STUDIES ON THE DIPTERA
BREEDING IN COWPATS IN SOUTH-EAST SCOTLAND
WITH PARTICULAR REFERENCE TO.
HARMATORIA STIMULANS MEIGEN.

by

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INTRODUCTION

The activity of fly-pests in summer and autumn is one of the most prominent and difficult of the problems with which animal husbandry is beset in most parts of the world. Among the wide range of types which contribute to the problem the dung-breeding Muscids constitute a well defined, and significant element. This group is world-wide in its distribution although it is represented by different species-components in different regions. In any given area, however, it is divisible into two main sections: the domestic species which frequent buildings and housed animals, and undergo development in middens and accumulation:of stored dung, and the pasture species which trouble animals in the field and breed in their droppings. The two sections may overlap to some degree, but in general they are quite distinct. Since it has a human - as well as an animal - health aspect, the domestic problem has hitherto received considerably more attention, and information concerning flies which breed in middens greatly exceeds that on flies which breed in droppings in the field.

The present investigation was started with the intention of examining the fly-pest problem, in the field, and in particular, to study the bionomics of the common blood-sucking stomoxidines of North Britain, Haematobia stimulans Mg. Unfortunately, in the course of the first year's study it became evident that the Edinburgh district did not provide suitable facilities for the purpose, since the species was nowhere sufficiently numerous to permit of continuous and profitable observation. The main intention/
intention of the work was, therefore, transferred to a study of the associated muscid flies of the cow-dropping community.

RÉAUMUR (1738) effectively initiated the study of the biology of dung-breeding flies with his remarkably acute observations on Scopemyia (stereorarium?), Mesembrina (meridiana?) and Rhingia sp. In spite of his commendation of the cow-pat as a fruitful source of biological subjects the field remained uncultivated until the end of the XIXth century when PORCHINSKI (1885) began his valuable series of contributions by drawing a broad comparison between necrophagous and coprophagous flies. In 1892 he recognised the carnivorous habit of Myospila meditabunda, and then in an appendix to his publication of 1910 established the fact that several of the dung-inhabiting dipterous larvae become zoophagous in their later instars. In his work, although he did not always distinguish between accumulated dung and fresh droppings, he was aware of some of the differences between the flies of the two types of medium, and knew well the differences between the faunas of dung of different animal species. For example, he states that Pseudomorellia albolineata breeds exclusively in horse-droppings and is as characteristic for that medium as Orthellia cornicina /= caesarion(?) is for cattle-droppings.

At the beginning of the present century the subject began to receive attention from several other workers including BOGDANOV (1901) in Russia, and HOWARD (1901) and PRATT (1912), in North America. All these workers give lists of the species encountered in cow-dung, and the first named includes some information/
information on seasonal incidence. Their work in all cases, unfortunately, contains the disadvantage that they do not specify when they were dealing with undisturbed cattle-droppings and when with accumulated manure of bovine origin.

Apart from these early contributions, almost all the work carried out on dung-breeding Diptera during the first thirty or so years of this century has been concerned with accumulated dung, and in particular with Musca domestica and Stomoxys calcitrans. The problems of fly-control during the First World War promoted a considerable volume of work on these species. Further work of this type was continued under the auspices of the League of Nations Health Organisation, until well after 1930. Dispersed throughout this large body of work there is information on many points of interest concerning various members of the dipterous community of cow-droppings. Reference to some of these items is made at appropriate points in the present account.

KEILIN(1914,1915, & 1917) and KEILIN & TATE(1930) in a series of papers on the anatomy of muscid larvae developed and amplified the morphological aspects of POKHINSKIY's work. KEILIN recognised and stressed the importance of the relationship between the structure of the buccopharyngeal skeleton and the feeding habits of muscid larvae. MUTHHEAD THOMSON(1937) continued this line of investigation and gave a very complete account of the preimaginal development and morphology of 13 muscid species of the cow-pat biocenose. His publication also contains quite extensive notes on field observations on these/
these species in Western Scotland, and included valuable information on seasonal incidence, oviposition and feeding habits of adults.

Biological and ecological investigations of individual members of the cow-pat community have been carried out from time to time, but nearly all of them are concerned with the stomoxidine species, (COTTERELL's (1920) study of Scopoeuma stercorarium is an exception), which have assumed such large pest proportions in the "new" continents. *Lyperosia irritans* in North America has been studied by, inter alia, MARLIATT (1910) and HASEMAN (1927), *Lyperosia exigua* in Australia and Indonesia has been extensively studied by many workers, including HILL (1917), TILLYARD (1931) and HANDSCHIN (1932, 1934), while in Europe *Haematobia stimulans* has received special study by THOMSEN (1935). The control of these pests by competitors, predators, and parasites was recognised particularly by the workers in Australia, and MYERS (1938) investigation, (concerned primarily with a search for new agents to control *L. exigua*), on *L. irritans* and the cow-pat community in Haiti, was one of the first to take account of the interactions between the constituent species, and to regard the cow-pat as an ecological entity.

It is in Denmark that the most detailed and intensive studies of the cow-pat biocoenose and its synecology have been carried out. This work was carried out contemporaneously with studies on the dipterous fauna of accumulated dung of various types by THOMSEN & HAMMER (1936). THOMSEN (1938) gave a preliminary account of some of the flies of cow-pats, and HAMMER (1941)
HAMMER (1941) published a very comprehensive account of an exhaustive investigation, the major contribution to date on the subject. HAMMER examined the physical conditions of cow-droppings, and their change with ageing of the droppings at different seasons. He recognised the differences between faunas in different regions and their relation, in particular, to conditions of shelter and exposure. His work was based largely on visual observation, and enumeration of adult flies, and of the species succession on the surface of cow-pats.

From these, and from some observations on the times of development of various species HAMMER drew his conclusions on the seasonal course of the life cycles. He gives very little information, however, on the developmental times of, or on the size and range of variation of the populations of the preimaginal instars.

Although the size of the problem compelled HAMMER to confine his attention to the Muscidae and the main acalyptrate and brachycerous species, he makes reference to the Coleoptera, and in a broad summary outlines the life together of the whole community.

MOHR (1943) working in North America (Illinois) made an ecological study of the Diptera, and Coleoptera, and their hymenopterous parasites, in cow-droppings. He regarded the pabulum as one part (microsere) of the environment of the biocoenose, and divided its temporary existence into 3 microseral stages. He includes details of the numbers of larvae of certain species in the "interior populations" and of adults in the "surface populations" at different seasons. He gives little evidence, however, concerning the seasonal course of the life cycles/
cycles (voltinism) of the species studied.

Lists of species occurring in the biotope in other parts of the world are recorded briefly by several authors, including RINGDAHL (1932) in Sweden and DUFFIELD (1937) in Norwegian Lapland, and in detail by LAURENCE (1953) in England. MUTIHEAD THOMSON (1947) continued his morphological studies on some of the species found in the biotope in Assam. HAFEZ (1939) in Egypt, and DERBENEVA-UKHova (1940) and others in Russia give information on the flies of accumulated cow-dung.

The outstanding deficiency in present knowledge of the dipterous flies of the cow-pat community concerns the duration of their developmental stages in the field, their voltinism, and the diapause phenomena associated with their hibernation. The present investigation was designed primarily to examine this aspect of the subject, since a comprehensive approach to the synecological problems can not profitably be undertaken until this aspect is more surely established.
Field observations were carried out during the years 1952 and 1953 at Bush, Miltonbridge, the Midlothian estate of the Edinburgh Centre of Rural Economy. The general topography of the immediate area is shown in the sketch map. Fields A - C were in grass and from late April to late October were grazed regularly by a herd of about 35 dairy cows. At various times they were accompanied by the two farm horses and a flock of upwards of two score sheep. From June to September an area was fenced off to accommodate four sty's of pigs, and moved three times during this period. Attention was largely confined to the cow-droppings, but occasional comparisons were made between their insect communities and those in the droppings of the other domestic animal species.

Qualitative comparisons were made periodically between the communities inhabiting the cow-droppings in these fields, and those occurring in the manure-heap at the farm (D), and the communities of both droppings and middens in other districts including Argyllshire, Ayrshire, and Hampshire.

Visual observations were regularly carried out on the activities of adult flies on cow-pats, cattle, fences, hedges, etc., but the system of uncontrolled grazing in Britain does not permit of so close a study as the tethering system employed in Denmark. The grazing system also prevented the study of the larval populations in the pats without removing them from the field.

At approximately weekly intervals cow-pats were marked immediately/
FIGURE 1. Sketchmap of field area (Midlothian).

D. = Midden site, E. = Enclosure, F. = Meat-bait trap sites.
FIGURE 2.
Field C.
Top-looking east.
Bottom - looking west.
immediately they were dropped, and then left undisturbed to permit access of all the flies of the community. Only compact, and well-formed pats were selected, and the intervals were not exact on all occasions since pats were only selected during periods of more favourable weather. In 1952 the pats were exposed for periods of up to one week, but the populations of these were not substantially different from those of pats exposed for 24 hours or 48 hours. In 1953, therefore, to reduce the variables pats were only exposed for the shorter periods before their removal. For the same reason all pats were marked in the forenoon. While it is probable that the time of day will have an important effect on specific composition of the ovipositing community this was one aspect which had to be omitted from the investigation. The pats studied were thus those which passed through their 'young stages' i.e. when they are most attractive to the majority of the dipterous species, during the middle of the day when fly activity was maximal. This policy of selection was compelled by the need to economise in cones for trapping and by the almost unmanageable proportions assumed by the task of enumeration and identification of material trapped.

On each occasion in 1953 a series of 9 pats was marked and these were removed on the following days, 3 to the field and 2 to the laboratory after 24 hours, and 3 to the field and 1 to the laboratory after 48 hours. The pats were removed undisturbed on a layer of underlying turf 1 foot square by 2 - 3" deep. Those maintained in the field were removed to an enclosure/
enclosure E (Fig. 1) in the adjacent park where they were countersunk in the ground to simulate their normal position. Each pat was covered with a perforated zinc cone trap of the pattern shown in figure 3. These were so constructed that the specimen tube, gauze cylinder and celluloid cone formed a rigid structure which could be removed and replaced readily each day. The gauze cone was of value in reducing condensation and so preventing damage to the trapped flies. From the experience obtained in 1952 it was found that the 2" rim of the zinc cone was inadequate to prevent migration of some larvae (e.g. Orthellia caesarion) prior to pupation. In 1953, therefore, each cone was sunk into a close-fitting zinc sleeve of 6" depth. The earlier cones were made from zinc with 9 perforations to the inch, but these were found to be too large to retain some of the species, and later cones were constructed from 12 mesh zinc. Even though the perforations allowed a fair degree of illumination within the cone, the flies readily passed into the more brightly lit trap so that no special steps were required to darken the cone. The pats removed to the laboratory were placed on their underturf on a gravel and sand base in trays, and surmounted by cones of the same pattern. These were kept in a constant temperature room at 23°C which was artificially illuminated during the daytime, and the turf was watered periodically to prevent desiccation. To save cones, qualitative results on the content of cow-pats from other districts, and horse-, sheep-, pig and midden-dung were obtained by keeping the dung in half-size biscuit tins (in which/
**FIGURE 3.**
Cone-trap.
FIGURE 4.
Cone-traps in enclosure.
which they were transferred to the laboratory) provided with Specimen tube traps of the same pattern as used on the cones.

A temperature record was kept in the field enclosure by two 'Edney' thermographs, shielded from direct sunshine by a slatted screen, in which the elements were contained in projecting arms. They were situated one above the other, one at ground level with its element among the grass layer, and the other one foot above the ground.

Several disadvantages may be envisaged in the use of the method to identify the time relations of developmental stages, and to obtain data representative of fly-populations developing in cow-pats in nature. First the temperature changes experienced by pats under cones are probably less marked than those occurring in pats in the open, since insolation is reduced during the daytime, and negative radiation is reduced at night. HAMMER(1941) using wire cones of 1.5 mm. mesh found no marked difference between the temperatures of pats inside and outside. (Perforated zinc probably gives less natural conditions than wire-cloth, but the cost of this material precluded its use).

Secondly, the rate of evaporation under cones is reduced, with the result that the pats remain compact for longer periods and disintegrate less rapidly than those in the open. It is possible that this condition might delay pupation of some of the species which normally migrate from the pat to select drier situations (e.g. Orthellia caesarion, Scopema stercorarium, Anisopus punctatus, Stratiomyidae etc.). The third obvious disadvantage is the fact that small flies such as Borboridae and/
and *Sepsidae* escape through the meshes very easily and the majority of them are lost. Their retention, however, is a special problem which seems not to be soluble without altering the physical conditions even more severely.

In addition to these disadvantages due to the method of trapping, there is the disadvantage due to the need to concentrate the pats within a relatively small enclosure. The cone perforations allow the passage of the smaller Staphylinid beetles. These are voracious carnivores, which are probably enabled to build up their numbers in the enclosure by the concentration of fly larvae there, and which probably exert a greater controlling influence there than in the open field. No concrete evidence was obtained regarding this possibility, however.

There is one source of potential error where the natural infestation of pats in open pasture is under examination, namely that some pats are dropped on the disintegrated remains of earlier droppings. These or the vegetation around them may contain preimaginal stages of flies which fed on the old pat but which have not yet completed their development. When these are later trapped they can be mistaken for individuals derived from the pat under study. Where they are obviously recognisable such records have been discounted, but it is impossible to be sure that they have all been excluded.

In the later part of the season, and in winter, when flies were no longer emerging as adults, the pats from the field were brought into the laboratory to carry out assessments of their dipterous faunas. Power washing through sieves, and flotation in/
in magnesium sulphate solutions were two methods which were examined for the extraction of larvae and pupae. They provided little assistance, however, since by the first method sieves which allowed the removal of the finer material permitted the passage of the smaller larvae, and the power sprays damaged the more fragile larvae. The flotation method was quite useless since the whole substance of the pat, being organic in nature, floated. Separation of larvae and pupae had, therefore, to be carried out by manual disintegration of the dung and turf-materials.

Opportunity was taken to use the results of other methods of fly-trapping in progress in the Department of Entomology. Two suction-traps of the type devised and described by JOHNSON (1950) were situated in the enclosure E where they were in continuous operation (Vide Fig. 5). These provided useful information on the seasonal incidence and behaviour of some of the cow-pat species (E.g., Dasyphora cyanella, Hylemya spp etc.)

Meat bait traps operated by Dr. J. A. Campbell on behalf of Dr. J. Macleod as part of a wide survey on Calliphorid flies contained varying numbers of some of the members of the cow-pat community including Dasyphora spp, Morellia spp, Pseudophaonia hirtiorura, Fannia spp, Hydrotæa spp, Scopeuma spp etc. These were small wire mesh balloon traps baited with rabbit flesh (Vide fig. 6). These traps when baited with fresh cow-dung collected very few flies, presumably because the amount of bait was far too small. Attempts to increase their attractiveness with scatole were quite unsuccessful. They were/
FIGURE 5.
Suction-trap.
FIGURE 6.
Meat-bait trap.
were, therefore, regularly employed with meat baits at the sites indicated in the sketchmap (Figure 1). Dr. Macleod also very kindly placed at our disposal the muscid material collected in his survey from other parts of Great Britain.

The method used to keep Haematobia stimulans and to obtain its eggs in the laboratory is described in Part IV.
PART II: SYSTEMATIC LIST, AND REMARKS ON SPECIES FOUND.

The species encountered in the investigation are given in the list which follows. Some of them appear not to have been recorded previously from cow-pats and are marked with an *.
The place occupied by the individual species in the community is indicated by a letter placed after the name, thus

C - regular breeder
O - occasional breeder
R - exceptional breeder
V - visitor only (non-breeder)
S - status uncertain

The additional letters H and L are used to indicate whether the species appears in the lists of HAMMER (1941) from Denmark and LAURENCE (1953), from England, respectively.

Obviously an arbitrary distinction between regular, occasional and exceptional breeders presents difficulties. For example, a species could be "occasional" rather than "regular" either if it used other breeding media or if it were absolutely less abundant in the district. *Haematobia stimulans* is "occasional" in Midlothian but "regular" in Ayrshire and Argyllshire because it is evidently less common in the first than in the other two counties, and not because it is thought to breed in any other medium there.

The list of *Coleoptera* is almost certainly very incomplete, and includes only the most commonly encountered species.

**DIPTERA**

*Tipulidae/*

**Thanks are due to Mr. N.W. Hussey for assistance in their identification.**
Tipulidae

* Rhipidia maculata (Meigen 1818) C

Trichoceridae

Trichocera annulata Meigen 1818 S

Anisopodidae

Anisopus punctatus (Fabricius 1787) C L

Ceratopogonidae

* Forcipomyia bipunctata (Linnaeus 1767) 0
Culicoides chiopterus (Meigen 1830) 0 L
Culicoides pseudochiopterus Downes & Kettle 1952 0 L

Bibionidae

* Bibio ferruginatus (Linnaeus 1767) 0
* Dilophus febrilis (Linnaeus 1758) C

Scatopsidae

* Scatopse notata (Linnaeus 1758) 0
* Scatopse fuscipes Meigen 1830 0

Stratiomyidae

* Beris vallata (Forster 1771) 0
* Beris fuscipes Meigen 1820 0
Microchrysa polita (Linnaeus 1758) 0 L
Microchrysa flavicornis (Meigen 1822) C H
* Microchrysa cyaneiventris (Zetterstedt 1842) C
Geosargus flavipes (Meigen 1822) C H L
* Geosargus nitidus (Meigen 1822) R
Chloromyia formosa (Scopoli 1763) R L

Rhamionidae (Leptidae)

Rhagio/
Rhagio tringaria (Linnaeus 1758)  S
Rhagio lineda Fabricius 1794  S

Empididae
Techydromia arrogans (Linnaeus 1761)  S
Platypalpus longicornis (Meigen 1822)  S
Platypalpus candidans (Fallen 1815)  S
Platypalpus pallidiventeris (Meigen 1822)  S
Ocydromia glabricula (Fallen 1816)  O  L

Doliichopodidae
Dolichopus popularis Wiedemann 1817  S
Dolichopus trivialis Haliday 1832  S
Gymnopternus cupreus (Fallen 1823)  S

Lonchopteridae
Lonchoptera lutea Panzer 1809  S

Syrphidae
Rhingia macrocephala (Harris, M. 1776)  C  H  L

Piophilidae
Piophila vulgaris Fallen 1820  S

Lauxaniidae (Sapromyzidae)
Lyciella subfasciata (Zetterstedt 1847)  (Collin, 1948)  S

Sepsidae
* Themira lucida (Staeger 1844)  O
Sepsis fulgens Meigen 1826  C  L
Sepsis punctum (Fabricius 1794)  O
Sepsis flavimana Meigen 1826  C  H  L
Sepsis cynipsea (Linnaeus 1758)  C  H  L

Helomyzidae
Neoleria/
Neoleria inscripta (Meigen 1830)  

Opomyzidae

† Opomyza germinationis (Linnaeus 1758)  
Geomyza apicalis (Meigen 1830)  

Sphaeroceridae (Borboridae)

Sphaerocera curvipes Latreille 1804  
Crumomyia nigra (Meigen 1830)  
Stratioborborus nitidus (Meigen 1830)  
Trichiaspis equina (Fallen 1820)  
Trichiaspis similis (Collin 1930)  
Coprophila pusilla (Meigen 1830)  

Cordiluridae (Scatophagidae)

Scopeuma stercorarium (Linnaeus 1758)  
Scopeuma squalidum (Meigen 1826)  
Scopeuma sp. non det.  

Calliphoridae

* Sarcophaga subvicina Rohdendorf 1937  

Muscidae

Orthellia caesarion (Meigen 1826)  
Orthellia cornicina (Fabricius 1781)  
Dasyphora cyanella (Meigen 1826)  
Myospila meditabunda (Fabricius 1781)  
Mesembrina meridiana (Linnaeus 1758)  
Muscina assimilis (Fallen 1823)  
Morellia hortorum (Fallen 1816)  
Morellia simplex (L3w 1857)  
Haematobia stimulans (Meigen 1824)  

Lasiopa/

† This species should probably be excluded, vide p. 20 re. Chlorops pumilionis.
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<tr>
<th>Species</th>
<th>Author</th>
<th>Key</th>
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†For *pagana* here and pp. 37 et seq. read *scutellaris*
Robineau-Desvoidy 1830 (= *pagana* Fabr.)
Hydrophilidae

Hylemya variata (Fallen 1823)
Hylemya variabilis (Stein 1916)
Egle cinerella (Fallen 1825)
Egle aestiva (Meigen 1826)
Hamaomyia grisea (Fallen 1823)
Macrochis meditata (Fallen 1825)
Caricca intermedia (Fallen 1825)

Coleoptera

Hydrophilidae

Sphaeridium bipustulatum (Fabricius 1792)
Sphaeridium lunatum (Fabricius 1792)
Cercyon lugubris (Olivier 1790) = obsoletus (Gyllenhal 1808)
Cercyon atomarius (Fabricius 1801) = impressus (Sturm 1807)
Cercyon melanocephalus (Linnaeus 1758)

Staphylinidae

Platystethus arenarius (Geoffroy in Fourcroy 1785)
Philonthus splendens (Fabricius 1792)
Philonthus fuscipennis (Mannerheim 1831)
Philonthus marginatus (Fabricius 1775)
Oxypoda opaca (Gravenhorst 1802)

Scarabaeidae

Aphodius depressus (Kugelann 1792)
Aphodius rufipes (Linnaeus 1758)
Aphodius sphacelatus (Panser 1798) = punctatosulcatus (Sturm 1802)
Aphodius scybalarius (Fabricius 1781)

As regards the Diptera this list bears a marked similarity to those of HAMMER and LAURENCE, and includes all the species studied by MUIRHEAD THOMSON (1937) in Western Scotland.

HAMMER/
HAMMER records only the families of the *Nematocera*, as also does THOMSEN (1938). The latter author, however, mentions that *Anisopus punctatus* is an abundant species.

Among the rarer flies recovered from cone-traps such species as the Larvaevoridae *Crocuta geniculata* (Degeer) parasitic on some *Tipula* species and a Noctuid (DAY 1948), and the Galliphoridae *Follenia rudis* (Fabr.) parasitic on an earthworm (KEILIN 1915) and *Morinia nana* (Meig.) obviously do not belong to the community and are, therefore, excluded from the list. The chloropid, *Chlorops pumilionis* (Sjerkander 1778) a grass parasite is similarly omitted.

**NEMATOCERA**

The list given of nematocerous species is very incomplete, since only those were identified whose numbers were such as to indicate a prominent part in the life of the community. No attempt was made to identify *Itioniidae* (Cecidomyidae) in view of their difficulty, and again although they are an important section of the fauna the *Sciarae* had to be neglected for the same reason.* Chironomidae* and *Psychodidae* are represented by some apparently quite regular breeders, (e.g. *Psychoda brevicornis* Tonnoir 1940, *inter alia* is frequently quite abundant) but the traps used did not permit their quantitative estimation, and their identification was therefore omitted. (The *Ceratopogonidae* were determined for the purpose of other studies in progress in the laboratory).

*Tipulidae* have been recorded by LAURENCE and by COE (1941 & 1950) but their records suggest that the species concerned

(Tipulines,/
(Tipulines, 1 Cylindrotomine and 1 Limoniine) are only casual inhabitants of the biotope. MOHR (1943) found Tipula bicornis Forbes as an irregular inhabitant of old dung in the U.S.A., but suggests that is not a true dung breeder. Tipuline larvae have been seen infrequently in the present studies, probably as irregular casualties. The Limoniine species Rhipidia maculata, on the other hand, is a regular member of the bioocoenose and has been bred from Midlothian and Ayrshire parishes in very large numbers.

BRACHYCEERA

Among the brachycerous families the Stratiomyidae greatly surpass the others in importance. In particular, members of the genera Geosargus and Microchrysa are regular dung breeders throughout most of the North Temperate Zone. In Britain G. flavipes has been recorded in cattle droppings by VERRALL (1909) and LAURENCE; while in accumulated manure MELLOR (1919) found G. cuprarius (L) to be the common species in East Anglia. In Denmark also, G. cuprarius is common in midden dung according to THOMSEN & HAMMER (1936) and THOMSEN (1938) while HAMMER (1941) found G. flavipes only in droppings. HAMMER emphasises that these two species were never encountered outside their characteristic biotopes. The earlier Russian workers FORCHINSKIĬ (1892) and BOGDANOV (1901) refer only to G. cuprarius (and G. infuscatus). It is probable, although not explicit, that they were dealing with accumulated dung, since DERBENIEVA-UKHOVA (1940) refers only G. cuprarius, but she states that it only/
only occurred in large dung-heaps, (cattle dung). G. flavipes appears not to be common in Russia. On the other hand, 
MOHR (1943) refers to G. cuprarius (together with the non-
-British species G. viridis Say and G. elegans Low) as a 
regular member of the dung-pat community. If his identification 
is correct then the North American representatives of this 
species must have developed a different breeding behaviour 
from the European. In the present investigation no Geosargus 
species with long postocular fringe was encountered (VERRALL's 
records suggest that G. cuprarius and G. iridatus are relatively 
scarce in the Edinburgh district), and G. flavipes was the 
species found on midden dung.

G. nitidus appears to be a new record for the cow-pat medium. It was only collected on rare occasions from pats 
dropped in Ayrshire.

Of the genus Microchrysa HAMMER records M. flavicornis 
only, and LAURENCE M. polita only. Both these species occurred 
in the present work but were accompanied by the much more 
abundant M. cyaneiventris. It is surprising that M. flavicornis 
(which was bred from both horse and cow droppings in Edinburgh) 
should be missing from LAURENCE's list since VERRALL records 
it as a very common British species, M. cyaneiventris on the 
other hand is stated to have a more northerly distribution, 
and is relatively scarce in the south. It may be scarce in 
Denmark, but HAMMER perhaps follows LUNDBECK (1907) in 
regarding cyaneiventris and flavicornis as a single species. 
In the Edinburgh district, M. polita appears to be a midden 
rather/
rather than a dung-pat breeder.

It is uncertain to what extent the Beris species are cow-
dung species. Both B. vallata and B. fuscipes were found
overwintering in several late season pats, but only in
Argyllshire. Chloromyia formosa was only found on one
occasion in September in Ayrshire. LAURENCE's Hertfordshire
record of this species is also a solitary one (June).

Rhagionidae, Empididae, & Dolichopodidae were never
numerous. Some species are evidently not uncommon in the
medium, but how far it serves as their regular breeding place
is impossible to say.

Appreciable numbers of Phoridae were sometimes bred but
their difficulty (and inadequate literature) prevented their
identification.

CYCLOPORRAPHI

Rhingia macrocephala is the only member of the Syrphidae
found in cow-pats in the present work. LAURENCE records
Syritta pipiens (Linn.) but we have found this only in middens
(cf. MELLOR 1919 and THOMSEN 1938).

The most important families of the Acalypterate series,
as in other lists, are the Sepsidae and Sphaeroceridae.
Rather fewer species were recognised here than are given in
the lists of HAMMER & LAURENCE. Large numbers were known
to escape from the traps on account of their small size and
it is possible that a larger list might have resulted had all
the flies been captured.

Nevertheless, many more of these flies were caught in
1952/
1952 when the traps were all of the larger mesh perforated zinc. A possible cause of the difference between the two years is that many of the 1952 piles were exposed to ovipositing flies for periods of over 48 hrs. whereas few in 1953 exceeded that period of exposure. That this explanation is not quite satisfactory however, is suggested by the failure to record early visiting species such as Pandora scutellaris (Fall.), & Sepsidimorpha pilipes (van der Wulp), among the Sepsids or Coprophila lugubris (Hal.) & Borborillus sordidus (Zett.) among the Sphaerocerids (cf. HAMMER). It is concluded that these families are less abundantly represented in this district than in Denmark, and certainly never achieve the prominence they are recorded as reaching in S. Russia (PORCHINSKII 1910) or Egypt (HAPEZ 1939).

The remaining acalypterate families contain only occasional breeding members but one absentee is worth mention namely the Dryomyzidae. LAURENCE records Dryomyza flaveola (and GRAHAM SMITH 1916) collected it on human dung). BOGDANOV (1901) and PORCHINSKII (1910) found Neuroctena anilis (Fall.) in cow-dung and human-dung, respectively. Both these species are abundant in the Edinburgh district, but were never found in dung.

Among the Cordiluridae, only four species have been recorded previously in cow-droppings, and even these are by no means confined to that medium. Scopeuma stercorarium is evidently much the most abundant of them in Europe, but in North America (Illinois) it is secondary in importance to S. aequalidum/
Squalidum (MOHR 1943). S. squalidum was only rarely observed in the present work. It does not appear in the lists of HAMMER or LAURENCE. The third Scopeuma species, observed by PORCHINSKII (1910) in forest districts only, and by DUFFIELD (1937) in the tundra of Northern Norway, namely S. suillum (Fabr.) was not seen here. A single male of an unidentified species of Scopeuma (subgenus Scatina) was bred. The remaining Cordilurid Phrosia albilabris (Fabr.) of HAMMER's list is apparently not present in Britain.

The fact that the Muscidae were studied more intensively than the other families may account for their greater representation in the list from the point of view of number of species. Nevertheless, apart from this, they do form with the Stratiomyidae and Cordiluridae the most prominent and generally abundant section of the dipterous inhabitants of the biotope.

Problems of recognition and identification have left their contribution in some of the anomalies and errors recorded in the literature. Some of these points merit note and are dealt with under the appropriate genera headings which follow.

Orthellia R - D. (= Cryptoluclilia B. & B., Pseudopyrellia Girschner)

The records of an Orthellia species feeding on and breeding in cow dung are very numerous. In many places it has been recognised as the most important, if not the dominant dipterous member of the community in summer. Among the earlier workers it was almost unanimously held that O. cornicóna was the species concerned, but some more recent workers have also named this species. E.g. PORCHINSKII (1892, 1910), HOWARD (1900), BRUES/
There is little doubt that some of these records are based upon misidentification, and confusion regarding the characters of the species. For example Graham Smith actually figures O. caesarion. Becquart (1922) drew attention to the absence of cornicina from North American collections which at that time were entirely composed of caesarion. The early N. American authors Howard, Brues, Pratt, & Banks must almost certainly have been concerned with caesarion. Mohr (1943) identifies his Illinois species as caesarion. Becquart's view that cornicina is not present in the New World is, nevertheless, contradicted by the recognition by Roberts (1930) of two specimens of cornicina during a survey in which caesarion was observed abundantly.

In Europe also the more recent workers identify the Orthellia of cow-dung as O. caesarion, they include Thomsen & Hammer (1936), Thomsen (1938), Derbeneva-Ukhoa (1940) Zimin (1948) and Laurence (1953).

Hammer questions whether the two species are distinct and emphasises the inconstancy of their distinguishing features. He is quite unsupported in this opinion, but the variability of their diagnostic characters certainly is marked, and may account for the unexpectedly marked difference in their distribution in France and Germany according to Seguy & Karl who state that cornicina is "très commun partout" and "seltener" while caesarion is "besonders häufig" and "assez rare".
HAMMER's alternative hypothesis is that *caesarion* is the normal cattle-dung species while *cornicina* belongs to a different biotope. In this he is supported by the results of DERBENYVA-UKHOVA (1940) who found that although *cornicina* is not common in Kabardino-Balkarsk (N. Caucasus) it is associated exclusively with horse-dung there.

In Midlothian both species were encountered, *caesarion* is the regular cow-dropping species, but *cornicina* occasionally feeds on cow pats. One specimen was actually bred from the medium. The only other record of both species breeding in the one area in cow-dung is that of VAINSHTEIN & RODOVA (1940) in Tadzhikistan (Central Asia). *Q. caesarion* was bred abundantly and exclusively from pats collected in Ayrshire, the district from which MUIRHEAD THOMSON's "cornicina" material originated. It is, therefore, most probable that his very complete account of the larval forms refers to *caesarion*, and the distinction drawn between *caesarion* and *cornicina* larvae by ZIMIN (1951) and HENNING (1952) is invalid, since their comparison uses MUIRHEAD THOMSON's description of "cornicina".

Although the thoracic chaetotaxy is inconstant, little difficulty was experienced in placing the specimens. The two are macroscopically distinct, *cornicina* being larger and bluer than *caesarion*.

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<th>Mean wing length (mm)</th>
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<td><em>Q. cornicina</em> Midlothian Collected</td>
<td>7.2(1) 7.7(3)</td>
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<td><em>Q. caesarion</em> Midlothian Collected</td>
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Figure/
FIGURE 7.
Variation in thoracic chaetotaxy
A - Orthellia caesarion
B - Orthellia cornicina.
Figure 7 indicates the variations (comparable with those noted by Hammer and Becquart) seen in the thoracic bristles.

It is interesting to note that the genus is represented in cow dung by two other species, *O. lucta* (Wied.) and *O. indica* R-D. in Assam (Muirhead Thomson 1947)

*Dasypohora cyanella*

This is a very prominent member of the biocoenose in Midlothian, but there are only two earlier records, both British, of its association with cow-pats, namely, Muirhead Thomson (1937) and Laurence (1953). It appears to be widespread in Britain and was collected in meat-bait traps in 1953 at 22 out of 52 stations distributed between Caithness and Dorset (The results of this survey are summarised in Map I).

In Europe it appears to have a mainly western distribution. Séguy (1923) states that it is quite common throughout France, but it appears not to extend far east from there since Schimer (1862) and Karl (1928) only know of it from the old record of Meigen in the Aachen district. Hammer (1953 - verbal communication) does not know the species; it must, therefore, be absent from or rare in Denmark. Zimin (1951) states that it has not yet been found in the U.S.S.R. although its occurrence is likely in the Caucasus since it is known from Iran. This raises doubt regarding the references by Porchinskii (1892 and 1910) who merely contrasts an oviparous species with the viviparous *D. pratorum* (Meig.) which breeds in cow dung. In 1892 he writes *D. lasiopthalmia*, whose breeding medium he did not know, and in 1910 it is *D. eriopthalmia*. Banks (1912) has obviously/
DASYPHORA CYANELLA

- Not recorded
- Recorded
- Abundant

MAP I
Broken line indicates approximate division between highland and lowland Britain.
obviously misquoted this author.

MUIRHEAD THOMSON repeats the misquotation, and regarding the three names as synonyms takes the species to be *D. cyanella*. More recently, however, ZIMIN has identified in Southern Russia (and 2 specimens from Austria) a species resembling but distinct from *D. cyanella* which he regards as *D. eriophthalma* (Macquart 1833), and which ZETTERSTEDT (1845) apparently recorded in Sweden as *Lucilia lasiophthalma*. (although *lasiophthalma* Macquart 1835 = *cyanella* Meigen). It may be this species, *D. eriophthalma* (Macquart 1833), Zimin 1951 of which PORCHINSKII wrote.

Another related species deserves comment, namely *D. serena* (Meigen 1826, Stein 1916; nec Séguy 1923, nec Karl 1928), Zimin 1951 = *Pyrellia cyanicolor* (Zetterstedt 1845), Séguy 1923, Karl 1928.

PRATT (1912) records this breeding in cow-dung in the U.S.A. (Texas). It is probable that this is an exceptional case, since no other observer has associated this widespread species (the only circumboreal member of the genus) with the medium. The species is generally distributed in France (Séguy) and Germany (Karl), is common in Denmark (Zetterstedt 1845 quoted by HOLMQUIST 1928), and in Russia extends from Murmansk to Kiev and across Asia to Kamchatka (Zimin). In Britain it is quite common in the Highland half, but apparently scarce in the lowland half of the country (The results of the bait-trapping survey of this species are given in map II).

The British distribution is unexpected in view of its occurrence elsewhere and suggests the possibility that this, the/
the European, and the American Fly may not be one species.

Some confusion still remains regarding the generic status of these species. Whereas most authors were agreed on regarding cyanella as a Dasyphora until PATTON & GIBRINS (1934) pointed out that the male abdominal terminalia are of Pyrellia type and accordingly transferred it to that genus, serena was generally included in Pyrellia. ZIMIN (1951) retains cyanella in Dasyphora with which it conforms in all other respects, and places serena in the same genus (van EMden 1952 verbal communication also regards this as a Dasyphora). All the specimens of D. serena collected in the present work bear bristles on the vein r₁ and support the opinion of these two dipterists.

Morellia

This genus contains several regular members of the cow-pat bioocoenose. It is represented by different species in various parts of the world, for example in N. America by M. micans (Macq.) (HOWARD 1901 - MOHR 1943), in Assam by M. hortensia (Wied.) (MUIRHEAD THOMSON 1947) and in Europe by three species M. aenescens (R-D.), M. hortorum, and M. simplex. Of these three the first was not seen in the present investigation and was not recorded by LAURENCE. In Denmark, HAMMER observed it only rarely (in cow-pats) while PORCHINSKII (1910) in Russia, found it only in horse-dung. The other two species have caused some difficulty in the past through their lack of distinguishing characters. For example, LAURENCE attempts no distinction and merely records Morellia as "hortorum or simplex"./
simplex". HAMMER encountered the same problem but discovered significant differences between the size of egg and numbers of eggs in the ovary, although this distinction has little value to the field observer.

ZIMIN (1951) describes a valuable distinguishing character which readily separates both males and females. \textit{M. (Dasysterna)} simplex bears a row of short bristles on the lateral margins of the pro sternum, while \textit{M. (Morellia)} hortorum has this selerite bare.

In the present investigation \textit{simplex} was the common species and \textit{hortorum} was only recognised once (4 specimens) in a Midlothian pat. Only \textit{simplex} was recovered from Ayrshire pats. Similarly, MUIRHEAD THOMSON (1937) identified \textit{simplex} only (males) in his Ayrshire studies.

In his trapping studies in Cambridge, GRAHAM SMITH (1916) recorded all his \textit{Morellia} captures as \textit{hortorum}. He found that it was more readily captured on dung (human) than on small animal carcasses (144:3). Only occasional specimens were caught in the meat-bait trap survey of 1953 and the catch contained: - \textit{hortorum} 13 specimens (46.9\%) and \textit{simplex} 6 specimens (14.5\%). The \textit{simplex} were all captured at Scottish stations. Thus, if GRAHAM SMITH is correct in calling all his material \textit{hortorum}, it may be that this species is commoner in the south, while \textit{simplex} is commoner in the north. (It should be noted, however, that in the Royal Scottish Museum collection the two species are equally well represented from Scottish localities.)

\textit{Pseudophaonia hirtiorum}
PSEUDOPHAONIA HIRTICRURA

p  Previous records
+  Bred from dung
●  Present in bait trap
○  Not in bait trap
Pseudophacelia hirticincta

Since the original discovery in Yorkshire by MEADE (1887) of a male of this species there have not been many records of the occurrence of this species. It remained unknown elsewhere until VERRALL (in GRIMSHAW 1901) found it in Ayrshire. The female was first described from a specimen from Arran by WATERSTON (1906). CARTER (1919) states that his record from Perthshire is only the second female record. Although it was known already from several localities (1) it was believed to be rare until MUIRHEAD THOMSON (1937) found it in fair quantities as a cow-pat breeder in Ayrshire. It was found in the present studies to be a common breeder in cow-pats in Midlothian and Argyll as well as Ayrshire. For example, 15 out of 30 pats in Midlothian in June 1953 were infested.

The species has not yet been recorded from any country other than Britain, and here it appears to be confined to the north. (It is absent from the Hertfordshire list of LAURENCE). The species is occasionally attracted to carcasses, and was recovered from some meat-bait trap stations. Its distribution identified from these and previous records, is shown in map 3.

Hydrotaea

The published keys are not entirely satisfactory for the identification of females of the genus Hydrotaea. Assistance from Dr. van Enden who confirmed their identification is, therefore, gratefully acknowledged.

Six/

(1) There are specimens in the Royal Scottish Museum, Edinburgh from Dunbartonshire (Malloch), Sutherland (Yerbury), and Midlothian, and in the King Collection, Glasgow University (MUIRHEAD THOMSON) from Inverness-shire.
Six *Hydrotaea* species were bred from cow-pats in the present work, but only one of them *H. albipuncta* is common to this and the lists of Hammer, and Laurence (and of Thomsen 1938). In Scotland it is the commonest *Hydrotaea*-species in the biotope and from the accounts of the authors concerned it is evidently common in England and Denmark. Outside these countries, it has not been recorded in cow-dung by any other observer. In Germany and France, however, it is stated to be uncommon or even rare (Karl, Seguy) and it is apparently absent from North America. In contrast to this distribution, *H. militaris* does not appear in any of the lists mentioned, although Seguy states it to be common in France, and in Germany it is widespread according to Karl. In Scotland it is well represented, and although it has a shorter active season it is probably no less abundant than the previous species.

Of the other four species *H. meteorica* was occasional, but *H. occulta*, *H. armipes* and *H. irritans* (Argyll only) were merely bred on one or two occasions. They were all, except *occulta* recorded by Hammer, but Laurence has none of them. Thomsen (1938) found *H. armipes* breeding in horse- and calf-dung in middens and Hammer states that it does not belong to the true dropping community. It is probable that some others of the numerous records refer to accumulated dung rather than to fresh droppings, for example those of Bogdanov (1901) and Howard (1901).

Nevertheless, as a true cow-dropping breeder it is the most widely recorded species of the genus, and is in fact the only one recorded hitherto in N. America (1) (Mohr, 1943) and Russia (Porokinskiy).

(1) It is probable that further studies in N. America will reveal other *Hydrotaea* species in cow-dung. Leonard (1928) records *tuberculata, occulta, militaris* and *meteorica* in the New York List.
(PORCHINSKII, 1910). (The latter author also found it in horse droppings in the field).

In view of its scarcity in cow-pats, there can be little doubt that H. irritans must belong normally to another biotope, at least in this area. Séguy (1923) states that it breeds in the excrement of domestic animals, and Karl (1928) repeats this statement. They give no evidence, however. In Midlothian it was not encountered in pig, sheep, or horse-droppings, and did not occur in middens. Thomsen (1938) does not describe its breeding habits. Unfortunately, Hammer does not indicate how frequently he found the species in cow-pats but he states "... H. irritans is not strictly confined to this biotope, but presumably develops also in others, e.g. in the manure and runs of small wild animals, or in decaying vegetable matter in which other fly larvae live." It is an abundant species everywhere in Britain and probably throughout much of Europe. It seems safe to conclude, therefore, that its breeding habits have yet to be identified.

Two species included in Hammer's list, namely H. velutina Rob. -Desv., and H. tuberculata Rond. were not seen in Scotland, and it is presumed that they are rare or absent here.

Grimshaw (1905) states the first of these is very rare in Britain, and his records of the second are all from Southern localities. This is of interest, since H. tuberculata was bred in the present work from pats obtained near Winchester, (Hampshire), and it is the only species other than albipuncta which appears in Laurence's (Hertfordshire) list. This species/
species probably has a fairly wide southern distribution in Britain. (Further south, it is rare in France according to Séguy).

Around buildings, and breeding in middens *F. dentipes* (Fabr.) is the typical member of the species. It has been recorded elsewhere by many workers, e.g. Forchinskij (1910 & 1911), MELLOR (1919) and THOMSEN (1933) and apparently never occurs outside this biotope.

The *Hydrotæa* species, with the exception of *arsipes*, have some economic importance. Adults of all the other species mentioned were collected from cattle. HAMMER also failed to find *arsipes* on cattle but he observed it on occasion as a pest of man.

**Fannia**

As in the foregoing, the females of this genus are difficult to distinguish, and it was necessary to seek the assistance of Dr. van Enden for confirmation of some determinations.

HAMMER merely refers to *Fannia* sp. and names no species. He does not indicate whether one or more species were encountered and records them as only occasional or accidental visitors. LAURENCE makes no reference to the genus. There is a paucity of evidence concerning this genus among the other authors to whom reference has been made, except in regard to midden breeders.

*F. mutica* in Scotland is a regular and typical member of the biocoenose and was present in upwards of 50% of the plots studied in summer, and it was never observed breeding outside this...
this biotope. *F. canicularis*, a well known midden fly occurred occasionally in cow-pats. It is, however, apparently attracted to older pats, since it was only bred in 1952 when some pats were exposed to ovipositing flies for periods of one week. The other species mentioned, namely *armata*, *monilis* and *serena* were only found on one or two occasions, and probably belong to some other biotope.

In middens the usual three species *canicularis*, *scalaris* (Fabr.) and *manicata* were frequently observed.

**Hebecnema**

Various species of this genus are associated with cow-pats in different parts of the world. The common species *umbra* bred in Scotland, although not particularly abundant has a frequency in pats of nearly 100% during its active season. It has a holarctic distribution and has been recorded by most students of the biotope. HAMMER also reports it as a frequent but not abundant species. It is not, however, confined to this biotope, but was bred from sheep dung and middens in this investigation, and has been recorded in middens by many other authors.

Of the other European species, *vespertina* (Fall.) has been recorded by the Russian workers Bogdanov (1901) and Porchinskii (1910) but, in spite of its wide distribution, not apparently elsewhere. (Since their records, however, Bazzi (1922) has shown that *vespertina* before 1920 also included *affinis* Malloch).

In the autumn of 1953 several specimens of *H. nigricolor* were bred from pats dropped between 5. x. and 13. xi. This species/
species appears not to have been recorded previously from the medium.

BEZZI in his review of the distribution of the genus (the same 5 species as in Britain) in Italy gives only the breeding habit of umbatica (cow-dung and manure).

In Assam MUIRHEAD THOMSON (1947) records H. nigrithorax Stein.

**Mydaea**

HAMMER includes two Mydaea species in his list, namely **urbana** and **pagana**, but he gives no indication as to their relative frequency. They were, he states, observed only a few times on the surface of droppings, but their avoidance of bright sunshine may account for this. (Both species extend far north into Swedish Lapland (RINGDAHL 1931)). It is not clear from HAMMER's account, however, whether he did actually observe pagana on droppings, since he states elsewhere (p. 100), "Mydaea urbana (and presumably also M. pagana) soon arrives at the fresh droppings". Since they are readily distinguishable species in the field his presumably cannot imply that they would be recorded together, as, for example, would be Morellia spp., but evidently means that actual observations were not made.

In Midlothian no evidence was found to suggest that pagana is a member of the cow-dung biocoenose although urbana is frequent there. **M. pagana** was never bred in the present investigation from cow pats (Midlothian, Ayrshire, Argyllshire & Hampshire), and only one specimen, a male, was ever seen on a cow pat. Nevertheless, the species is common in Midlothian and/
and was regularly observed resting on bushes. LAURENCE did not breed it from pats in Hertfordshire, and MUIRHEAD THOMSON (1937) found it to be rare in Ayrshire pats. On the other hand this author found it more commonly in the Island of Arran. Although he succeeded in raising larvae of the species in cow-dung for his anatomical studies it is not definite from his account whether the fly was actually breeding in that medium in the field. If it was, then in Scotland, it seems that the species must vary in habit according to the locality in which it lives.

**Hylemya**

The two species *strenua* R. D. (*= strigosa* Fabr.) and *variata* are recorded in the HAMMER and LAURENCE lists and are evidently widespread (PORCHINSKI (1910) found the first in human- and horse-dung as well as cow). The species *nigrimana* (Meig.) which is very similar to *strenua* was trapped in suction traps in Midlothian. It may be included in the present observations in the *strenua* record but its presence in cow-pats was not positively confirmed. HAMMER notes the possibility that his record embraced the two species under one heading (*strigosa*) and refers to the opinion of RINGDAHL (1933) that the two may merely be varieties of a single species.

On the other hand, the record of *variata* in the present work definitely includes both *variata* (Fall) and *variabilis* Stein. The male hypopygia of these specimens do not agree well with the rather diagrammatic figures given by KARL (1928). They bear a similar relationship however. That of *variata* agrees with the figure of SCHNABEL & DZIDZICKI (1911) and is shown together with/
FIGURE 8.
Male terminalia
A - Hylemya variata
B - Hylemya variabilis.
with variabilis in figure 8. The lack of distinction between the females of these species compelled their joint treatment.

NOTE

Musca autumnalis Degeer and Lyperosia irritans (Linn.), two species of economic importance, which are prominent members of the cow-dropping community elsewhere were never observed in this investigation. They are presumed to be very rare or absent from the Scottish Fauna (Vide infra).

TAXONOMIC LITERATURE

The nomenclature of Kloet & HINCKS (1945) is employed throughout, with the exception of those few cases where a contrary indication is given.

In addition to the works already quoted, the following were consulted for identification purposes:

Diptera (General) OLDROYD (1949), and CURRAN (1934);
Tipulidae and Trichoceridae (COE) and Anisopodidae (FREEMAN) in COE, FREEMAN & MATTINGLEY (1950); Ceratopogonidae EDWARDS (1926) and DOWNES & KETTLE (1952); Bibionidae and Scatopsidae EDWARDS (1925); Stratiomyidae LUNDBECK (1907); Empididae LUNDBECK (1910) and COLLIN (1926-27); Dolichopodidae LUNDBECK (1912) and PARENT (1938); Lonchopteridae COLLIN (1938); Syrphidae LUNDBECK (1916) and COE (1953); Acalyptera SEUBY (1934); Sapromyzidae COLLIN (1948);
Helomyzidae COLLIN (1943); Opomyzidae COLLIN (1945); Sepsidae GOETGHEBUE & BASTIN (1925) and DUDA (1925); Sphaeroceridae RICHARDS (1930); Larvaeororidae and Calliphoridae DAY (1948); and Muscidae (Fannia) MALLOCH (1912) and COLLIN (1939), & (Hydrotaea) RINGDAHL (1925).
PART III: LIFE HISTORIES OF THE DIPTERA.

1. General features

Apart from scattered information given by MUIRHEAD THOMSON (1937) and MOHR (1943), the only attempt to describe the time relations and succession of generations of the dipterous species of the cow-pat biocoenose is that of HAMMER (1941).

HAMMER based his conclusions mainly on a study of the surface populations and their seasonal incidence. He supplemented his information by observations on developmental rates under laboratory conditions, and states "Knowing the time of development at constant temperatures in the laboratory it is found possible to estimate fairly correctly the time of development in the field, provided that the maximum and minimum temperatures of the places where the larvae live are known".

This procedure contains two serious disadvantages. First, for most species the curve of seasonal incidence consists of a series of peaks and troughs which are the immediate result of climatic variations, but which form broadly what HAMMER terms "an even one-peaked curve". Against this background the component curves representing the rise and fall of successive generations are not readily recognised. Occasionally a key is provided by periodic variations in the abundance of males, e.g. in Musca autumnalis, or in other species when the individuals change their appearance as they age e.g. Orthellia caesarion and Dasyphora cyanella. These are bright metallic green flies when newly-emerged but they change to a duller red-copper colour as they age. Secondly, extrapolation of curves relating developmental/
developmental rates to temperature can be misleading since simple relations which apparently obtain over the medial temperature range are sometimes inapplicable at lower temperatures (KROGH, 1914, SHELFORD, 1918, BĚLEHRÁDEK, 1930 & 1935), and simple extrapolation from laboratory-derived results ignores the possibility of the intervention of diapause phenomena. From the results obtained in Midlothian it seems certain that this last is the most important source of error in HAMMER'S method.

Very few of the species of this community have been studied under controlled temperature conditions, and the data of BRO LARSEN & THOMSEN (1940) appears to be the only published information. They refer only to H. stimulans, L. irritans, and S. stercorarium of the biotope proper, but they compare these with the related saprophagous species Stomoxys calcitrans and Musca domestica. KOBAYASHI & MIZUSHIMA (1937) also studied M. domestica together with two saprophages Muscina stabulans and a Sarcoptes sp. The Danish authors applied the exponential formula of JANISCH (1932), but found a linear relationship between temperature and reciprocal of time (cf. PHAIRS, 1927,) to provide a satisfactory interpretation of their data. The Japanese workers applied the formula for the empirical hyperbola of BĚLEHRÁDEK (1926) \( (\text{Time} = \text{Constant} / (\text{temperature})^b) \) but the value of \( b \) in all their examples is so close to unity that their results also may be regarded as satisfactorily representing a linear relationship. For all these species, therefore, the rule of thermal summation is applicable over the medial temperature.
temperature range at least, and the calculated "thresholds" are:

<table>
<thead>
<tr>
<th>Species</th>
<th>BRO LARSEN et al.</th>
<th>MIZUSHIMA et al.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lyperosia irritans</td>
<td>12.9°C</td>
<td></td>
</tr>
<tr>
<td>Stomoxys calcitrans</td>
<td>12.3°C</td>
<td></td>
</tr>
<tr>
<td>Musca domestica</td>
<td>12.2°C</td>
<td>12.1°C</td>
</tr>
<tr>
<td>Haematobia stimulana</td>
<td>10.7°C</td>
<td></td>
</tr>
<tr>
<td>Sarcophaga sp.</td>
<td></td>
<td>8°C</td>
</tr>
<tr>
<td>Muscina stabulans</td>
<td></td>
<td>5°C</td>
</tr>
<tr>
<td>Scopeuma stercorarium</td>
<td>2.1°C</td>
<td></td>
</tr>
</tbody>
</table>

Now it is somewhat surprising that the difference in developmental threshold between two species of the same biotope should be as great as that shown between the results for Scopeuma and Haematobia (or Lyperosia) particularly since they do not show very marked differences in their developmental rates under field conditions. Using data collected in the field in Midlothian and utilising a check point at 23°C the "thresholds" obtained assuming a linear relationship were much lower, and lay within a much smaller range, thus:

- Scopeuma: 2.0 - 2.5°C
- Dasyphora: 2.0 - 4.5°C
- Mesembrina: 4.0 - 4.5°C
- Orthellia: 6.5°C
- Haematobia: 6.5°C

(It is interesting to note that PEAIRS (1927) also found a linear temperature relationship for development of Musca domestica, but his "threshold" (c 7°C) was much lower than that/
that of the Danish and Japanese authors.)

It is apparent, therefore, that laboratory data, even in the absence of diapause phenomena, can fail to provide a sound clue to field phenomena.

HAMMER concluded that with few exceptions the diptera of the biocenose are multivoltine with 4 or 5 generations per annum. His exceptions include Morellia bortorum with 3 generations, 3 bivoltine species, Polistes lardaria, Rhingia, & Microchrysa flavicornis, and one univoltine species Geosargus flavipes. The field observations in the present work lead to conclusions which are in disagreement with HAMMER's in nearly all cases.

Considering the range of variety of individual characteristics and of the environmental factors which influence them, it might be expected that the different species would show considerable differences between their developmental time relations. The fauna includes purely saprophagous species such as Eapyphora, Orthellia, Morellia, Haematobia, Hylomyia spp, Fannia spp, Anisopus, Stratophyidae, etc., and species such as Hydraetae spp, Mydaea urbana, Hyospila, Hebeconema, in which the third stage larva is an obligate carnivore. Carnivorous species tend to vary in their developmental rates to a greater degree than saprophages, through the limiting factor of food availability.

Some species, e.g. Mesembrina meridiana, Pseudophania hirticrura (Muirhead Thomson, 1937), and Polistes lardaria (Séguy, 1923) have been described as facultative carnivores. Ksulin (1915, 1917) has demonstrated the anatomical characters which/
which distinguish carnivorous from saprophagous muscid larvae, namely the presence of ventral pharyngeal ridges in saprophages, and of accessory oral sclerites (median ventral arc, oral bars and anterior and posterior ribbons) and unequal lateral hooks in carnivores. A combination of these characters is found in *R. hirticrura* (MUIRHEAD THOMSON), and *R. lardaria* & *Mesembrina* (KEILIN & TATE, 1930) and thus supports the suggestion that they can live both as saprophages and as carnivores. HAMMER (1941) is of the opinion that in the last two species carnivorism is unusual, a view which is confirmed by the present study. *R. hirticrura* on the other hand appears to behave as a zoophage more frequently.

The patterns of life-cycle vary from typical oviparous species such as *Dasyphora*, *Orthellia*, *Haematobia*, etc., with three larval instars to larviparous ones such as *Hylemyx a variata* and *stremona* which deposit late first instar larvae, through an intermediate form such as *Mesembrina* whose egg contains a fully developed larva. Some species exhibit a 'condensed' cycle in which the first instar is suppressed, e.g. *Hebeconema*, *Myospila* and *Mydaea*. In general, however, the variation in length of the total life cycle due to such differences as these is not of great importance since the egg and larval stages are short in comparison with the pupal stage.

Where species exhibit marked sun- (e.g. *Orthellia*, etc.) or shade-preferences (e.g. *Haematobia*, *Aselia*, *Hylemyx* spp. etc.) their larval environments will be warmer or cooler according to the amount of insolation they enjoy, and their developmental periods/
periods will have a general tendency to be correspondingly longer or shorter.

Notwithstanding the possible variations described, in general the duration of preimaginal development in the cow-pat in the early part of the year is short and remarkably close for a large number of the species. The remainder show great diversity, some are slow, some are extremely variable, and some require to pass a winter before they complete development. The population contains the following classes:

a) Development uniformly rapid:
   - Orthellia, Haematobia, Hebeconema, Hylemyza spp., Scopeuma

b) Development rather less rapid:
   - Myospila, Mesembrina, Morellia, Anisopus

c) Development uniform but slow:
   - Dasyphora

d) Development very variable, moderate to very slow:
   - P. hirticrura, H. albipunica, F. mutica

e) Development completed only after winter:
   - P. lardaria, H. militaris, Stratiomyidae

The last of these groups contains species in which a diapause occurs in every generation, and in which every generation passes the winter, i.e. species with a univoltine life cycle. It will be shown later that Dasyphora is also a univoltine species. The other three groups contain species which are multivoltine, but they also exhibit diapause phenomena in varying degrees. These species vary in the intensity as well as in time of incidence of their diapause, but with few exceptions they are destined for after all, in diapause, by the middle of August. In 1952 no individuals of/
of any species completed their development from eggs laid on or after 6th August, while in 1953 only 2 individuals of *Hebecnema umbratica* and a few *Anisopus punctatus* completed their development in the same year from eggs laid on or after 14th August.

To save unnecessary repetition it is proposed to describe the life history of certain of the multivoltine species (*Hebecnema* and *Scopeuma*) individually and to deal with the remainder together. The principal univoltine species (*P. lardaria* and *D. cyanella*) will be individually treated, and the remainder together.

It would be impracticable to give the detailed results of the emergence of the different species in the field and the data are, therefore, presented graphically (vide figs. 9, 11, 14 etc.). Each series includes the pats dropped on the given date, and contains 6 pats in all but 3 cases in 1953, those of 18.5, 24.5, and 13.7, which contain only 4.

The population of each species is summed for each series, and its daily adult emergence represented as a histogram. Each series is placed upon its own baseline, beginning at the arrow which indicated the date of pat deposition. Where the baseline is extended beyond the histogram as an interrupted line it indicated the presence of individuals in diapause which do not emerge until the following year. In the case of *Scopeuma* the numbers of individuals per pat reach such levels that it is necessary to express the emergence as means/pat and not totals/series.

2. *Hebecnema umbratica* Mg.
In spite of its appearance in the lists of earlier workers, the biology of this species in nature has received comparatively little attention. Porchinskiy (1910) suspected the larva of being carnivorous and this was confirmed by Muirhead Thomson (1937), who described the larval stages and eggs in great detail. The adults are small inconspicuous flies which although they are never abundant are the most frequent visitors to cow-pats in the Midlothian area. Between May and October there were very few cow-pats studied which were not infested. Thus, for example, from 2nd May when the first pats were infested in 1953, until 31st October when the last pats were infested, 112 out of 126 pats (89%) contained Hebeonema-larvae.

Muirhead Thomson records a comparable degree of frequency in Ayrshire, and states that "males and females can be seen on nearly every dung-cake during summer from June until September..."

In Midlothian, however, males were only rarely seen on or collected from dung-pats; a feature which was also noted by Hammer (1941) who presumes that the males feed on nectar. Seguy (1923) quotes Bezzi (1922) who states that this fly alights on mammals to suck blood from wounds left by stomoxydine and tabanid flies. Karl (1928) makes literally the same statement but cites no authority. Observations here confirm Hammer's opinion that these statements are erroneous. Females were regularly seen feeding on dung but were never seen on or collected among samples of flies from cattle or horses.

This species is not confined to the cow-dung biotope, but breeds frequently in sheep-droppings and in dung in middens. In common with other flies (e.g. Myospila) which can use different/
different breeding media, Helycorma shows less discrimination in its association with cow-pats. Whereas obligate cow-pat breeders (e.g., Haematobia, Artharia casearia) are restricted to pats of a definite age and oviposit only over a very limited period, Helycorma will oviposit readily on pats up to 48 hours old, and sometimes on even older ones. MURHEAD THOMSON even considered it to occur most abundantly on dung a day or two old. HAMMER, on the contrary found the maximum incidence within 10 minutes of dropping of the pat. The Midlothian results are in agreement with the second rather than the first of these authors, although the pattern of pat-incidence was never so well defined here as HAMMER found it in Denmark.

Undoubtedly the greater part of oviposition occurs on pats within the first 24 hours after their deposition, and very little takes place after 48 hours. The results in 1952 suggested that a substantial part of the infestation derives from eggs laid on the second day, but this was not confirmed in 1953 when a much larger series was examined with little difference in numbers of adults emerging from day old and 2 day old pats. Thus we have

<table>
<thead>
<tr>
<th>Pats exposed 24 hours</th>
<th>Pats exposed 48 hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>Mean Flies/Fat</td>
</tr>
<tr>
<td>1952</td>
<td>7</td>
</tr>
<tr>
<td>1953</td>
<td>28</td>
</tr>
</tbody>
</table>

The diapause-point in the life-cycle of this species is the white-eyed pupa, and it is in this stage that it overwinters. Development is resumed in spring, and adult flies emerge during May. In 1953 the period of emergence of overwintered flies
in cone-traps ranged from 15th May to 5th June and oviposition was in full course by 24th May. Occasional pats were infested before this date; one dropped as early as 2nd May produced 3 flies, and some flies were actually observed on 6th May. Although it is apparent that flies emerged earlier than the population in the traps, in general it is probable that its emergence took place contemporaneously with the bulk of emergence of the wild population. From 24th May onwards the level of pat-infestation fluctuated irregularly such that no clear pattern of variation was evident. No break in the course of infestation was recognised between this date and the end of October. Population density in the pats, therefore, provided no clue to the time limits of the overlapping generations.

Pats infested in June and July, which produced populations with an interrupted course of development contained rather fewer individuals than those dropped in the period August-September when the whole population entered diapause at the appropriate point. Compare for example:-

<table>
<thead>
<tr>
<th>Number of Pats producing</th>
<th>Nil</th>
<th>1-10</th>
<th>11-20</th>
<th>21+</th>
<th>flies per pat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dropped June</td>
<td>2</td>
<td>20</td>
<td>7</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>1</td>
<td>19</td>
<td>10</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>August/ October</td>
<td>1</td>
<td>10</td>
<td>9</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

About 84% of the pats, therefore, produced from 1-20 Hebecnema-adults and of these about two thirds produced less than 10 flies. While these numbers are small in comparison with some other diptera of the community (e.g. Scopeluma, Stratiomyidae, /
FIGURE 9.
*Hebecnema umbratica* - Adult emergence in field.
Stratiomyidae, Anisopus, etc.), they are, nevertheless, greater than those of any other muscid fly in spite of the inconspicuous part they play in the surface community. No more than 5-6 adults were ever observed at one time on a dropping but HAMMER records up to 22 exceptionally. The largest emergence from single pats were 95, 47, 35, 30, 29, 28, 28, etc. The species is evidently a successful one which suffers a comparatively low mortality rate among the Muscidae in its preimaginal instars. Figure 9 records the emergence of adults from the successive series of pats placed under cone-traps in 1953. The emergence of the 1st (overwintered) generation has been mentioned above. The earliest emergence of second generation adults took place in the cone-traps on 26th June, and it is not likely that this generation could have begun to appear much earlier. It is probable, therefore, that the 5 series of pats infested between 24th May and 22nd June inclusive contained the progeny of the first generation only. Now, the pattern of emergence of the second generation adults from these successive series shows a notable trend. Thus, in the 1st series dropped 24th May, adult emergence extended over 13 days (from 26.6 to 8.7). In the next three series the length of the emergence period is more or less the same, but in the 4th series dropped 7th June, although emergence was spread over only 15 days (from 13.7 - 27.7) the distribution did not show so distinct a mode as the earlier ones. The 5th series, dropped 22nd June, however, gave an emergence pattern of quite a different type from the earlier ones. The emergence period extended over an interval of 34 days (22.7 - 24.8) in spite of the warmer conditions over this period, and not only/
only did the distribution show a bimodal tendency, but the population median lay within the later half (i.e. skewness was in the reverse direction to that of earlier series).

The 6th series, dropped 29th June, showed a return to the earlier pattern, with emergence spread over 15 days (except for 2 isolated individuals) from 26th July to 10th August and with the normal left-skewed distribution. The date of dropping of this series is several days later than the emergence of 2nd generation individuals and it is possible and indeed probable that the bulk of its infestation represents the first part of the 3rd generation. In this series the phenomenon of diapause appears for the first time, a small number of individuals failing to complete development beyond the pupal stage. Their viability was confirmed after their transfer to the laboratory in December. Diapausing individuals formed a progressively larger proportion of the population in the later series of pests until on 14th August and thereafter to 10th October, when the latest eggs were laid, the whole population was in diapause. (Diapause in this as well as the other species is discussed separately in Section 9 later). It is not possible to recognise so clearly the occurrence of a trend in the later series comparable to that described for the first six. It may be, however, that there is a difference between the series of 26th July and 7th August indicating a possible fourth generation appearing on the later date. The succession of generations may therefore be summarised as follows:-

Generation 1/
<table>
<thead>
<tr>
<th>Generation 1 (overwintered)</th>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early May - 5th June</td>
<td>Mid May - 22nd June (and possibly with remnants) on 29th June</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Generation 2</th>
<th>26th June - 24th Aug.</th>
<th>29th June - (?)</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Generation 3</th>
<th>26th July - 20th Sep.</th>
<th>29th July (?) - (?) or 7th Aug. - 10th Oct.</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Generation 4 (? or 11th Sep.)</th>
<th>27th Aug. (?) or 25th Sep.</th>
<th>10th Oct.</th>
</tr>
</thead>
</table>

It is impossible to recognise which generation gives rise to the diapausing individuals in any given series. Certainly the later series must in many cases contain populations of mixed composition as regards generations. The limits of oviposition activity suggested are, therefore, only approximate and arbitrary. The diapausing individuals of the series dropped on 29th June might be the progeny of the first generation in which case we should have a small part of the population behaving as a univoltine species. Further work would be necessary to decide upon this point, however. Nevertheless the population contains proportions whose life cycle definitely varies from bivoltine to three-voltine and probably also four-voltine.

HAMMER's interpretation of his observations on the appearance of adults in the surface populations is in substantial agreement with the present findings. He identified three main generations appearing respectively in early May, early July, and early August and a small fourth generation in early September. His results, however, do not contain evidence (apart from the third-fourth succession) to suggest that in Denmark each generation of adults represents only a part of the progeny of its predecessor.
3. **Scopeuma stercorarium** L. ("The Yellow Dung Fly")

REAUMUR (1736) made the first contribution, a remarkable one in its detail and accuracy, to the biology of this widely distributed species. It has received attention from many later authors in various parts of the world, who have recorded it as breeding on a range of materials including many types of dung and manure, or even (MAXWELL LEFROY in COTTERELL 1920) sludge in septic tanks. In Midlothian it has been found breeding in cow-, horse-, and sheep-dung, in middens, and in a pig wallow. In its larval stages it is entirely saprophagous (HANDSCHIN (1934) is in error in supposing it to be carnivorous) while in the adult state it feeds on nectar, and as a blood-sucking predator of other insects.

The predatory habit of the adult has been referred to by many authors, including inter alia KIRBY & SPENCE (1828), SCHINER (1864), POULTON (1906) HEWITT (1914), HOBBY (1931), and HAMMER (1941), and a large list is recorded of species which can fall victim. A change in behaviour from blood- to nectar-sucking has been shown from the laboratory work of COTTERELL (1920), who has described the blood-sucking process in detail, and BRO LARSEN & THOMSEN (1940) to be associated with sexual maturity. AUSTEN (1921) summarises earlier evidence and concludes that small flies are the commonest victims. He criticises severely the view of MAXWELL LEFROY that Calliphora is so regularly attacked that Scopeuma activity may provide a "possible blow-fly control". In the present investigation, it has been seen attaching most of the dipterous species of the cow-pat community.
Its attacks are most readily seen on flies visiting the pats to feed or oviposit, but it has been observed on bushes and other vegetation, and it attacks newly-emerged flies (Anisopus punctatus in particular) in the cone traps, i.e. when it is less than 24 hours old.

There is little evidence to suggest that Scopeuma is selective of its prey, but rather that it is indiscriminate and attacks whatever species presents itself. Even so large a fly as Mesembrina meridiana may be attacked although rarely if ever with success (cf. also HAMMER). In the early part of the season Borboridae and Dasyphora cyanella are the chief victims, but as the composition of the dung community changes with the season so the variety of prey is altered. After the earliest phase Anisopodidae, Bibionidae, Scatopsidae, Mycetophilidae, and Muscidae contribute in varying degrees to the diet. In the late season such large species as Polistes lardaria and Pseudophasia hirticrura are regularly attacked. BARAUD (1923) and MYERS (1938) claim that Scopeuma does not hunt its prey, but awaits it at the dung-pat. While this is probably usual in the high season when prey is abundant, a different type of behaviour was observed in the early spring in Midlothian. In 1953 the cattle were not out until 25th April and before that date when dung was not available Scopeuma was regularly observed on ivy and rhododendrons, hunting and feeding upon Dasyphora cyanella which frequented those situations in the course of their mating behaviour.

The yellow dung fly is the first of the larger flies to make/
make its appearance at the beginning of the season, and is one of the latest to disappear at the end of the year. During summer there is a period when it is extremely scarce, although in spring and autumn it is the most abundant and conspicuous species of the biocoenose. Evidence of a summer decline has been noted by Bogdanov (1901) in Russia, Graham-Smith (1916) in England, Thomsen (1938) in Denmark, and Mohr (1943) in the U.S.A., who also records a similar seasonal pattern in the related species S. squalidum (Mg.). Closer attention to the phenomenon was paid by the Danish workers Bro Larsen & Thomsen (1940) who emphasise the absence of evidence of a diapause associated with high temperature (a preimaginal diapause is presumably meant), and by Hammer (1941). The former workers conclude that the summer decline is explicable simply by the fact that the species has a low tolerance of temperatures in excess of 25°C, and that the mortality (of pupae in particular) is increased during the heat of summer. Hammer recognises that the biotope is not continuously subjected to high temperature but suggests the possibility of a cumulative lethal effect of exposure to supra-optimal temperatures on successive days, such as Nash (1936) described for Glossina submorsitans Newst., and G. tachinoides Westw. He concludes that although a number of successive generations occurs during the year the numerical dimensions of these are influenced by climatic conditions, such that high summer temperatures are lethal to a large proportion of newly emerged larvae and adults.
Other factors can be envisaged which might produce or contribute to a marked reduction in size of the summer generation, for example, infection by the fungus *Empusa muscae* (cf. HOBBY & ELTON 1935 and HAMMER) or the activity of predators or parasites. No evidence was obtained in the present investigation of infection by fungi or infestation by parasites which would account for the summer decline in 1952 and 1953. 

*Scopeuma* eggs fall victim in large numbers to the Staphylinid *Philonthus marginatus* (Fabr.) but the activity of this beetle is not confined to summer and even appears to be greater in autumn.

Nevertheless, whatever the cause, a material reduction in numbers of the summer generation implies a build-up of the population after the removal of the restricting factor in autumn. In view of the very considerable difference between the numbers seen in summer and autumn this build-up can only be envisaged through the occurrence of more than one generation after summer. GOTTRELL (1920) estimates a probable succession of five generations for the whole season, but his estimate is evidently based on laboratory observations, since he was apparently unaware of any decline in summer, and states that "breeding takes place regularly from April to October".

HAMMER bases his interpretation of the seasonal appearance upon an estimated succession of five generations, although his data do not contain evidence of their occurrence, and concludes that the fourth and fifth generations together comprise the autumn culmination.

Theories/
Theories which seek to base the summer decline upon an actual reduction in fly numbers are inapplicable to the phenomena observed in Scotland in 1952 and 1953 since there was no evidence for the uninterrupted succession of generations which they presuppose.

Flies were first observed on the wing in 1953 in mid-March, and by mid-April they were common. In cone-traps the peak period of emergence of the overwintered generation was late-March and early April. The length of the preoviposition period could not be ascertained since dung-pats were not available for oviposition until late April when the cattle were first turned out to graze. By this time a considerable part of the female population was gravid; the first pats collected (25th April) were the most heavily infested of the early part of the year.

Nine pats dropped on 25th April produced from 165 to 495 flies per pat, the mean being 246 ± 33. From that date the rate of infestation gradually declined so that by 12th June a series of pats produced 16 ± 88 flies. Throughout June the level of infestation of all pats remained at a very low level until on 29th June some pats again contained very large numbers. With a range of 7 to 552 the mean of six pats was 146 ± 81. Thereafter, the infestation level declined rapidly so that with very few exceptions the cow-pats dropped between early August and early October were quite devoid of *Sceoperna* larvae.

From early October until late November pats were again heavily infested, and some contained even larger numbers than the most heavily infested spring ones. (612 flies were bred from one pat/)

*Standard error (± σ/√n)*
The seasonal variation in infestation levels in 1952 differed from this in two respects, namely, the smaller peak of late June 1953 was not recognised in that year, and the autumn oviposition phase began earlier.

From the 1953 pats, adult flies emerged during the period 6.vi to 20.viii, and corresponding with the bimodal course of the infestation levels there was a bimodal emergence pattern. The course of infestation and of adult emergence throughout the year are shown diagramatically in figures 10 and 11 respectively. It is apparent from the figures that the second phase of infestation (beginning 29th June) follows the first phase of emergence (beginning 5th June) after an interval of from 2 to 3 weeks (compare overwintered generation where it was within 4 weeks, late March to 25th April, which compares with the times quoted by Cotterell(1920) and Bro Larsen & Thomsen(1940) as the preoviposition period. This second phase of emergence evidently represents the progeny of the first, and its completion terminates adult emergence for the year. We thus have evidence of three generations, and no suggestion of one or more autumn emergences representing the fourth and fifth generations of Hammer's (1941) hypothesis.

From this it follows that the ovipositing generation of autumn must have passed the late summer period in the adult instar, and must have emerged before the end of August. It appears unlikely, however, that this autumn population could have been composed solely of third generation individuals.

The third generation was notably smaller than either the first (overwintered)/
FIGURE 10.
_Scopeuma stercorarium_- Seasonal course of infestation of pats.
FIGURE 11.
Scopeuma stercorarium - Adult emergence in field.
(overwintered) or second and it is doubtful whether it represents the whole progeny of the second or that it is large enough to account for the abundance of flies observed in autumn. It is, therefore, assumed that the second generation in part matured without delay to produce the third, while in the remainder of the second, and in the third generation, sexual maturity was delayed so that oviposition did not take place until October. On the other hand in 1952 the third generation was not recognised; the autumn ovipositing generation must therefore have been composed entirely of second generation flies.

It is of interest to note that the frequency of pat infestation by the progeny of Generation 1 is greater than that found with the early summer progeny of Generation 2, and consequently the coefficient of variation is greater in the second than in the first phase of infestation.

Compare for example the coefficient of variation at the peak periods:

<table>
<thead>
<tr>
<th>Progeny of Generation</th>
<th>Date of Pats</th>
<th>Mean Infestation</th>
<th>S.D.</th>
<th>Coeff. of Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation 1</td>
<td>25 April</td>
<td>24.6</td>
<td>98</td>
<td>40%</td>
</tr>
<tr>
<td></td>
<td>9 May</td>
<td>16.1</td>
<td>84</td>
<td>52%</td>
</tr>
<tr>
<td>Generation 2</td>
<td>29 June</td>
<td>14.6</td>
<td>207</td>
<td>140%</td>
</tr>
</tbody>
</table>

If this interpretation be correct, (and there seems to be no other possible unless the species has an unrecognised breeding medium in August and September) then it follows that the preoviposition period in the field of the third and second generations (in part or wholly according to the year) must be prolonged considerably beyond the limits which normally obtain in the first (overwintered) generation, or which other workers have/
have observed in laboratory studies. HAMMER's (1941) observations provide good supporting evidence for the hypothesis that a large part of the second generation sustains delayed sexual maturation. He found that between 14 June and 22 July, 52 out of 62 females swept from grass were immature (i.e. over 80%). If all the second generation developed sexually without delay no immature specimens would be expected to occur in late July. As regards the assumed prolongation of adult life it is notable that COTTERELL (1920) kept individuals for as long as 2 months at 18 - 23°C.

Unfortunately, although all the evidence suggests strongly that immature adults aestivate, we have found no evidence regarding the mode or location of their so doing.

The course of events in 1953 is summarised diagrammatically in Fig12.

BRO LARSEN & THOMSEN (1940) studied the effect of temperature on the rate of development of this species and basing their conclusions on the minimal periods elapsing between oviposition and adult eclosion identified a linear relationship (i.e. rule of thermal summation was applicable). The threshold (or alpha point of SHELFORD 1927) was 2.1°C and the thermal sum (or constant) 372 Day - Degrees C. The results obtained in the field in 1953 and at a constant 23°C in the laboratory for the generations emerging in that year were plotted against the Temperature Velocity (i.e. Reciprocal of Time) Line constructed on the data of these authors and are shown in figure13. Since the minimal times found in the field were erratic/
Plies on Cowpats.

Flies rare on Cowpats.

Flies on Cowpats.

Generation 1 oviposits.
Peak period

Generation 1 (overwintering) emerges.
Peak period

Generation 2 oviposits (part.)

Generation 2 emerges.
Peak period

Generation 3 emerges.
Peak period

Generation 3 oviposits (Progeny overwinter)

FIGURE 12.
Scopeuma stercorarium -
Life cycle (diagrammatic).
Scopoeuma stercorarium - Effect of temperature on rate of preimaginal development.

FIGURE 13.
erratic, some individuals preceding the main population by several days, the medial values for each population were used, and the temperatures were taken as the mean air temperatures near the cones for the periods in question. The plotted points lie in striking conformity with the findings of the Danish workers and warrant the conclusion that their results apply broadly to the uninterrupted development of the species when exposed to the fluctuating temperatures of the field.

When, on the other hand, the population developing from autumn-laid eggs is considered, the characteristics $a = 2.1^\circ C$ and Thermal sum 372 Day - Degrees Centigrade quite obviously do not apply. The effective day-degrees for the autumn-winter months were as follows:

<table>
<thead>
<tr>
<th>Month</th>
<th>1952/3</th>
<th>1953/4</th>
</tr>
</thead>
<tbody>
<tr>
<td>October</td>
<td>176</td>
<td>245</td>
</tr>
<tr>
<td>November</td>
<td>70</td>
<td>177</td>
</tr>
<tr>
<td>December</td>
<td>40</td>
<td>132</td>
</tr>
<tr>
<td>January</td>
<td>85</td>
<td>96</td>
</tr>
</tbody>
</table>

From this, emergence of adults would be expected as follows if the temperature characteristics of early summer were applicable:

<table>
<thead>
<tr>
<th>Time</th>
<th>Expected emergence</th>
<th>Observed emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td>26. ix. 52</td>
<td>31. i. 53</td>
<td>After 15. iii. 53</td>
</tr>
<tr>
<td>8. x. 52</td>
<td>25. ii. 53</td>
<td>do.</td>
</tr>
<tr>
<td>10. x. 53</td>
<td>10. xii. 53</td>
<td>After 15. iii. 54</td>
</tr>
<tr>
<td>31. x. 53</td>
<td>20. i. 54</td>
<td>do.</td>
</tr>
</tbody>
</table>

The actual appearance of adults was thus delayed in the different series by periods of from 6 to 12 weeks. The delay occurs in the pupal instar and is evidently a diapause effect. BRO LARSEN & THOMSEN found evidence of a pupal diapause (at the white/
white eye stage) in one series only of the many they examined, and they suggest that a part of the pupal population must pass into diapause in the field. The remainder, they suggest, probably continues to develop without interruption. In the example they give, the diapause lasted for about 10 weeks at 15°C. It is significant that these authors found no indication of the occurrence of diapause at high temperatures. In the present work no significant delay in adult emergence was ever observed at 23°C. In the field, however, all individuals exhibited diapause characteristics to some degree. When transferred to the laboratory as pupae in mid-December and maintained at laboratory temperatures of 10°C - 19°C (mean c. 15°C) their emergence as adults was delayed by periods of from 10 - 54 days beyond the expected time. The thermal sums for the whole development period were from 140 to 250% of the sums for early season development. (In BRO LARSEN & THOMSEN's example it amounts to 330%).

Although the factors which induce the pupal diapause are not known the following features are evident:-

a) At high temperatures it does not develop (23°C), or when in course in field material it is readily broken (HAMMER obtained adults from diapausing pupae within 7 days of transferring them to 22°C in early February).

b) At 15°C diapause can develop (BRO LARSEN & THOMSEN) but only does so in a minority.

c) In the field at mean temperatures between 7°C and 13°C all individuals (from autumn-laid eggs) go into diapause when the pupal stage is reached (Midlothian).

d) The intensity of the diapause varies individually; the time/
time required for its completion shows a great range for any set of conditions at 15°C or less (c.f. ANDREWARTH 1952).

As regards items (c) and (d) the views of BRO LARSEN & THOMSEN (1946) and HAMMER (1941) are not in complete agreement with those stated here. The joint authors assume that only part of the population sustains a diapause, but they were not concerned with development in the field. Their suggestion that continuous slow development can take place throughout winter was not supported by the Midlothian data in the particularly mild winter of 1953/4 when for weeks on end the temperature remained continuously above the morphogenetic threshold of 2°C. To account for the appearance of flies in late January & February such as COTTERELL (1920) and (1) KOYAYASHI (1921) mention, and he himself observed, HAMMER says "Such early occurrences are unquestionably due to the fact that the pupae … have had no diapause". One cannot be so certain as this, however, since without diapause adults would be expected even earlier than this. It is likely that these are examples of a less intense diapause which had been completed in time for the individuals to resume morphogenesis during warmer periods in late winter. Nevertheless HAMMER and MELLOR (1919) are correct in their view that the species overwinters in the pupal instar and not as adults as COTTERELL (1920) suggests.

In 1952 the population was bivoltine and the succession...

---

(1) KOYAYASHI does not as HAMMER states, express the view that the adults hibernate, he merely records finding an adult in late January.
of events was probably as follows:

Generation 1 adults matured without delay  Preimaginal development of progeny uninterrupted  Generation 2 sexual maturity delayed  Autumn eggs developed with pupal diapause & overwintered.

Thus we have a clear-cut alternation of generations in which:

**WINTER**
- Preimaginal development interrupted (= hibernal pupal diapause)
- Adults mature directly
- Preimaginal development uninterrupted
- Adults with delayed maturity (= aestival imaginal "diapause")

Since nothing is known yet of the imaginal aestivation it may be premature to term it diapause. Nevertheless the species displays the unusual phenomenon of interrupted morphogenesis at two possible points in its life-cycle. (ANDREWARTHA (1952) points out that for any given life cycle diapause occurs only at one stage in nearly all known cases. Apparent exceptions include Reduvius personatus which at 22°C according to READIO's (1931) findings may diapause in the fourth or third plus fifth instars, and Popillia japonica in which LUDWIG (1932) found the duration of diapause in the third instar to vary inversely with the duration of the second.). Polistes lardaria (vide infra) presents a similar feature.
The significance of the third generation of 1953 presents an additional problem whose solution clearly requires further work. Present discussion of the possible interpretation of its significance in the life cycle of the species would serve little purpose since we have only the evidence of two years, and consequently do not know which pattern is the more usual.

The species is biologically one of the most interesting of the biocoenose, and evidently has a life cycle of such complexity that it requires more experimental study. Interpretations along the simple lines proposed by the Danish workers are untenable.

4. Other Multivoltine Species

The fact that the successive generations overlap to some extent makes it difficult to recognise their limits. This problem has been encountered already in the case of *Hebecnema*, but it becomes more acute when we consider the other multivoltine species on account of their smaller numbers, and less regular pattern of pat-infestation. The variable incidence of diapause is a further complicating factor, in that it causes variability in the voltinism of some species. The multivoltine species may be classified in the following groups

**Group I.** - includes those forms which resemble *Hebecnema* with a series of at least three generations in which preimaginal diapause occurs in increasing proportions in each successive brood. It contains *Myospila meditabunda*, *Morellia simplex*, *Hylemya strenua*, and *Anisopus punctatus*.

**Group II.** - includes species with three or more generations in which/
which the onset of preimaginal diapause in the population is not gradual, but comparatively rapid. Eggs laid before a given date develop without interruption to produce an adult generation, whereas eggs laid at a later date produce individuals whose development is arrested at the appropriate diapause stage. *Mesembrina meridiana, Azelia macquarti* and *Hylemya variata* are contained in this group.

**Group III.** - contains *Orthellia caesarion* (and probably *Musca autumnalis*) in which the adult overwinters, and in which, therefore, the diapause stage occurs outside the biotope. It is not possible, to decide from the evidence in this work whether the onset of diapause is confined to individuals of one (as in group II) or several generations (as in group I).

**Group IV.** - includes species in which no more than two generations per annum are developed, but in which a proportion of the population is definitely univoltine. It embraces a range of forms from the substantially bivoltine species *Pseudophona hirtiorum* to those in which the second generation is of negligible dimensions such that the species are virtually univoltine. Some species included below in the univoltine class could equally well be considered here as the extreme examples of the present group (e.g. *Microchrysia polita*).

The group also includes *Hydrotæa albipuncta, Pannia mutica* and *Rhingia macrocephala*.

**Multivoltine Group I**

*Myospila meditabunda* Fabr.

This species is not confined to cow-pats; it was also bred from/
from pig- and sheep-dung. (Together with Egle aestiva it appears to be more abundant in sheep-droppings than in cow-pats). Although it is a regular and frequent member of the surface-community of cow-pats its numbers are never greater than 6 per pat. Individual pats have yielded as many as 20-25 individuals, but in the majority the number is well below 10 per pat.

Figure 14 summarises the data of emergence of flies in cone-traps. Although only a small number of flies were obtained from overwintering pats in spring 1953, it is notable that they all emerged in late May and early June. This was, however, appreciably later than the emergence of "wild" flies in the area. Flies were actually observed in the shade of bushes as early as 24th April 1953, and in the open on pats on 6th May. The first infestation was in pats of 2nd May. It is apparent that the results of emergence of overwintered flies in the cones are misleading in this case. The discrepancy between cone and wild emergences is far greater for this than for any other species.

Muirhead Thomson (1937) states that Myospila appears as early as the second week in April, but does not become frequent until late May. This accords quite well with the observations in 1953 in Midlothian.

The evidence presented justifies the conclusion that the species has three main generations per annum and a possible very small fourth. Hammer (1941) presumed five generations. The cycle is summarised as follows:-

<table>
<thead>
<tr>
<th>Generation</th>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Late Apr. - Early June</td>
<td>Early May - late June</td>
</tr>
<tr>
<td>2</td>
<td>19 June - 28 July</td>
<td>29 June - ?</td>
</tr>
<tr>
<td>3</td>
<td>29 July - 16 Sep.</td>
<td>7 Aug. - ?</td>
</tr>
<tr>
<td>(?)</td>
<td>4</td>
<td>2 Sep. - 16 Sep.</td>
</tr>
<tr>
<td></td>
<td>(?)</td>
<td>(? - 19th Oct.</td>
</tr>
</tbody>
</table>

A/
FIGURE 14.
*Myospila meditabunda* - Adult emergence in field.
A small part of the progeny of the second generation, most of the third and all of the progeny of the fourth enter diapause in the pupal instar, (Fig. 34 shows the relation between development and temperature for non-diapausing individuals and the developmental threshold is in the region of 4-5°C.)

*Morellia simplex* Low

This species was recovered much more frequently from August and September pots than from those of the early part of the season. In spite of the fact that the fly lays eggs in batches of up to 25, most pots produced only small numbers (less than 10). The highest numbers recovered were 42, 32, 30, 24, 23, 20, 18, 17, 17, etc.

The data for emergence of this fly are given in Figure 15. Unfortunately, this evidence is too scanty to be conclusive, and only broad limits can be suggested for the generations. We have evidence for three generations only, thus:

**Emergence**

<table>
<thead>
<tr>
<th>Generation</th>
<th>Emergence</th>
<th>Progeny Diapause</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation 1</td>
<td>Early May - Early June</td>
<td>some progeny diapause(?)</td>
</tr>
<tr>
<td>Generation 2</td>
<td>Early June - late Aug.</td>
<td>most progeny diapause</td>
</tr>
<tr>
<td>Generation 3</td>
<td>September</td>
<td>all progeny diapause</td>
</tr>
</tbody>
</table>

The last generation is evidently much smaller than the second, the bulk of whose progeny enter diapause when the prepupal larval stage is reached. Some pots as early as 7th July contain a few diapausing individuals, and these could be the progeny of first generation flies. This suggests the possibility of a small proportion of univoltine individuals. By 28th July all pots contain only diapausing larvae.

Hammer suggests that *M. simplex* has 4 generations, whereas *M. hortorum* /
FIGURE 15.
Morellia simplex - Adult emergence in field.
M. hortorum which develops more slowly has only three. The
times he gives are considerably shorter, however, than those
determined here. For example M. simplex emerged in 23 days in
each case from pats of 14 June, 26 June and 3 Aug. in Denmark,
(the conditions under which they were kept are not indicated but
in the laboratory seems probable), whereas in Midlothian pats of
6 June, 22 June, and 20 July did not produce flies in less than
37, 54 and 44 days respectively. M. hortorum was only identified
here from 3 diapausing pupae in a pat of 7 July. HAMMER states
that the diapause point is different in the two species, and
this was confirmed in the present work.

Hylemya strenua R-D

This species is not particularly frequent and never abundant
in the pabulum. It was collected abundantly, on the other hand,
in meat-bait and suction traps, and the use of other breeding
media is, therefore, probable. From the summary of emergence
data in Fig. 16 it is concluded that there are three generations,
as follows:

<table>
<thead>
<tr>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation 1</td>
<td>Early May - Early June-</td>
</tr>
<tr>
<td>Generation 2</td>
<td>12 July - 11 Aug.</td>
</tr>
<tr>
<td></td>
<td>6 June - 29 June</td>
</tr>
<tr>
<td></td>
<td>13 July - 14 Aug. (+?)</td>
</tr>
</tbody>
</table>

From the suction trapping catches it would appear that the
species reaches its peak of abundance from late September - mid
November. The size of these catches, however, cannot be directly
related to abundance of the fly since the sex ratios show so
remarkable/
FIGURE 16. *Hylemya strenua* - Adult emergence in field.
FIGURE 17.
*Hylemya strenua* - Suction-trap catch.

Mean air temperature - 10 day periods - (above).
remarkable a pattern (Figure 17). The first generation is represented by males almost entirely in 1952 and by males in the proportion of 2:1 female in 1953 (May - June). Of the later generations a higher proportion of females are caught (July - August). The females are apparently longer lived than males and so the later catches (Sept.-Nov.) contain increasingly greater proportions of females, but these show an increasing tendency to be caught, their numbers in the traps becoming greater as the population ages. These catches are evidently related to an unknown behaviour-climate complex as well as to actual population dimensions, and they provide no assistance in determining the generation limits.

Anisopus punctatus Fabr.

This species was represented by the greatest numbers of all the species studied. It was present in nearly all the pats examined between mid-May and mid-October except for a short period in early-mid-June. Late season pats are particularly heavily infested by populations of larvae destined to overwinter. The heaviest infestations were 3820, 2770, 2500, 2360, 2230, 2160, etc. It appears to be rather more abundant in Ayrshire than in Midlothian. For example, 10 late August pats from Ayrshire contained a mean of 1400 larvae against a mean of 850 larvae in 7 Midlothian pats of the same date.

In view of these very large numbers a complete record of emergence in the field was not kept. The course of events (1953) is, therefore, summarised from qualitative evidence as follows:

<table>
<thead>
<tr>
<th>Generation 1</th>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May</td>
<td>Mid - late May</td>
</tr>
<tr>
<td>Generation 2</td>
<td>Late June - Late July</td>
<td>July - August</td>
</tr>
<tr>
<td>Generation 3</td>
<td>Early Aug. - Late Sep.</td>
<td>August - Early Oct. (Oct. 10)</td>
</tr>
</tbody>
</table>

Prepupal/
Prepupal larvae in diapause were found first in pats of 7th July. Their numbers increased in pats of later date until by the end of July all individuals were in diapause. On 7th and 14th August again, however, some few flies developed without diapause, and these could represent a 4th generation. Diapause clearly appears in the progeny of all generations except the one which overwintered, and the species contains bivoltine and three-voltine groups (plus a possible four-voltine one).

**Multivoltine Group II.**

It may be that the distinction drawn between this and the previous group is an unreal one, it is, nevertheless, a convenient one for descriptive purposes. *(Vide infra, Section 9)*

Mesembrina meridiana L.

This very conspicuous species is frequent but never abundant on cow-pats in Midlothian. It appears to be confined to this breeding medium here, a fact which is also maintained by PORCHINSKII (1910). HAMMER (1941) emphasises the shade preference of this species, and states that the surface populations in shade reached 5 or 6 and exceptionally 9, while in the open only one per pat in summer and 2 or 3 in autumn were seen. No such difference was observed in this area. The populations only occasionally exceeded 2 - 3 anywhere; the highest number observed was 6 and this was in the open on a bright sunny day. Infested pats usually produce less than 5 flies. This number was only reached or exceeded in eight examples of pats which produced 9,7,7,6,5,5,5,5 respectively.

This species is remarkable in the degree of uniformity of development rates of individuals maintained under the same conditions/
conditions. The relation of temperature to developmental velocity is consequently identifiable with more confidence for this than for most other species. Figure 18 shows this relationship and indicates a threshold point a little below $5^\circ$C.

The emergence data in the field are summarised in Figure 19. The overwintering generation appears in late May and early June in the cone-traps (1953). Again (cf. *Myospila*) this emergence is slightly later than that of the 'wild' population, of which occasional flies were seen on hedges and tree-trunks as early as 8th May. The cone-trap emergence, however, coincides with the appearance of the bulk of the wild population. No infested pats were discovered until 31st May.

The outstanding feature of this life cycle is that only one out of all the series of pats contained both diapausing and non-diapausing individuals namely that of 6.8.52 which contained one individual in diapause as well as those shown emerging on 19 and 20 Sept. In 1953 the pats of 7th Aug. contained only non-diapausing while those of 14th Aug. contained only diapausing forms.

The cycle (1953) may be summarised as follows:

<table>
<thead>
<tr>
<th>Generation</th>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation 1</td>
<td>Mid May - Early June</td>
<td>(Before?) 31 May - 29 June</td>
</tr>
<tr>
<td>Generation 2</td>
<td>11 July - 12 Aug.</td>
<td>20 July - 14 Aug. (or 21 Aug?)</td>
</tr>
</tbody>
</table>

Although a small number of the progeny of generation 2, namely those from larvae /the species is ovolarviparous, cf. KErLIN/
Figure 18: Mesembrina meridiana - Effect of temperature on rate of preimaginal development.

Temperature
0°C 20°C 30°C 40°C 50°C

Time (1953)

\[ a = 7.2^\circ C \]
FIGURE 19.
Mesembrina meridiana - Adult emergence in field.
KEMLIN(1916) & MUIRHEAD THOMSON(1937) deposited on 14, and perhaps 21 August, enter diapause, the bulk of the overwintering population derives from the 3rd generation.

HAMMER estimates 4 or even 5 generations for the species in Denmark.

_Hylemya variata_ Fall.

Like the closely related _H. strenua_ this species is not very numerous on or in cow-dung, but is readily collected in large numbers in bait and suction traps. It is less numerous than _strenua_ but its flight season definitely longer, both beginning earlier and finishing later. The suction trap catches (Fig. 20) resemble closely in their sex ratios the catches of _H. strenua_. Here again little assistance is to be found towards the interpretation of the voltinism. Individual cow-pats rarely contain more than 5 individuals of this species.

Emergence data in the field are summarised in Figure 21.

The incompleteness of the 1953 record is readily detected from the gap which exists between the emergence of the overwintered generation and the earliest date of oviposition. Nevertheless although their limits cannot be accurately defined it is probable that the active succession comprises 3 main generations thus:

<table>
<thead>
<tr>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation 1</td>
<td>Late April - Late May</td>
</tr>
<tr>
<td></td>
<td>Mid-May - late June (cf. 1952)</td>
</tr>
<tr>
<td>Generation 2</td>
<td>Late June - Mid July</td>
</tr>
<tr>
<td>Generation 3</td>
<td>Late July - Mid Aug.</td>
</tr>
<tr>
<td></td>
<td>Early or Mid Aug. - Mid Nov.</td>
</tr>
</tbody>
</table>

Pats up to and including 7th August contained forms whose development was uninterrupted. Those of 14th August and after contained only forms destined to overwinter. The series of 7th August may be the progeny of 2nd generation flies and thus diapause would/
FIGURE 20.

_Hylemya variata - Suction-trap catch._

Mean air temperature - 10 day periods - (above).
FIGURE 21. Hylemya variata - Adult emergence in field.
would appear to be confined to and universal in third generation progeny, or they might be a minor part of the progeny of the 3rd generation representing a fractional 4th generation. HAMMER (1941) suggests 4 or 5 generations for this species, *Azelia macquarti* Stal.

HAMMER (1941) describes *Azelia ciliipes* as one of the species with a two-peaked curve of incidence. His account implies that other *Azelia* spp. are similar. His interpretation of the observations is that the species have two main generations incident on the droppings in June-July, and August-October respectively, and he states "This method of reproduction causes the curve to be two-peaked, but this effect is amplified by the delicacy of the species". The species *macquarti* is also one with a strong shade preference such that in open situations its incidence on the pats is low in mid-season. In Midlothian the two-peaked effect is probably due entirely to what HAMMER terms "the delicacy of the species". The species was only bred in ones and twos from open situation pats until October when the infestation rose to levels of 10-14 per pat. On the other hand pats from shade situations contained such numbers in mid-late July.

Figure 22 summarises the data for field-emergence in 1953, and warrants the conclusion that there are three generations in this area, thus:

<table>
<thead>
<tr>
<th>Generation 1</th>
<th>Emergence</th>
<th>Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early May - Early June</td>
<td>Late May - Mid-June</td>
<td></td>
</tr>
<tr>
<td>Generation 2</td>
<td>Early ? - Late July</td>
<td>July</td>
</tr>
<tr>
<td>Generation 3</td>
<td>Mid - late Aug.</td>
<td>Late Aug. - Mid Nov.</td>
</tr>
</tbody>
</table>

Diapause appears only in the progeny of third generation flies.
FIGURE 22. \textit{Azelia macquarti} - Adult emergence in field.
flies, and in them it is universal. It occurs in the pupal stage.

**Multivoltine Group III**

*Orthellia caesarion* Mg.

MUIRHEAD THOMSON (1937) referred to the larvae of this species as "... probably the most generally dominant inhabitants of cow-dung, and not only do they play an important part in the eventual consumption and disintegration of the dung-cake, but they also,... form the principal basic food of all dung-frequenting carnivorous larvae". He observed surface populations of up to 30 adults per pat at the peak of activity in Ayrshire. Even higher levels of infestation have been described by MOHR (1943) in N. America (up to 60 per pat) and by HAMMER in Denmark (up to 100 and 200 per pat). Numbers of this order were never observed in 1952 and 1953 in Midlothian; the largest infestation seen was 6 flies per pat in August 1953 whereas in the same month CAMPBELL (personal communication) observed from 30-40 per pat in Denmark. It is clear that in this area the species plays a much less significant role and certainly has not the importance that MUIRHEAD THOMSON attributed to it in Ayrshire.

There can be little doubt that the species hibernates in the adult instar although the discovery of hibernating forms has eluded nearly every worker. They were not found in the present investigation, but success here could hardly have been expected since HAMMER failed to find them in an area where the species is considerably more abundant. The few individuals found on pats in September and October were all immature, and no pats were infested after August. In common with the experience/

* O. cornicina (see p. 27)
experience of earlier workers all pats examined during winter were found devoid of preimaginal stages. There appears to be no European record of hibernation of *Orthellia*. Two American workers, however, have recorded finds of hibernating adults namely HÖLQUIST (1926) and MOHR (1943) who found two and one individual respectively in leaf-drifts in woodland, and three (MOHR) beneath burlap bands on apple trees. The paucity of records, and the fact that the only extant records are of isolated individuals suggest that the species is non-gregarious in hibernation, a feature which distinguishes its behaviour from that of such forms as *Dasyphora cyanella*, *Dasyphora serena*, *Musca autumnalis*, *Pollenia rudis*, etc.

Figure 23 summarises the data for emergence in the field. On account of its comparative scarcity, the record of emergence in Midlothian is very incomplete, and its interpretation must remain largely conjectural. The species was not trapped in either meat bait or suction traps. In 1952, 5 out of 50 summer pats produced 11 individuals while in 1953, 13 out of 120 summer pats produced 47 flies. Flies were first observed on dung on 6th May in 1953, and thereafter they were regularly present in small numbers until August when their numbers were maximal. The population on dung-pats declined throughout September and flies were last observed on 9th October.

The earliest infested pats discovered were those of 6th June, but it is probable that these represent the later part of the oviposition of the first generation (overwintered) flies. The earlier part of the oviposition has evidently been missed. If this supposition is correct then we have:-

Generation 1/
FIGURE 23.
Orthellia caesarion - Adult emergence in field.
Generation 1  Becomes active  Oviposition
(overwintered adults)  Early May  May - Early June (6 June)

Emergence

Generation 2  Late June - Mid July  Late June - Mid July
(not seen)

Generation 3  Late July - Mid August  August

Generation 4  September  Overwinters.

The latest pats from which adults emerged were those of 7th August 1953. The last emergence was in mid-September. HAMMER considered the last emergence in mid-late September to be the fifth generation. In North America this species apparently continues to breed until a much later date. MOHR (1943) found larvae as late as 5th November in Illinois, while, HUTCHINSON (1918) actually records an emergence between 4th November and 3rd December in Maryland.

Multivoltine Group IV

Pseudophaonta hirticrura Meade

MUIRHEAD THOMSON (1937) gives the only published record of observations on the habits of this fly, but his account does not include information on the duration of developmental stages or on the voltinism of the species. Abundant opportunity was provided by the present work to observe the activity and oviposition behaviour of the fly, since it is quite a common one in Midlothian. These observations were generally in agreement with MUIRHEAD THOMSON's findings. The gravid females invariably traverse the surface of the dung-pat with the ovipositor trailing before they proceed to egg-laying. This stage may last for up to several minutes. Eggs are invariably laid on the/
The ground deep in the grass layer, usually below the overhanging margin of the pat. We have never seen egg batches such as MUIRHEAD THOMSON describes; eggs were always observed singly in ones and twos. Even when kept in tubes gravid females have only been seen to lay their eggs individually, although up to 20 eggs may be scattered around the tube within a few minutes. (This is in marked contrast to Rhingia or Stomoxys, for example, which will deposit their eggs in typical batches in tubes). MUIRHEAD THOMSON only refers to males on bushes, fences, etc. They have been observed not infrequently in Midlothian feeding on dung, but they do not mate on the dung.

The flies are common on the pats in two main phases, the first in June, and the second in August and September. In July there are few flies to be seen. The infestation of pats follows the same pattern thus:

From 31st May - 12th June
12 pats out of 18 produced 60 flies (3.3 per pat)
22nd June - 21st August
9 pats out of 54 produced 24 flies (0.5 per pat)
28th August - 26th September
23 pats out of 24 produced 179 flies (7.5 per pat)

The largest infestations were: 31, 25, 16, 14, 13, 11, 10, 8, 6, 7, flies per pat.

Figure 24 summarises the data of emergence in the field. The first generation emerged between 21st May and 6th June (the first wild flies were seen on 24th May and laid its eggs between 31st May and 13th July. The earlier laid eggs (31 May - 12 June) developed to produce the second generation, but many of those laid later (22 June - 13 July) entered diapause when the pupal stage was reached.
FIGURE 24.

_Pseudophonia hirtiorura_ - Adult emergence in field.
The second generation flies emerged between 15 July and 4th September and laid their eggs between 7th August and 3rd October. Two eggs laid on 7th August developed without interruption to emerge as adults on 25th September, the remainder all entered diapause. The two apparently represent a fractional third generation.

*Hydrotaea albipuncta* Zett.

The data concerning this species are among the most difficult to understand. First, the individual variations of developmental times under any given conditions are very great, and secondly the larvae in the third stage are markedly cannibalistic so that comparatively few flies emerge from a particular larval population. Finally, as figure 25 shows, the emergence of second generation flies was substantially earlier in 1952, (2nd July - 30th August) than in 1953 (5th August - 19th September). No obvious climatic difference between the two years can be suggested to account for these differences. (The possibility that some of the earlier emergences in 1952 are of overwintered flies present in the turf before the pat was dropped should be mentioned.) Only a very small number of flies were recovered in the cone-traps from overwintered pats, and these emerged during the very short period 8th June - 20th June, 1953. It is almost certain that the period both begins earlier and finishes later than these limits suggest.

*Hammer* (1941) states that the species begins to appear in early May (while *H. meteorica* emerges late in that month) but does not become numerous until June. Although perhaps not appearing/
FIGURE 25.
Hydrotaea albipuncta - Adult emergence in field.
appearing so early as the beginning of May the species was already active in May in Midlothian since pats were infested on 31 May 1953 and 23 May 1952. The bulk of emergence, nevertheless must have occurred in June, as indicated by the trap records, since infestation of the pats was not marked until that month. Second generation flies emerged from these pats in August and September. But whereas 26 flies completed development from eggs laid in June, the same pats contained a much greater number of larvae in diapause when brought into the laboratory in winter. Only a very small number of them, however, completed development successfully under the new conditions. 19 adults emerged from a population of 107 larvae. It is impossible to determine what is the true proportion of actively developing to diapausing individuals in this generation since we have no information on mortalities under field conditions of the non-diapausing section of the population. Nevertheless, it is quite clear that the diapausing section is very large and probably as large as or perhaps larger than that section which emerges to produce the second generation of adult flies. In the 1953 record, one fly emerged on 20th September from a pat dropped on 28th July. This could derive either from a late oviposition by a 1st generation or from an early oviposition by a 2nd generation fly, probably the former. It could conceivably represent a fractional third generation, but is more probably a second generation individual.

HAMMER(1941) was unable to recognise much change in the numbers of adults of this species throughout the summer, but he identifies/
FIGURE 26. *Fannia mutica* - Adult emergence in field.
identifies two summer generations emerging in late July - early August, and late August - early September respectively. The emergence periods given correspond quite well with those found in Midlothian, but they represent one generation here. It is important to note that this is one of the few species in which HAMMER refers to early season flies entering diapause. He states "The last generation is not particularly numerous, as a number of larvae, even from the 2nd generation, and still more from the 3rd generation remain in the dropping in order to hibernate".

It is concluded that the species has too slow a development rate to enable it to develop more than one active generation in Scotland, and that the species is bivoltine, but it contains a large proportion (perhaps the larger proportion) of univoltine individuals Fannia mutica Zett.

There appears to be no published record of the life cycle of this species in the field. It has an irregular incidence in the pats, and the infestation levels throughout the year do not show any obvious seasonal variations. Usually about 60% of the pats are infested. Pats from late June and early July contained no representatives, and those dropped in late summer often contained larger numbers than those of the early summer. The highest numbers of larvae found were 23, 20, 18, 17, 13, 12 per pat, but the majority examined contained less than 5. Under any given set of conditions the period of development may vary between very wide limits (e.g. from 42 - 85 days in field from pats/
pats of 31st May) but it is always a comparatively long one. Larval populations contained individuals in diapause from as early as 6th June 1953.

The data for emergence in the field are summarised in Figure 26. Adults developed from overwintered larvae emerged between 21st May and 26th July. The blank period in June is unexpected. No explanation can be offered other than to suggest that it is probably not significant as regards the emergence of the species in nature. Of the eggs laid by this generation between 31st May and 13th July 33 developed to the adult instar and produced a second generation emerging between 12th July and 14th September, and at least 14 (25 out of 38 pats examined) remained in larval diapause throughout the next winter.

The species may be represented in this area by both univoltine and bivoltine strains.

**Phinga macrocephala** Harris.

Although REAUMUR (1738) recognised this species as a member of the cow-dung community, it was not until quite recently that the fact was confirmed, and the details of its life history were established. KRUGER (1926) knew the larvae. MULHEAD THOMSON (1937) referred briefly to its oviposition habits, and HAMMER (1941) and COE (1942) have described the life-cycle independently. COE found the species to be bivoltine in Southern England with a brood of adults in the period mid-June to early July, and a second brood in the period early August - mid-September. He does not refer to the relative abundance of the broods. Figure 27 illustrates the habit of ovipositing in consecutive batches as/
FIGURE 27.
Rhingia macrocephala - Eggs on vegetation.
as described by COE. The eggs shown on clover and grass leaves were all laid by one female within a few minutes. Three further small batches were laid on another adjacent grass leaf the total amounting to about 150 eggs (108 are shown). In Denmark HAMMER also identified two broods occurring in late May-early June, and in August. He, however, found the first to be the larger and states "It seems as if only a small percentage of the progeny of the first generation emerges as a second generation, while the greater part remains in the dung in order to hibernate."

The record obtained in the present studies is a very incomplete one and may be summarised thus:—

Pats were infested in 1952 on 4 June, 24 July, and 10 Nov. (*) and in 1953 on 12, 22, & 29 June, 7 July, 7, & 14 August, 4 & 26 Sept. and 10 October.

From all these only three individuals emerged in the field in the same year that eggs were laid, namely,

<table>
<thead>
<tr>
<th>Egg laid</th>
<th>Fly emerged</th>
</tr>
</thead>
<tbody>
<tr>
<td>24.7.52</td>
<td>25.8.52</td>
</tr>
<tr>
<td>do.</td>
<td>27.8.52</td>
</tr>
<tr>
<td>7.7.53</td>
<td>23.8.53</td>
</tr>
</tbody>
</table>

Some of these pats when dissected in November & December were found to contain quite large numbers of prepupal larvae (up to 21, 17, 15, 12, 7, etc.) and many contained ones and twos. It would appear, therefore, that the life-cycle in this area resembles that described by HAMMER in Denmark more closely than that described by COE in Southern England. A small second generation/

(*) A single male emerged from this pat in 1953 but whether from an egg laid on or after that date (10.11.52) is open to question, although COE (1953) gives April-November as extremes of dates of capture. It may have been present from an earlier date, as a larva in diapause, in the turf on which the pat was dropped.
generation is developed and appears in August and it continues to lay eggs until early October, and perhaps until November. HAMMER is probably in error in referring to the pupa as the overwintering stage. All our examples entered diapause in the prepupal-larva stage thus confirming COE(1942) who states "it appears probable that the larvae pass the winter in the torpid, prepupal condition, becoming pupae in the spring."

5. Polistes lardaria Fabr.

In its seasonal incidence among the surface populations of newly dropped cow-pats, Polistes lardaria shows a pronounced bimodal pattern. In Scotland both sexes are regularly observed feeding on the dung from late May to early July. During most of July and up to about mid-August they are rarely seen. They reappear in late August and from then are common until late October or continue even into November, and during this period females lay their eggs. In the early period oviposition was never observed, nor were pats of this period ever found infested by larvae. GRAHAM SMITH(1916) records a similar seasonal pattern of incidence in dung-traps. HAMMER(1941) found the species abundantly (up to 300 per pat) in June, scarce during July and August and common again in September. PORCHINSKII(1910) records the presence of the flies on dung in mid-June in the Leningrad district but asserts that they do not lay their eggs until late July and early August, and that larvae are not found in pats until August.

MUIRHEAD THOMSON(1937) and HAMMER have both described the oviposition/
oviposition habit of this fly, which lays its eggs on the ground below the edge of the pat. (cf. Pseudophaonia). It has often been observed in the present studies to lay the eggs in the dung at the margin of, and even occasionally on the disc of the pat, as well as on the ground.

Figure 28 summarises the evidence of field emergence and pat-infestation. This, together with the laboratory evidence of a firm and invariable diapause in the prepupal larvae permits only one conclusion, that the species is strictly univoltine.

Yet HAMMER with very similar evidence states "This occurrence of P. lardaria can only be explained by the fact that it has only two generations a year". At several points in his account he refers to bivoltinism in this species. The fact that dissection of 21 individuals caught between 18 June and 6 July revealed sexual immaturity, and his observation that in spite of its large numbers the species was never seen to oviposit in the early summer, led HAMMER to conclude that the species must have a very long prepupation period. It is, therefore, difficult to appreciate how with these facts at his disposal he should have reached so obvious a non sequitur as the view that the species is bivoltine.

The length of the prepupation period, which is evidently greater in Britain and Denmark than in N. Ruália, is a feature of great interest. This period is coincident with the summer phase of scarcity of the fly which is a shade-seeker. The species clearly deserves further study since it would be of great value to know whether this aestivation phenomenon is associated with a true adult diapause (in addition to the hibernal larval one).
FIGURE 28.
Univoltine species - Adult emergence in field.
or whether it is merely an example of direct inactivation by unsuitable conditions of temperature, light, etc. (cf. Scopemia). It is perhaps significant in this connection to note that attempts to rear the preimaginal stages at 23°C have consistently failed.

The incidence of P. lardaria in September - October pats in 1953 was about 7%. The numbers were never so high as those of Pseudophaonias, the most heavily infested pats producing 15, 12, 10, 8, 8, 7, 6, etc., flies per pat.

6. Dasyphora cynanella Mg.

Apart from its habit of adult hibernation, and the fact that it breeds in cow-dung, the life-cycle of this species in nature has not previously been described. The larval and pupal stages have been described in detail by Muirhead Thomson (1937) who also recorded a few observations on the behaviour of the fly.

Several authors, including Ashworth (1916), Gaskell (1916), Graham Smith (1919) and Muirhead Thomson (1937) have recorded the presence of hibernating adults of both sexes in houses and buildings, but there is apparently no record of its hibernation out of doors. (The related species P. serena has been recorded by Holmquist (1928) hibernating gregariously in rotten logs.)

In March 1952 a colleague E.G. Pelham-Clinton obtained upwards of a dozen specimens from a number of abandoned bird-nests (mostly blackbird) collected from a thicket of sea buckthorn and hawthorn growing near the seashore at Whitekirk, East Lothian. The flies emerged from the nests about 3 weeks after their removal to the laboratory. The same type of nest collected in late/
late February 1954 produced no flies, but a pigeon nest (of much more open texture) yielded from 80-100 individuals which became active immediately upon transfer to warm conditions. About a dozen flies were also found hibernating in late March in the open structure of a "witches' broom" on a birch tree at Annbank, Ayrshire.

No opportunity was provided to search for hibernating forms in buildings, but they were observed in large numbers in the ivy on a Midlothian house in October presumably in search of winter quarters. Large numbers fell victim to spiders here. The flies were caught in fairly large numbers in suction traps adjacent to this house in early spring and late autumn but not in summer, and during the same periods they were abundantly observed resting on rhododendrons around the traps. Figure 29 summarises the record of the suction trap catches. A very significant difference is evident between the autumn of 1952 when fair numbers of flies were caught in October, and the same period in 1953 when none were caught. Nevertheless, the flies were equally common on the rhododendrons in the two years. Their absence from the traps in 1953 is probably due to a more vigorous flight associated with the unusually high temperatures of that year. (E.g. the mean air temperatures for October were 1952 - 7.8°C, and 1953 - 10.1°C).

Hibernating adults often become active in warm periods during winter. In 1953 such individuals were even trapped in the suction traps as early as January and February. By March appreciable numbers had emerged and were trapped, but the flies did not become visibly numerous until mid-April. On 14th April/
FIGURE 29.

_Dasyphora cyanella_ - Suction-trap catch.

Mean air temperature - 10 day periods - (above).
April large numbers of both sexes were observed on rhododendron leaves, and on this date the commencement of mating behaviour was observed.

On certain leaves the mature male flies congregate and there take up a characteristic stance. They rest in file along the mid-rib, 'head to tail' on the upper surface of the leaf, facing outwards away from the petiole (Fig. 30). The files may number up to 8 individuals. When a female passes in flight they all rise and approach her. The successful male contacts the female in flight then together they return to the undersurface of a leaf where mating takes place. The remainder of the males return ultimately to resume their waiting attitude. Mating was most observed to be most active on 22nd April.

Flies were first observed on cow-dung on 21st April, and of the first pats examined (25th April) one out of six was infested. Both sexes may be observed on dung but they were never seen to mate there. _D. cyanella_ frequents dung only after a crust has begun to form and the bulk of _Scopeuma_ activity has subsided i.e. upwards of one hour old. They are not uncommonly seen on scattered droppings (dropped by moving animals) where they often feed. As many as 6 flies were seen together sucking fluid from such small droppings. They have never been seen to lay eggs, however, except on properly formed pats.

In preparing to lay their eggs the females walk over the surface of the pat testing the surface with the ovipositor. They may take up to 5 minutes before they select the precise site/
FIGURE 30.
*Dasyphora cyanella* - Males on rhododendron leaves.
site. This is always a crevice or hole in the crust towards the centre, and never at the margin, of the pat. The egg batch is then deposited in this below the surface, by the motionless female. When Scopeuma is present on the pat it does not attack these females when they are actually engaged in egg laying; on one occasion a Scopeuma was observed to walk over an ovipositing Dasyphora without attacking it. An example of oviposition may be quoted. The fly alighted on the pat at 2.31 p.m., and for the next four minutes wandered to and fro exploring the pat until it found a crack in the crust. Then standing motionless it proceeded to lay its eggs there until disturbed by an Aphodius. The Dasyphora moved away and spent the next half minute seeking the crack again. It resumed its egg-laying at the same site and completed the process at 2.44 p.m., having deposited a cluster of 39 eggs. Normally this species is not so readily disturbed during oviposition as some others e.g. Orthellia, and it is not uncommon to see two or more females ovipositing at the same time in the same hole. A mass of 58 eggs was taken from one such hole where 2 flies had laid their eggs together. On one occasion six females were seen standing in a circle with their ovipositors inserted into a common hole, their wings actually overlapping.

The peak of abundance of the species in the surface community of the pats was in early May, when the maximum numbers simultaneously present were 2/5 - 10, 3/5 - 12, 4/5 - 12, 8/5 - 16, 9/5 - 6, etc. By the end of May the numbers had fallen to twos and threes. Thereafter their incidence became less frequent until/
until in July they had become quite rare, presumably because the greater part of the overwintered generation had died out. In July, however, the emergence of the second generation of adults begins. Figure 31 shows the seasonal incidence of pat infestation and emergence of adults. In 1953 the new generation emerged between 2nd July and 16th August, while in 1952 for which the record is less complete emergence was between 12th July and 8th August. The developmental time is comparatively long in spite of the low threshold (Fig. 32). By the end of July Dasyphora again appears regularly on cow-pats and continues to be present until the end of September (23.9.1953). In late September and October they again congregate on the rhododendron and are no longer seen on dung.

In late July and early August, large numbers of young adults are readily trapped in meat-bait traps, but after mid-August although occasional specimens are taken they cease to be attracted by this bait. Only immature individuals are caught in these traps.

The second generation adults were never observed to lay eggs on dung and no infested pats were found later than 6th June. One specimen emerged on 7th August from a pat dropped on 7th July, but from comparison with the other field and laboratory data it appears highly improbable that the egg from which it emerged could have been laid as late as 7th July since its whole development would only have occupied 31 days. It is presumed that the pat in question was dropped on the remains of an earlier one. In any case it is almost certainly the progeny of an overwintered female. A series of dissections between 31 July and/
FIGURE 31.

*Dasyphora cyanella* - Adult emergence in field.
FIGURE 32.
*Dasyphora cyanella* - Effect of temperature on rate of preimaginal development.
and 23 September revealed 3 flies, 2 on 31 July, and one on 3 August, which were gravid out of the 212 examined. The remainder were all immature. The three mature ones were obviously recognisable as old individuals from their torn wings and brownish-copper tinge. Evidently the overwintered generation contains some longer lived individuals than the pat-infestation record indicates. The immature new-generation flies were found to contain increasing quantities of stored fats as the year advanced. There can be little doubt that the new-generation each year merely prepares to overwinter, and does not become sexually mature (both sexes) until the following spring. It is interesting to note that HOLMQUIST (1928) failed to promote maturity in individuals of D. serena captured in the late summer & autumn.

The species is considered to be a univoltine one in which sexual maturity is delayed until the adult has hibernated.

The account given is slightly at variance with the details quoted by MUIRHEAD THOMSON (1937). He states that "During the summer from the end of May onwards, females may be seen ovipositing... it is only very occasionally that two females are seen ovipositing on the same dung-cake". On the other hand, he observed the flies in April and even as early as March. It seems unlikely that the preoviposition period could be so long as these two observations together suggest, and it implies quite a different behaviour if oviposition during the summer did take place. The most likely interpretation is that the peak of activity and egg-laying was missed by this author. By the end of May, the numbers would be, as he says, low. The flies observed during summer were probably the/
the new-generation adults feeding but not egg-laying.

7. Other Univoltine Species.

The evidence given in figure 28 points to the probable univoltinism of *Hydrotæa militaris* and *Geosargs flavipes*. The development of adults from overwintered larvae is completed comparatively late in the year, and no examples were seen of individuals completing their whole development within one season. The cycle of these two species differs from that of *P. lardaria*, however, in that they do not have the same uniformly prolonged preoviposition period, oviposition and pat-infestation, therefore, terminate for them somewhat earlier.

Adults of *H. militaris* were on the wing from June-August (1952) and June-September (1953). GRIMSHAW (1906) gives the dates 8 June - 20 August. They appear earlier in France (May-Sept.) according to SEGUY (1923), and in Sweden continue active longer (June-Oct.) according to RINGDAHL (1925). Since *H. militaris* is a carnivore which displays cannibalism, estimates of infestation levels based on emerged adults are probably low. Up to 12 adults per pat have been recorded. *G. flavipes* adults occurred from July - early October 1952 and 3. VERRALL’s (1909) dates are 6 July - 22 September. In Denmark HAMMER (1941) states the active period as July-September while LUNDBEK (1907) only records the species from 12 August - 3 September, but mentions ZETTERSTEDT’s dates as 12 July - 6 September.

The other Stratimyids are, from the field evidence in the present work, mainly univoltine, but there are some indications that *Microchrysa polita* may contain potentially bivoltine forms/
forms, and from laboratory records the same may also be true of *Geosargus flavipes*. (Vide section 9). *Microchrysa* spp. have presented a serious difficulty in that they migrate from the pat prior to pupation, and on account of their size can escape through the perforations of the cone-traps either as larvae, (or as adults in those few cases which pupate inside the cone). Consequently, despite the large numbers of larvae which occurred, the emergence of adults was rarely observed in the field.

The appearance of adults after winter (of *Microchrysa* spp.) must be considerably earlier than that of the other univoltine species, since pats of late May and early June contained larvae of all three species. The dates of earlier authors also show these species to precede *Geosargus*, for example, by quite a long time, thus:

<table>
<thead>
<tr>
<th>Species</th>
<th>Verrall (1909)</th>
<th>Lundbeck (1907)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. cyaneiventralis</em></td>
<td>6 Jun. - 1 Sep.</td>
<td>——</td>
</tr>
</tbody>
</table>

The evidence from the present studies is that *M. polita* occurs between late May and 4 September, while the other two occur between late May and 11 September. One or more of these, however, continued longer than those dates since the pats of 3 October were infested with larvae (which have not emerged to date).

Hammer regards *G. flavipes* as univoltine, and considers that *M. flavicornis* has one main generation a year, but regarding/
regarding the latter he adds "... numbers occur also in August. This must be the 2nd generation, which, however, is not numerous, it being usual for larvae which have hatched even early in summer to hibernate." It is difficult to appreciate how, in spite of the same type of evidence for both species he can make any sort of distinction between them. Their summer period is of the same length in both cases except that the limits of Microchrysea are one month earlier, and in the laboratory HAMMER found both to have a very strict and practically unchangeable rhythm.

The possible multivoltinism (bivoltine) of M. polita is suggested by the very wide limits of the adult appearances given by VERRALL and by the capture of one individual on 4 Sept. 1953 in a cone-trap over a pat of 31 May 1953. (Although by that date the pat would not be attractive to flies the possibility of an entry from outside by this individual cannot be excluded). Evidence, on the other hand, from laboratory observations suggests that all three species of Microchrysea have an invariable prolonged diapause, whereas G. flavipes is much more variable in this respect (Vide section 9).

The Stratiomyids may reach very high larval population densities as follows: - G. flavipes 36, 28, 26, 15, 12 etc. larvae per pat in Midlothian, and 93, 86, 78, 40, 33, etc. in Ayrshire; Microchrysea spp. appeared in similar numbers in both areas, the highest counts being 703, 631, 321, 295, 284 etc., larvae per pat. The proportion of species emerging in the laboratory was cyaniventris - 81%, flavicornis - 11%, and polita 9% /
3. **Other Species.**

Appreciable numbers of several other species were identified in the pabulum, but their occurrence was too irregular to permit conclusions regarding their seasonal cycle and voltinism. Some forms were only observed in late season pats in which they overwintered and were not seen at other times of the year. Among these may be mentioned the Bibionidae of which Dilophus fébrilis was particularly common in autumn pats where the larval populations reached 100 per pat, the Dolichopodidae and Empididae.

An even more impressive example of a species with very large pat populations in autumn and winter was the Tipulid Rhipidia maculata. This species occurred in nearly all pats examined in late August and September in both Midlothian and Ayrshire. From these pats it emerged quite readily after development at 23°C and numbers as high as 534, 353, 226, 183 etc., adults per pat were obtained. Although their emergence after winter in the field was not recorded adults of the overwintered generation almost certainly emerge in May - June since the species was captured in the suction traps in late May and June. It is most unlikely that so fragile a fly could persist in the adult instar from then until September, and multivoltinism must be presumed. The complete absence of the species from cow-pats during the rest of the year suggests that it may utilise a different pabulum for its summer breeding.

Two other muscids may be mentioned of which scattered records/
records permit only of tentative conclusions, namely:

**Mydaea urbana** with 2 generations emerging in June - July and late August-September, and

**Egle aestiva** with 2 generations with approximately the same times of appearance, Both these species continue to lay eggs into October.

HAMMER (1941) also had incomplete evidence for these species. He concluded that **Mydaea** has 2 generations and **Egle** has 3 plus a partial fourth generation.

9. **Discussion.**

ANDREWARTHA (1952) recognises four types of insect life-cycle, namely,

Type I, strictly univoltine, with a firm obligate diapause in all individuals;

Type II, virtually univoltine, with most individuals of every generation entering diapause;

Type III, multivoltine, with facultative diapause in some individuals of most generations, and most individuals of some generations; and

Type IV, univoltine or multivoltine, with diapause in a few individuals of some generations.

Only I - III of these types were recognised in the **Diptera** of the cow-pat community. Type I is, of its nature, comparatively well defined but it is not always possible to know whether a given form is referable to it or to Type II. Between Types II and III, on the other hand, the division is often an arbitrary/
arbitrary one.

The Stratiomyidae occupy a bridge position between types I and II since evidence concerning them appears to vary in different localities. In Midlothian *M. polita* is probably type II while the other two *Microchrysa* spp. are evidently type I. In Denmark, HAMMER's evidence indicates that *M. flavicornis* is type II. On the other hand, HAMMER found *Geosargus flavipes* to be of type I, with an invariable firm diapause, but in Midlothian, and even more markedly in Ayrshire the populations appear to be of type II. Although no individuals were reared in the field in the same season during 1952 or 3, when reared from the egg at 23°C a few individuals from the first, and up to 14% from the second locality developed so rapidly (adults emerged in 36 to 51 days) that the diapause must either have been omitted, or completed with an abnormal rapidity (usual time of emergence 120 days plus). This is in marked contrast to the definite type I species, *H. militaris* of which only a small proportion could complete development at 23°C, and *P. lardaria* which never succeeded in pupating at 23°C but which developed quite normally (Fig. 36) at room temperature with a mean around 15-16°C. It appears that the upper temperature limit for diapause development of the true uni-voltine species is appreciably lower than for the other species of the biocoenose. (cf. ANDREWARTHA on *Austroicetes cruciata*).

It has been pointed out above (p.66) that the bivoltine series of species including *Pseudophaonia*, and *H. albipuncta* which/
FIGURE 33.
Hebeunema umbratica - Length of preimaginal development in field.
Myospila meditabunda - Effect of temperature on rate of development (above); and duration of preimaginal development A - at 23°C and B - in field (below).
FIGURE 35.
Development and adult emergence at 23°C of Morellia simplex, Pseudophilia hirticrura, Hylemya strenua and Hylemya variata.
Development and adult emergence at room temperature of Autumn-laid eggs of various Muscid species.
FIGURE 37.
Emergence of 1st generation adults of various Muscid species in 1953.
O - Species first observed, S - Species first caught in suction-trap.
which have type III life cycles, merges through *Fannia mutica* to *Rhingia macrocephala* which in the present and in *HAMMER*’s work is virtually univoltine, i.e. type II but in Southern England was found by COE to be bivoltine, i.e. type III. In this group of species we have the interesting possibility that in different localities there is a tendency for the development of geographical races. Compared with many of the distinctly multivoltine life cycles which will be discussed later, these bivoltine species have two quite distinct features, namely, they show a much slower developmental rate, a feature which could account for the restriction of their multivoltine strains to 2 generations, and their diapause when it develops is a very firm one, so that they are among the latest species to emerge in the field after overwintering (*Vide* fig. 37 - *H. albipuncta* and *F. mutica*). There was a substantial proportion in all these species which in 1952 and 3 developed only one generation. It would be of considerable interest to know to what extent these proportions vary from place to place, and from year to year, and to what extent the tendencies to uni- or multi-voltinism are heritable. Although it may be a chance phenomenon, it is interesting to note that in *F. mutica* the univoltine "strain" was numerically greater than the multivoltine "strain". The emergence pattern in the field after winter was markedly bimodal, indicating a possible difference in diapause intensity in the two groups (cf. other species in the laboratory mentioned below). If it could be established that these groups were also different as regards their voltinism we/
we should have a species with two distinct races in one area, the univoltine strain being the more successful in the area.

Again it may be fortuitous but it is worth mentioning that in the records from various parts of the world the most conspicuous and consistent members of the biocoenose are the multivoltine or type IV species. Those in which the tendency to enter diapause is most strongly developed are much less conspicuous, either because they are absent in many localities or because they are less numerous and are therefore overlooked. This gives point to Bonnemaison's (1945) remark that "La diapause est nuisible à l'extension d'une espèce en diminuant le nombre possible des générations, elle est utile en plaçant l'insecte dans des conditions physiologiques particulières qui lui permettent de résister au froid de l'hiver ou à la sécheresse de l'été."

Diapause phenomena display the greatest variability in incidence and intensity among populations of the multivoltine species. These have been divided (pp. 65, 66) into two main groups according to the manner in which the population is transformed from a developing summer one to a diapausing winter one. The Hébecnema - Myospila etc. group (1) comprises forms with a characteristic type III (ANDREWATHA) life-cycle in which some diapausing individuals occur in each generation. Their number increases progressively in populations of progressively later date. The seasonal pattern here is thus comparable, for example, to that described by Theodor (1934) for Phlebotomus papatasii although we have no evidence regarding the occurrence of an inherent rhythm such as he describes. In the Mesembrine - /
Mesembrina-Azelia group (2) on the other hand no diapausing individuals were recognised among populations in the early season, but in early August within a very short period from 7th - 14th circa the later populations changed from entirely active to entirely diapausing. This pattern resembles that described by ANDREWARTHA from the data of GARLICK (1948) on Cydia pomonella in which the time of year determined the inception of diapause. It is, of course, possible that a small number of individuals of these species in the earlier generations do enter diapause but the number is so small that they were missed. Nevertheless, it is apparent that the characteristics of the group 2 species are much less variable than those of group 1. In the active developing state, for example, Mesembrina displays the greatest degree of uniformity in the temperature relations of its developmental velocity.

Furthermore, the group 2 species when developed at 25°C showed a greater uniformity than the group 1 species in populations which enter diapause and overwinter in the field. Figure 35 shows the difference in range between September populations of H. strenua (Group 1) and H. variata (Group 2) when developed at 25°C, at which temperature early summer populations show little difference, with H. strenua ranging from 17-27 days and H. variata from 14-21 days.

Unfortunately, lack of constant temperature facilities prevented a proper experimental study of the onset and duration of diapause in the multivoltine species. Observations on their development at 25°C and at room temperature, however, provide some/
some pointers towards an understanding of the factors which operate.

HAMMER (1941) inclines to the view that diapause is induced in the multivoltine species of the biocoenose by the direct action of low temperature on the developing instars before they reach the diapause point. He states "In the late summer and autumn the larvae stop development, presumably owing to climatic influences, among which it is most likely that the first really low temperature minima are of importance." At other places in his account, however, he suggests that the phenomena are more complex than this implies.

The present investigation produced no evidence to suggest a direct action of unfavourable developmental conditions on larval forms as the cause of inception in them of diapause. In all the species described, eggs laid after 7th August produced only diapausing individuals, yet this "critical" date was at the hottest period of the year in 1953. The mean temperature remained well above the mid-June (11-20) level of 12.5°C until mid-October (11-20) when some colder nights were first experienced. We should, therefore, not expect to encounter diapausing individuals until October if a direct action of temperature were the provoking factor.

In no species did eggs laid in the later part of the year produce marked evidence of diapause when the whole preimaginal development took place at 25°C. In most of them, however, development was relatively slower than in individuals deriving from early season eggs. An example, in the Hylemya spp. has been/
been quoted above. Figure 35 shows two other species, Morellia simplex and Pseudophaonia, in which retardation of development at 23°C becomes progressively more marked in later-season egg batches. When individuals from late season eggs of these species are developed at room temperature c.15°C, on the other hand, diapause is clearly evident. (Vide fig. 36). These findings compel the conclusion that while the temperature level may have an effect on the manifestation or otherwise of diapause, it does not induce it directly.

It seems improbable that there is any other factor which induces diapause by its direct action on the developing larvae. Light, which has a direct action on developing larvae of some insects, e.g. Cydia pomonella (DICKSON, 1949), in the nature or quality of the food supply which are important in many species, e.g. Euproctis chrysorrhoea (GRISON, 1947). This might be a factor operating in this community since there is a definite change in the consistency and appearance of dung as the year advances. How far such changes imply a change in the nutritive quality is unknown. This factor, however, would be expected to be of greater significance to the coprophagous than to the zoophagous species. No consistent difference in their diapause features was noted.

Those forms which develop more slowly at 23°C and which actually enter diapause at 15°C must already have had the tendency to diapause developed in their egg stage, since it is improbable that it could have been induced later. The tendency to diapause must, therefore, be maternally induced. Diapause of maternal origin has been identified in various insects: among/
among them Lucilia sericata (CRAGG & COLE, 1952), presents closely similar features to some of the dung-pat species.

The tendency towards diapause (or the diapause towards which the individual tends) is a variable characteristic as between species, or as between individuals of a species of the multivoltine group. The species Pseudophaonia, Morellia and Hebeconema form a series with diapause of decreasing intensity. Fig. 36 shows the effect of room temperature on populations developing from late season eggs. The whole Pseudophaonia population entered diapause, nearly all the Morellia population entered diapause, but in Hebeconema only 50% entered diapause. Material of the same origin (late Sept.) when reared at 25°C although not showing a distinct break in development was comparatively retarded, (Fig. 35) the degree of delay being in the same order for the three, namely greatest in Pseudophaonia, and least in Hebeconema.

When eggs laid in September were allowed to undergo development to the late larval instars in the field, and after one month transferred to room temperature, it was found that all individuals in all three species had entered diapause.

From these results we may conclude that the temperature at which the larvae develop can determine whether they will or will not enter diapause. High temperatures can prevent its occurrence but the diapause tendency is manifest in retardation of the developmental rate, the level required to achieve this depends upon the intensity of the tendency to diapause. Hebeconema illustrates this concept most clearly. Maintenance at 23°C prevents diapause, and the tendency is not intense enough/
enough to retard development to any marked extent in most individuals. Maintenance at 15-16° *circa* prevents diapause in 50% of the population, whereas field temperatures (13° mean) are too low to prevent its occurrence in any.

Once established at field temperature, diapause duration at lab. temperature is as long as in populations maintained throughout from the egg at lab. temperature. If kept in the field for 80 days before transference to laboratory conditions, the completion of development presented a bimodal pattern, and required from 16 to 47 days in the earlier group and 70 to 100 days in the later group, the two groups being in the proportion 80% - 20% respectively. Thus we have in comparable populations for total development to adult

Days in Field + Days in Laboratory

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In the individuals entering diapause the total developmental periods range from 96 - 180 days when 80 days were spent in the field, and from 119 - 210 days when the whole period was spent in the lab. The limits are perhaps not significantly different but the field group contains a much higher proportion near the lower limit than the lab. group. It is, therefore, probable that once established the diapause development (or physiogenesis of ANDREWARTHA) is completed more rapidly at field temperatures than at the higher laboratory temperatures.

As regards the genesis of maternal induction of diapause in/
in the progeny, it can only be assumed that this is related to the complex of factors, environmental and nutritional which change with the changing season. SIMMOND (1948) found that in Spalangia drosophila the incidence of diapause-tendency in the progeny increased with the ageing of the mother, but the manifestation of diapause was related to the temperature conditions. CRAGG & COLE (1952) found no evidence of a correlation between the incidence of diapause in the progeny and the age of the mother in Lucilia sericata. It is clear that from August onwards the incidence of diapause in the multivoltine species of the dung-pat community is unrelated to maternal age, since the whole progeny of the latest generation is a uniformly diapausing one. In the early part of the season, however, there is some evidence in Hebecnema that the progeny of the older flies of the first generation began to show a diapause tendency. The diapausing tendency is associated in the laboratory with a retardation in developmental rate in those individuals which escape diapause. It is reasonable to assume that a slower rate in the field (not due to actual temperature conditions) indicates the same. Figures 33 and 34 show examples of retarded development of some individuals in populations where diapause is incipient or occurring. This is particularly well marked in the Hebecnema populations originating from eggs of 22 June (Fig. 33). These were laid by flies of at least 1 month old - the end of the first generation. In the population of 29th June, the bulk of which is the progeny of 2nd generation flies, two individuals completed development with delay and a few actually entered diapause. These/
These also are probably the progeny of even older 1st generation flies. It seems likely, therefore, that in the first generation the diapausing tendency only began to appear in progeny of the oldest flies. The same could be true of the second generation but overlapping of generations obscures it.

Discussion of the peculiarities of life cycles of *Scopeuma*, *Orthellia* and *Eaeyphora* has been included in the appropriate foregoing sections. *Hagmatobia* has been reserved for the section which follows,
PART IV: HAEMATOBIA STIMULANS MG., AND THE MUSCID STOCK-PESTS.

Haematobia stimulans is the sole representative of the blood-sucking Muscidae encountered in the field in Midlothian. Its numbers here were much smaller than in Western Scotland, and never approached the numbers of 100 or more per beast recorded by HAMMER (1941) and figured by THOMSEN (1938) in Denmark. The largest infestation observed in 1953 was 15 per animal in mid-afternoon on 24th May. At other times the species occurred in twos and threes and rarely exceeded five. To collect adults for experimental work it was, therefore, necessary to make periodic excursions to Argyll where under favourable conditions infestations of 20-50 were regularly encountered. MUIRHEAD THOMSON (1937) records up to 25 per cow in Ayrshire.

Stomoxys calcitrans although abundant here was not found to extend its activity beyond the immediate neighbourhood of the farm buildings. Apparently in other countries, for example the U.S.A. (BISHOFF, 1929), and to a lesser extent in Denmark (HAMMER) this species regularly follows stock for quite long distances into the fields, a habit presumably associated with climatic differences. The other Stomoxydine species of the British Fauna, Lyperosia irritans was not observed, and apparently has not yet been recorded from Scotland. SMART (1939) states that it is uncommon and confined to the south, whereas H. stimulans is generally distributed throughout the British Isles.

As concerns their blood-sucking habits, there are several conflicting statements in the writings of earlier authors on Haematobia.
Haematobia. All workers are agreed that it is predominantly a cattle pest, but SEGUY(1923) states that "L'Homme est assez souvent piqué..." and NEVEU-LENAIRE(1933) goes further in saying "Elle pique également l'homme". In Scotland, present experience agrees with that of colleagues in the Department of Entomology, and with that of MUIRHEAD THOMSON(1937) who states "... despite innumerable opportunities, I have never been bitten..." HAMMER observed only a few on horses in the presence of cattle, while MUIRHEAD THOMSON found none on horses. Our experience is in agreement with HAMMER's in that they are scarce on horses grazing areas in common with cows. In the absence of cattle in early May 1952 Haematobia was quite frequent on horses in Midlothian. Dr. J.A. Campbell and Mr. J.D. Matthew (verbal information) found horses regularly attacked in Orkney in June 1949; the cattle here being turned out to graze at a much later date than in south Scotland.

The second point of difference arises from the statement by BEZZI(1911) that only the females suck blood from cattle. This is repeated by SEGUY(1923). HAMMER apparently does not agree with the absolute denial that the males never occur on cattle, but he agrees with BEZZI to the extent that Haematobia is unique among the Stomoxynidae in that the males spend most of their time away from the cattle. MUIRHEAD THOMSON asserts that "Both males and females, with the latter predominating, occur commonly on the cow...Males and females swollen with blood are frequently seen on wooden gates etc..." The present investigation gives complete confirmation of MUIRHEAD THOMSON's findings,
findings, and offers a basis for the apparently contradictory findings of the earlier workers (vide infra).

All earlier authors are agreed that Halmatobia is reluctant to enter buildings. They were regularly observed to follow the cattle herd, but when the animals entered the byre the flies quitted them and remained on the outside walls and door of the building. In contrast, Eyperosia irritans was readily collected from cows in the byre at a Berkshire farm.

In the two years 1952 and 3 the fly was first observed at the beginning of May, the dates being 5 May 1952, and 2 May 1953. Muirhead Thomson was impressed by the constancy of the first dates of appearance, namely 5th and 10th May in two consecutive years. These Ayrshire dates correspond very closely to our Midlothian ones, but with one important difference between them. Whereas Muirhead Thomson did not observe the flies on stock until the end of May, although cows were in the field from the first or second week of that month, in Midlothian it was on stock that they were first observed, and they were continuously present on stock thereafter. This suggests that in this area eclosion of adults from overwintered pupae (not larvae as Muirhead Thomson presumed) was followed quite soon by their feeding, and no evidence was found for the long interval implied by Muirhead Thomson's observations. In the laboratory, flies of both sexes accepted blood quite readily within 48 hours of their emergence.

The first observation of flies on dung was on 21st May 1953, nineteen days after flies were seen in the field, and eggs were not seen until 24th May, 22 days from the first appearance/
appearance of flies. The preoviposition period in the laboratory was from three to four weeks.

Both sexes visit cow droppings where they suck the fluid parts. They were never seen to mate at this or any other situation in the present work. HAMMER, who reports their mating on one occasion, appears to be the only worker to have observed the phenomenon. The males, according to him, congregate at certain chosen sites and await the approach of females when they all take to flight (cf. Dasyphora p. 88).

The gravid female lays her eggs singly, or occasionally in pairs, near the edge of freshly-dropped pats. Six was the largest number seen on a single pat laid by one female. They arrive at the pat almost as soon as it is dropped and rarely remain there (nor are others attracted) after about 5-6 minutes. Occasional flies seen by this time (in the early season) were disturbed by the newly arrived Scopeuma and failed to lay. The speed with which the females arrive at newly dropped pats is remarkable. Scopeuma which can be watched approaching the pats upwind takes several minutes to arrive, but Haematobia like (but slightly slower than) Lyperosia arrives almost instantaneously. Since Haematobia is regularly observed resting without feeding on the flanks and shoulders of cattle, it seems probable that they are awaiting the opportunity to lay eggs, and that they are primarily attracted to the dropping via the cow. The white eggs are completely buried in the surface layer of the dung. ZIMIN (1951) apparently overlooks PORCHINSKII's own correction (1913) of his earlier (1910) mistake in describing the eggs as reddish, when drawing/
drawing attention to that worker's probable confusion of
Haematobia with Lyperosia.

There is no evidence as to the frequency of oviposition
in the field, but MUIRHEAD THOMSON refers to the regularity
with which captured females lay egg-batches of very constant
number (25-29), which he believes to be the full complement,
when confined in tubes in the dark, and states that the
stimulus to oviposit is very strong, thereby implying that
oviposition is a comparatively rapid process. He gives no
evidence as to whether or not further egg batches are developed.
When wild females are brought into the laboratory, they do tend
to lay all their developed eggs in a batch in the course of
from 10-15 minutes, but when fed (vide infra) they are readily
induced after some 7-14 days to lay further egg batches. Some
individuals are reluctant when newly captured to oviposit but
appear to be encouraged to lay in the dark by intermittent
exposure for 10 minute periods to bright light. Their failure
to lay in the light is presumed to be due to inhibition by
their active flight under these conditions. Their egg-batches
were not found to be so regular in number as MUIRHEAD THOMSON
reports: a random group of 22 wild females may be quoted
which laid 35, 26, 22, 22, 21, 20, 20, 16, 16, 16, 15, 11, 11,
11, 11, 11, 11, 10, 8, 5, 3, 3, eggs respectively. Females
bred and maintained in the laboratory laid very many more eggs
during the course of their life, although they were unmated and
the eggs were infertile. The most fecund individual observed
had the following history:-

0 days/
0 days  Female emerged (after 19 days preimaginal development at 23°C)
1-2 days  Began feeding
25 days  First oviposition  Egg batch = 38 eggs
+ 11 days  Second "  " = 25 eggs
+ 14 days  Third "  " = 29 eggs
+ 8 days  Fourth "  " = 32 eggs
+ 8 days  Fifth "  " = 38 eggs
+ 14 days  Died.

Total imaginal life 80 days  Total 160 eggs.

This individual was kept in isolation in a 21b. Kilner Jar at room temperature (15-16°C mean) and fed daily. On the first occasion the egg batch was laid within 30 minutes; on subsequent occasions the actual oviposition was not observed, but definitely occurred within a few hours. It is difficult to see how the fly with its characteristic oviposition habit could possibly find the opportunities to lay all its developed eggs within so short a period as it does in the laboratory. It seems probable that this habit of depositing a batch of eggs is abnormal; it does not take place under normal conditions, and it is probably provoked by abnormal stimuli. It is, therefore, most likely that the fly in the field takes longer to lay its complement of eggs than observations on captured flies suggest.

The method developed by Mr. L.C. Stones* of the Cooper Technical Bureau for the laboratory rearing of Stomoxys calcitrans was employed for the maintenance of Haematobia stimulans. Adult flies were kept in boxes of the type shown in figure 38 and fed on defibrinated ox-blood and diluted ox-dung supplied in tubes with their open ends resting on the perforated zinc slide. The flies were attracted to the feeding tubes.

* To whom thanks are due for permission to use unpublished information.
FIGURE 38. Feeding box, and feeding jar used for laboratory maintenance of *Haematobia stimulans.*
tubes by darkening the front of the box and illuminating the tubes. To maintain individuals in isolation Kilner Jars with perforated zinc tops and feeding tube attachment were found invaluable (Fig. 38). Both species will feed readily and deposit eggs under these conditions, but whereas *Stomoxys* eggs remain viable for quite long periods and can be collected from the sides of the box each day. *Haematobia* eggs (from captured wild females) desiccate with exceptional rapidity, and only those dropped on a moistened cloth on the floor of the box can be used. (A collection of *Lyperosia* on one occasion was placed in one of these boxes, but was unfortunately lost through the too large perforations in the zinc. They were, however, observed to feed and it is believed that *Lyperosia* adults could also be kept in this way).

*Stomoxys calcitrans* mates and breeds readily under laboratory conditions and can be reared quite easily on artificial breeding media. When testing the method, this species was bred through several generations without any difficulty. Attempts to breed *Haematobia* ended uniformly in failure on account of their complete refusal to mate in captivity under any conditions of light, temperature, humidity and space (They were allowed the freedom of a room 12 ft x 6 ft on occasion). Furthermore, it is a relatively difficult problem to raise *Haematobia* larvae to maturity under laboratory conditions (as Muterhead Thomson (1937) and Bro Larsen & Thomsen (1940) have already pointed out). They failed to develop in any medium other than fresh cow-dung, but even in this medium a large proportion/
proportion of failures was encountered. In spite of their pronounced mobility and activity (cf. PORCHINSKII, 1910) the larvae are quite inept at penetrating and burrowing in compact dung except of the most fluid consistency. They are more successful in the presence of other insects which break up and mine the dung (BRO LARSEN et al. used Aphodius sp.), or when the dung is tunneled by needle or wire "pricks". Of the flies raised in pure culture in the laboratory (15-16, or 23°C) many were distinctly undersized (cf. BRO LARSEN et al.), a probable indication of the imperfect conditions.

The series of cow-pats exposed to natural oviposition in the field in 1952 produced disappointingly few flies of this species. Out of 87 pats kept under cones, only 9 flies were obtained. These were developed from eggs of 4 June - 2, 24 July - 1, and 25 August-6. Three of the last date over-wintered as pupae in diapause in the field, while the other three, transferred straight away to 23°C, developed without delay. In 1953, pats were regularly infested with eggs from wild females maintained in the laboratory. Aliquot samples of the batches were reserved for viability tests. In all, 47 pats were infested between May and July about 700 eggs in groups of from 10 to 25. Again the emergence rate of adult flies was most disappointing. Throughout the year from pats artifically infested and/or naturally infested only 8 adults were obtained from 160 pats kept in the field, and 30 from 62 pats kept at 23°C (23 of these would have entered diapause under field conditions).
From such results, it is clearly impossible to attempt a recognition of the life-cycle. Fortunately, the incidence of flies in the field offers some assistance in this connection.

In its broad outlines the life-cycle resembles that of *Hebecnema*, in that under field conditions its preimaginal development is quite rapid, and in the late autumn there is a maternally induced pupal diapause whose development may sometimes be prevented by high temperature. For example, at 23°C the retardation in the developmental rate of individuals derived from eggs of September-caught females was slight: at room temperature diapause was manifest in about 2/3rds of the population. From eggs of this period, 24 adults developed in from 28 to 35 days while 52 had a preimaginal life of from 128 days to 220 days. These findings suggest a multivoltine life-cycle of the *Hebecnema* type.

The Danish workers are unanimous in describing the occurrence of *Haematobia* adults, on stock and dung as bimodal, with early Summer and Autumn peaks. Thomsen(1938) considers the second peak as containing the more numerous population and gives the species the popular Danish name "Efterårs-Stikfluen". (autumn biting-fly). In summer they record the fly as scarce or even absent. It is, thus, comparable in its incidence to *Scopeuma stercorarium*, although the peaks are not so widely separated as in that species. They seek to explain the incidence along similar lines to their explanation of *Scopeuma*'s incidence, namely by depressed activity or increased mortality due to high summer temperature. Bro Larsen & Thomsen(1940) write "*Haematobia*'s slight resistance to temperatures above 30°C may/
may probably be the cause of the characteristical summer depression of this species... It is probable... that a number of pupae are simply killed by the heat, and that the adults hatched are mainly debilitated individuals with reduced fertility". HAMMER (1941), after considering and rejecting an alternative hypothesis that the species has two main generations with aestivating and hibernating pupae respectively, adopts more or less the same viewpoint. The difficulty of such a hypothesis lies in the question, where do the autumn populations come from? This has already been emphasised in connection with Scopeuma (p. 56), it applies with added force to this species which has a much lower reproductive potential.

The Danish hypothesis is further based on laboratory evidence, that Haematobia has a lower threshold (10.7°C) a lower optimum (28.3°C) (BRO LARSEN & THOMSEN); and a lower larval preferendum 15.4 to 26.4°C with a mode between 19° & 22.8°C, (THOMSEN & THOMSEN 1937) than the other Muscids studied. This is particularly marked in comparison with Lyperosia which is also confined to the cow-pat biotope, and which has a mid-summer peak of incidence. These workers consider Lyperosia to be a warm-adapted and Haematobia to be a cold-adapted species. They cite geographical distribution as further evidence. While this may be true in a broad sense, there is reason to doubt the validity of the figures upon which the view is based. First the thermal preferendum of Haematobia larvae is so high that it is difficult to appreciate its significance vis-à-vis the ecology of the species. Secondly the figures quoted as threshold/
FIGURE 39.
Haematobia stimulans - Effect of temperature on rate of preimaginal development.
threshold values are far too high to be applicable to the development in the field in Scotland. On the basis of BRO LARSEN & THOMSEN's figures (Threshold 10.7 and Constant 189) Haematobia would require some 90 days to complete development at the mean summer temperatures recorded in Midlothian.

Figure 39 shows the development rate/temperature relationship obtained from the results in the present work, and this indicates a probable threshold of about 5°C. BRO LARSEN & THOMSEN's own results throw grave doubt upon their conclusions, since they observed complete development at 9.5°C and larval development and pupation at 7.5°C. It has been mentioned above (p 42) that their threshold value for total preimaginal development of Musca is markedly higher than that obtained by another worker. Further evidence may be mentioned in the temperature characteristics of incubation of eggs. The thresholds calculated from the data of various workers, assuming a linear temperature relationship, are:

**Lyperosia**
- From MELVIN & BECK (1931) - 2 points only - 11.0°C.
- From BRO LARSEN & THOMSEN - 5 scattered points - 11.0°C.
- From MELVIN (1934) - 3 points - 6.5°C.

**Stomoxys**
- BRO LARSEN & THOMSEN's calculation - 12.4°C.
- From MELVIN (1931) - 5.0°C.

**Haematobia**
- Present investigation - two points - 5°C.

This last is based upon means of 25 hours at 23°C and 40 hours at c.15°C. BRO LARSEN & THOMSEN give one reliable point namely 22 hours at 25°C which is in agreement with our findings, and two approximate points of 32 hours at 21°C and
3 days at 16° which are considerably lower than would be expected from the present conclusions.

It must be accepted that the laboratory evidence concerning the temperature relations of the various species is too conflicting to be of much significance in the interpretation of field phenomena. Nevertheless, it is believed that the threshold value for Haematobia at least is much lower than the Danish work suggests, and is of the same order as that found for other species of the biotope.

In Britain, the evidence for a summer decline in numbers of Haematobia is not so positive as in Denmark. MUIRHEAD THOMSON (1937) makes no reference to the phenomenon. In Midlothian, there was a definite decline on the cows in fields A-C, but a less marked one on the calves in the park (vide fig. 1). For example on 24th July 14 per beast were seen in the park, as against the year's maximum of 15 in late May. (In May the numbers were continuously high for a longer period than in July). In the fields the flies were present in only ones and twos at this time. Now HAMMER also found evidence of Haematobia activity in July and August which he regards as exceptional on one of his farms, where woodland shade was abundant. (THOMSEN & HAMMER (1936) also record an exceptional oviposition on horse dung in late July). HAMMER assumes that cooler shade conditions facilitate survival, and recognises that Haematobia is always more abundant near woodland than in the open. It is of interest to mention the depression of Lyperosia activity in summer in Texas (MARLATT, 1910) and Puerto Rico (WOLCOTT, quoted by MYERS, 1938). MYERS also believes/
believes that a depression occurs in Haiti and states that the fly becomes abundant in the rainy season both there and in Puerto Rico.

It seems probable that **Haematobia** which in Britain is more abundant in the moister west than in the drier east, and is more abundant in wooded than in open areas is limited by humidity rather than temperature considerations, and that the depression of cattle-infestation in summer is due not to a reduced population but to a depressed activity such as we have presumed for **Scopeuma**, i.e. not that high temperature kills them, but that low humidities inactivate them. This could also account for the even greater depression found in the continental summer.

As regards the probable course of its life cycle three main types of evidence may be used and they all lead to the conclusion that the species has 3 generations, but the succession may be modified by summer inactivation in open localities.

(1) The period of activity (blood-sucking) extends from early May to late October and is rather longer than either **Muirhead Thomson** (1937) or **Smart** (1938) suggest. Two main periods of incidence May-early June, and September-October are separated by a period of relatively lower incidence. The intervening period is interrupted in shaded regions by a smaller peak of incidence in mid - late July. These peaks are thought to represent the adult activity of three principal generations.

(2) The scanty data on adult emergence in the field are in agreement with a three generation hypothesis. Thus:

Eggs/
Eggs laid          Adults emerged

7 July 1952       2 August 1952 (1) = Third gen. 1952
25 August 1952    Late May 1953 (3) = First gen. 1953
6 June 1953       3, 9 July 1953 (2) = Second gen. 1953
29 June 1953      8 August 1953 (1) = ?
7-20 July 1953    10-28 August 1953 (4) = Third gen. 1953

Individuals which would have overwintered to emerge in 1954 were bred in the laboratory from pats of the following dates:


(3) The sex ratios of samples captured when feeding on cattle vary significantly. In the peak periods of May-June and July males are frequent, but in the third, much longer, period of September-October males become markedly scarce. A series of small samples collected at intervals throughout the year in 1949 (Campbell & Matthew - unpublished) illustrates the variation in the sex ratio.

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th>Females</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>May - June</td>
<td>35</td>
<td>56</td>
<td>(1 : 1.4)</td>
</tr>
<tr>
<td>(first date 1.5.49)</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late June - early July</td>
<td>12</td>
<td>36</td>
<td>(1 : 3.0)</td>
</tr>
<tr>
<td>Mid - late July</td>
<td>14</td>
<td>25</td>
<td>(1 : 1.8)</td>
</tr>
<tr>
<td>August</td>
<td>2</td>
<td>18</td>
<td>(1 : 9.0)</td>
</tr>
<tr>
<td>September</td>
<td>6</td>
<td>12</td>
<td>(1 : 2.0)</td>
</tr>
<tr>
<td>October</td>
<td>1</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>(last date 24.10.49)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The males are most numerous in the three periods May-June,
June, mid-late July and September, the periods presumed from the other evidence to be the main times of incidence of the three generations.

The males are evidently less long-lived than females (cf. *Hylemya* spp.) and their occurrence on the stock probably indicates the presence of a young population. In the autumn especially, males disappear to leave a long-lived almost pure female population, and since the autumn infestations are more numerous in some regions (e.g. Denmark) this might lead to the impression that males do not often bite.

The problem remains concerning the course of events where a July peak is not evident. This is explicable on the basis that the bulk of the second generation flies aestivate and the minority produce the third generation. In this case the autumn infestation would be composed of third generation males, and third and second generation females. Laboratory evidence on the relative longevity of bred males and females support the hypothesis.

An interesting piece of evidence for the possible heterogeneous nature of the autumn culmination is to hand in the course of mortality of a laboratory maintained random sample of flies collected on 29 Sept. 1953.

<table>
<thead>
<tr>
<th>Date</th>
<th>Males (alive)</th>
<th>Males (Mortality)</th>
<th>Females (alive)</th>
<th>Females (Mortality)</th>
</tr>
</thead>
<tbody>
<tr>
<td>29 Sept.</td>
<td>9</td>
<td></td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>9 Oct.</td>
<td>7</td>
<td>(2)</td>
<td>23</td>
<td>(46)</td>
</tr>
<tr>
<td>15 Oct.</td>
<td>4</td>
<td>(3)</td>
<td>16</td>
<td>(7)</td>
</tr>
<tr>
<td>24 Oct.</td>
<td>2</td>
<td>(2)</td>
<td>9</td>
<td>(7)</td>
</tr>
<tr>
<td>31 Oct.</td>
<td>0</td>
<td>(2)</td>
<td>5</td>
<td>(4)</td>
</tr>
<tr>
<td>8 Nov.</td>
<td>-</td>
<td></td>
<td>3</td>
<td>(2)</td>
</tr>
<tr>
<td>12 Nov.</td>
<td>-</td>
<td></td>
<td>0</td>
<td>(3)</td>
</tr>
</tbody>
</table>

In the first 10 days the female mortality was considerably higher.
higher than the male mortality, thereafter the males died more rapidly than the females. This is strong presumptive evidence for the view that while the males were all young, the females included a high proportion (about 50% at least) of old individuals.

(It is of interest to note that Haemotobia is absent from the Hertfordshire list of Laurence (1953) but Lyperosia is included).

The stomoxydine species are not alone among the Muscidae in contributing to the fly-pest problem of cattle in Scotland. In fact, the Stomoxidini in the field probably take second place to the non-biting species in their nuisance value. The most important species, in respect of numbers and disturbance of cows is Hydrotaea irritans, a species which is not a normal cow-pat breeder. Four cow-pat breeders contribute the problem, namely, Hydrotaea albipuncta, H. militaris, H. meteorica and Morellia simplex. They are frequently observed clustered around wounds, or blood points left by stomoxydine and tabanid biters, but probably cause the greatest annoyance to the animals by their habit of congregating on the head and feeding on eye exudates. Fig. 40 illustrates this feature which is in marked contrast to the restriction of Haemotobia to the shoulders, flanks and legs.
FIGURE 40.
Morellia sp. (probably simplex) and Hydrotaea spp. (mainly irritans) on cow, July 1953.
SUMMARY.

1. Observations on the insect fauna of cow-droppings in the field in Midlothian in 1952 and 3 are recorded. Attention was mainly given to the Diptera and of them to the family Muscidae. Newly-dropped pats were exposed to fly activity for periods of 24 or 48 hours then transferred to an enclosure and isolated under perforated zinc cone-traps. Other pats were transferred to the laboratory and maintained at 23°C or room-temperature.

2. 93 species of Diptera were identified breeding in the pabulum, including Nematocera-10 species, Brachycera - 19 species, Cyclorrhapha - 64 species (of which 43 were Muscidae). 23 of these species were recorded as common. The method of trapping was not satisfactory for the smaller flies, and the list is recognised as deficient in respect of Sphaeroceridae, Sepsidae and Nematocera. Only the commonest Coleoptera were identified and they numbered 14 species.

3. The seasonal course of the life-cycles of 20 of the principal dipterous species was studied and is discussed in detail. The main features include:

   a) The time/temperature relations are linear over the medial range, and the threshold for preimaginal development lies in the region of 5°C for most species.

   b) The flies overwinter as larvae or pupae in diapause according to the species, and in two cases, Orthellia and Dasyphora, as adults.

   c) The factors which induce diapause are not clearly understood, but are complex, and in no case is low temperature
a direct causal factor. There is evidence that the state is maternally induced

e) The events of the two years for any given species correspond very closely.

f) The fauna includes, univoltine, bivoltine and multivoltine species. In the multivoltine species no further generations are produced after about 7-14th August since diapause becomes universal in populations derived from eggs laid later than these dates.

g) In addition to a preimaginal diapause, three species, _Polistes lardaria_, _Scopeuma stercorarium_, and _Haematobia stimulans_ are believed to undergo an imaginal inactivation characterised by a prolonged preoviposition period in summer.

4. An attempt was made to breed _Haematobia stimulans_ in the laboratory, but although adults could be maintained for long periods (up to 80 days) and captured wild ones could be induced to lay viable eggs, it failed through the refusal of the flies to mate.

5. Although the significance of competition between coprophages, the balance between them and carnivores, and of parasitism (Ichneumonids, Braconids, and Chaleids were recovered in small numbers) was recognised a review of the synecology of the biotope could not be attempted in the absence of information of the size of Coleopterous populations, the predators among which are probably the most important biotic factor in regulating the size of fly populations. The trapping method used was unsuited to this purpose.
ACKNOWLEDGEMENTS.

I wish to thank the Egyptian Education Bureau with whose financial assistance this work was carried out. I am greatly indebted to Mr. J.W. McHardy and his colleagues of the Department of Agricultural & Forest Entomology, and in particular to Dr. J. Allan Campbell for continued and invaluable help. I also wish to thank Mr. A.R. Waterston of the Royal Scottish Museum, and Dr. J. MacLeod of the Ministry of Agriculture and Fisheries for putting much material at my disposal, and The Edinburgh Centre of Rural Economy, the West of Scotland Agricultural College and several farmers for permission to work on their land and collect material from their livestock.
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Publication marked * not seen, those marked otherwise known through translation by Dr. C. Rayski (a) and Dr. J. Allan Campbell (b) to whom thanks are due.