td>1953</td>
</tr>
<tr>
<td>72</td>
<td>Wolfram Noodt</td>
<td>Entromastreaceae aus dem Litoral und dem Küstengrundwasser des Finnischen Meerbusens.</td>
<td>12</td>
<td>1953</td>
</tr>
<tr>
<td>73</td>
<td>Sebastian A. Gerlach</td>
<td>Die Nematodenfauna der Uferzonen und des Küstengrundwassers am Finnischen Meerbusen.</td>
<td>32</td>
<td>1953</td>
</tr>
<tr>
<td>75</td>
<td>T. H. Järvi</td>
<td>Über die Coregonen s.str. im Päijänne und in einigen anderen Gewässern Mittelfinnlands.</td>
<td>33</td>
<td>1953</td>
</tr>
<tr>
<td>76</td>
<td>Björn Kurtén</td>
<td>On the Variation and Population Dynamics of Fossil and Recent Mammal Populations.</td>
<td>122</td>
<td>1953</td>
</tr>
<tr>
<td>77</td>
<td>Göran Bergman</td>
<td>Verhalten und Biologie der Raubseeschwalbe (Hydroprogne teshcragava).</td>
<td>50</td>
<td>1953</td>
</tr>
<tr>
<td>78</td>
<td>Floriano Papi</td>
<td>Beiträge zur Kenntnis der Macrostomiden (Turbellarien).</td>
<td>32</td>
<td>1953</td>
</tr>
<tr>
<td>79</td>
<td>Walter Hackman</td>
<td>The Spiders of Newfoundland.</td>
<td>99</td>
<td>1954</td>
</tr>
<tr>
<td>80</td>
<td>Karl Schmölzer</td>
<td>Beitrag zur Kenntnis der Gattung Armadillidium Latr. 1804 (Isopoda terrestria).</td>
<td>63</td>
<td>1954</td>
</tr>
<tr>
<td>81</td>
<td>Peter Ax</td>
<td>Die Turbellarienfauna des Küstengrundwassers am Finnischen Meerbusen.</td>
<td>54</td>
<td>1954</td>
</tr>
<tr>
<td>82</td>
<td>Harry Krogerus</td>
<td>Investigations on the Lepidoptera of Newfoundland. I. Macrolepidoptera.</td>
<td>80</td>
<td>1954</td>
</tr>
</tbody>
</table>


STUDIES ON THE DIPTEROUS FAUNA IN
BURROWS OF VOGES (MICROTUS,
CLETHRIONOMYS) IN FINLAND

BY

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ZOLOGICAL MUSEUM OF THE UNIVERSITY, HELSINGFORS

WITH 21 FIGURES AND 11 TABLES

HELSINKI—HELSINGFORS

1963
I. Introduction

Among the many papers published about insects in nests and burrows of small mammals, only a few deal with the Diptera and in very few have the ecological factors influencing the composition of the fauna been analysed. FALCOZ (1915, 1921) has reviewed most older records on this subject and introduced an ecological terminology for the arthropod fauna of subterranean nests and burrows of warm-blooded animals. LELEUP (1948) adds a few Diptera mainly from nests of the Mole (Talpa europaea). The nest fauna of several small rodent species has been studied quantitatively by GENSICKE (1960) in Germany but the Diptera were only identified as to the family and the collecting method used (Berlese funnel) was less suited for imagines of Diptera. Insects from runways of voles have been collected by ISRAELSON (1960) in Sweden but only the Coleoptera have been considered by him. Mr. E. B. BASDEN, of Edinburgh, many years ago collected Diptera from nests of numerous mammals and birds but has not published the results of his studies. Scattered
records about his finds have appeared in taxonomic or faunistic papers by other authors (COLLICK 1933, 1939, 1943, SCHMITZ 1938—50) as well as notes by himself (BADSEN 1961). Records of Borboridae in the burrows of various mammals were given by RICHARDS (1930). Oestrid parasites of voles and marmots have been studied by ŽURČEK (1951) and GRUNIN (1958, 1962). The following is a list of papers primarily concerned with the ecology of the arthropods of subterranean nests of rodents: MARIE (1927, 1930) and IHSSEN (1940) on the burrow fauna of the Alp Marmot (Marmota marmota), HUBBEL & GOFF (1939) on the fauna of nests and runways of the Florida Pocket Gopher (Geomys floridanus), Ross (1944) on those of the Texas Pocket Gopher (Geomys breviceps attwateri), MEDVEDEV (1944), who gives temperature and moisture data for burrows of the Suslik (Citellus pygmaeus brauneri) of the Ukraine, AGRELL (1945) dealing with the Collembola of vole nests, BARABASCH-NIKIFOROV (1949), who deals with the animal community in Beaver lodges. WIREN (1961) gives outlines for an ecological classification of the fauna of rodent nests. A useful review about the ecology of the Diptera in nests and burrows in given by SEGUY (1950) in «La Biologie des Diptères».

The present investigation made during the period 1959—1961 deals almost exclusively with the Diptera of burrows of Microtus arvalis Pall., M. agrestis L. and Clethrionomys glareolus SchrkJ in Finland. The fauna of the nests of these rodents has not been included in this study, because Microtus arvalis, at least, often builds them separate from the burrows at the soil surface (in decaying stumps of trees, in heaps of hay or other suitable material). The autecological conditions of the nests are thus far more variable than those of the burrows. The dipterous fauna of the nests outside the burrows also seems to be of a more fortuitous composition and forms no stable part of a community. The burrows, on the other hand, are more favourable for a study, their arthropod communities being persistent normally for periods of at least a year and their microclimatic conditions being less variable.

The sampling of the Diptera in burrows of the Common Vole (Microtus arvalis) was made during the summer and autumn of 1959 and 1960 on a small island, Småholmen (in the commune of Esbo) not far from Helsinki/Helsingfors on the south coast of Finland. In 1960, my assistant, Mr. HANS JUNGERSTAM, collected for me samples of Diptera from burrows of the Field Vole (Microtus agrestis) and the Bank Vole (Clethrionomys glareolus) throughout the warm season in Bonäs (near Nykarleby) on the Gulf of Bothnia. In 1961, the investigation was completed by rearing experiments and the use of special traps. This was done mainly in Evitskog (commune of Kyrkslätt, S. Finland).

The microclimatic conditions in vole burrows being but poorly known, at least in northern Europe, measurements were made of the main variable abiotic factor, the temperature, in Småholmen in 1959 and 1960. In Bonäs,
observations were made regularly from May to September, 1960, by Mr. Jungerstam. Completing measurements were made in Evitskog in 1961.

I wish here to express my gratitude to the following persons and institutions: to the Finnish State Committee for Natural Sciences, which paid the salary of my assistant, to Societas Scientiarum Fenniae for a grant in 1961, to Prof. Pontus Palmgren and Prof. Paavo Suomalainen and their departments in the Zoological Institute of the University for facilitating my work, to my assistant, Mr. Hans Jungerstam, for his excellent sampling work, and further to Prof. Risto Tuomikoski for valuable help in identification of certain difficult groups among the Nematocera.

II. Vole burrows and their microclimatic conditions

Småholmen Island, where a great part of the investigation was made, is about 200 metres from the mainland. It is mainly covered by conifer wood growing on rock but across this runs a dell, once a garden plantation, and now with a vegetation of bushes (Alnus, Salix, Ribes) and ruderal plants. The ground here is to a large extent undermined by galleries of the Common Vole. In the Alnus thickets closer to the shore a number of vole burrows were also found. In the forest parts there are numerous burrows under trees and stumps. These burrows were probably all dug by the Bank Vole but in 1959 many of them apparently were used by the Common Vole. Abandoned vole nests were found under logs and in decaying stumps in this area of the island. The Bank Vole was observed on the island in 1958 but disappeared in 1959. The Common Vole was extremely abundant in 1959 but was not observed on the island in 1960. In 1961, at least a few burrows in the forest were inhabited by the Bank Vole. Sudden changes of size are a well known feature of the vole populations.

The typical summer burrows of the Common Vole in the dell of Småholmen run 10 to 15 cm under the surface in grassy soil. Their length seems to vary greatly and as the galleries run under roots and stones, they are difficult to dig open. Often the burrows have more than one entrance. The diameter is usually 4—5 cm. In 1959, 11 burrows were studied in grassy soil under bushes, several of them inhabited by voles. In 1960, 15 were studied (partly the same as in 1959). Before the summer of 1960 they had all been abandoned by the voles.

The runs beginning in stumps or under the roots of living trees and continuing along more or less decayed roots — containing plenty of decaying wood — differ from vole burrows in garden or meadow soil as a habitat for Diptera and their larvae. 17 burrows under roots were studied in 1959 and 16 in 1960.

The localities of the vole burrows studied in Bonäs in 1960 are on the mainland. The Field Vole burrows were in meadows surrounded by forest. In all,
24 burrows were investigated, most of them situated in the banks of ditches. The 6 Bank Vole burrows investigated were in shady places in the wood, some of them on the western slope rather close to the shore.

In Evitskog in 1961 samples were mainly taken from burrows in the banks of ditches on a Phleum meadow. The burrows were probably made by the Field Vole.

Of the three most important abiotic factors influencing the insect fauna of a terrestrial biotope, namely light, temperature and moisture, the first and third are in most cases practically constant in the burrows, with exception of the entrance zone. At 10 or 20 cm in a burrow in grassy soil, the air is normally already saturated with moisture. In August during a rainless period in the exceptionally dry summer of 1959 the relative humidity in the entrance zone of a burrow in open wood on Småholmen was measured and found to be about 80%. In some burrows (probably made by Microtus) in rather dry soil at the edge of a wheat field in Evitskog 1961 the humidity must have been below 100% even deeper in the runway. This must be regarded as an exception, however.

The temperature. For the study of the diurnal changes, a thermograph (»Fernthermograph») was used. Its measuring head is connected to the apparatus by a cable 6 m long and measurements can thus be made deep in narrow cavities. For other measurements maximum-minimum thermometers were used (in 1961 a special type of these, German »Jumo« thermometers provided with a thin cable and measuring head). In 1959, the thermograph was used from the beginning of July to the end of August, in 1960, from June 15 to August 15. All measurements were made about 30 cm inside the burrow and at a depth of about 10–15 cm.

The general features of the diurnal temperature variation in a typical burrow of the Common Vole during the warm period are illustrated by a curve obtained on a sunny day, July 6, 1960, from a burrow in grassy soil on Småholmen (fig.1). For comparison, curves for the temperature at the soil surface by the same burrow are given for a sunny day (July 15) and for a rainy day (July 11) in figs. 2 and 3. The diurnal curve in fig. 1 shows an amplitude of 4°C (+10°–+14°). In a burrow in a shady thicket on Småholmen a diurnal temperature range of 3° was observed on a sunny day, June 22, 1960. In burrows under roots in sun-exposed places on Småholmen on August 15–20 a maximal diurnal range of 5° was observed. In Evitskog, the thermograph was used during the period June 12–15, 1961, in a burrow on a sun-exposed meadow. The temperature range on a sunny day (June 13) was 3° (+16°–+19°) and on a rainy day (June 14) 2° (+14°–+16°). In 1959 and 1960, thermograms were taken from a number of different burrows on Småholmen but the above-mentioned examples already show their essential features.
It is obvious that, with rather small deviations, the air temperature in the burrow follows the temperature of the surrounding compact soil. Juusela (1945) has investigated the soil temperature of certain agricultural experimental fields (meadows with different degrees of draining) situated about 20 km from Småholmen and 10 km from the coast. His diurnal summer thermograms for compact soil at a depth of 10–15 cm. agree well with those from the vole burrows in comparable cases. Juusela points out that the water content of the soil is an important factor influencing the thermal conditions. At a higher water content the soil temperature (at 10–20 cm depth) will follow more sensitively the changes of the air temperature at the surface than at a lower water content. Some observations in this connection were made in Evitskog and on Småholmen 1961. In a Microtus burrow in a meadow in Evitskog the diurnal range of temperature on June 12 (during a warm, almost rainless week) was +14°–+18°, with a daily peak at 1 p.m. In the surrounding soil the range was +14°–+16°, with the peak at 2 p.m. During the following rainy week period the thermograms taken from compact soil in the same place on the few sunny days showed a peak at noon or even earlier. In Småholmen on July 2, 1961 (during a rainy period) the temperature in a burrow in grassy soil under a bush was compared with that in compact soil at the same place at the same depth (10 cm). The data are given in the diagram in fig. 4. Here the compact soil shows slightly more variation of temperature than the burrow air. The specific warmth of the burrow air saturated with humidity will remain constant, but that of the surrounding soil will vary with the water content.

The seasonal variation of the burrow temperatures was studied on Småholmen in 1959 and 1960 and in Bonäs in 1960. On Småholmen in June 1959,
Fig. 4. Day temperature from 10 a.m. to 3 p.m. in a burrow and in the surrounding compact soil July 2, 1961 on Småholmen. Further explanation in the text p. 7.

the lowest temperature measured was +9° C (in a root cavity inhabited by Microtus arvalis, June 5—10) and the highest +15° (root cavity, June 13—17). In July, the lowest was +10° (root cavity, N.W. slope, 18th—25th) and the highest +19° (burrow in grassy soil, July 6). In August: lowest +10° (burrow in open forest, 28th—31st), highest +19° (grassy soil, August 4—6). In September—October, maxima and minima were measured in a single wide burrow under decaying roots of a birch at about 20 cm depth. The burrow was probably made by the Brown Rat (Rattus norvegicus) but in 1960 possibly used by voles (this burrow was chosen because its diameter allowed insertion of a usual maximum-minimum thermometer). The observations were the following:

<table>
<thead>
<tr>
<th>Month</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>September</td>
<td>-2°</td>
<td>+11°</td>
</tr>
<tr>
<td>5—9</td>
<td>+4°</td>
<td>+7°</td>
</tr>
<tr>
<td>10—15</td>
<td>+6°</td>
<td>+9°</td>
</tr>
<tr>
<td>16—30</td>
<td>+8°</td>
<td>+10°</td>
</tr>
<tr>
<td>October</td>
<td>-1°</td>
<td>+11°</td>
</tr>
<tr>
<td>1—6</td>
<td>+4°</td>
<td>+7°</td>
</tr>
<tr>
<td>7—18</td>
<td>+4°</td>
<td>+9°</td>
</tr>
<tr>
<td>19—31</td>
<td>+6°</td>
<td>+10°</td>
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</table>

The thermometer was left there over the winter and showed a minimum of -2° in spite of several cold periods, when the air temperature must have been below -10° at the snow surface.

On Småholmen in 1960 temperatures were measured in a vole burrow in grass soil under a bush in a sun-exposed place during three periods. During the first period, June 25 — July 10, the minimum was +9° (June 25) and the maximum +15° (June 26, July 1, 2, 7, 8, 9). During the second period, July 25 — August 15, the minimum was +11° (August 5) and the maximum +18° (July 28, August 2). The third period, October 5—15, showed a minimum +16° and a maximum +11°. During the mild winter of 1960—1961, the minimum in the same burrow was 0°. In spring 1961 the island was visited on April 29 and a maximum of +7° was recorded.

In Bonäs in 1960 temperatures were measured at almost regular intervals from the middle of May to the end of August in three vole burrows, 1) a
Clethrionomys glareolus burrow under a stump (shady wood, W. slope), 2) a Microtus agrestis burrow in a ditch bank on a well drained meadow, 3) another Field Vole burrow in a similar situation. The temperatures were taken at 3 p.m. Further maxima and minima were measured from the beginning of June to the end of August in a Field Vole burrow in a ditch bank of a less well drained meadow. The maxima and minima were taken for about ten day periods. The results are given in the tables 1 and 2. The maximum-minimum thermometer was left in that same burrow over the winter 1960–61. The winter minimum was 0°, the same as in Småholmen in a burrow in grassy soil under a bush.

The seasonal fluctuations of the soil temperature at 10–20 cm depth are also influenced to some extent by the water content of the soil. Juusela (op.cit.) points out that until the point is reached when the frozen soil has thawed wetter soil will warm up more slowly in the spring. On the other hand, the rise of temperature after the thaw will be more rapid at higher water contents.

The essential facts about the microclimatic conditions in vole burrows as revealed by the data from Småholmen and Bonäs, can be summed up as follows: In all kinds of vole burrows (in the areas of the investigation) extremes in the outside temperature will be evened out. In a normal burrow (depth 10–15 cm) the temperature will hardly rise above +20°C even on a hot summer day. During the winter the burrow temperature will sink by at most a

| TABLE 1. Temperatures measured in vole burrows in Bonäs 1960 at 3 p.m. |
|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Bank Vole burrow            | Field Vole burrow, well drained meadow | Field Vole burrow, similar situation |
| (forest, W. slope)          | well drained meadow          | similar situation           |
| +1° + 8° + 8° + 10°         | +9° + 11° + 13° + 14°        | +8° +10° +12° +13° +14°    |
| June 16th 31th              | June 20th 30th               | June 10th 20th 31th        |
| +12° +13° +14°              | +16° +17° +18°              | +12° +14° +10° +8°        |
| July 10th 20th 31th         | July 10th 20th 31th          | August 10th 20th 31th      |
| +12° +14° +10° +8°          | +15° +16° +12°              | +15° +16° +12°            |
| Sept. 7th                   |                             |                             |

| TABLE 2. Temperature maxima and minima of 10 day periods measured in a Field Vole burrow in a ditch bank of a less drained meadow in Bonäs in 1960. |
|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Maximum +12° +12° +13°      | Maximum +14° +15° +15°      | Maximum +16° +15° +12°     |
| Minimum +9° +9° +11°        | Minimum +12° +13° +13°      | Minimum +12° +11° +9°      |
|                             |                             |                             |
few degrees below zero. The length of the warm season with temperatures suitable for active insect life in the burrows will depend on several factors, the macroclimate, sun exposure, nature and water content of the soil. In the inner parts of the burrow the air humidity will in most cases remain high and constant throughout the warm season. The entrance zone will show a gradient for temperature as well as for moisture. As a biotope a vole burrow is by no means extreme and exclusive in a climatic respect and this will be reflected in the composition of its dipterous fauna.

III. Sampling methods and material

The dipterous material was collected in the vole burrows with the aid of various kinds of traps described below:

1) A funnel trap (fig. 5) consisting of a cylinder of metal gauze closed with corks at both ends and provided with a plastic funnel (diameter 6 cm). The trap was placed in the entrance of a burrow as shown in fig. 5. For killing the Diptera, the trap was removed from the funnel and placed in a large jar with chloroform vapour. Used on Småholmen in 1959 and 1960 and in Bonäs 1960.

2) A funnel trap functioning on the same principle, but the metal gauze cylinder replaced by a plastic jar (diameter 5 cm), its bottom covered with metal gauze. The insects were killed by placing the jar with the bottom against a cyanide bottle. Used on Småholmen in 1960 and in Bonäs 1960.

3) A funnel trap made of the same material as type 2, but with a funnel of metal gauze inside the jar. Used in Evitskog in 1961.

4) Pitfall trap (Barber trap, see for example HEYDEMANN 1958) made of a plastic jar (diameter 5 cm) half filled with ethylene glycol and provided with a roof protecting against falling soil particles (see fig. 6). The trap was sunk in the floor of the burrow about 10—15 cm from the entrance and under a removable roof of soil (see fig. 6). Used in 1960 on Småholmen and in Bonäs.

On Småholmen in 1959 funnel traps were used from mid-June to the end of October. Almost every vole burrow discovered during the summer was provided with a trap and by the end of August there were 30 traps in use. The traps were examined for Diptera at least once a week. In October, two pitfall traps were tried and proved effective. In 1960, the sampling was made from the end of May to the end of October. In all, 31 traps were used, 11 of them pitfall traps. The traps were investigated at least once a week and during the period June 15 — August 12 twice a week.

In Bonäs in 1960, 15 funnel traps and 9 pitfall traps were in use from May 15 to September 24 (a few traps even later, to November 6). Until the end of August the traps were investigated every third day and in the autumn at longer intervals.
In Evitskog in 1961 21 funnel traps (type 3) with or without bait were used from June to August mainly for collecting living flies for rearing experiments. Traps with bait (figs. 7 and 8) were also used on Småholmen and to a lesser extent in Bonäs in 1960. Among the various baits tried (decaying fruit, fungus, cheese, meat, rodent droppings) meat proved the most successful.
W. Hackman: The dipterous fauna in burrows of voles

The material from Småholmen in 1959 contained about 95 species of Diptera and in all 424 specimens. In 1960, sampling was begun earlier and with numerous and more effective traps from the beginning. If the bait trap material (more than 200 specimens) is excluded, remains a collection containing about 150 species and 801 individuals. The material collected by Mr. Jungerstam in Bonäs in 1960 (24 traps without bait throughout the season) contains about 90 species and 642 individuals (only a small number of individuals collected in traps with bait).

It is clear that the samples obtained by the methods described above cannot give an exact picture of the quantitative composition of the dipterous fauna of the burrows. The funnel traps without bait will only collect individuals moving towards the entrance, thus favouring species with imagines that have hatched in the burrows and are seeking their way out. The pitfall traps catch flies moving in both directions but might be avoided by some species. The bait traps catch certain categories of feeders and occasionally other species and also attract specimens from outside. The material from bait traps must, of course, be kept apart from the other samples. Rather frequently spiders (Linyphiidae and Microryphantidae) get into the funnel traps and kill and distort small Diptera so that they are not longer recognizable, and might cause much damage if the traps are not investigated at short intervals. In the pitfall traps this is avoided, the spiders being killed in ethylene glycol.

Considering the above facts, it is clear that the material can only approximately show which species are abundant in the burrows. The material from Småholmen in 1959 and 1960, mainly collected from the same burrows in both years, can only be compared from mid-July onwards. The material from Bonäs is at least somewhat more suited for quantitative studies, since the same number of traps was used throughout the collecting season, but even here the calculated dominance and constancy percentages must be accepted with great reserve. The composition of the dipterous fauna in vole burrows of different kinds show considerable differences. The fauna has therefore been treated here under three main headings: 1) The Diptera in burrows under stumps and living trees, 2) those in burrows in grassy soil under bushes (typical Microtus burrows on Småholmen), 3) those in burrows in meadows.

IV. Dipterous fauna in burrows under stumps and living trees

On Småholmen 17 burrows under stumps or living trees were studied in 1959 (number of traps increased successively during the summer), and in 1960 16 burrows. In 1959, these burrows under stumps of Betula, Pinus and Picea
and under living pines were mostly inhabited by *Microtus arvalis* but probably all made by *Clethrionomys glareolus* (observed 1958 and again 1961). In 1960, most or possibly all of the 16 burrows studied had been abandoned by the voles. In Bonäs in 1960, all the burrows of this type (6 investigated) were made and at least two inhabited by the Bank Vole. Especially those under decaying stumps form larger cavities, usually with more than one opening and the soil is mixed with numerous pieces of wood in various degrees of decomposition. On Småholmen the microclimatic conditions in these burrows were less homogenous because of variation in exposure to sun. In Bonäs, 5 of these cavities were in shady places and only one in open forest.

A list of the dipterous families and numbers of species and specimens captured in burrows of the type described above is given in table 3. On Småholmen only 45% of the species taken in 1959 were recaptured in 1960, in spite of the fact that the 1960 material was larger in amount and richer in species and that the sampling began earlier in the summer. The summer of 1959, especially in its latter half, was extremely dry, that of 1960 rainy. The vole population (*Microtus arvalis*) reached a peak in 1959 but crashed in 1960. To what extent these two factors are responsible for the changes in the fauna is a question which can only be solved by study of the occurrence and biology of the individual species.

The vast majority of the species collected in burrows of this type on Småholmen and in Bonäs are represented by 1—3 specimens and higher dominance and constancy is shown by comparatively few species. The sources of error for a quantitative analysis based on the present material have already been pointed out in the previous section. Therefore the species have been divided in only three roughly approximate dominance and constancy groups:

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<thead>
<tr>
<th>Småholmen</th>
<th>Bonäs</th>
</tr>
</thead>
<tbody>
<tr>
<td>d+ = dominance 11—20%</td>
<td>c+ = in 9—16 burrows</td>
</tr>
<tr>
<td>d = &gt; 5—10%</td>
<td>c = in 5—8</td>
</tr>
<tr>
<td>d— = &lt; 5%</td>
<td>c— = in 1—4</td>
</tr>
</tbody>
</table>

The dominance and constancy values for the species from Småholmen in 1959 are based on material caught in 16 traps, which were set up in the first half of July. The values for 1960 are based on samples from 16 traps used from the beginning of June. The values for Bonäs in 1960 are based on the samples from all six burrows from May 15 to the beginning of September. Table 4 gives the species with dominance values above d- or constancy values above c- in 1959 or 1960. (The numbers of individuals for all species identified and the number and kind of burrows in which they have been trapped are given in the list of species in section XIII). Significant changes can be noted for the following species: *Rhagio lineola*, fairly common (d) and constant (c+) in 1959,
W. Hackman: The dipterous fauna in burrows of voles

TABLE 3. The dipterous families, numbers of species and individuals in the collections from burrows under stumps and trees. Sp. = species, Ind. = individuals, Sp.c. = species common to the collections on Småholmen 1959 and 1960, Småholmen & Bonäs sp.c. = in both Småholmen and Bonäs.

<table>
<thead>
<tr>
<th>Family</th>
<th>Småholmen</th>
<th>Total</th>
<th>Bonäs</th>
<th>Småholmen &amp; Bonäs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tipulidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Limoniidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Trichoceridae</td>
<td>2</td>
<td>7</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>Anisopodidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Psychodidae</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Culicidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5</td>
</tr>
<tr>
<td>Ceratopogonidae</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bibionidae</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Mycetophilidae</td>
<td>3</td>
<td>5</td>
<td>24</td>
<td>61</td>
</tr>
<tr>
<td>Sciaridae</td>
<td>4</td>
<td>25</td>
<td>17</td>
<td>193</td>
</tr>
<tr>
<td>Cecidomyiidae</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Rhagionidae</td>
<td>1</td>
<td>10</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Empididae</td>
<td>13</td>
<td>46</td>
<td>8</td>
<td>23</td>
</tr>
<tr>
<td>Dolichopodidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Phoridae 1)</td>
<td>123</td>
<td>22</td>
<td>30</td>
<td>248</td>
</tr>
<tr>
<td>Syrphidae</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Dryomyzidae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Helomyzidae</td>
<td>6</td>
<td>15</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Borboridae</td>
<td>7</td>
<td>29</td>
<td>4</td>
<td>14</td>
</tr>
<tr>
<td>Diastatidae</td>
<td>1</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Chloropidae</td>
<td>2</td>
<td>5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tachinidae</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Calliphoridae</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Muscidae</td>
<td>5</td>
<td>40</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>64</strong></td>
<td><strong>218</strong></td>
<td><strong>113</strong></td>
<td><strong>603</strong></td>
</tr>
</tbody>
</table>

1) The Megaselia (s.str.) species in the 1959 samples were sent to a specialist for identification but not returned. Therefore the number of species remains uncertain.

totally lacking in the samples from 1960. The larva of this species is a common inhabitant of the litter layer in various ground biotopes, being raptorial and thus not dependent on the presence of voles. *Limosina talparum* was fairly common and fairly constant in 1959, but lacking in 1960. This is one of the few cases when the absence of a species can be attributed directly to the crash of the Common Vole population in 1960. In the case of the two *Lasiops* species the decrease in dominance may have had climatic causes. As only females of
**Table 4.** Species from the burrows under stumps and trees. Only those species are listed which show a dominance value above d- or a constancy value above c- in 1959 or 1960. Explanation of the d and c values in the text (p. 13).

<table>
<thead>
<tr>
<th>Species from the burrows</th>
<th>Småholmen VII—X 1959</th>
<th>VI—X 1960</th>
<th>Bonäs V—I X 1960</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ormosia pseudosimilis</em> Lundstr.</td>
<td>—</td>
<td>—</td>
<td>d— c</td>
</tr>
<tr>
<td><em>Lycoriella brevipila</em> Tuom.</td>
<td>—</td>
<td>—</td>
<td>d— c</td>
</tr>
<tr>
<td><em>Corynoptera camptochaeta</em> Tuom.</td>
<td>—</td>
<td>—</td>
<td>d— c</td>
</tr>
<tr>
<td><em>Ctenosciara hyalipennis</em> Meig.</td>
<td>d+ c— d+ c+</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Bradysia bicolor</em> Meig.</td>
<td>d— c— d — e—</td>
<td>d+ c—</td>
<td>—</td>
</tr>
<tr>
<td><em>Scaptosciara vivida</em> Winn.</td>
<td>—</td>
<td>—</td>
<td>d— c—</td>
</tr>
<tr>
<td><em>Rhagio lineola</em> F.</td>
<td>d c+ — —</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Tachydomia ciliaris</em> Fall.</td>
<td>d c d— c</td>
<td>d— c—</td>
<td>——</td>
</tr>
<tr>
<td><em>Tachydomia ecalceata</em> Zett.</td>
<td>d— c— d— c</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Anevrina thoracica</em> Meig.</td>
<td>d— c— d+ c+ d+ c+</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Conicera floricola</em> Schmitz</td>
<td>— — d e d— c—</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Megaselia giraudi</em> Egg.</td>
<td>——</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Megaselia flavicaxa</em> Zett.</td>
<td>——</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Megaselia rufipes</em> Meig.</td>
<td>d— c— d— c ——</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Megaselia sp. (pr. pulicaria)</em></td>
<td>? ? d— c—</td>
<td>d— c—</td>
<td>——</td>
</tr>
<tr>
<td><em>Heteromyza oculata</em> Fall.</td>
<td>d— c— ——</td>
<td>d e—</td>
<td>——</td>
</tr>
<tr>
<td><em>Eccoptomera ornata</em> Loew.</td>
<td>d— c— d— c— d— c—</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Cromomyia glacialis</em> Meig.</td>
<td>d c— d— c— c— d c</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Limosina palmata</em> Rich.</td>
<td>— — d— c— d— c—</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Limosina talparum</em> Rich.</td>
<td>d c— —— d— c—</td>
<td>d— c—</td>
<td>——</td>
</tr>
<tr>
<td><em>Lasiops seminervius</em> Wied.</td>
<td>d+ c+ — — d+ c</td>
<td>——</td>
<td>——</td>
</tr>
<tr>
<td><em>Lasiops hirsutulus</em> Zett.</td>
<td>d c d— c— d— c—</td>
<td>——</td>
<td>——</td>
</tr>
</tbody>
</table>

1) See footnote to table 3.

These species were trapped, it is most likely that these flies are visitors from outside searching for moisture or for a suitable place for oviposition in moist soil. During the dry warm summer of 1959, the numerous vole burrows must have been more important as refuges from drought than in 1960. Possibly the changes concerning *Rhagio lineola* (only females in the samples) also has a microclimatic explanation. The phorid *Anevrina thoracica* seems to have been more abundant and constant in burrows under stumps and trees than in other kinds of burrows (see pp. 18 and 19). In the material of 1959 the species might be underrepresented because effective sampling began rather late for it.

Stumps of trees themselves form compound biocenoses with successive changes (*Krogerus* 1927, *Brauns* 1954a). Numerous species associated with decaying wood or else belonging to the stump biocenosis will also occur, at least in small numbers, in the entrance zones of burrows of the type considered
here. Among the species in table 4 *Ctenosciara hyalipennis* and the *Tachydomia* species might belong to this category. Further several fungus gnats belong here (in Småholmen 1960 more than 20 species) but it can be noted that no *Mycetophilidae* (sensu lat.) species show a dominance or constancy high enough to warrant their inclusion in the table.

The instability and heterogeneity of the dipterous fauna in this kind of burrows could be demonstrated by using AGRELL’s (1945) method for a coenological analysis. Among the species present in at least 25% of the burrows on Småholmen there are only two, *Ctenosciara hyalipennis* and *Tachydomia ciliaris*, common to 1959 and 1960. These two species do not show a strong affinity (1959 about 40%, in 1960 about 10%).

V. Dipterous fauna of burrows in grassy soil under bushes

The burrows mentioned in the heading are *Microtus arvalis* runways in garden soil and in grassy soil in shady places on Småholmen. The soil in these cases is not much mixed with pieces of decaying wood and the burrows are thus less favourable for xylosaprophagous and fungivorous Diptera. Samples of Diptera were taken from 11 burrows in 1959 (number of traps increased successively during the summer) and from 15 in 1960. The list of the dipterous families and numbers of species and individuals is given in table 5. The list shows that the important groups are in general the same as in the burrows under stumps and trees. The *Mycetophilidae* are, however, in the samples of 1960 only 2.

Table 6 gives the approximate dominance and constancy for a number of species selected from the material, following the same principles as for the Diptera of the burrows under stumps and trees (table 4). The dominance values (d+, d, d-) are calculated as before, the constancy values are given according to the scale below:

<table>
<thead>
<tr>
<th></th>
<th>1959</th>
<th>1960</th>
</tr>
</thead>
<tbody>
<tr>
<td>c+</td>
<td>in 6—11 burrows</td>
<td>in 8—15 burrows</td>
</tr>
<tr>
<td>c</td>
<td>in 3—5</td>
<td>in 4—7</td>
</tr>
<tr>
<td>c−</td>
<td>in 1—2</td>
<td>in 1—3</td>
</tr>
</tbody>
</table>

If the d and c values of 1959 and 1960 for the species are compared, at least the following significant change can be noted: *Limosina talparum* which was common and constant (in 6 burrows out of 11) in 1959, was found in only
TABLE 5. The dipterous families, numbers of species and individuals in the collections from burrows in grassy soil under bushes in Småholmen. The abbreviations are the same as in table 3.

<table>
<thead>
<tr>
<th>Family</th>
<th>1959</th>
<th>1960</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tipulidae</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Trichoceridae</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Anisopodidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Bibionidae</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Mycetophilidae</td>
<td>4</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Sciaridae</td>
<td>6</td>
<td>19</td>
<td>13</td>
</tr>
<tr>
<td>Rhagionidae</td>
<td>1</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Empididae</td>
<td>9</td>
<td>31</td>
<td>3</td>
</tr>
<tr>
<td>Dolichopodidae</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Phoridae</td>
<td>7?</td>
<td>26</td>
<td>12</td>
</tr>
<tr>
<td>Sciomyzidae</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Helomyzidae</td>
<td>8</td>
<td>19</td>
<td>4</td>
</tr>
<tr>
<td>Borboridae</td>
<td>7</td>
<td>57</td>
<td>5</td>
</tr>
<tr>
<td>Drosophilidae</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Chloropidae</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Calliphoridae</td>
<td>4</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Muscidae</td>
<td>5</td>
<td>22</td>
<td>5</td>
</tr>
</tbody>
</table>

1) Larvae, the other numbers of individuals refer to imagines.
2) See footnote to table 3.

2 burrows out of 15 in 1960. It is possible that these two burrows were still inhabited by voles in the spring of 1960. After July 10, no specimens were trapped (in 1959 the species was still found in late August). Conicera floricola is lacking in the samples of 1959 but might have been present in May—June that year before the trapping began.

It seems that burrows of this kind are less rich in species than those under stumps and trees, especially if the material of 1960 is considered. Xylosaprophagous and fungivorous elements occur in smaller numbers. Among the species found in at least 25% of the burrows in 1959 and 1960, three species are common to both years: Bradysia bicolor, Anevrina thoracica and Crumomyia glacialis. In the samples of 1960, these species show a mutual association of 50% (Agrell's method), whilst in the samples of 1959 the association is much lower.
TABLE 6. Dominance and constancy of species in the samples from burrows in grassy soil under bushes, in Småholmen. The species are selected following the same principles as in table 4. Explanation of the d values in the text (p. 13) and the c values on p. 16.

<table>
<thead>
<tr>
<th>Species</th>
<th>1959</th>
<th>1960</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>VII—X</td>
<td>VI—X</td>
</tr>
<tr>
<td><strong>Bradysia bicolor</strong> Meig.</td>
<td>d—</td>
<td>d—</td>
</tr>
<tr>
<td><strong>Scaptosciara vivida</strong> Winn.</td>
<td>d—</td>
<td>d—</td>
</tr>
<tr>
<td><strong>Platypalpus luteus</strong> Meig.</td>
<td>d—</td>
<td>d—</td>
</tr>
<tr>
<td><strong>Platypalpus ecalceatus</strong> Zett.</td>
<td>d—</td>
<td>d—</td>
</tr>
<tr>
<td><strong>Anevrina thoracica</strong> Meig.</td>
<td>d</td>
<td>d</td>
</tr>
<tr>
<td><strong>Conicera floricola</strong> Schmitz</td>
<td>—</td>
<td>d+</td>
</tr>
<tr>
<td><strong>Megastoma sp. (pr. pulicaria)</strong></td>
<td>?</td>
<td>d</td>
</tr>
<tr>
<td><strong>Eccoptomera ornata</strong> Loew</td>
<td>d</td>
<td>c</td>
</tr>
<tr>
<td><strong>Crumomyia glacialis</strong> Meig.</td>
<td>d</td>
<td>c</td>
</tr>
<tr>
<td><strong>Copromyza stercoraria</strong> Meig.</td>
<td>d—</td>
<td>d—</td>
</tr>
<tr>
<td><strong>Limosina talparum</strong> Rich.</td>
<td>d+</td>
<td>c+</td>
</tr>
<tr>
<td><strong>Cynomyia mortuorum</strong> L.</td>
<td>d</td>
<td>c</td>
</tr>
<tr>
<td><strong>Alloestylus sudeticus</strong> Schnabl</td>
<td>d</td>
<td>c</td>
</tr>
</tbody>
</table>

VI. Diptera of burrows in meadows

In Bonäs the burrows investigated in meadows were made by the Field Vole and several of them were used by voles in 1960. 9 burrows were on comparatively well drained meadows, mainly in the banks of ditches, 7 on a less well drained meadow in the banks of a large ditch (containing water throughout the summer). The numbers of species and individuals are given in table 7. The important groups are the Trichoceridae, Sciaridae, Phoridae, Borboridae.

The more abundant or at least fairly constant species, selected according to the same principles as before, are listed in table 8. As one species shows a dominance value above 20 %, the class d++ has been added indicating a dominance between 20 and 25 %. The c values mean:

- c+ = in 9—16 burrows, c = in 5—8 burrows, c— = in 1—4 burrows

The high dominance value for *Trichocera regelationis* attracts attention, but it must be mentioned that 87 individuals of this species were trapped in one burrow. Obviously there had been a local congregation of larvae in the soil (possibly in an old food store of the voles). The great number of *T. regelationis* individuals markedly depresses the d values for other species in a collection of 456 specimens, but as this does not affect the c values, important species will hardly have been omitted from the list. In these burrows, *Limosina talparum,*
### Table 7. Dipterous families and numbers of species and individuals in the collection from burrows of the Field Vole in meadows in Bondä.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Limoniidae</td>
<td>2</td>
<td>16</td>
<td>Dolichopodidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Trichoceridae</td>
<td>1</td>
<td>100</td>
<td>Phoridae</td>
<td>13</td>
<td>77</td>
</tr>
<tr>
<td>Culicidae</td>
<td>1</td>
<td>22</td>
<td>Syrphidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>3</td>
<td>11</td>
<td>Helomyzidae</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>Mycetophilidae</td>
<td>3</td>
<td>3</td>
<td>Borboridae</td>
<td>10</td>
<td>91</td>
</tr>
<tr>
<td>Sciaridae</td>
<td>6</td>
<td>99</td>
<td>Chloropidae</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Cecidomyiidae</td>
<td>2</td>
<td>6</td>
<td>Calliphoridae</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Empididae</td>
<td>6</td>
<td>10</td>
<td>Muscidae</td>
<td>3</td>
<td>22</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Family</th>
<th>Sp.</th>
<th>Ind.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Limosina claviventris Strobl.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limosina talparum Rich.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cynomyia mortuorum L.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The characteristic species of runways of various micromammals, is both common and constant (in 12 out of 16 burrows). *Bradysia bicolor*, fairly constant in burrows in grassy soil on Småholmen, has been trapped in 11 out of 16 burrows on meadows in Bondäs. *Anevrina thoracica* is fairly constant (in 8 out of 16 burrows) but seems to have its highest dominance and constancy in burrows under stumps and trees.

In Evitskog in 1961, 8 burrows on a comparatively well drained meadow area were studied from June 8 to August 25, but in several of the traps bait was used for shorter periods. The burrows were obviously largely used by voles, probably *Microtus agrestis*. The dipterous material trapped here was small, however, (about a hundred individuals) and covered only a part of the warm season. The number of species was surprisingly low. To calculate d values from such a collection would be meaningless but it can be noted that the common species showing high constancy were:

- *Anevrina thoracica* and *Bradysia bicolor* were not captured there at all.
- *Crumomyia glacialis* was taken in several burrows in June but its main time of occurrence is before and after the period investigated.
If Agrell's method for a coenological analysis is applied to the material from meadows in Bonäs and the flies from each burrow considered as a sample, 11 species present in at least 25% of the samples can be selected for study of mutual association. The single pair of species associated to over 70% is the stenotropic Limosina talparum and a probably ubiquitous phorid, a Megaselia sp. of the pulicaria group (breviterga Schmitz?). No other groups of species showing higher association (>50%) can be demonstrated by application of this method.

VII. Diptera trapped with bait

1. Bait of decaying fruit. On Småholmen 1960, bait of decaying apples was placed in 5 funnel traps June 7 (removed from 4 traps in beginning of July). The funnel end was directed inwards in the burrow, blocking the entrance. The results were poor and hardly more Diptera were collected than if the traps had been without bait:

Anisopus fenestralis 2♀, Ctenosciara hyalipennis 1♀, Corynoptera boletiphaga 1♀, C. piniphila 1♀, Megaselia angusta 1♀, M. sp. 2♂ 3♀, M. fusc 1♀, M. rufipes 1♀, Plastophora sp. 3♀, Chaetomus confusus 1♀, Crumomyia glacialis 3♀, Leptocera coenosa 2♀, Limosina claviventris 1♀, Drosophila fasciata 2♀, Fannia hamata 1♀, F. coracina 1♀ and Alloeostylus sudeticus 1♀.

2. Bait of decaying fungi. On Småholmen in 1960, portions of a myxomycete were used as bait in 2 traps from June 7 until July 7. These fungi decay rapidly and then smell strongly and the smell remains in the trap for months. The traps were placed with the funnel end inwards into the runway. The species trapped were:

Scaptosciara vivida 2♀, Corynoptera fulvicollis 1♀, Bradysia confinis 2♀, Conicera floricola 1♂ 3♀, Megaselia barbulata 1♀, M. woodi 1♀ and Crumomyia glacialis 1♀.

All species trapped are saprophagous but the numbers of individuals are too small to show anything of significance.

In Evitskog 1960, rotten mushrooms (Psalliota) were tried as bait in 4 traps July 23 — August 15 (metal gauze funnel, funnel end inwards in the vole burrow). The following species were trapped:

Megaselia giraudi 2♀, Limosina talparum 4♀, Cynomyia mortuorum 6♀, Lucilia silvarum 1♀ and Pegohylomyia fugax 1♀.

3. Bait of rodent droppings. On Småholmen in 1960, droppings of guinea-pig were used as bait in one trap (July 7 — August 31). The trap was placed in a Microtus arvalis burrow with funnel end inwards. The following species were trapped:
In Evitskog in 1961, 4 traps with droppings of white laboratory mice as bait were used in the period July 19 — August 25. The traps were placed at the entrances of the vole burrows but not so as to block them. The following species were trapped:


4. Bait of cheese. In Evitskog in 1961, a cheese of Port Salut type (strongly smelling) was used as bait in one trap August 5—25 in a vole burrow. The funnel trap was placed so that it did not block the entrance. Two species were trapped: *Limosina talparum* 1♂ 5♀, and *L. pullula* 1♀.

A trap with the same kind of bait was placed in an artificial burrow in a garden in Evitskog (not close to any vole burrows). The funnel side of the trap was directed outwards and the Diptera trapped thus came from outside. The trap was set up on August 28 and during the next two weeks gave the following result:

- *Gymnophora arcuata* 1♂ 2♀♀
- *Megaselia giraudi* 2♀♀
- *Oechthea fenestralis* 1♂ 4♀♀
- *Stratioborborus fimbriatus* 1♀
- *Leptocera fontinalis* 3♀♀
- *Limosina claviventris* 6♀♀
- *Piephila vulgaris* 1♂ 1♀

5. Bait of meat. On Småholmen in 1960, meat was tried as bait in different trap arrangements: a) In a runway of *Microtus arvalis* as in fig. 7. The funnel blocks the runway and Diptera from outside can get at the bait but are not trapped. The trap thus collects only individuals coming from the inner parts of the burrow. b) Bait in a closed plastic jar outside a burrow (see fig. 8). The funnel of the trap was placed some centimetres from the entrance to a burrow under a stump. After some weeks the bait was almost liquid. c) Similar trap arrangement at the entrance of a burrow under a tree. The bait was in a metal gauze container and did not decay to liquid consistency. The trapping was started on June 7. The trap with bait in the burrow (a) gave good results until the beginning of July. Then the bait was renewed, but towards the end of July it ceased to attract any Diptera. In cases b and c the bait was not changed until late October. The results are given in table 9.
TABLE 9. *Species trapped on meat bait in various arrangements (a, b and c on Småholmen 1960). The trap arrangements are explained in the text (p. 21). The species are placed in two groups, I) species trapped in burrows also without using meat baits, II) species not trapped in vole burrows in the areas of investigation.*

<table>
<thead>
<tr>
<th>Species trapped</th>
<th>Bait in the burrow (a)</th>
<th>Bait outside arrangement b</th>
<th>Bait outside arrangement c</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Within 30 days</td>
<td>Within 30 days</td>
<td>After 30 days</td>
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<td></td>
<td></td>
<td>After 30 days</td>
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<tr>
<td><strong>Group I.</strong></td>
<td></td>
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<tr>
<td>Lycoriella brevipila</td>
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<td>-</td>
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<tr>
<td>Corynoptera boletiphaga</td>
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<td>-</td>
</tr>
<tr>
<td>Ctenosciara hyalipennis</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Scaptosciara vivida</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Anerovia thoracica</strong></td>
<td>1♂</td>
<td>2♀</td>
<td>1♂</td>
</tr>
<tr>
<td><strong>unispinosa</strong></td>
<td>1♂, 16♀</td>
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<tr>
<td>Conicer a floricola</td>
<td>10♂, 64♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>pauxilla</strong></td>
<td>5♀</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Megaselia barbulata</td>
<td>-</td>
<td>-</td>
<td>1♂</td>
</tr>
<tr>
<td><strong>nigripalpis</strong></td>
<td>1♂</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>hyalipennis</strong></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>ruficornis</strong></td>
<td>-</td>
<td>-</td>
<td>1♂</td>
</tr>
<tr>
<td><strong>giraudi</strong></td>
<td>3♀, 1♀, 5♂</td>
<td>4♂</td>
<td>1♂</td>
</tr>
<tr>
<td><strong>rupipes</strong></td>
<td>4♀, 1♀</td>
<td>9♂, 28♀</td>
<td>2♂</td>
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<tr>
<td><strong>sp. (pr. pulicaria)</strong></td>
<td>3♂, 2♀</td>
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<td>1♂</td>
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<tr>
<td>Dryomyza anilis</td>
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</tr>
<tr>
<td>Tephroclamys flavipes</td>
<td>-</td>
<td>-</td>
<td>1♀</td>
</tr>
<tr>
<td>Neoteria inscripta</td>
<td>-</td>
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<tr>
<td>Stratioborborus fimbriarius</td>
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<td>Crumomyia gracialis</td>
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</tr>
<tr>
<td>Limosina claviventris</td>
<td>-</td>
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</tr>
<tr>
<td><strong>flavipes</strong></td>
<td>-</td>
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</tr>
<tr>
<td><strong>palmata</strong></td>
<td>-</td>
<td>3♂, 2♀</td>
<td>-</td>
</tr>
<tr>
<td>Calliphora erythrocephala</td>
<td>-</td>
<td>-</td>
<td>1♀</td>
</tr>
<tr>
<td>Cynomyia mortuorum</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td>Fannia hamata</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>coracina</strong></td>
<td>-</td>
<td>2♀</td>
<td>4♀</td>
</tr>
<tr>
<td><strong>Group II.</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnophora arcuata</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Mycteaulus bipunctatus</td>
<td>-</td>
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</tr>
<tr>
<td>Piophila vulgaris</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Acartophthalmus bicolor</td>
<td>-</td>
<td>-</td>
<td>4♂, 1♀</td>
</tr>
<tr>
<td>Drosophila testacea</td>
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<td>Fannia sp. (difficilis?)</td>
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<tr>
<td><strong>speciosa</strong></td>
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<td>2♀</td>
</tr>
<tr>
<td>Hydrotæa oculata</td>
<td>-</td>
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</tr>
</tbody>
</table>
5. Micromammalian carrion as bait. On Småholmen August 10, 1959 a freshly killed Microtus arvalis was placed in a burrow and the opening blocked by a funnel trap (funnel inwards). The very few specimens trapped belonged to typically necrophagous species:

- *Dryomyza anilis* 1♀ 11—20. VIII
- *Cynomyia mortuorum* 1♀ 28. X
- *Calliphora erythrocephala* 1♀ subalpina 28. IX

In Bonäs in 1960, a Bank Vole was used as bait in a burrow in similar way. Three ♀ of *Anevrina unispinosa* were trapped.

In Evitskog in 1961, a dead shrew was placed about 15 cm deep in a *Microtus* burrow and the entrance blocked by a funnel trap with the funnel end outwards (both funnel and bottom of the trap made of metal gauze). The experiment was made to see which species enter burrows containing dead micromammals and was started on June 18. Only one species of Diptera was trapped: *Cynomyia mortuorum*, 15 ♀ during the period June 20 — July 26.

VIII. Traps without bait in artificial burrows

On Småholmen in 1960, a special trap arrangement was used in order to see which Diptera enter holes in the ground even if the holes are not made or inhabited by micromammals. The traps were metal gauze cylinders ending in a container (pitfall trap) with ethylene glycol placed in a hole as in fig. 9. 30 traps of this type were set out in various places on the island and were mainly sunk in shady places under bushes or at roots of trees. In 20 of the traps Diptera were captured. Altogether 45 species were obtained (123 individuals):

- *Polypedilum sp.* 1♀
- *Bibio claviges* Meig. 1♀
- *Macroceria lutea* Meig. 1♀
- *Mycomia fusca* Meig. 3♀
  * incisurata Zett. 1♀
- *Rhynosia fasciata* Meig. 1♀
- *Polyxena fasciata* Meig. 1♂
  * fissa Edv. 1♀
- *Corynoptera sp.* 2♀
- *Lycoriella brevipila* Tuom. 1♀
  * sp. 1♀
- *Ctenosciara hyalipennis* Meig. 1♂ 2♀
- *Brady sia bicolor* Meig. 4♀
  * nocturna* Tuom. 1♀
  * sp. 2♀
- *Scaptosciara vivida* Winn. 2♀
- *Rhagio lineola* F. 1♀
- *Platypalpus ciliaris* Fall. 2♀
- *Tachypena nubila* Meig. 1♀
- *Xanthochlorus tenellus* Wied. 1♀
- *Anevrina thoracica* Meig. 16♂
- *Coniceria floricola* Schmitz 2♀ 16♀
- *Triphleba bicornuta* Strobl 3♀ 5♀
- *Phora pubipes* Schmitz 1♂
  * sp. 4♀
- *Megaselia pleuralis* Wood. 1♂
  * barbulata* Wood. 1♂
  * coaequalis* Schmitz 2♂
  * hyalipennis* Wood. 1♂
  * unicolor* Schmitz 1♂
The vast majority are species also trapped in real vole burrows. The great number of males among the Phoridae is noteworthy. As in the vole burrows the Muscidae (Alloeostylus, Lasiops) are represented by females.

IX. Rearing experiments

For rearing dipterous species belonging to the vole burrow fauna and to obtain information as to which kinds of substrate can serve as food for the larvae, the following methods were used: 1) Bait of the same kind as was used in the bait traps was put in small containers of coarse metal gauze (length about 6—8 cm, diameter about 3 cm, mesh big enough for medium-sized Diptera to get at the bait) and exposed for egg-laying 7—10 days in a vole burrow (about 30 cm inside the burrow). The bait container attached to a metal thread was then removed and the contents put in a rearing cage and more of the substrate added. The cage (fig. 10) was sunk in the soil at a suitable place with only a small vial (in which the emerging imagines are trapped) above the surface. In some cases the cages were kept in flower-pots in a laboratory room (temperature kept at +12°C). 2) Females of dipterous species (caught in the funnel traps) were placed in the same kind of rearing cages provided with the substrate and sunk in the soil.

The methods were tried with meat bait already in Småholmen in 1960 but used on a larger scale in Evitskog in 1961, with several kinds of bait.

If the rearing cages are kept in the open sunk in the soil, the risk of secondary infection from outside is considerable. Small dipterous larvae can creep through the meshes into the substrate. It is obvious that this has taken place in some of the experiments. Females of certain species are attracted by the smell from the cages and lay their eggs on the metal gauze of the cage. If, on the other hand, the cages are too air-tight (jars of plastic instead of metal gauze cylinders) the substrate will grow a culture of mould and the dipterous larvae die. If meat is used as substrate the decaying process in air-tight jars will also be unfavourable for the larvae and kill most of them. In these experi-
ments, however, the disadvantage of secondary infection by Diptera was of lesser importance since the main purpose of the experiments was to find out the feeding biology of certain species and not to prove the presence of the species in the burrows where the bait had been exposed for oviposition. In the cultures started in September 1961 with bait exposed in Clethrionomys glareolus burrows on Småholmen and then kept in flower-pots in the laboratory, the risk of secondary infection was practically nil.

1. Vegetable substrates. On Småholmen in 1960 bait consisting of rottening grass was placed in 3 burrows of Clethrionomys type (in forest) but the cultures gave no results. Two females of Limosina talparum were placed in one culture with grass as a substrate (July 7) and a number of specimens were reared after a month (see table 10).

In Evitskog in 1961, 3 cultures were started on banana peel exposed in Microtus burrow. Two gave results (Limosina moesta and L. claviventris, table 10), one mouldered entirely. Mushrooms (Psalliota) were used in one culture after exposure in a vole burrow, Drosophila transversa and a phorid were reared (see table 10).

2. Rodent excrement as substrate. Droppings of white mice (from laboratory culture) was used in most of the experiments:

a) Bait exposed in vole burrows:
   Småholmen 1961, 4 cultures in laboratory, 3 with positive results
   Bonäs 1961, 2 in the open, 2
   Evitskog 1961, 7 in the open, 6

b) Diptera introduced into cages with the substrate:
   Evitskog 1961, 20 cultures. Same species reared in 7, other species (secondary infection) in 9 cases.

The species introduced were:

- Limosina claviventris, 14 cultures, positive results in 10.
- L. talparum, 5 cultures, positive results in 3.
- Megaselia giraudi 4 cultures, positive results in 3.
- Crummomyia glacialis, 5 cultures, negative results.

3. Cheese as substrate. A Port Salut cheese was used both as bait and as substrate for the larvae.

a) Bait exposed in vole burrows:
   Småholmen 1961, 2 cultures kept in laboratory, positive results in one.
   Evitskog 1961, 2 cultures kept in the open, positive results in one.

b) Diptera introduced:
   Evitskog 1961, Anervina urbana 12, culture in the open, negative result, but secondary infection by other species (mainly Oecothea fenestralis).
TABLE 10. The results of the rearing experiments. Abbreviations: Rd. excr. = rodent excrement, D. ins. = dead insects, Rt. grass = Rotten grass, L = Locality, E = Evitskog, S = Småholmen, B = Bonäs. In the column marked with L the numbers of cultures are given in which the species in question was reared. E:8 means that the species was reared in 8 cultures in Evitskog.

<table>
<thead>
<tr>
<th>CHIRONOMIDAE</th>
<th>Substrate</th>
<th>L</th>
<th>Time from start of culture to hatching of imagines and number of individuals reared</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smittia sp.</td>
<td>Rd. excr.</td>
<td>E:1</td>
<td>3–4 weeks</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MYCETOPHILIDAE</td>
<td>Cheese</td>
<td>S:1</td>
<td></td>
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<tr>
<td>SCIARIDAE</td>
<td>Lycoriella brevipila Tuom.</td>
<td>Rd. excr.</td>
<td>S:1</td>
</tr>
<tr>
<td></td>
<td>Lycoriella brevipila</td>
<td>Rd. excr.</td>
<td>B:1</td>
</tr>
<tr>
<td></td>
<td>Lycoriella hundstroemi Frey.</td>
<td>Rd. excr.</td>
<td>E:1</td>
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<td></td>
<td>Braldysia nocturna Tuom...</td>
<td>Rd. excr.</td>
<td>E:1</td>
</tr>
<tr>
<td></td>
<td>Braldysia trivittata Staeg...</td>
<td>Rd. excr.</td>
<td>E:1</td>
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<td>Scaptosciara vivida Winn.</td>
<td>Rd. excr.</td>
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<td></td>
<td>Scaptosciara vivida</td>
<td>Meat</td>
<td>E:2</td>
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<tr>
<td>EMPIDIDAE</td>
<td>Unidentified species</td>
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<td>E:1</td>
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<td>PHORIDAE</td>
<td>Triphleba bicornuta Strobl.</td>
<td>Rd. excr.</td>
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<td>Coniceria fallens Schmitz ...</td>
<td>Cheese</td>
<td>E:2</td>
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<td>Conigeria pau. Schmitz (?)</td>
<td>Meat</td>
<td>S:1</td>
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<td>Megasia laevis Meig.</td>
<td>D.ins.</td>
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<td>Megasia giraudi Egg......</td>
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<td>E:1</td>
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<td>Rd. excr.</td>
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<td>Megasia fusca Wood.....</td>
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<td>E:1</td>
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<td>Megasia sp.</td>
<td>Muschr.</td>
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<td></td>
<td>Megasia sp.</td>
<td>Rd. excr.</td>
<td>E:1</td>
</tr>
</tbody>
</table>

Remarks

- Culture started 13.VI., larva from outside.
- Bait exposed 7–18.IX., laboratory culture. Hatched after 12 weeks.
- Bait exposed 7–18.IX., laboratory culture. Time of hatching not known.
- Culture started 13.VI., larva from outside.
- Culture started 15.VIII., larva from outside.
- Culture started 14.VI., larva from outside.
- In 6 cases bait exposed in June 8 cases: larvae from outside.
- Bait exposed 7–18.IX., laboratory culture.
- Bait exposed 18–25.VI.
- 3 larvae, probably from outside.
- Bait exposed 7–18.IX., laboratory culture, 1♂ in April 1962.
- Larvae in at least one culture from outside, possibly a second generation in the other culture.
- Bait exposed 18–25.VI.
- Bait exposed 1–8.VII.1960.
- Bait exposed 14–24.VIII., laboratory culture.
- Bait exposed 1–4.VII.
- Culture started 8.VII.
- Cultures started in June, larvae from outside.
- Culture started 4.VI., larva from outside.
- Bait exposed 18–25.VI.
- Bait exposed 1–8.VIII.
- Bait exposed 13–29.VIII.
<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Type</th>
<th>Bait Exposed</th>
<th>Larvae from Outside</th>
<th>Culture Started</th>
<th>Remarks</th>
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<td>Heteromyza oculata</td>
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<td>Cheese</td>
<td>7-18 IX</td>
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<td>Tephroclamys flavipes</td>
<td>Zett.</td>
<td>Cheese</td>
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<td></td>
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<td>Tephroclamys flavipes</td>
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<td>E:3</td>
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<td><strong>BORBORIDAE</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limosina moesta</td>
<td>Villen</td>
<td>Banana</td>
<td>7-18 IX</td>
<td></td>
<td>1♀</td>
<td></td>
</tr>
<tr>
<td>Limosina claviventris</td>
<td>Strobl.</td>
<td>Banana</td>
<td></td>
<td></td>
<td>1♀</td>
<td></td>
</tr>
<tr>
<td>Limosina claviventris</td>
<td></td>
<td>Rd.excr.</td>
<td>E:9</td>
<td></td>
<td>1♀</td>
<td></td>
</tr>
<tr>
<td>Limosina claviventris</td>
<td></td>
<td>Rd.excr.</td>
<td>B:1</td>
<td></td>
<td>1♀</td>
<td></td>
</tr>
<tr>
<td>Limosina claviventris</td>
<td></td>
<td>D.ins.</td>
<td></td>
<td></td>
<td>2♀</td>
<td></td>
</tr>
<tr>
<td>Limosina claviventris</td>
<td></td>
<td>Meat</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limosina pullula</td>
<td>Zett.</td>
<td>Rd.excr.</td>
<td>E:4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limosina talparum</td>
<td>Rich</td>
<td>Rt.grass</td>
<td>13-10 VI</td>
<td></td>
<td>1♀</td>
<td></td>
</tr>
<tr>
<td>Limosina talparum</td>
<td></td>
<td>Rd.excr.</td>
<td>E:4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limosina palmata</td>
<td>Rich</td>
<td>Meat</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>DROSOPHILIDAE</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Drosophila transversa</td>
<td>Fall</td>
<td>Meat</td>
<td>18-25 VI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drosophila transversa</td>
<td></td>
<td>Mushr.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>CALYPTRATA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sarcophaga coparia</td>
<td>Pand.</td>
<td>Meat</td>
<td>18-25 VI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Muscina assimilis</td>
<td>Fall</td>
<td>Rd.excr.</td>
<td>1♀</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fannia canicularis</td>
<td>L.</td>
<td>Rd.excr.</td>
<td>4-25 VIII</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fannia coracina</td>
<td>Loew</td>
<td>Meat</td>
<td>18-25 VI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fannia coracina</td>
<td></td>
<td>Meat</td>
<td>18-25 VI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pegohylemyia fugax</td>
<td>Meig.</td>
<td>Rd.excr.</td>
<td>2♀</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Cultures started in June, larvae from outside.

Bait exposed 7-18 IX, laboratory culture. 1♀ in January 1962.
Bait exposed 7-18 IX, laboratory culture. 1♀ in February 1962.
Bait exposed 7-18 IX, laboratory culture. 1♂ in February 1962.

In 3 cases bait exposed in June, in 5 cases females introduced, in 1 case larva from outside.

Bait exposed 24 VI-12 VII.
Bait exposed 24 VI-12 VII.

In 3 cases bait exposed in June, in 5 cases females introduced, in 1 case larva from outside.

Time of hatching unknown.
Bait exposed 14-24 VIII, laboratory culture.
Bait exposed in May, 1 ♀, time of hatching not known.

In 3 cases bait exposed in June, in 1 case larva from outside.

2 ♀ implanted 10 VII 1960.
In 1 case bait exposed 13-20 VI, in 2 cases larvae from outside.

Bait exposed 18-25 VI.

Baits exposed 18-25 VI.
Bait exposed 1-10 VIII.

Bait exposed 18-25 VI. Culture from 25 VIII in laboratory, 2 ♀ 1 ♀ in January 1962.
Culture started 13 VI, larvae from outside.

In 2 cases bait exposed in June, 2 cases culture started in June, larvae from outside.

Bait exposed in June, 1960.
Baits exposed 18-25 VI.

In one case bait exp. 5-13 VI, in the other one culture started 13 VI and larva from outside.
4. **Meat as substrate:**

Bait exposed in vole burrows:
- Småholmen 1960, 3 cultures in the open, positive results in 2.
- Bonäs 1961, 2 cultures in the open, positive results in 1.
- Evitskog 1961, 3 cultures in the open, positive results in 2.

5. **Dead insects as substrate:** Killed flies (*Musca domestica*), about 50 specimens, were used as bait and as substrate in the culture.

Evitskog 1961, 1 culture kept in laboratory, positive result (two phorid species reared).

The results of the rearing experiments are listed in table 10.

The number of specimens reared was in most cases low. The cultures in the open were in many cases invaded by predators (larvae of staphylinid beetles, mites and also raptorial dipterous larvae). Some predators may already have been introduced with the bait into the culture. In one case 3 dipterous larvae most probably belonging to Empididae were found (larvae of Dolichopodidae, not separable morphologically from those of Empididae, can hardly be expected in this case). Some of the Phoridae (*Megaselia* spp.) reared are known to be facultative predators as larvae. Further, a certain degree of cannibalism can be expected in some cases. In one culture with meat as substrate some hymenopterous parasites appeared.

**X. The phenology of Diptera in vole burrows**

Only in the case of the more abundant species the data obtained from the present material give a clear picture of the phenology of the species. For a number of species the rearing experiments give an approximate idea of the duration of development from egg to imago. There is no reason to consider here the phenology of occasional visitors and thus the item is restricted to the species which are able to develop in the burrows. On Småholmen in 1959, the trapped material covers the period July—October, and in 1960 from the end of May to the end of October, in Bonäs from mid-May to mid-September 1960. The spring aspect is thus insufficiently known.

During the winter the temperature in the burrows keeps around 0° and at most the imagines of some Diptera known as winter insects might show some activity. In the winter of 1960—1961, 11 pitfall traps were left in burrows on Småholmen and searched for Diptera on April 29, 1961. Most of the traps were filled with earth particles or flooded with water but four of them contained a few Diptera still floating on the surface of the ethylene glycol. These must
Fig. 11. Phenological histograms of Sciaridae in burrows, on Småholmen in 1960 (S 1960) above and in Bonäš 1960 (B) below. On the ordinates the numbers of individuals. On the abscisse between the two diagrams the collecting periods are given. Each month is divided in three periods (10—11 days). The figures above the columns indicate the numbers of species trapped during each period. The numbers of traps (in the upper histogram 24, 30, 31) are on the abscisse under the histograms. Bradysia bicolor marked with white, Ctenosciara hyalipennis striated, other species of Sciaridae black.

have been trapped at most a week before the visit to the island. The species were Crumomyia glacialis and Limosina claviventris. The temperature in one of the burrows was +4° at 1 p.m. that day (a sunny day).

In the material from Bonäš the spring aspect is represented by the species trapped in Clethrionomys burrows in shady wood May 15—20 (burrow temperature only a few degrees above zero):

<table>
<thead>
<tr>
<th>Trichocera regulationis</th>
<th>Megaselia sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>salitator</td>
<td>Heteromyza oculata</td>
</tr>
<tr>
<td>fuscata</td>
<td>Copromyza borealis</td>
</tr>
<tr>
<td></td>
<td>Stratiobborborus fimetarius</td>
</tr>
</tbody>
</table>

The Trichocera species are typical winter insects, but their phenology is far from clear. It is possible that even in one and the same population some individuals hatch in the autumn, others in the spring. In Bonäš, however, no specimens were trapped in September but obviously newly hatched specimens were trapped in great numbers (Trichocera regulationis) as late as in the end of
May and beginning of June. These specimens were from burrows in meadows which had already warmed up to about +8° by the middle of May. On Småholmen the *Trichocera* species were trapped in smaller numbers in the autumn but not any more in the end of May (when the trapping began on Småholmen 1960).

Among the Helomyzidae there are also species occurring in autumn and spring and supposed to be imago hibernators. The rearing experiments made in this investigation, however, have thrown more light on the phenology of one of them, *Heteromyza oculata*. On Småholmen 1959 and 1960, a few specimens were trapped in August and September, in Evitskog a couple in July 1961. In Bonäs 1960, *Heteromyza oculata* was only trapped in May. In a laboratory culture (see table 10) started from a cheese bait exposed for oviposition in a burrow on Småholmen in September 1961 a specimen of this species was reared in January 1962. This shows that females occurring in autumn are able to lay eggs before the winter that possibly do not give rise to a new generation until the following summer (Evitskog finds in July). In Bonäs, the species was only trapped in May and in burrows warming up very slowly during the spring. It seems as if *H. oculata* might be able to develop two generations in Southern Finland hibernating as larva or puparium but as far north as Bonäs only one, hibernating as the puparium and hatching in the spring.
Fig. 13. Phenological histograms of Helomyzidae in vole burrows. S. 1959 — on Småholmen in 1959, S. 1960 — on Småholmen in 1960, B. 1960 — in Bonäsv in 1960. Striated — *Eccoptomera ornata*, black — other species. For further explanations, see fig. 11.

The Borboridae *Crumomyia glacialis*, *Copromyza borealis*, *Stratioborborus fimetarius* and *Limosina claviventris* taken in traps in the spring had probably hibernated as imagines.

When later in the spring the temperature reaches a diurnal maximum of about +8° — +10°, numerous species appear and among them pupal hibernators as, for example, *Anevrina thoracica* and *Megaselia* spp. *Limosina talparum* showed its highest abundance in Bonäsv in the burrows in meadows in mid-May (see fig. 14). Towards the end of May the Sciariidae increase in numbers (Corynoptera spp., *Lycoriella brevipila*, some *Brady sia* spp., *Scaptosciara vivida*). The occurrence of *Trichocera regelationis* in Bonäsv during this period has already been mentioned. *Muscina assimilis* was trapped in numbers (1511♀♀) in the second half of May in Bonäsv. The hibernating instar is not known.

On Småholmen and in Bonäsv the period from mid-June to mid-July gave the best trapping results as regards both species and individuals. The Phoridae show a clear peak (see fig. 12), the sciarid gnats *Brady sia bicolor* has its maximum (see fig. 11) and a new generation of *Crumomyia glacialis* occurs.

Concerning some groups the late summer—autumn aspect of the fauna differs remarkably in Småholmen and Bonäsv. The Sciariidae show a peak during this period in Småholmen (especially in the 1960 material, see fig. 11) caused by the second generation of some species and a maximum of *Ctenosciara*.
hyalipennis (occurring throughout the season). In Bonäs there is no peak of Sciaridae during the late summer and beginning of the autumn (see fig.11). The Helomyzidae (fig.13) form a characteristic part of the autumn fauna in the burrows on Småholmen but are not found among the flies trapped in
September in Bonä. *Hetromyza oculata* has already been dealt with in connection with the spring aspect. *Tephroclamys flavipes*, occurring in burrows on Smäholmen in September (and October 1959), was reared from bait exposed in burrows September 7–18 1961 (see table 10) and is thus able to oviposit before the winter in S. Finland. The phenology of the *Eccoptomera* species (*ornata* and *infuscata*) is less clear, as these occur in very small numbers in the samples from the end of June to late autumn. A further helomyzid fly, *Oecotheca fenestralis*, represented by very few specimens in the trapping material (Smäholmen, Bonä), was reared in cultures in Evitskog. It obviously has two generations in South Finland, imagines in June and August—September (in Bonä taken in May). The duration of its development is about two months during the summer. This species is mentioned here because it is known from burrows of various mammals (Falcoz 1915, 1921, Gorodkov 1959). Séguy (1950) reports that in mammal burrows in France this species develops generation after generation without any long winter pause.

The following species occur as imagines in overlapping generations throughout the warm season:

- *Plastosciara nobilis*
- *Lycoriella brevipila*
- *Ctenosciara hyaliennis*
- *Scaptosciara vivida*
- *Corynoptera tetrachaeta*
- *Megaselia sp.* (pr. *pulicaria*)
- *Conicera floricola*
- *Leptocera fontinalis*
- *Limosina claviventris*
- *Limosina talparum*

*Plastosciara nobilis* is present in only very few samples but its phenology is known (Tuomikoski 1961). *Lycoriella brevipila*, *Scaptosciara vivida*, *Limosina claviventris* and *L. talparum* were reared in cultures in the open in 1961. The development of these species takes approximately a month.

The few species of Calliphoridae and Muscidae frequently trapped in the burrows or reared from bait are mainly represented by females entering the burrows from outside. Among these *Cynomyia mortuorum* occurs throughout the summer. *Fannia coracina* has a developmental period of two months (see table 10) and imagines occur at least in the end of June and in August in South Finland. The *Lasiops* species and *Alloestylus sudeticus* were trapped in July—August, the last-mentioned even later in the autumn. The tachinid fly *Sarcophaga scoparia*, as the rearing experiments show, has only one generation a year. The bait from which the species was reared was exposed for oviposition in the end of June.

The differences in the phenology of certain groups of Diptera on Smäholmen and in Bonä, most clearly seen in the Sciaridae (fig.11) but also as
Fig. 15. The phenology of 8 dipterous species in three kinds of burrows in Bonás 1960. Under the histograms (on abscisse) the period with temperatures above +10°C is indicated. A — burrows in well drained meadows (10 traps), B — burrows in the banks of a large water ditch in a meadow (7 traps), C — burrows under stumps and trees in shady wood. Numbers of individuals and species and the collecting periods indicated as in fig. 11. See further the text on p. 34.

A tendency in the Phoridae (fig. 12), are naturally due to the difference in length of the warm period. It is obvious, however, that microclimatic differences between burrows in the same locality cause some differences in the phenology of the species inhabiting them. This is demonstrated in fig. 15, where the trapping records for 8 species in three types of burrows in Bonäs are compared: a) burrows in well drained meadow soil, b) in less well drained meadow soil and c) under roots of stumps and trees in shady woodland. The 8 species are Bradysia bicolor, Anevrina thoracica, Megaselia flavicosa, M. sp. (pr. pulicaria), Crumomyia glacialis, Leptocera fontinalis, Limosina claviventris and L. talparum. In types a) and b) activity begins and reaches the peak earlier than in case c).
XI. Ecological classification of vole burrow Diptera.
Notes about certain species

A. Wirén’s classification

An ecological classification of insects occurring in vole burrows can be made along different lines. Wirén (1961) has suggested a useful classification based mainly on the feeding habits. Wirén’s groups of insects in burrows systems of small rodents are as follows:

1. Food store insects (»Vorratsinsekten»).
2. Necrophagous insects (»Aaslebende insekten»).
3. Species feeding on refuse and saprophytes (»Abfalls- und saprophyten-lebende Arten»).
4. Insects in nests for breeding and hibernation and floating nests (»Insekten in Brutnestern, Winternestern und Schwimmnestern»).
5. Occasional visitors (»Zufälligen Besuchen»).

As a criticism it might be mentioned that there are no groups for raptorial species and parasites of other members of the community. As far as the Diptera are concerned raptorial species are mainly represented in the burrows by Empididae (imagines and larvae), Rhagionidae (larvae), Phoridae (facultatively raptorial larvae), Muscidae (larvae) and Mycetophilidae (Macrocer a larvae). These can hardly all be considered as occasional visitors. In the present material parasitic forms are represented by a few blood-sucking Culicidae and Ceratopogonidae and some Phoridae (larvae facultative parasites on other invertebrates). The Ceratopogonidae are probably here truely occasional visitors. The Culicidae might to some extent use the burrows as hibernating place. Observations of this kind have been made in U.S.A. (Bennington & al., 1958)

In the following the ecological groups will be treated in greater detail according to Wirén’s classification.

1. Food store Diptera.

The Bank Vole often collects large stores of various vegetables in its burrows for the winter. This is also but less often done by the two Microtus species. The mortality of voles being high during the winter, many such stores will not be entirely used up and will be in various stages of decomposition by the next spring. Such stores of rotten vegetables will provide a suitable substrate for phytosaprophagous Diptera. It must be admitted that no special search was made for such stores on Småholmen and they were not found in the few burrows systems opened during summer 1960. On the other hand, some of the
samples from Bonäs in 1960 may indicate which species may be of importance as feeders in vegetable stores of this kind:

<table>
<thead>
<tr>
<th>Species</th>
<th>Burrow nr 12</th>
<th>Burrow nr 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trichocera regelationis</td>
<td>2♂ 5♀</td>
<td>36♂ 51♀</td>
</tr>
<tr>
<td>Bradysia bicolor</td>
<td>17♂ 4♀</td>
<td></td>
</tr>
<tr>
<td>Ormosia pseudosimilis</td>
<td>13♀</td>
<td></td>
</tr>
</tbody>
</table>

The above three species (phytosophagous as larvae) were conspicuously numerous in certain burrows of *Microtus agrestis* (burrows no. 6 and 12).

*Limosina talparum*, highly constant inhabitant in *Microtus* burrows, was reared on decaying grass and can thus be expected to be a store insect.

Some other saprotophagous species trapped in the burrows (for example *Anisopus fenestralis* and various Sciaridae) might feed as larvae in vegetable stores but do not congregate locally like *Trichocera* and *Bradysia bicolor* in Bonäs.

2. Necrophagous species

Dead voles in the burrows will within a short time attract necrophagous Diptera. The experiments with carrion and meat bait indicated that at least the following species are important in the localities where the investigation was made:

- *Anevrina unispinosa toracica*
- *Conicera floricola fallnes*
- *Megaselia rufipes*
- *Dryomyza anilis*
- *Neoteria inscripta*
- *Limosina palmata*
- *Cynomyia mortuorum*
- *Sarcophaga scoparia*
- *Fannia coracina*

There were a number of further species trapped on meat bait at the entrance of burrows, but whether these species are adapted to oviposit in the darkness deeper in the burrows remains uncertain. As a facultatively necrophagous species *Drosophila transversa* Fall. was reared in two cultures in Evitskog. Usually this species feeds on decaying fungi.

3. Diptera feeding on refuse and on saprophytes in the burrows

Burrows inhabited by voles contain various types of refuse: vegetable remains from meals and excrement. The decaying process of the vegetables will be accelerated by the urine of the voles and there will be suitable substrates for a fungal flora. In burrows made by *Clethrionomys glareolus* under stumps and trees fungal hyphae will also be abundant.
In the usual type of Microtus burrows in grassy soil there will be fewer fungi and mycetophagous Diptera will be less numerous. The majority of the coprophagous and phytosaprophagous species in the burrows are obviously members of the local terricolous fauna and may invade the burrows either as larvae from the surrounding soil or as egg-laying females from outside. If species that are occasional visitors and those whose biology is insufficiently known are excluded, the following saprophagous species from the present material can be listed in this category (B = Bonäs, E = Evitskog, S = Småholmen, copr. = coprophagous, phytosapr. = phytosaprophagous, zoosapr. = zoosaprophagous, sapr. = saprophagous in general):

- Smittia sp. (copr., E,B)
- Docosia gilvipes (copr., S)
- Lycoriella brevipila (copr., S)
- Bradysia bicolor (phytosapr., S,B)
- Lycoriella brevipila nocturna (copr., S,E)
- Scaptosciara vivida (copr., S,E)
- Megaselia pleuralis (sapr., S,B)
- Heteromyza oculata (zoosapr., S,E,B)
- Tephroclamys flavipes (zoosapr., S)
- Oeothea fenestralis (zoosapr., S,E,B)
- Copromyza stercoraria (copr., S)
- → borealis (copr., S,B)
- Leptocera coenosa (zoosapr., B)
- → fontinalis (sapr., S)
- Limosina claviventris (sapr., S,E,B)
- → pullula (sapr., E,B)
- → talparum (sapr., S,E,B)
- Muscina assimilis (sapr., E,B)
- Fannia canicularis (sapr., E)
- Pegohylemyia fugax (copr., E)

Very possibly the Eccoptomera species and Crumomyia glacialis belong to this group, but their larval habits are not yet known (see further remarks about these flies on p. 41).

In burrows with a richer fungus flora and decaying pieces of wood, numerous species of Mycetophilidae (sensu lat.) and certain Sciaridae occur. The Mycetophilidae in the present material, however, are represented by very few individuals of each species. In the following species more than 5 individuals have been trapped in more than two burrows:

- Mycomyia fusca (Småholmen)
- Exechia subulata (Småholmen)
- Rhymosia fasciata (Småholmen)

Among the Sciaridae, one xylosaprophagous species is of importance: *Clenosciara hyalipennis*

This species is dominant and constant in burrows under roots in Småholmen. It has been reared by Tuomikoski (1961) from decaying wood.

4. Diptera in vole nests

The few (three) nests of Microtus arvalis investigated on Småholmen in August 1959 were separated from the burrow systems and at the soil surface under logs and pieces of decaying wood. They were newly abandoned and only one of them contained some Diptera
imagines, Phoridae, the only one captured being a female of *Megaselia aequalis* Wood. The nest material contained numerous empty puparia of phorids and in one of the nests two larvae of a tipulid species. As already mentioned in the introduction, the nest fauna has not been included within the scope of this study. *Gensicke* (1960), in his study of the nest fauna of various small rodents, has identified the Diptera only as to family and the specimens in his samples are rather few.

5. Occasional visitors

The vole burrows being by no means isolated from neighbouring habitats and not extreme or exclusive as far as abiotic factors are concerned, one can reckon with numerous occasional visitors in the samples. The following subcategories can be separated:

a) *Newly hatched imagines of terricolous species using the burrows as passages out of the soil.* In the present material this group includes Tipulidae, Limoniidae, Empididae (*Hilara* spp., *Rhamphomyia* spp., *Bicellaria* spp.), Dolichopodidae (*Diaphorus* sp.), Syrphidae (*Chilosia* sp., *Syrphus* torvus), Diastatidae (*Diastata fuscula*), Chloropidae (*Aphanetrignonum* sp., *Tricima lineata*, *Cocosiscinella frontella*).

b) *Female Diptera entering the burrows from outside for oviposition in moist soil.* As examples may be mentioned *Bibio clavipes*, *B. nigriventris*, *Helomyza humilis*, *Lasops* spp. and *Alloeostylus sudeticus*. Possibly some of the numerous Phoridae belong to this group.

c) *Raptorial dipterous imagines which might chase various small arthropods in the entrance zone of the burrows:* Empididae of the genera *Tachydromia*, *Tachista*, *Tachypeza* and *Trichina* and the dolichopolid fly *Xanthochlorus tenellus*.

d) *Larvae of terricolous species from the surrounding soil.* A few larvae of *Rhagio lineola* captured in the pitfall traps represent this group.


f) *Dipterous imagines searching for moisture or protection against unsuitable weather.* The occurrence of a few Chironomidae with aquatic larval habits (*Limnochironomus nervosus*, *Tanytarsus* sp., *Paratanytarsus* sp.) might have this explanation.

B. Coenological classification

In his important work *Falcoz* (1915) introduced an ecological terminology for classifying the Arthropoda in vertebrate burrows and this terminology has been adopted by later authors (*Marié* 1930, *Ihssen* 1940, *Seguy* 1950). *Falcoz*
used the term microcaverns (Microcavernes) for subterranean animal burrows and nests in order to separate these from larger subterranean cavities of other kinds (natural caves, cellars made by man, etc.). On analogy to the classification of cave animals (troglobionts, troglophiles and trogloxenes) he introduced the terms pholeobionts (Pholeobies), pholeophiles and pholeoxenes for animals living in subterranean nests and burrows of vertebrates. The original definitions are given below (op. cit. p. 70):

1. Les Pholeobies, qui vivent et se développent exclusivement dans les terriers;
2. Les Pholeophiles, qu'on observe fréquemment dans ce milieu, mais qui peuvent aussi se rencontrer ailleurs;
3. Les Pholeoxenes, dont la présence dans les terriers est purement accidentelle.

IHSSEN (1940, p. 461) used these terms for beetles in Marmot nests and runways in a somewhat different sense and defined them as follows:

A) Pholeobionten (Pholeobies), deren biologischer Lebenszyklus sich vollständig in den Bauen (terriers) abspielt,
B) Pholeophilen, welche gewöhnlich ganz in den Bauen lebend sich davon von Zeit zu Zeit entfernen können,
C) Pholeoxenen, welche nur gelegentliche Bewohner der Microcavernen sind.

In connexion with a study on Catopidae beetles, SOKOLOWSKI (1942) severely criticized FALCOZ' terminology. Among other things, he pointed out that the concepts pholeobionts, pholeophiles and pholeoxenes do not fully correspond with the terms for cave animals. Further, SOKOLOWSKI put forward logical reasons for dropping the term microcavern. HESSELHAUS (1915) had already pointed out that the stem of the word pholeophile does not at all express the restriction of the term to animals in vertebrate burrows.

The essential point is to arrive at a classification expressing the different degrees of adaption of animals to the habitat. The further question arises of whether it is necessary or even advisable to keep up or create a separate terminology for each special habitat like vertebrate burrows. HESSÉ's (1924) general terms eucoenic, tychoenic and xenocoenic have been used by several ecologists, including BACKLUND (1945), to express the relation of the animal to a given biotope when three degrees are needed. In the present paper this terminology is used as defined by BACKLUND (op. cit., p. 176):

Eucoenic species: Animals which occur only in the community in question or at least are much commoner there than in any other biotope.
Tychoenic species: Animals which occur both in the community in question and in other related communities. They are fully adapted to the biotope, but their ecological range is wider than that of the eucoenic animals, therefore they can also thrive in other similar biotopes.
Xenocoenic species: Animals which are foreign to the community. These species are adapted to life in other biotopes and cannot live and multiply continually in the biotope in question.

The classification of the species in the present material according to these principles must in many cases be based on subjective estimation or be impossible because of lack of knowledge of the life habits of the species in question.

1. Eucoenic species

*Limosina talparum* Rich. Imagines are frequently found in the entrance zone of vole burrows and it seems possible that mating takes place here. *L. talparum* shows a high constancy in inhabited *Microtus* burrows but is less common in the rodent burrows in the wood. The investigation on Småholmen in 1960 showed that the species had disappeared from abandoned burrows. It is both phytosaprophagous and coprophagous. Richards (1930) mentioned that the species occurs more frequently in mole nests than in rodent burrows. *L. talparum* shows to some degree the characteristic morphological features of flies with a subterranean mode of life, already pointed out by Falcoz (1915): reduced eyes, prolonged arista (see fig. 16—21) and comparatively long legs. It can, for example, be compared with the related *L. crassimana* Halid. (only an occasional visitor in subterranean cavities) and on the other hand, with *L. racowitzi* Bezzi (occurring in both caves and mammalian burrows) showing these features still more strongly. It is evident that *L. talparum* is highly adapted for life in micromammalian burrows. Teschner (1961, p. 4), however, reports the species from a scrap-heap near Hamburg (a number of specimens trapped on bait), but there too the occurrence might be associated with rodent burrows, for example those of the Brown Rat.

2. Tychocoenic species

a. Species showing as imagines such characters as reduced eyes, long arista or reduction of wings.

*Oecothea fenestralis* Fall. A helomyzid with reduced eyes and long arista. Trapped in small numbers in Småholmen and in Bonäs. In Evitskog, imagines were captured in traps with cheese as bait (not near vole burrows) and small larvae of the species invaded some of the rearing cages baited with mouse droppings or cheese and developed there to imagines. The flies were rather sluggish and did not even climb up to the light in the collecting vials of the cages. The species may be underrepresented in the trapped material because of this habit. There are numerous records in the literature about its occurrence in the burrows of various mammals and it also occurs in natural caves (Falcoz 1915, 1921, Leleuf 1948, Séguy 1950, Gorodkov 1959). The species is highly adapted to life in subterranean cavities and being zoosaprophagous it might, in Finland at least, prefer mammalian burrows.
Eccoptomera ornata Loew and E. intuscata Wahlgr. Reduced eyes and long arista are features common to the entire genus Eccoptomera. The eyes are especially small in E. microps Meig., eucoenic for mole nests, and in some cavernicolous species from Southern Europe (for example E. filata Loew., fig. 18). E. ornata showed a medium degree of constancy in burrows of various kinds on Småholmen in both 1959 (voles frequent) and 1960 (voles almost absent) but was trapped in small numbers (1959: 12 individuals, 1960: 8 individuals). In Bonäs, the species was extremely rare and in Evitskog it was not trapped at all. Two females were caught on Småholmen in September 1960 in an artificial burrow (without bait), which indicates that the species enters various cavities in the soil and not only vole burrows. E. intuscata was trapped on Småholmen and in Bonäs but in very small numbers. The feeding habits of the larvae of the two species are not known. Two further species of the genus are present in the material, E. pallescens Meig. (1 specimen) and E. longiseta Meig. (2 specimens). The Eccoptomera species occurring in vole burrows show features indicating adaption to life in cavities in the soil but are possibly not dependant on the presence of micromammals.

Crumomyia glacialis Meig. This borborid fly shows a fair constancy in vole burrows on Småholmen, in Bonäs and in Evitskog. The species has a long arista but the eyes are not much reduced. The wings are comparatively short and the fly runs more than it flies. It is fully active at temperatures as low as +3°C and sometimes observed on snow. The larval habits are not known but probably saprophagous. It has been observed by the author on Småholmen in 1958 on a rotten fungus (Boletus sp.).

Brady sia albanensis Ldf. A species with narrow wings and a reduced ability to fly (Tuomikoski 1960, p. 148). Terricolous and probably phytosaprophagous. In the present material in two samples from Småholmen.
W. Hackman: The dipterous fauna in burrows of voles

*Pteremis fenestralis* Fall. Showing polymorphism in reduction of wings. Larvae saprophagous. In the present material only in one sample from Bonäs and in one from Evitskog. On the other hand, known previously from micromammalian burrows (RICHARDS 1930).

*Ormosia pseudosimilis* Lundstr. A sluggish, rather short-winged species of Limoniidae trapped in 4 burrows in Bonäs and in one in Evitskog. The *Ormosia* larvae are probably phytosaprophagous.

b. *Saprophagous species showing a fair or high constancy as imagines in the burrows. Not known to be common in other kinds of natural habitats.*

*Anevrina thoracica* Meig. This phorid fly was dominant in vole burrows in forest soil in Bonäs and on Småholmen in 1960 and also fairly common in other kinds of burrows that year. With few exceptions, the trapped specimens were males. In artificial burrows (without bait) 16 ♂♂ were trapped on Småholmen in 1960. According to SCHMITZ (1938—58), the species is necrophagous, but it is captured only in small numbers on micromammalian carrion at the soil surface. Only two females were trapped on meat bait on Småholmen (1960). Probably the species is not obligatorily necrophagous. The males are often found in the entrance zone of burrows and run out when alarmed. It seems possible that the females usually remain deeper in cavities in the soil and leave these only for mating. Pairs of this fly in copula have been observed by LUNDBECK (1922) on stems of trees.

*Coniceria floricolor* Schmitz. This phorid fly was trapped in large numbers with meat bait in burrows (11♂♂ 62♀♀ in a single burrow) on Småholmen in 1960 and also occurred on bait consisting on rodent excrement. 2 ♂♂ and 16 ♀♀ were trapped in artificial burrows without bait (Småholmen, 1960), thus invading various cavities in the soil from outside. SCHMITZ (1938—58) mentions that the species is sometimes observed on flowers but that in general comparatively few specimens have been collected by net sweeping. There are no previous records about this species in Finland.

*Bradysia bicolor* Meig. This sciarid gnat was trapped in burrows of various kind both on Småholmen and in Bonäs but not in Evitskog. The species showed high constancy in burrows in ditch banks of meadows in Bonäs and the large number in one burrow has already been commented (p. 36). In the artificial burrows on Småholmen 5 ♀♀ were captured. *B. bicolor* has been observed by Prof. R. TUOMIKOSKI (verbal communication) in a potato cellar in Vihti (S. Finland) in large numbers and its larva is probably phytosaprophagous. Obviously the species develops in cavities in the soil. The imagines seem to have predominately nocturnal habits and leave the cavities for mating.

*Megaselia flavicosa* Zett. The *Megaselia* species are in general saprophagous but with a rather wide range of food choice. The biology of this species is not known, but its fairly frequent occurrence in the Bonäs material and the fact that the species is rarely taken in other habitats suggests it insertion among the tychocoenic species.

c. *Species with wide ecological range and able to feed as larvae on substrates constantly present in burrows inhabited by voles. Imagines showing a fair or high constancy in the samples.*

*Scaptosciara vivida* Winn. A sciarid fairly common in some vole burrows on Småholmen and reared from numerous baits exposed in vole burrows in Evitskog. Not in the Bonäs material. A mainly coprophagous terricolous species which is able to multiply in vole burrows.
Lycoriella brevipila Tuom. This sciarid has been reared from mouse droppings (Småholmen, Bonäs). The species was common in certain burrows on Småholmen and was also trapped in artificial burrows without bait. Its ecological range seems to be almost the same as that of Scaptosciara vivida.

Limosina claviventris Strobl. A common terricolous species, in Evitskog dominant and constant in Microtus burrows but less common in the samples from Småholmen and Bonäs. The species was also found in large numbers in a burrow system of the Brown Rat on Småholmen in 1959. In 1961, L. claviventris was reared from bait of different kinds. The species is able to multiply in burrows as well as in other terricolous habitats.

Muscina assimilis Fall. A ubiquitous saprophagous species trapped in 8 burrows in Bonäs. A few specimens were reared from bait of mouse droppings in Evitskog.

Megaselia sp. (pr. pulicaria). A very common species trapped in numerous burrows on Småholmen and in Bonäs.

d. Xylosaprophagous species showing fairly high constancy in burrows under stumps and trees.

Ctenosciara hyalipennis Meig. Taken on Småholmen in 1959 in 5 burrows, in 1960 in 12 burrows and dominant in the samples from root burrows in August—September. Not in the samples from Bonäs.

e. Species showing low constancy in the samples but which for various reasons could be classified as tychocoenic.

Trichocera regelationis L. The local mass occurrence in a burrow in Bonäs (see p. 36) suggests that this species may infest old food stores of the voles. Trichocera larvae are common members of the terricolous fauna and are sometimes found in potato cellars. Imagines occurred in various kinds of vole burrows in Småholmen and in Bonäs. The species might be classified here as tychocoenic.

Macrocer a fasciata Meig., M. lutea Meig., M. vittata Meig., M. parva Lundstr. and M. stigma Meig. The larvae of the genus Macrocer a are raptorial and are known to live on walls of various subterranean cavities, even caves (ENSlin 1916). They spin webs in which they catch small arthropods. Some individuals of the species mentioned above were trapped as imagines in the burrows and it is most probable that they have lived there as larvae. One specimen of M. lutea was caught in an artificial burrow.

Docosia gilvipes Halid. This fungus gnat was reared from a cheese bait exposed in a Clathri onomys burrow on Småholmen. The same species has also been reared from an Amanita sp. by Mr. P. LASTOWKA (Checkoslovakia, letter communication). Another species (reported as D. sciarina) has been found in a nest of Talpa (Falcoz 1921) and D. fumosa is known from birds' nests (Edwa rds 1925).


Triphleba bicornuta Strobl. In Småholmen in burrows under stumps, 8 specimens in artificial burrows. Reared from bait of mouse droppings.

Megaselia pleuralis Wood. A saprophagous species repeatedly found in various micromammalian burrows (Schmitz 1938—1950). Present in samples from various kinds of burrows in Småholmen and in Bonäs.

Megaselia rufipes Meig. Trapped in vole burrows on Småholmen, especially on meat bait. In Evitskog, reared from a bait of dead insects. The species is common in dark places
(cellars, birds' nests near the ground, etc.). The larva is mainly zoosaprophagous, but also phytosaprophagous and even raptorial, killing dipterous and coleopterous larvae (MoRGE 1956). The species thus has a wide ecological range and is able to multiply in vole burrows.

*Megaselia giraudi* Egg. Like the preceding species with wide ecological range. Trapped on meat and cheese bait on Småholmen. In Evitskog the species was reared from bait of mouse droppings.

*Megaselia fuscata* Wood. In samples both from Småholmen and Bonä. Reared from bait of various type in Evitskog.

*Heteromyza oculata* Fall. Trapped in various burrows on Småholmen, in Evitskog (few specimens) and in Bonä (7 ♀♀). A single ♀ was reared from cheese bait.

*Tephroclamys flavipes* Zett. The species occurred on Småholmen, especially in burrows under stumps and trees, and was reared from baits of both mouse droppings and cheese (2 specimens). It is known from various habitats, including birds' nests. The rearing experiments show that this species is able to oviposit and live as larva in burrows.

*Scoliocentra scutellaris* Zett. From one burrow in Bonä. RICHARDS (1930) reported the species from rabbit holes.

*Limosina palmata* Rich. In various kinds of vole burrows in Bonä, rare on Småholmen (2 ♀♀ in one burrow) and reared from meat bait in Evitskog. A mainly necrophagous species previously known from rodent burrows (RICHARDS 1930) but also from other habitats.

*Leptocera coenosa* Rond. Only a few specimens in the samples from Småholmen. It is interesting to note that this species was found in a laboratory culture of *Cethridonomys glareolus* in the Zoological Institution of the University in Helsingfors 1960. The species is previously known from various mammalian burrows but also from other habitats.

*Borborus ater* Meig., *Stratioborborus fimetarius*, *Copromyza stercoraria* Meig., *C. borealis* Zett. and *Limosina schmitz* Duda. Mainly coprophagous species previously known from micromammalian burrows (RICHARDS 1930, DUDA 1938) but also found in other habitats.

*Fannia canicularis* L. Only a small number of specimens belonging to the genus *Fannia* have been trapped in vole burrows but, on the other hand, several of my cultures with mouse droppings kept in the close vicinity of vole burrows were infested from outside by *Fannia canicularis* larvae. The *Fannia* larvae, especially those of *F. canicularis* are constant members of the soil fauna in many situations and can be reckoned as members of the vole burrow community.

A number of the other species of Sciariidae, Phoridae, Helomyzidae and Borboridae represented by a few specimens in the samples might be able to develop in the vole burrows. As these species have neither been reared from bait nor previously known as inquilines, they have been omitted from this classification.

3. Xenocoenic species

a. *Species from outside which are able to feed as larvae in the burrows under certain circumstances*. In this group the necrophagous species are included which invade the burrows in cases when a vole has died in the runway. The
most important necrophagous species in the present material have already been dealt with in connexion with WIREN's classification (see p. 36) but a few of them deserve some comment:

_Anerina unispinosa_ Zett. Trapped in the burrows only in the presence of meat or carrion bait. The species is obligatorily necrophagous.

_Conicera fallens_ Schmitz. Reared from bait of meat or cheese in Evitskog. Egg-laying females of the _Conicera_ species are obviously able to locate even buried carrion (Schmitz 1938—50).

_Drosophila transversa_ Fall. This drosophilid fly, usually feeding as a larva on decaying fungi, was twice reared from meat bait in Evitskog. On Småholmen this fly was very common on various fungi (_Boletus_ spp., _Russula_ spp.) but no specimens were trapped in vole burrows. Hennig (1950) has trapped two _Drosophila_ species (_D. buscki_ and _D. melangaster_) on a rabbit carrion but states that _Drosophila_ species have never been found feeding as larvae on carrion.

_Sarcophaga scaparia_ Pand. Reared from meat bait exposed in a _Microtus_ burrow in Evitskog. Two imagines were trapped in a burrow in the same locality.

_Cynomyia mortuorum_ L. In Evitskog this calliphorid fly was among the dominant species in _Microtus_ burrows. On Småholmen and in Bonäs this species was trapped in smaller numbers, possibly because the trap funnels were too narrow. The experiment with carrion as bait (see p. 23) indicates that this species might be important as a necrophage from outside. _C. mortuorum_ was not reared from any bait, however. Nuorteva's (1959) trapping experiments made in several localities in Finland show that this species plays a minor part among the blow-flies attracted to carrion at the soil surface. In Nuorteva's samples, 19.4% of the _C. mortuorum_ specimens were males. In the present material all the specimens were females and obviously the males do not enter dark burrows. It is known that Calliphoridae maggots ready for pupation leave the carrion and crawl restlessly about for several days before they choose a place for pupation. If they develop in a carrion in a burrow, they probably do not stay there for pupation and newly hatched ♂♂ and ♀♀ can hardly be expected in traps at the entrance.

_Fannia coracina_ Loew. Reared from meat bait exposed in burrows (Småholmen and Evitskog). In his monograph on the Fanniinae, Chillcott (1960) mentions that this species has been reared in association with _Neodiprion lecontei_ Fitch, but otherwise very little is known about this rare but widely distributed species.

b. _Species using the burrows as passages when hatching or for oviposition_.

This group has already been dealt with on p. 38, but the following species merit further comments:

_Rhagio lineola_ F. On Småholmen in 1959, 17 ♀♀ of this species were trapped in various burrows. Further, a few larvae were found in burrow litter in both 1959 and 1960. The larva is mainly raptorial and occurs in litter in a variety of forest biotopes. The absence of males in the samples calls for comment. In the Finnish collection of the Zoological Museum, Helsingfors, the species is represented by 87 ♂♂ and 90 ♀♀ (brought together by the usual collecting methods), thus indicating a normal sex-ratio. It seems likely that the trapped females are mainly individuals that have invaded the burrows from outside for oviposition in moist soil. In 1960, (when the summer was rainy) no specimens were trapped in vole burrows, but one female was caught in an artificial burrow.
Alloestylus sudeticus Schnabl, Lasiops seminereus and L. hirsutulus. These three Muscidae species are represented in the samples from Småholmen in 1959 by numerous specimens, but exclusively females. Their larval habits are not known in detail, they belong to the terricolous fauna. During the rainy summer of 1960 very few individuals (♀) were trapped on Småholmen and in Bonäs. In 1960, these flies occurred abundantly on flowers on Småholmen. It seems obvious that here we have to do with a parallel case to that of Rhagio lineola: In dry summers the females use the vole burrows as passages to moist soil for oviposition.

c. Raptorial species the imagines of which chase their prey in the entrance zone of the burrows.

Tachypeza nubila Meig. and the Tachydromia species. Tachypeza nubila is a common empidid fly on Småholmen, especially on old stumps of threes. In 1959, 24 individuals were captured in 11 burrows, whereas in 1960, only a few were captured in the traps. It is possible that these flies hunt small Diptera and other insects in the entrance zone of the burrows. This might also be the case with Tachydromia lutea Meig., T. ciliaris Fall. and T. ecalceata Zett. The larvae are supposed to be terricolous and raptorial. Why Tachypeza nubila was much more common in the samples of 1959 than in those of 1960 might have some microclimatic explanation. In both years the species was very common on stumps on the island.

d. Species using the burrows for hibernating as imagines. The group includes at least Culex pipiens L. (see p. 38).

e. Casual visitors which do not live in the burrows as larvae. Imagines seeking refuge against drought or accidentally present. Examples are already mentioned in connexion with WRÉN's classification (p. 38).

The majority of the Mycetophilidae (sensu lat.) numerous in species in the burrows under stumps and trees are most probably xenocoenic, using the burrows as passages or as refuges against drought.

The numbers of species in coenological cathegories are given in table 11.

<table>
<thead>
<tr>
<th></th>
<th>Eu</th>
<th>Ty</th>
<th>Ty?</th>
<th>Eu+Ty+Ty?</th>
<th>Xe</th>
<th>Xe?</th>
<th>Xe+Xe?</th>
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<td>24</td>
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<td>6</td>
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<td>48</td>
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<tr>
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<td>30</td>
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<td>4</td>
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<td>60</td>
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<td>58=25%</td>
<td>140</td>
<td>39</td>
<td>179=75%</td>
<td>237</td>
</tr>
</tbody>
</table>

Table 11. The numbers of species in the coenological categories. Eu = eucoenic, Ty = tychocoenic, Ty? = probably tychocoenic, Xe = xenocoenic, Xe? = Probably xenocoenic, Rb = burrows under stumps or living trees, Gb = burrows in grassy soil under bushes, Mb = burrows in meadows, Ns = total number of identified species.
The percentage of xenocoenic species is sometimes (BACKLUND 1945) used as a measure of the specificity of the biotope, but in such cases as the present this can be erroneous. The percentage of xenocoenic species will increase to some extent with the amount of material and may only be significant in very large collections. The small number of eucoenic species (a single one) and the comparatively large number of tychocoenic ones (40—58) are typical of an impermanent biotope, which is not extreme.

XII. Factors influencing the dipterous fauna of vole burrows

AGRELL (1945) points out in connexion with the collembolous fauna that the subterranean nests and burrows of Microtus and Talpa are not extreme environments. The study corroborates this statement. On the other hand, in every special niche in nature there are a number of factors which require special adaptions of the insects which are constant members of the community. An attempt is made here to analyse some of these factors, but admittedly on the basis of rather few observations.

1. The light factor. The larvae, for example, of Trichocera, the sciarids Scaptosciara vivida and Lycoriella brevipila, the phorids Conicera fallens and Megaselia rufipes, the helomyzid Oecothea femestralis, the borborids Limosina talparum and L. claviventris and of the muscid Fannia coracina are adapted to life in darkness. This is a general feature of terricolous dipterous larvae and, for example, larvae of certain Mycetophilidae and Sciaridae are readily killed by the ultraviolet rays of direct sunlight (BRAUNS 1954, p. 130—131). The imagines of the vole burrow Diptera show very different degrees of adaption to the darkness. The Trichocera gnats leave the burrows when newly hatched and swarm in the open. The females enter dark (and moist) holes in the soil, including vole burrows, for oviposition. This same type of imaginal behaviour is probably the rule among many of the Sciaridae (Ctenosciara hyalipennis, Scaptosciara vivida, Lycoriella brevipila, to name a few examples). Some of the species swarming outside the burrows seem to have nocturnal habits: Bradysia bicolor, B. nocturna and B. nitidicollis. These species have been captured with a lamp (TUOMIKOSKI 1960). Some phorid flies swarm at daytime outside the burrow and males of Anevrina thoracica and Conicera floricola are often found in the entrance zone, probably waiting for emerging females. Males of these species and many other phorids invade burrows and other dark holes in the soil from outside. The Borboridae of the vole burrows, including the eucoenic species Limosina talparum, are often found in both sexes in the entrance zone of the burrows. Possibly mating takes place here. Also specimens (both sexes)
of the helomyzid fly *Eccoptomera ornata* have been observed in the entrance zone. It was noted that this species as well as *Limosina* spp. and *Anevrina thoracica* males, when alarmed, did not try to escape into the dark burrow but flew out towards the light. In the rearing cages (sunk in the soil) newly hatched males and females of *Limosina talparum*, *L. claviventris* and *Conicera jallens* in most cases move towards the light and so into the collecting vials.

Among the species studied here, the helomyzid fly *Oecothea fenestralis* seems to be more strongly adapted to darkness. The species is very characteristic of various micromammalian burrows and other dark places (caves). Very few specimens were obtained in unbaited traps probably because of the slugish habits of this fly. In the rearing cages the hatching imagines rarely climbed towards the light. As previously mentioned in this paper the species has reduced eyes and long arista. *O. fenestralis* is sometimes trapped with a lamp by night. An other helomyzid in the present collection, *Heteromyza oculata*, also able to develop in the burrows, but of which only a few specimens were trapped, shows a peculiarity concerning its light sense organs. The males have larger eyes than in any other species of the family, rather like those of Muscidae males. This species seems also to have nocturnal habits and has been trapped with a lamp (in Helsingfors, Botany Garden). Mating probably takes place outside the burrows.

The experiments with carrion or meat bait made in the present investigation indicate that the light factor has a strongly selective effect on necrophagous fly visitors from outside. Among the blow-flies (Calliphoridae) only *Cynomyia mortuorum* entered the burrows in any considerable numbers and the only *Lucilia* species trapped was *L. silvarum*. Probably other more common Calliphoridae do not oviposit in the dark. Male blow-flies were not trapped at all in the burrows.

2. **Moisture.** The larvae of terricolous Diptera in general are strongly hygrophilous (BRAUNS 1954, p. 131). Moisture experiments have not been made in the present investigation but it seems clear that the humidity (100% RH) in the burrows is favourable for the larvae and imagines of most species found there. It has already been pointed out that on warm and sunny summer days a number of occasional visitors from outside may take refuge from drought in these burrows and that females of Muscidae might react to the moisture gradient in the opening zone in their search for suitable place for oviposition in moist soil.

3. **Temperature.** The temperature conditions in the burrows have been dealt with in greater detail earlier in this paper (p. 6—10). The important features are: a) that in the places where this study was done the temperature in the burrows did not rise above 20°C even on warm summer days, b) that the winter temperature sinks at most a few degrees below zero. In this con-
nexion are a number of problems, to be solved by experiments: a) To what extent is larval development of the constant dipterous inhabitants possible during the winter half of the year at a temperature of a few degrees above zero? Oecotheca fenestralis would be a suitable species for study. b) Which are the temperature preferenda of imagines of Limosina talparum, L. claviventris, Crumomyia glacialis and other constant inhabitants? c) Which are the limits of toleration of higher temperatures (above +20°) for these species?

Field observations show that Crumomyia glacialis imagines at least are fully active at a temperature of +3°. A few preliminary experiments to determine the upper limits of temperature tolerance of Limosina talparum, Eccoptomerora ornata and Crumomyia glacialis were made in 1960.1) These indicate that the temperature for the heat collapse for these species lies between +30° and +38°, thus far above the maximal temperatures in the burrows. As the summer temperature in the burrows usually remains near +10° fluctuating only by a few degrees, Limosina talparum and tychocoenic species as Lycoriella brevipila, Scaptosciara vivida and others must be able to develop at normal rate at least at this temperature.

4. Food resources. This is the most important factor governing the composition of the dipterous fauna in the biocoenosis. Burrows inhabited or at least frequently visited by voles contain excrement scattered around the runways. The amounts must be comparatively small per burrow and only enough for the nutrition of small populations of small sized Diptera. It can be noted that Limosina talparum, L. claviventris, Scaptosciara vivida and other species species feeding as larvae on excrement are not exclusively coprophagous. Limosina talparum has also been reared on decaying vegetables and L. claviventris is rather polyphagous. Decaying vegetables are usually left over in small amounts from the meals of the voles, but larger quantities are abandoned in winter stores. In these, for example, large colonies of Trichocera larvae and possibly also of Bradysia bicolor might find their nutrition. The Clethrionomys burrows under stumps and trees contain pieces of rotten wood and a comparatively rich fungous flora. The nutrition of the xylosaprophagous and fungivorous elements among the Diptera is here secured independently of the presence of voles.

The mortality of voles is known to be high in the winter, but to what extent they die in the burrows is not known. In any case carrion of voles can hardly be regarded as a regularly occurring food resource for necrophagous Diptera in the deeper summer runways studied. The only necrophagous species regarded here as tychocoenic are Anevrina thoracica and Conicera floricola.

1) 3—4 specimens of these species were heated in glass tubes with moist cotton wool on a water bath. The individual variation for heat collapse seems to be considerable but more material and better equipment are needed for obtaining more exact results.
At least the latter phorid fly seems not to be exclusively necrophagous and the life habits of the former are still unsufficiently known.

5. The fluctuations of the vole populations. This is a factor causing a certain lability in the community, especially as the fluctuations are often drastic. The years 1959 and 1960 showed a good example of this on Småholmen. In 1959, the population of Microtus arvalis had a peak and the single eucuenic species among the Diptera, Limosina talparum showed high constancy in the burrows. In 1960, no voles were seen and probably most burrows were abandoned. Limosina talparum occurred in only two burrows of those investigated and no specimens were trapped after mid-July. As strong fluctuations of the vole populations are the rule, this means that burrows will often be abandoned for one to several years and devoid of food resources for Diptera feeding on excrement and refuse of voles. The high constancy of Limosina talparum in Småholmen in 1959, in Bonås in 1960 and in Evitskog in 1961 shows that the species is able to spread rapidly to new burrows or to old ones inhabited anew when the vole population increases again. Many of the tychocoenic species among the Diptera are able to survive as populations even in abandoned burrows, since their larvae feed on other substrates besides vole excrement and refuse.

6. Invasion of social Hymenoptera. Abandoned vole burrows are not infrequently invaded in the spring by female wasps (Vespula sp.) or bumble bees (Bombus spp.) which build their nests there. On Småholmen, a pitfall trap was placed in one burrow inhabited by wasps and the Diptera collected from May 26 to October 30, 1960. The material (kept apart from the other collections and not included in the list of species in section XIV) contained one specific dipterous inquiline of wasp nests, the phorid fly Triphleba lugubris Meig. In Evitskog, some Diptera were collected from a Microtus burrow inhabited by a Bombus sp. Among these was a specimen of Volucella bombylans L. Invasion of ants in burrows also occurs. In Bonås, a Formica sp. (rufa group) was trapped in numbers in a Clethronomys burrow, and on Småholmen one of the Microtus arvalis burrows studied was invaded by a Myrmica sp. In neither case were myrmecophilous Diptera trapped, but on the other hand, the effect of ants as predators on dipterous larvae might have been considerable.

7. Predators and parasites. In the traps raptorial beetles, Carabidae and Staphylinidae, were frequently captured. Among lesser Carabidae Trechus secalis was common in Microtus burrows on Småholmen. In Evitskog, Lasio­trechus discus was trapped in numbers. The importance of these beetles as predators of dipterous larvae, such as those of sciarid gnats and borborids, is not known. Some of the cultures in the rearing experiments were invaded by small Staphylinidae larvae and gave poor results. In one of the cultures,
started from a meat bait, an imago of a *Quedius* sp. was found and it must have developed in the culture. Predators among the Diptera themselves have already been considered in this paper.

Among the Arthropoda other than insects the spiders are important predators of the dipteron imagines in the burrows. Especially *Leptophyantes* and *Bathyphantes*, species and some Micryphantidae (for. example *Gonatium rubellum*) entered the funnel traps and caused losses in the dipterous material. The predatory effect of certain mites on dipterous larvae must also be taken in consideration.

Quite a number of parasitic Hymenoptera were trapped in the burrows on Småholmen and in Bonäs and also some small species of those were observed in the cultures kept in the open. Which species of these parasitize Diptera is not known, but it can be assumed that the group is of importance.

**XIII. Remarks about Diptera in other micromammalian burrows**

Among the Diptera known from burrows or nests of voles (*Clethrionomys* spp., *Microtus* spp. and *Arvicola* spp.) no species is associated exclusively with a single vole genus. *Limosina talparum*, the only species in the present material eucoenic for micromammalian burrows, also occurs abundantly in mole nests and galleries. *Oestromyia leporina* Pall. (in Central and S.E. Europe and in Asia) parasitizes not only *Microtus* spp. but also *Ochtona* spp., *Citellus undulatus* and other rodents (GRUNIN 1962).

Concerning the dipterous fauna of burrows of Muridae (s.str.) very little is known. In the summer of 1959, samples of Diptera were taken from the entrance zone of some burrows of the Brown Rat on Småholmen. Among the species which can be associated with the rats there were only three not found in the vole burrows: *Orbellia nivicola* Frey (Helomyzidae), *Limosina racowitzi microps* Duda and *L. bequaerti* Villen. About the biology of the first of those little is known, but *Limosina bequaerti* is obviously eucoenic for micromammalian burrows and *L. racowitzi* is strongly adapted to subsoil biotopes (the nominate form in caves, ssp. *microps* in micromammalian burrows and wasps' nests).

The nests and galleries of the mole (*Talpa europea*) have several dipterous inquilines in common with the vole burrows, but as biocoenoses they are more stable and more favourable for the evolution of stenotopic Diptera. They also contain refuse of animal origin (other than excrements) in contrast to the vegetable refuse in vole burrows. The helomyzid *Eccoptomera microps* and
Limosina pseudonivalis Duda have been found exclusively in association with moles.

In mammalian burrows larger and deeper than those of the voles the helomyzid flies are characteristic inhabitants and probably more abundant than in the vole burrows. Some of the species are also known from caves. A few examples may be mentioned here:

- Orbellia cuniculorum Ro-D. in burrows of Oryctolagus cuniculus, Central and W. Europe (SÉGUY 1934).
- Amoebaleria mariae Ség., burrows of Marmota marmota in the Alps (SÉGUY 1934).
- Oecocthea praecox Loew, burrows of Oryctolagus cuniculus, W. Europe (COLLIN 1943).
- Oecocthea aristata Mall., burrows of Marmota spp. in Asia (GORODKOV 1959).
- Pseudoleria pectinata Loew, burrows of Geomys breviceps, N. America: Texas (ROSS 1944).

Among the Helomyzidae, entire genera such as Scoliocentra, Amoebaleria, Orbellia, Oecocthea and Eccoptomera, show imaginal features connected with subterranean habits: The eyes are more or less reduced and the arista, especially in Oecocthea and Eccoptomera, conspicuously long.

Although the Borboridae are important elements in the burrow faunas it seems that the eucoenic species are few in this family.

It is further interesting to note that among the flies in the burrows of the Florida Pocket-Gopher (Geomys floridanus) the single species observed is a muscid fly, a Pegomyia sp. (HUBBEL & GOFF 1939). No Borboridae or Helomyzidae were collected there.

Megaseilia species (Phoridae) of the ciliata group have been observed in burrows of various European mammals (SCHMITZ 1938–50) and also in North America one species of this group was taken in such a situation: Megaseilia subciliata Mall. in burrows of Marmota monax in Canada (JUDD 1961).

The larvae of certain Central African Calliphoridae (Stasia spp., Choeromyia spp.) are blood-sucking parasites of rodents of the genus Cricetomys and edentates of the genus Orycteropus in the burrows of these mammals (SÉGUY 1950 p. 354). The Stasia spp. are exclusively associated with Cricetomys, Choeromyia with Orycteropus.

XIV. List of species

In the following list all the species collected in vole burrows in Småholmen, Evitskog and Bonäs are recorded in systematic sequence. The following abbreviations are used: Rb = Burrows under roots of trees or stumps (made by Clethrionomys glareolus), Gb = Burrows in garden soil or in thickets (Alnus) on Småholmen (burrows made by Microtus arvalis), Mb = Burrows on open meadows (in Bonäs made by Microtus agrestis, in Evitskog probably by this Microtus species). Ab = Artificial burrows. The Roman numerals indicate the months May to October and the immediately following numbers (1, 2 or 3).
the first, second or third ten-day period. After the number of specimens the number of burrows in which the species has been found is given. Eu = eucoenic, Ty = tychoenic, Xe = xenocoenic. An example: Ormosia lineata Meig. Bonäs 1960: VI:1, Mb 3 ♀♂/2 Xe means that 3 ♀♂ of the species are present in the samples from two burrows on meadows in Bonäs during the first third of June, 1960 and that the species is considered xenocoenic.

TIPULIDAE

Tipula sp. Småholmen 1960: VII:2, Rb 1 ♂/1, Xe.
Tipulidae sp. Småholmen 1960, Gb 2 larvae/2. (2 larvae in 1959 in a nest of Microtus arvalis).

LIMONIIDAE

Limonia sp. Småholmen 1960: VI:3, Rb 1 ♀ 2 ♀♂/2, Xe.
Chionea lutescens Lundstr. Småholmen 1959: X:3, Rb 1 ♀/1, Xe.
Limnophila sp. Bonäs 1960: VII:3, Rb 1 ♀/1, Xe.

TRICHOERIDAE

Trichocera hiemalis Deg. Småholmen 1959: X:3, Rb 2 ♂♂ 1 ♀/1; 1960: IX:3—X:1, Rb 4 ♂♂ 2 ♀♀/4, Gb 1 ♂/1. Ty?

ANISOPODIDAE


PSYCHODIDAE

Species not identified. Småholmen 1959: 2 specimens, 1960: 6 specimens, in both years from a single burrow (Rb).

CULICIDAE

Aedes sp. Bonäs 1960: VI:3—VII:1, Rb 1 ♀/1, Mb 2 ♀♀/2. Xe.

CHIRONOMIDAE

Cricotopus sp. Småholmen 1960: VII:3, Rb 1 ♀/1. Xe.
Eudactylocladius sp. (scanicus Bajno?). Småholmen 1960: VI:1, Rb 1 ♂/1. Xe.
Smittia sp. Bonäs 1960: VI:2, VI:2, VIII:1, VII:2, Mb 2 ♂♂ 6 ♀♀/5. Ty?
Orthocladiinae sp. Bonäs 1960: VI:1, Mb 2 ♀♀/1. Xe.
Polypedilum sp. Småholmen 1959: VIII:1 Gb ♀. Xe.
W. Hackman: The dipterous fauna in burrows of voles

*Limnochironomus nervosus* Staeg. Småholmen 1960:VIII:1—2, Rb 1 ♀/1, Gb 1 ♂/1. Xe.
*Tanytarsus* sp. Småholmen 1960:VIII:3, Rb 1 ♀. Xe.
*Paratanytarsus* sp. Småholmen 1960:VIII:3, Rb 1 ♂/1. Xe.
*Paratanytarsus* sp. Bonäs 1960:VII:3, Mb 1 ♂/1. Xe.

**Ceratopogonidae**

*Ceratopogon* sp. *(minutus Meig.?) Småholmen 1959:VI:3 Rb 1 ♀/1.
*Forcipomyia* sp. *(ciliata Winn.?) Bonäs 1960, Rb 1 larva.

**Bibionidae**

*Bibio clavipes* Meig. Småholmen 1960: IX:1—3 Rb 1 ♀ 2 ♀♀/3, Ab 1 ♀, Xe.

**Mycetophilidae** *(sensu lát.)*


*Mycomyia tumida* Winn. Småholmen 1960:X:1, Rb 1 ♀/1. Xe.
*Boletina* sp. Småholmen 1960:VI:2, Rb 1 ♀/1. Xe.

*Trichonta* sp. Småholmen 1959:VII:2, Rb 2 ♀♀/1. Xe.
*Phronia* sp. Småholmen 1960:VII:2, Rb 1 ♀/1. Xe.
*Phronia* sp. Småholmen 1960:IX:3—X:1, Rb 2 ♀♀ 2 ♀♀/1. Xe.
*Phronia* sp. Småholmen 1960:IX:1, Rb 1 ♀/1. Xe.
*Phronia* sp. Bonäs 1960:VIII:3, Rb 1 ♀/1. Xe.


Alloedia sp. (sericoma Meig.?) Bonäs 1960: VIII: 2, Mb 1 ♂/1. Xe.

Alloedia sp. Bonäs 1960: V: 3, Mb 1 ♂/1. Xe.

Polychaena fasciata Meig. Småholmen 1960: VII: 2, X: 1, Rb 1 ♂/1, Ab 1 ♂. Xe.

Polychaena sp. Bonäs 1960: VIII: 2, Rb 1 ♀/1. Xe.


Allodia sp. (sericoma Meig.?) Bonäs 1960: VIII: 2, ‘lib 1 ♀/1. Xe.


Polychaena fasciata Meig. Småholmen 1960: VII: 2, X: 1, Rb 1 ♂/1, Ab 1 ♂. Xe.


Polychaena sp. Bonäs 1960: VIII: 2, Rb 1 ♀/1. Xe.

Polychaena fasciata Meig. Småholmen 1960: VII: 2, X: 1, Rb 1 ♂/1, Ab 1 ♂. Xe.

Polychaena sp. Bonäs 1960: VIII: 2, Rb 1 ♀/1. Xe.

Rhymosia fuscata L. Småholmen 1960: VII: 1, Rb 1 ♂ 4 ♀♀/1 (also some larvae possibly of the same species). Xe.


Plastosciara brachyptera Kieff. Småholmen 1959: VII: 2, Gb 2 ♂♂/1. Ty?


Corynoptera piniphila Ldf. Småholmen 1960: VIII: 2, Rb 1 ♂/1. Xe.

Corynoptera tetrachaeta Tuom. Bonäs 1960: V: 3 — VI: 2, VII: 1 — VIII: 2, Rb 1 ♂ 2 ♀♀/2, Mb 7 ♂♂ 12 ♀♀/8. Ty?

Corynoptera boletiphaga Ldf. Småholmen 1960: VI: 2, VIII: 2, Rb 1 ♂/1, Gb 1 ♀/1. Xe.

Corynoptera fusiceps Tuom. Småholmen 1959: VIII: 1, Gb 1 ♂/1; 1960: VI: 1 — 2, Rb 1 ♂/1, Gb 1 ♂/1; 1960: VI: 1 — 2, Rb 1 ♂/1.

Corynoptera verrucifera Ldf. Småholmen 1960: V: 3 — VI: 1, Rb 6 ♂♂ 5 ♀♀/1, Gb 1 ♂/1. Ty?

Corynoptera camptochaeta Tuom. Bonäs 1960: VI: 3, Rb 5 ♂♂ 9 ♀♀/1. Ty?

Corynoptera sp. Bonäs 1960: VII: 1 — 2, Mb 7 ♂♂ 2 ♀♀/2. Ty?

Corynoptera sp. Bonäs: 1960: VI: 3 — VI: 1, Mb 18 ♂♂ 8 ♀♀/1. Ty?


Bradysia fungicola Winn. Småholmen 1960: VIII: 2, Gb 1 ♂/1. Xe.

Bradysia nitidicollis Meig. Småholmen 1960: VI: 2, IX: 1, Rb 2 ♀♀/2. Ty?


Bradysia confinis Winn. Småholmen 1960: V: 3 — VI: 2, Rb 1 ♀/1, Gb 6 ♀♀/5. Ty?


**CECIDOMYIIDAE**

The comparatively few specimens (possibly 4 species) have not been identified (Småholmen 1960, Rb, Bonä 1960 Rb and Mb).

**RHAGIONIDAE**

*Rhagio lineola* F. Småholmen 1959:VII:3—VIII:1, Rb 1 ♂ ♀♀/9 (and 2 larvae), Gb 7 ♀♀/1; 1960:VII:3 Ab 1 ♂ (Gb: 2 larvae). Xe.

**EMPIDIDAE**

*Hilara interstincta* Fall. Småholmen 1960:VI:2, Rb 1 ♂/1. Xe.
*Hilara* sp. Småholmen 1960:VI:3, VII:3, Rb 1 ♂ 1 ♀/2. Xe.
*Rhamphomyia simplex* Zett. Småholmen 1959:VI:3, Rb 1 ♀/1. Xe.
*Rhamphomyia* sp. Bonä 1960:V:3, Mb 2 ♀♀/2. Xe.
*Bicellaria spuria* Fall. Småholmen 1959:VII:3—VIII:1, Rb 1 ♂/1, Gb 1 ♀/1. Xe.
*Bicellaria nigra* Meig. Småholmen 1959:VI:3, Gb 1 ♀/1. Xe.
*Tachydromia commutata* Strobl. Småholmen 1959:VIII:2, Rb 2 ♀♀/1. Xe.
*Tachydromia candidans* Fall. Bonä 1960:VI:3, Mb 1 ♀/1. Xe.
*Symballophthalmus dissimilis* Fall. Bonä 1960:VI:2, Mb 1 ♀/1. Xe.
*Tachista arrogans* L. Småholmen 1959:VII:1, VII:3—VIII:2, Rb2 ♀♀ 1/, Gb 2 ♀♀/1. Xe.
*Trichina clavipes* Meig. Bonä 1960:VII:2, Mb 1 ♂ 1 ♀/1. Xe.
*Phyllodromia melanocephala* F. Småholmen 1959:VII:3, Rb 1 ♀/1. Xe.

**DOLICHOPODIDAE**

*Diaphorus* sp. Bonä 1960:VII:1, Mb 1 ♂/1. Xe.
*Xanthochlorus tenellus* Wied. Småholmen 1959:VII:3, Rb 1 ♂/1, Gb 2 ♀♀/2; 1960: VII:2—3, Rb 1 ♂/1, Ab 1 ♀. Xe.

**Anevrina urbana** Meig. Evitskog 1961:VI:1, Rb 3 ♀♂/1. Ty?


**Triphleba gracilis** Wood. Småholmen 1959:VIII:1, Rb 1 ♀♂/1. Xe.

**Triphleba distinguenda** Strobl. Småholmen 1960:VII:2, Gb 1 ♀♂/1. Xe.

**Triphleba bicornuta** Strobl. Småholmen 1959:IX:3, Rb 1 ♀♂/1; 1960:IX:1—3, Rb 5 ♀♂ 1 ♀/3, Ab 3 ♀♂ 5 ♀♂; 1961: reared from bait exposed in IX. Ty.

**Conicera floricola** Schmitz. Småholmen 1960:V:3—VII:3, Rb 16 ♀♂ 64 ♀♂/5 (out of these 13 ♀♂ 63 ♀♂ on bait), Gb 10 ♀♂ 47 ♀♂/6 (out of these 2 ♀♂ 12 ♀♂ on bait), Ab 2 ♀♂ 16 ♀♂. Bonäs 1960:VI:2—3, Rb 3 ♀♂ 2 ♀♂/2, Mb 1 ♀♂ 2 ♀♂/3. Ty.

**Conicera pauxilla** Schmitz. Småholmen 1959:VII:2, Gb 1 ♀♂/1; 1960:VI:3—VII:1, VIII:1—3, Mb 1 ♀♂ 7 ♀♂ on bait, reared from meat bait. Xe.

**Conicera fallens** Schmitz. Evitskog. 1961: Mb reared from meat bait. Xe.

**Phora pubipes** Schmitz, Småholmen 1959:VIII:2, Gb 1 ♀♂/1; 1960:VII:2—3 Rb 1 ♀♂, Ab 1 ♀♂. Xe.

**Phora obscura** Zettl. Småholmen 1960:VI:1, Rb 1 ♀♂/1. Xe.

**Phora spp.** (unidentified) Småholmen 1960. 13 ♀♂, Bonäs 1960, 2 ♀♂ (possibly different species).


**Megaselia projecta** Becker (?). Småholmen 1960:VIII:3—IX:1, Rb 2 ♀♂/1. Xe.

**Megaselia specularis** Schmitz (?). Småholmen 1960:VII:2, Rb 1 ♀♂/1. Xe.


**Megaselia meconicera** Speiser (?) Bonäs 1960:VI:3, Mb 1 ♀♂/1. Xe.


**Megaselia major** Wood. Småholmen 1959:VIII:3, Rb 1 ♀♂/1; 1960:VIII:1, Rb 1 ♀♂/1.

**Megaselia aequalis** Wood. Småholmen 1959:VIII:3, 1 ♀ in a Microtus nest.


**Megaselia fungivora** Wood (?). Småholmen 1959:VIII:1, Rb 1 ♀♂/1. Xe.

**Megaselia (Aphiocoeta) sp.** Bonäs 1960:V:2, Mb 1 ♀♂/1. Xe.

**Megaselia angularis** Schmitz. Småholmen 1960:VI:3, Rb 1 ♀♂/1. Xe.

**Megaselia hyalipennis** Wood (?). Småholmen 1960:VII:2, VIII:1, IX:1, Rb 1 ♀♂/1, Gb 1 ♀♂/1, Ab 1 ♀♂.

**Megaselia unicolor** Schmitz. Småholmen 1960:IX:3, Rb 1 ♀♂/1, Ab 1 ♀♂. Xe.


**Megaselia fusciptalpis** Wood (?). Småholmen 1960:VIII:3, Rb 1 ♀♂/1. Xe.

**Megaselia pumila** Meig. Bonäs 1960:VI:1, Rb 1 ♀♂/1. Xe.


**Megaselia affinis** Wood (?). Småholmen 1960:VII:1, Rb 1 ♀♂/1. Xe.


**Megaselia rustipes** Meig. Småholmen 1959: Rb 1 ♂; 1960:VII:1—VIII:3, IX:2, Rb 11 ♂ 8♀/7 (out of these 4 ♂ 6♀ on meat bait), Gb 5♀/2. Evitskog 1961: reared from bait. Ty.


**Megaselia longiseta** Wood. Småholmen 1960:IX:3, Rb 1 ♂/1. Xe.

**Megaselia minor** Zett. Bonäs 1960:VI:3, VIII:1, Rb 1 ♀/1, Mb 1 ♀/1. Xe.


**Megaselia sp. (maura** Wood?). Småholmen 1960:VIII:3, Gb 1 ♀/1. Xe.

**Megaselia sp. (impolluta** Schmitz?). Småholmen 1960:VI:2, VIII:1, Rb 1 ♂ 1♀/2.

**Plastophora sp. (brevicornis group).** Bonäs 1960:VIII:3, Mb 1 ♀/1. Xe.

**Plastophora sp. (spinigera** Wood?). Småholmen 1959:VI:2, Rb 1 ♀/1. Xe.

**SYRPHIDAE**

**Chilosia** sp. Bonäs 1960:VI:1, Mb 1 ♀/1. Xe.

**Syrphus torvus** O. Sack. Småholmen 1959:VIII:1, Rb 1 ♀/1. Xe.

**DRYOMYZIDAE**


**SCIOMYZIDAE**

**Hemitelopteryx brevipennis** Zett. Småholmen 1960:VII:1, Gb 1 ♀/1. Xe.

**HELOMYZIDAE**

**Helomyza pallida** Fall. Småholmen 1959:X:3, Gb 6 ♀/1. Xe.

**Helomyza humilis** Meig. Småholmen 1959:X:3, Gb 1 ♀/1; 1960: IX:1, Ab 1 ♀. Xe.


**Tephroclamys rufiventris** Meig. Bonäs 1960:V:3, Rb 1 ♀/1. Ty?

**Tephroclamys flavipes** Zett. Småholmen 1959:IX:1, 3, X:1, 3, Rb 6 ♀/3, Gb 2 ♀/1; 1960:IX:1—3, Rb 8 ♀/2, Ab 1 ♀; IX:2, Rb 1 ♀/1, reared from bait exposed in September. Ty.
Neoleria inscripta Meig. Småholmen 1959: VII: 3, Gb 1 $\varphi$ /1; 1960: VIII: 1, Gb 1 $\varphi$ /1. Xe.

Eccoptotera ornata Loew. Småholmen 1959: VII: 3—VIII: 3, IX: 3, Rb 2 $\varphi$ /5, Gb 1 $\varphi$ /4. 1960: VI: 2, VII: 1—3, IX: 2—X: 2, Rb 1 $\varphi$, Gb 4 $\varphi$ /3 in Ab /3, Ab 2 $\varphi$. Bonäs 1960: VI: 3, VIII: 3, Rb 1 $\varphi$ /1, Mb 1 $\varphi$ /1. Ty.


Eccoptotera longiseta Meig. Småholmen 1959: X: 3, Gb 2 $\varphi$ /1. Ty.

Chaetomus confusus Wahlgr. Småholmen 1960: IX: 1, Rb 1 $\varphi$ /1. Xe.

Leria serrata L. Evitskog 1961: VII: 2, Rb 1 $\varphi$ /1. Ty?


Amoebaleria amplicornis Cz. Bonäs 1960: V: 3—VI: 1, Rb 1 $\varphi$ /2. Ty.

BORBORIDAE

Spaerocera nitida Duda. Småholmen 1959: VI: 3, Rb 1 $\varphi$ /1.

Borborus alt Meig. Småholmen 1959: IX: 3—X: 1, Rb 1 $\varphi$ /1, Gb 1 $\varphi$ /1. Ty.

Copromyza stercoraria Meig. Småholmen 1959: VI: 1—2, VII: 1, Gb 4 $\varphi$ /7 in Ab /2; 1960: VIII: 1, Gb 1 $\varphi$ /1. Ty.


Leptocera fontinalis Fall. Bonäs 1960: V: 2—VI: 1, VII: 1, VIII: 1—2, Rb 2 $\varphi$ /2. Mb 7 $\varphi$ /8 in Ab with bait. Ty?

Piteremis fenestralis Fall. Bonäs 1960: VII: 3, Mb 1 $\varphi$ /1. Evitskog 1961: VI: 3, Mb 1 $\varphi$ /1. Ty?

Limosina schmitzi Duda. Småholmen 1959: VII: 2—3, Rb 1 $\varphi$ /1, Gb 1 $\varphi$ /1. Bonäs 1960: VII: 1, VIII: 2, IX: 1, Rb 2 $\varphi$ /1, Mb 1 $\varphi$ /1. Ty.


Limosina flavipes Meig. Bonäs 1960: VII: 1, Mb 1 $\varphi$ /1. Xe.


DROSOPHILIDAE

Drosophila obscura Fall. Småholmen 1960:VIII:1, Gb 1♀/1. Xe.
Drosophila transversa Fall. Evitskog 1961: reared from bait. Xe.

DIASTATIDAE


CHLOROPIDAE

Aphanitrigonum sp. Bonäs 1960:V:3, Mb 1♀/1. Xe.
Conioscinella frontella Fall. Småholmen 1959:VIII:1, Rb 1♀/1. Xe.

TACHINIDAE

Sarcophaga scaparia Pand. Evitskog 1961:VII:2, VIII:1, Mb 2♀/1, reared from meat bait. Xe.

CALLIPHORIDAE

Pollenia varia Meig. Bonäs 1960:VIII:2, Mb 1♀/1. Xe.
Calliphora uralensis Villen. Småholmen 1960:VII:2, VIII:1, Rb 1♀/1, Gb 1♀/1. Xe.
Calliphora subalpina Ringd. Småholmen 1959:IX:3, Gb 1♀/1. Xe.

MUSCIDAE

Fannia hamata Macq. Småholmen 1960:VI:3, Rb 1♀/1. Xe.
Fannia pallitibia Rond.(?). Småholmen 1959:VI:3, Rb 1♀/1. Xe.
Helina lucorum Fall. Småholmen 1960:VII:1, VIII:1, Gb 1 ♀ 1 ♂̄/1. Xe.
Spilogona sp. Småholmen 1960:VII:2, Gb 1 ♀/1. Xe.
Coenosia mollicula Fall. Småholmen 1959:VII:3—VIII:1, Gb 2 ♀♀/2. Xe.
Phaonia scutellaris Fall. Småholmen 1959:IX:1, Rb 1 ♀/1. Xe.
Lasiops inocuss Zett.(?). Småholmen 1960:VII:1—2, Rb 1 ♀/1, Ab 1 ♀/1. Xe.
Lasiops variabilis Fall. Småholmen 1960:VII:3, Gb 1 ♀/1. Xe.
Hylonymia variata Fall. Småholmen 1959:VIII:1,3, Rb 2 ♀♀/2; 1960:VI:3, Gb 2 ♀♀/2. Xe.
Hylonymia sp. Bonäs 1960:VI:2, Mb 1 ♀/1. Xe.

XV. Summary

The present paper deals with the dipterous fauna of the subterranean burrows of voles (Microtus arvalis, M. agrestis and Clethrionomys glareolus). The investigation was made in the years 1959—1961 and in three places in Finland, on Småholmen Island (commune of Esbo), in Evitskog (commune of Kyrkslätt) and in Bonäs near Nykarleby town. The Diptera were collected with the aid of funnel and Barber traps. Various types of bait were also tried. In 1959 and 1960, the field work was done during the warm season and continued until the end of October. In 1961 rearing experiments were mainly done, in the field during the summer months and in the laboratory in the autumn. Measurements of the temperatures in the burrows were made with maximum-minimum thermometers and a thermograph.

In the types of burrows studied, the temperature fluctuations are small in comparison with those outside at the soil surface. In a normal Microtus burrow (depth 10—15 cm) on Småholmen (about 60°10' N.lat.) and in Bonäs (63°30' N.lat.) the temperature will hardly rise above +20°C even on hot summer days. During the winter the burrow temperature will sink at most a few degrees below zero. The length of the season with temperatures at least around +10°C will depend on several factors, macroclimate, sun exposure, nature of the ground and water content of the soil.

The material collected, about 240 species, includes representatives of 27 families and the number of individuals is about 2000. Owing to the sampling methods used, this material allows a quantitative treatment only to a limited
extent. Three types of vole burrows have been distinguished and the dipterous fauna of these treated in separate sections of this paper. The burrow types are 1) burrows under stumps and trees (Småholmen, Bonäs) 2) burrows in grassy soil under bushes (Småholmen), 3) burrows in meadows (Bonäs, Evit-skog).

Burrows of the first type form rather heterogeneous and unstable biocoenoses, where the fungivorous and xylosaprophagous elements are numerous. The only species of these showing fair dominance (on Småholmen) is *Ctenosciata hyalipennis* (Sciariidae). In the second and third types the fungivorous elements are few. The dominant or constant elements are saprophagous species of Trichoceridae (in type 3), Sciariidae, Phoridae, Helomyzidae, Borboridae and Muscidae.

Species common to all three kinds of burrows studied on Småholmen and in Bonäs are:

- *Bradyisia bicolor* Meig. (Sciariidae)
- *Anevrina thoracica* Meig. (Phoridae)
- *Conicera floricola* Schmitz
- *Megaselia sp. (pr. pulicaria)*
- *Eccoptomera ornata* Loew. (Helomyzidae)
- *Copromyzia borealis* Zett. (Borboridae)
- *Crumomyia glacialis* Meig.
- *Limosina claviventris* Strobl.
- *Lasiops semicinereus* Wied. (Muscidae)

A coenological analysis after AGRELL’s method was tried on the samples from burrows of the three kinds. No strong affinity between more than couples of species was found.

The biology of various species was studied with the aid of different kinds of bait in the traps, by rearing experiments and by using artificial burrows combined with Barber traps. 27 species were reared on various substrates, mainly mouse droppings.

Phenological aspects of the dipterous fauna are dealt with and differences in phenology attributable to microclimatic factors demonstrated.

Principles for an ecological classification of the species are discussed. A classification suggested by WIREN for insects in rodent burrows is applied to the present material. An attempt has been made to classify the species as eucoenic, tychoecoenic and xenocoenic. Only *Limosina talparum* Rich. in the present material is considered eucoenic for micromammalian burrows. The tychoecoenic or probably tychoecoinic species are 57. For numerous species, the reasons for their insertion in the ecological groups are given in short notes.

Various factors influencing the dipterous fauna of vole burrows are discussed. Among these factors the fluctuations of the vole populations are of especial importance.

A list of all species identified is given, including phenological and other data.
XVI. References


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W. Hackman: The dipterous fauna in burrows of voles


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