CATTLE DROPPINGS AS ECOLOGICAL UNITS

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TABLE OF CONTENTS

PAGE

Introduction 277

Habitat and Methods 277

Account of Weather and Its Possible Effect 277

Systematic Table of Arthropods Collected 278

Surface Succession During Summer 279

Surface Succession During Spring and Fall 282

Hibernating Insects in Fresh Droppings 283

Physical Changes of Droppings 283

The Microsere and Its Stages 283

Species Components of the First Microseral Stage 284

Species Components of the Second Microseral Stage 292

Species Components of the Third Microseral Stage 294

Irregular Influents 296

Relative Abundance of Larvae of the First Microseral Stage 296

Ecological Positions of Larvae 296

Bovine Dung as a Structural Unit of the Prairie 297

Summary 297

Bibliography 298

CATTLE DROPPINGS AS ECOLOGICAL UNITS

INTRODUCTION

This study is presented as a contribution to a knowledge of the succession and relative numbers of animals as illustrated by the assembly in the dung of cattle in open pastures.

Choice of this microhabitat was governed by the faith that small, fast-changing environments, which harbor a few familiar insects, can be made to supply quick knowledge concerning principles of succession; that a detailed structural study of communities is necessary to a better understanding of their make-up and that possibility of experimental manipulation of its fauna, based on knowledge of its normal succession and numbers, is of great value.

Since a knowledge of life cycles and habits is fundamental to an understanding of presence and numbers of animals, it is supplied in some detail for each species found in the early stages of change which dung undergoes.

The author expresses his gratitude to Professor C. L. Metcalf, of the Department of Entomology, and to Professor V. E. Shelford, of the Department of Zoology, for suggestions and support during the course of this investigation; and to Dr. H. H. Ross of the Illinois Natural History Survey for much advice, technical help and encouragement.

Gratitude is tendered to each of the following taxonomists, without whose experience and patience in naming selected specimens this study would have been impossible: J. M. Aldrich, U. S. National Museum, Diptera; H. S. Barber, U. S. Department of Agriculture, Ptiliidae; W. J. Brown, Canadian Department of Agriculture, Aphodiinae; H. E. Ewing, U. S. Department of Agriculture, Acarina; J. W. Folsom, U. S. Department of Agriculture, Collembola; C. A. Frost, Framingham, Massachusetts, Coleoptera; A. B. Gahan, U. S. Department of Agriculture, Cynipiodea; C. T. Greene, U. S. Department of Agriculture, Psychodidae; W. P. Hayes, University of Illinois, Coprinae and Geotrupinae; O. A. Johannsen, New York State College of Agriculture, Chironomidae; C. F. W. Muesebeck, U. S. National Museum, Cynipoidea; H. H. Ross, Illinois Natural History Survey, Diptera and Hymenoptera; L. H. Weld, Figitidae.

HABITAT AND METHODS

The following notes on succession and numbers of bucoprophilous insects, i.e., those having a liking for cow dung, were drawn almost entirely from droppings of cattle in unwooded pastures at Urbana, Illinois, between October 1, 1930 and January 1, 1934. The notes on surface populations were drawn from droppings between 18 centimeters and 23 centimeters in diameter, a normal size; and those on internal populations were drawn from 1000 cubic centimeters of dung, which in most cases included from one half to one third of the droppings. The surface counts were made on sunny days when there was relatively little wind. Very strong wind affected populations greatly and it was not possible to make a complete study under such conditions.

Estimates of internal populations were generally obtained by counting insects reared in the laboratory to any stage which separated itself from dung. For this purpose the dung was placed on a wire holder in a glass cage covered with a paper towel. Since some species like Aphodius beetles separated out completely within a few hours, and others like Sepsis and anthomyid flies, only after some deaths accompanying complete growth and development, the count is somewhat differential. In order to guard against abnormal death rates, the dung was placed in cages shortly before the particular group of species for study were due to emerge.

The larger species were frequently picked out by hand with equal accuracy, but with greater loss of time.

In order to get a preliminary estimate of the relation of populations to habitat, Dr. H. H. Ross and the writer examined a considerable number of cattle droppings under dense shade on low moist ground in a swamp in Johnson County, Illinois, and others on dry sunny hillside pastures in the same county.

Droppings on the sunny hillsides had approximately the same fly fauna found so familiar at Urbana, namely, horn flies (Haematobia); sarcophagid flies; false bluebottles (Cryptolucilia); and others. The adult flies were numerous on the fresh droppings and their larvae were common in the droppings. Sepsis flies swarmed over many of the droppings. The tumblebug (Canthon) was abundant.

Droppings in the shady swamp were extremely different. No horn flies were bred from them; sarcophagid flies were not ovipositing in numbers so familiar in the sun; false blowflies were absent, and Sepsis flies were not swarming over the droppings. The surface of the droppings had a dearth of fauna.

Inside, instead of the larvae named above, was a population of entirely different make-up. *Morellia micans* was the most numerous muscoid maggot, apparently replacing false blowfly and sarcophagid maggots. Aphodius larvae were abundant. So also were larvae of the fly Rhyphus, probably *punctatus*.

Only in the later stages did the fauna resemble that of the dry pastures. Stratiomyiid larvae and pupae were abundant in these but they were *Geosargus elegans* Lw., not *G. cuprarius* Linn.

ACCOUNT OF WEATHER AND ITS POSSIBLE EFFECT

During the period of this investigation, from October 1, 1930 to January 1, 1934, the weather was dry and warm, remarkably so in 1930.

The following accounts taken from the United States Department of Agriculture weather report for the Illinois section pictures the trend of the weather.

"Never before [1930] so far as climatological records show, has there been a year of such diverse temperature extremes or with a drought of such severity." "The central division [of Illinois] suffered severely. January was cold, wet, and snowy. February was unusually mild with light snowfall. A remarkably severe snowstorm occurred on March 25th and 26th. April was warm. During July and August there were numerous days with the temperature exceeding 100°." Root (1930).

"This year 1931 was unusually warm, the temperature being above normal in all months but March and May. January, February, September, November, and December show excesses of 6° to 9°. In general, precipitation was below normal the first half of the year, and above the latter half. For the state it was the warmest year except 1921." Root (1931).

"Temperature, considering the entire year [1932] averaged slightly above normal; however, there were unusual contrasts. January and February were the mildest first two months of the year in the climatological history of the state. March averaged not only colder than any month of the winter of 1931-1932, but was the fourth coldest month of the year. Mostly seasonable temperatures were the general rule from April to November inclusive. November averaged unseasonably cold, while in December temperature contrasts were marked. The precipitation average for 1932 for the state was slightly in excess of normal, this excess being due to considerably heavier precipitation in the southern than in the northern divisions in January, September, and December." Holcomb (1932).

"The year 1933 as a whole was warm and dry, with snowfall only approximately half of the normal. January was exceptionally mild, and June, September, and December also averaged much above normal. It was the warmest June in 56 years. There was an exceptionally large number of days with 90° or higher. October was the only month of the year with temperature definitely below normal, although the first half of February was severely cold which was largely offset by mildness the latter part of that month. An exceptionally wet spring was followed by persistent deficiency of precipitation which continued quite generally during the remainder of the year." Holcomb (1933).

Since the observations on bucoprophilous insects were intended to discover the order of succession and relative numbers, no elaborate effort was made to discover how weather affected their numbers. The above weather records are offered only to show whether or not the conditions were extreme or otherwise.

That the faunal composition may change greatly even within the range of weather changes that one regards as not very extreme, is shown by the fact that droppings remained in moist condition much longer during the cool rainy summer of 1942 than during the period described above; this permitted Sepsis and Leptocera to breed continuously in a given dropping for a week or more longer than they were found to breed in a given dropping during the period when most of this study was being carried on.

There are certain indications, not proven however, that *Sarcophaga lherminieri* might be more common in droppings at Urbana during 1942, than when the writer did most of his work. Aldrich, 1916, stated that this form "seems to become rare southward at about the latitude of Washington and the Ohio River," and that farther south it is replaced by the variety known at that time as *ochracea* and now known as *sueta*. In our own collecting Dr. Ross and I have found *lherminieri* with greater ease in northern than in southern Illinois.

It is my impression that the false bluebottle fares better during dry than during wet seasons and Pratt, 1912, stated that dry weather prevents development of the horn fly whereas a series of showers invariably brought about a sudden and conspicuous increase in numbers.

SYSTEMATIC TABLE OF ARTHROPODS COLLECTED

ACARINA — PAGE

Parasitidae

Parasitus sp. 292

COLLEMBOLA

Achorutes maturus Folsom 296

Proisotoma immersa (Folsom) 296

COLEOPTERA

Hydrophilidae

Sphaeridium scarabaeoides (Linnaeus) 290

Sphaeridium bipustulatum Fabricius 293

Cercyon haemorrhoidalis (Fabricius) 294

Cercyon pygmaeus (Illiger) 294

Cercyon quisquillius (Linnaeus) 293

Staphylinidae

Oxytelus sp. 00

Platystethus americanus Erichson 291

Philonthus tetragonocephalus Notman 294

Philonthus varians (Paykull) 294

Quedius capucinus (Gravenhorst) 00

Tachyporus jocosus Say 00

Metaxaya sp. 00

Dimetrota recondita Erichson 00

Falagria dissecta Erichson 00

Baryodma bimaculata Gravenhorst 00

Ptiliidae

Acrotrichis aspera (Harold) 296

Histeridae

Hister abbreviatus Fabricius 293

Hister americanus Paykull 293

Scarabaeidae

Canthon laevis (Drury) 296

Pinotus carolinus (Linnaeus) 296

Copris tullius Oliver 296

Onthophagus hecate Panzer 296

Onthophagus pennsylvanicus Harold 296

Aphodius terminalis Say 292

Aphodius haemorrhoidalis (Linnaeus) 295

Aphodius fimetarius (Linnaeus) 294

Aphodius ruricola Melsheimer 295

Aphodius granarius (Linnaeus) 292

Aphodius vittatus Say 292

Aphodius sterocorosus Melsheimer 292

Aphodius bicolor Say 292

Aphodius distinctus Mueller 291

Aphodius femoralis Say 291

Ataenius strigatus (Say) 292

Geotrupes splendidus (Fabricius) 296

Geotrupes blackburni (Fabricius) 296

SYSTEMATIC TABLE OF ARTHROPODS COLLECTED
(Continued)

PAGE

Ligyrus gibbosus De Geer....296
Euphoria inda (Linnaeus)....295

DIPTERA

Rhyphidae
Rhyphus near *punctatus* (Fabricius).... 00

Tipulidae
Tipula bicornis Forbes....296

Psychodidae
Psychoda cinerea Banks....296

Chironomidae
Smittia sterocorarius De Geer....296

Cecidomyiidae
Monardia illinoensis Felt.... 00

Sciaridae
Sciara sp....296

Scatopsidae
Rhegmoclema atrata (Say)....296

Stratiomyiidae
Geosargus elegans Loew.... 00
Geosargus cuprarius (Linnaeus)....292
Geosargus viridis (Say)....293

Sarcophagidae
Sarcophaga sueta Van der Wulp....284
Sarcophaga lherminieri Desvoidy....285
Sarcophaga pusiola Van der Wulp....285
Sarcophaga ventricosa Van der Wulp....285
Sarcophaga stimulans Walker....285

Calliphoridae
Cochliomyia macellaria Fabricius....287

Muscidae
Haematobia irritans (Linnaeus)....284
Stomaxys calcitrans (Linnaeus)....287
Cryptolucilia caesarion Meigen =
Pseudopyrellia cornicina of authors....287
Musca domestica Linnaeus....286
Morellia micans (Macquart).... 00

Anthomyiidae
Myiospila meditabunda (Fabricius)....288
Hydrotaea armipes Fallen....287
Paregle cinerella (Fallen)....286
Hylemyia cilicrura (Rondani)....286

Borboridae
Leptocera sp....288
Coprophila equinus (Fallen)....289
Coprophila sp. undescribed....289
Borborus marmoratus Beck....289
Borborus geniculatus Macquart....289

Scatophagidae
Scatophaga furcata Say....289
Scatophaga sterocoraria (Linnaeus)....290

Lonchaeidae
Lonchaea polita Say....296

Sepsidae
Sepsis violacea Meigen....287

Drosophilidae
Drosophila busckii Coquillett....286

HYMENOPTERA

Alysiidae
Aphaereta muscae Ashmead....286
Asobara lineata Viereck....284
Idiasta or *Phaenocarpa* sp. undescribed....286

Diapriidae
Phaenopria sp....284

Figitidae
Xyalophora quinquelineata Say....285
Kleidotoma sp. undescribed....284
Figites sp....286

SURFACE SUCCESSION DURING SUMMER

Adult flies, parasitoid wasps, and beetles visit cattle droppings in numbers. Most of the beetles arrive singly or in small numbers, and soon enter the droppings so that only a few individuals, if any, may be seen on the surface at any given time. Stated in another way, the representation of any one species of beetle on the surface is likely to be discontinuous. Much the same condition has been found true of the parasitoid wasps.

Flies, on the other hand, are more numerous, usually attain continuous representation, and show a distinct and gradual increase to a peak of abundance followed by a decline. The peak occurs roughly about half way between the beginning of period representation (Fig. 1) and the end. The peaks are most evident early in the succession.

Some species reach this peak early, and others reach it late, but no two appear to reach their peaks at the same time, there being a definite succession of such peaks determined by the species involved.

During June, July, August, and part of September, such a surface succession on a new dropping begins with that constant attendant and pest of cattle, the horn fly, *Haematobia irritans,* which reaches its peak of abundance almost instantly and disappears entirely before two minutes have passed.

Details of its activity are well described by Riley and Howard (1889) who wrote "One animal was fortunately observed, from close quarters, in the act of passing her dung. As the operation commenced, forty or fifty of the flies moved from the flank to the back of the thigh near the 'milk mirror' and at the close of the operation they were seen to dart instantly to the dung and to move quickly over its surface, stopping but an instant to deposit an egg. Most of them had left the dung at the expiration of thirty seconds, while a few still remained at the expiration of a minute. Every individual had returned to the cow, however, in little more than a minute."

Many individuals are prepared for even faster action, for some move from the flank to the ankle to await the close of the operation.

The remainder of the succession determined by periods of abundance of common flies is shown in the accompanying table (Fig. 1.)

It often happens that a new cake is dropped near one or more older ones bearing flies which prefer the older dung for oviposition but which swarm to the new dropping, thereby introducing an apparent deviation from the order listed above. Observation will show that oviposition does not take place immediately and that the peak is not reached immediately even under these conditions. Early individuals of Cryptolucilia, for example, may actually arrive before Sarcophaga under such circumstances simply because they happened to be on nearby dung.

The nature of a succession depends somewhat on seasonal variation in the numbers of individuals of the different species concerned.

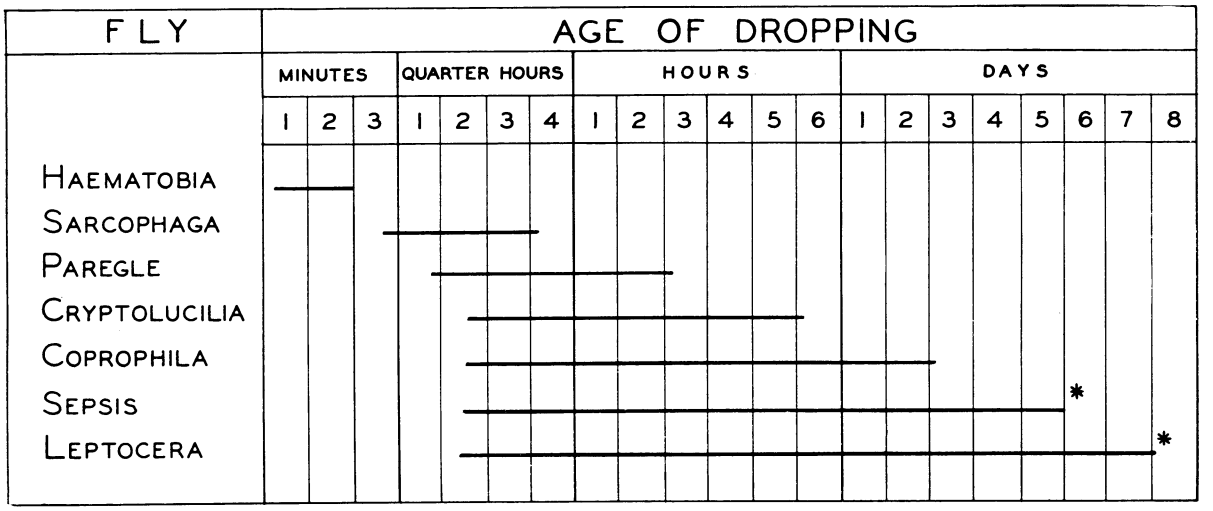

FIG. 1. Periods during which adult flies were present on droppings.

Haematobia is, for instance, the most available insect by position, and undoubtedly by its desire for freshness of the breeding medium; but when the beetle, *Aphodius distinctus,* flies in enormous numbers during the fall it is frequently present on a new dropping before the horn fly.

Such irregularity does not, however, apply to peaks of abundance. These succeed one another in definite order, whether the dung changes slowly or rapidly, even if the relative numbers of individuals of each species varies greatly.

A gradual increase in both numbers of species and numbers of individuals accompanies the physical changes and increment of time for somewhat over a week. From this time on a gradual decline takes place as the dung becomes very dry, or as it becomes more like the soil; though as it approaches the latter condition, it actually becomes available to a greater possible range of animals. When dropped in a forest, soil insects characteristic of woods invade it; when dropped in a field, soil insects characteristic of fields invade it.

In densely shaded woods, the physical changes noted above do not obtain. Rain affects the changes considerably.

After Haematobia adults have reached their peak in the cake, there follow abundance peaks for Sarcophaga, Paregle, and Cryptolucilia. The various species of Sarcophaga arrive at the cake at the same time and show little difference among themselves in succession; on this basis these different species of Sarcophaga appear to be ecological equivalents.

The other flies, *Sepsis violacea,* a small black slender fly, and *Leptocera* sp., a minute fly, reach their peak in three or four days, but have not been studied adequately to warrant more than descriptive summary beyond the first few hours. Rainfall, wind, sunshine, and humidity greatly affect the duration of visits by Sepsis and Leptocera.

Sepsis has been found to be uncommonly abundant during the latter part of April and in May. When a cake is in proper condition late in the first day or during the second day of exposure it may bear around 45 adults, but the number is highly variable due largely to diurnal rhythm. Leptocera, common throughout the season, builds up to a peak of over a hundred individuals during the first day of exposure of a dropping but presents such difficulty in counting due to the habit of hiding in crevices, that insufficient data have been gathered. Both of these flies are abundant early visitors which remain several days longer than any of the others. The passing of Leptocera from the surface marks the end of continuous surface representation by any insect.

DURATION OF SURFACE SUCCESSION

The succession sketched above, beginning with Haematobia and ending with Leptocera, usually requires from five to eight days (Fig. 1), depending upon the degree of wetness of the dung and the drying power of the weather. In one observed case thirty-five minutes passed before either Sarcophaga or Paregle found the surface sufficiently dry to attain continuous representation and to begin breeding. Many individuals of each species accumulated on nearby grass blades and occasional individuals tried the surface lightly from time to time but left immediately. When, however, the dung did become dry enough, Sarcophaga, delayed ten minutes, reached its peak at one hour and twenty minutes and was continuously present for three hours and thirty minutes. Pareglea reached its peak at one hour and forty minutes and Cryptolucilia reached its peak at around eight hours. The last, Leptocera, were present on the fifth day.

In another case when the dropping was relatively dry, the whole succession was telescoped, Sarcophaga having reached its peak in ten minutes, Paregle in forty-five minutes, Cryptolucilia in three hours, and Leptocera by the middle of the third day.

It is a common occurrence for cattle to drop dung around dusk when drying is slow. Small numbers of Haematobia oviposit if the evening is warm, but if

cool they do not oviposit. In either case, the dropping is frequently suitable for the succession to begin on the next day, with Sarcophaga or Paregle, but occasionally only with Cryptolucilia or later flies and beetles. Such a condition commonly accounts for much variation in future larval populations.

Dung frequently is so wet that, when dropped, it spreads thinly. Sarcophaga flies seem to avoid such droppings for some reason, but the Paregle usually lay great numbers of eggs in it before early drying kills the eggs and prevents Cryptolucilia from carrying on the succession.

TYPES OF POPULATION CHANGES

Comparison of numerical changes of these species show two well-defined types. One, illustrated by the activities of Haematobia, Paregle, Sarcophaga, and Cryptolucilia, is characterized by a relatively rapid rise to a peak population and a rapid decline; and the other, common to most of the other flies, is characterized by a relatively slow rise and a relatively slow decline.

It is important to note that those species with the shortest period of representation on the surface of a droppings are the early visitors with limited oviposition or larvaposition periods somewhat corresponding to relatively rapid changes in the early physical conditions of dung and that no species with such sudden changes in numbers has been found late in a succession. These species with relatively gradual fluctuations, Sepsis and Leptocera, may oviposit early, but early oviposition is not obligatory to them, their range or adaptability being greater than that of the early flies. Adults of these species are present on droppings for a week or even longer and evidently oviposit under the edges and in beetle runways during most of that time. The earlier stages in a succession are the most ephemeral while the later stages are the longer lasting.

INTERIOR SUCCESSION

Interior succession (Fig. 2) during the summer begins, like surface succession, with the larvae of Haematobia, the eggs of this species being the first insect life present. Before five minutes have elapsed, larvae of Sarcophaga are likely to be present, followed by eggs of Paregle, Sepsis, Cryptolucilia, and possibly Leptocera. The hydrophilid beetle, *Sphaeridium scarabaeoides*, soon arrives to oviposit and is followed in the next few days by others, mostly Aphodius and short-winged beetles, many of them carrying mites. The wasp, *Xyalophora quinquelineata*, arrives soon after Sarcophaga to parasitize its newly laid larvae, and is followed during the next few days by wasp-parasites of other flies. Over a hundred and fifty insects more or less characteristic of dung make up a complete succession in the weeks during which droppings gradually lose their individuality and become restored to the soil, and inhabited by soil animals.

Since this study was chosen in an effort to establish a near optimum balance between a study of the biologies of the inhabitants and their niche in the succession, it was limited, not too arbitrarily, to include that period in which Cryptolucilia or Sarcophaga maggots are present, which is about five days long during the summer, and which is here considered to constitute the first microseral stage of which these two flies are zoometers.

The two species were chosen because at least one of them is present at almost any time during the growing season; because they are considered to exert a large influence over the course of a succession by reason of their bulk, numbers, and activity; and because they are early species and cease their activity at very nearly the same time as do the early flies and beetles which live with them.

RELATIONS OF FLIES, BEETLES, AND PARASITOID WASPS

When a four-day-old dropping is opened, many larvae of flies, and adults and larvae of beetles are exposed. Staphylinid larvae and adults run wildly over the surface until they dash into a newly found burrow or crevice, while the slow-moving larvae of flies, and hydrophilid and histerid beetles are more likely to dig their way in.

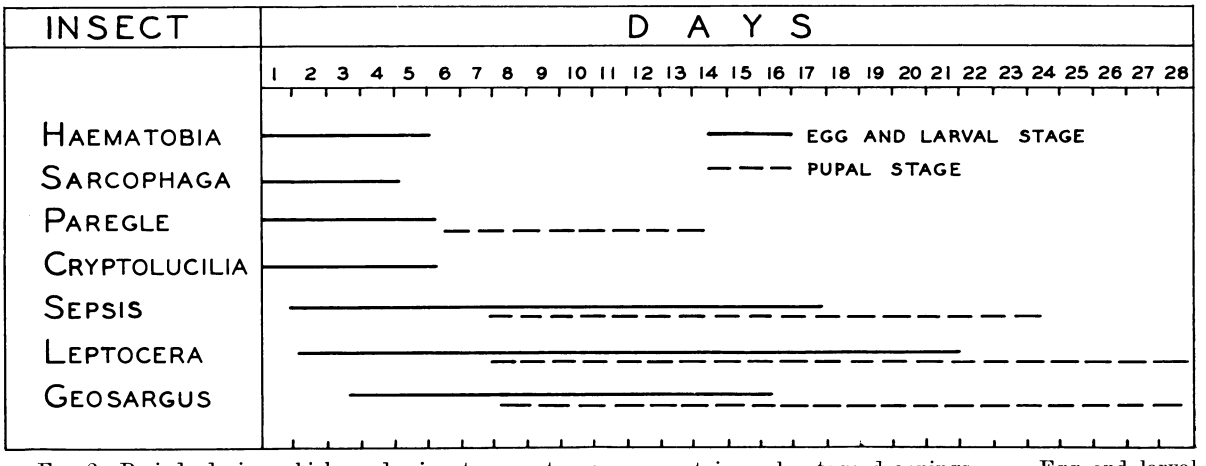

FIG. 2. Periods during which predominant maggots were present in early stage droppings. ——Egg and larval stage; – – –Pupal stage.

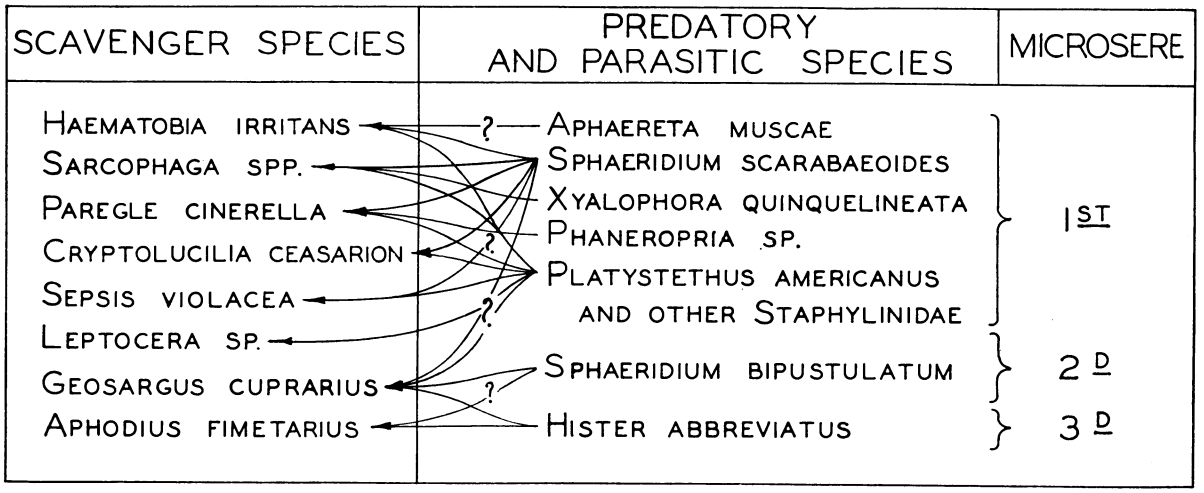

FIG. 3. Predator and parasite relations of the immature stages of common scavenger species in droppings.

The burrows which are found in such a dropping form a great network left by larvae of at least half a dozen flies, and of the Sphaeridium beetles, most of which preceded the staphylinids in the succession. The latter are therefore dependent to some extent on activities of the former.

When the Philonthus staphylinids arrive at newly dropped dung, they dash, as described before, over its surface and enter the burrow of Sphaeridium, or run under the edge where they work between the soil and the dropping. When the parasitoid wasp, Xyalophora, arrives, it walks slowly over the dung and frequently walks down the burrows of Sphaeridium, probably ovipositing. The dependence of Xyalophora on beetle burrows is evident and possibly measurable.

Probably the most obvious relation between the flies, beetles and parasitoid wasps is the predator-prey one, such as exists between the hydrophilid larva, *Sphaeridium scarabaeoides,* and dipterous larvae (Fig. 3) or such as exists between the parasitoid wasp, *Xyalophora quinquelineata,* and the larvae of *Sarcophaga sueta* which is slowly killed by parasitoid activities of the wasp. In the first case an individual substitutes itself in the biologic system for several individuals of another species by its predatory activities. In the second case an individual substitutes itself for a single individual of another species by similar activities.

Nearly as obvious are certain cases of competition for food. The large beetle, *Pinotus carolinus,* for example, removes so much of a dropping in a single night that larvae of flies, if not removed with it and destroyed in the process, are left to starve and sometimes to dry beneath an inedible crust. The destruction of life by one beetle commonly amounts to that contained in an entire cake.

Competition for space becomes particularly obvious and measurable during the fall when the beetle, *Aphodius distinctus,* mills about on the surface of a dropping, jostling flies which come to oviposit and breaking up any egg masses which have been laid. During the height of their activity, droppings are completely riddled by the Aphodius.

SURFACE SUCCESSION DURING SPRING AND FALL

Flies have been observed to show the following seasonal presence as adults on cow dung in the open pasture near Urbana.

Scatophaga furcata, a large yellowish, hairy fly; *Myiospila meditabunda,* a large dusky fly; and *Coprophila equinus,* a dark, medium-sized, angular-legged fly, are the most conspicuous part of the fauna during early spring (Fig. 4.) *M. meditabunda* may breed throughout the summer under suitable climatic or environmental conditions but when the summer became warm and dry, it disappeared from the open pasture. It has however been found in densely shaded pastures. *B. geniculatus,* with its smaller relative, *B. marmoratus* are usually very numerous, frequently reaching numbers well above fifty.

Paregle and Sepsis are at this time uncommon on dung, though adults appear early in the growing season and become very common. Borborus, apparently non-breeders, are commonly but irregularly abundant, while Scatophaga and Myiospila, less common but very regular in representation, reach their peaks of abundance slowly but at separate periods; Myiospila being the latest fly. In early spring, these two flies have approximately the same successional position on the surface as Cryptolucilia does in summer.

Late fall successions on newly dropped dung are similar to the late March or early April successions. The Borborus and Scatophaga, having disappeared from fresh droppings during the summer, are again represented in numbers during the fall and Myiospila again increases in numbers. The summer fauna has disappeared and the succession of common ovipositing flies is again Scatophaga and Myiospila.

The likely species composition of successions at any time of a year may be judged by use of the table (Fig. 3).

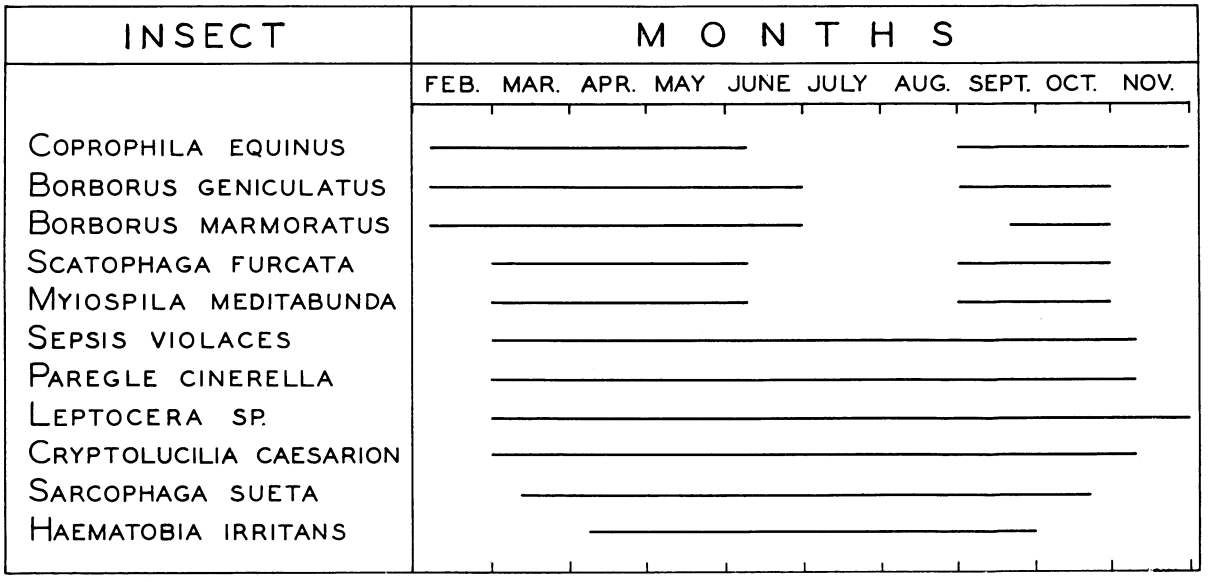

FIG. 4. The likely species composition of successions at any time of a year may be judged by use of this table.

HIBERNATING INSECTS IN FRESH DROPPINGS

Any dung which is dropped shortly before the first killing frosts usually contains the following insects hibernating in numbers:

Pink cecidomyid larvae (nearly 1 millimeter long) of *Monardia illinoensis*
Puparia of *Sepsis violacea*
Adults of *Cercyon quisquillius*
Puparia of *Paregle cinerella*
Adults and pearly round eggs of *Aphodius fimetarius*
Puparia of *Scatophaga furcata,* and *Myiospila meditabunda.*

PHYSICAL CHANGES OF DROPPINGS

Although droppings vary greatly in water content and are exposed to variable drying conditions, they show similar changes in color and consistency. When dropped they are usually gleaming wet and greenish brown, and pass through the following more or less distinct stages:

Greenish brown with distinct tarnish and film
Uniformly brown and moist
Blackish brown with moist depressions
Brown with distinctly dry crust
Light brown with very thick crust
Light brown chip, dry throughout.

The first three changes occur during the first day when the dung is dropped early in a forenoon. If it is dropped later in the day, night conditions greatly slow the process. The fourth condition progresses to such a degree during the third day as to become unattractive even to the long-staying Leptocera. Complete drying depends largely on the weather, but frequently progresses to a degree which destroys the slow growing *Aphodius fimetarius* in thirty days.

The earlier stages are the shorter ones, corresponding somewhat to the time selected for oviposition by the flies. Haematobia lays its eggs while the cake is gleaming wet and untarnished; Sarcophaga after tarnishing and filming occur and while the dropping is uniformly brown and continues until a distinct crust is formed. Sepsis and Leptocera continue to oviposit for many days, making use of moist crevices and beetle holes.

All but one species of insect were observed to arrive at droppings by flying or walking up-wind, possibly in response to wind-blown odors, the nature of which changes during the first day from a musky sweetness to an unpleasant stink. All of the large flies finish laying their eggs during the first day, but strangely enough may reappear later in large numbers if the crust, which seals in much of the odor, is removed, though they will not again oviposit unless the operation is performed very soon after their natural peak is passed.

Haematobia is the only insect observed which was not highly dependent upon the wind, and perhaps upon odor, for its direction of approach. This is possibly due to its close presence at the time of dropping and conditioning to the movements of its host.

THE MICROSERE AND ITS STAGES

Larvae of *Haematobia irritans, Sarcophaga sueta, Paregle cinerella, Cryptolucilia caesarion, Sepsis violacea, Myiospila meditabunda, Sphaeridium scarabaeoides* and other insects associated with them form such a well-defined group which attain their growth together and pupate at about the same time. Though it is true that, before they attain their complete growth, young larvae of *Geosargus cuprarius, Sphaeridium bipustulatum, Hister abbreviatus* and others are found associated with them, the pupation of the first group leaves the latter isolated, distinct, inter-

dependent among themselves and therefore components of a distinct second stage.

Before the second group attains its growth, larvae of *Aphodius fimetarius* and *A. haemorrhoidalis* begin their growth; these in turn, are isolated by the pupation and emergence as adults of the group preceding it in the succession.

Since these groups seem sufficiently distinct and since microhabitat eventually becomes a homogeneous part of the larger community, the entire change may be called a *microsere* and each distinct division or stage of it, a microseral stage. These terms were suggested by Professor V. E. Shelford.

The first stage has received the most consideration during the course of this study because of its chronological position; because of its complexity; and because it is made up of some, if not all, of the insects specific to cow dung.

SPECIES COMPONENTS OF THE FIRST MICROSERAL STAGE

Haematobia irritans Linnaeus

Successional Position: During its active season the horn fly is the first insect to visit newly dropped cow dung. Females lay small numbers of eggs singly and horizontally on the shining wet surface during the first two minutes and usually within a minute and a half, after which adults of this species disappear from the dropping. Representation was relatively irregular, though continuous.

Breeding Media and Food: This fly is known to breed naturally only in fresh cow dung. Riley and Howard (1889) managed to rear four adults from horse dung under unnatural conditions by confining many adults in breeding cages containing only horse dung. Larvae, boiled in an aqueous solution of potassium hydroxide, reveal masses of ingested matter looking like fine particles of cellular material in dung. They evidently ingest this with other fecal contents. Any ingested matter is regarded as food in this paper. Blood of living cattle is the natural food of the adult fly which is a pest of cattle.

Appearance and Activity: Adults are medium-sized gray flies nearly four millimeters in length, which flutter their wings as they move quickly over the shining wet and untarnished surface of the dropping while laying their eggs. The larva is whitish and attains a length of seven millimeters. Puparia are brown and oval, and are best identified by examination of their stigmal plates which are similar to those of the larva.

Numbers of Adults: One hundred and sixty-three larvae were recovered shortly before pupation from a cake dropped at noon, June 20, 1931. The average from twenty-five cakes is 151.7, dropped between nine o'clock, forenoon, and four o'clock, afternoon, during the summer months. Since all observations on abundance were made in an area where cattle are treated to repel the fly, this figure is very probably an unnatural one, lower than that which the fly maintains when not interfered with by man.

Pupation: Riley and Howard found that pupation took place in loose soil under dung placed in breeding cages. Several dozen reared by the writer had pupated in the dropping but this is not the common habit.

Seasonal Activity: The species hibernates in its puparium chiefly in the soil beneath its breeding medium. Emergence of adults takes place during April or early May. Breeding is continuous until the early frosts of October.

Life Span: About twenty days according to Riley and Howard and twelve days in the laboratory at room temperature from eggs laid at Urbana on October 26, 1932. The egg and larval stage usually require five days of this period and the presence of any developmental stages in numbers indicates that droppings containing them are less old than the time required for those stages to complete their growth.

Sex Ratio: Fifty-six percent were females as determined from 225 individuals reared between March and July.

Kleidotoma sp. undescribed

Host: Haematobia irritans. Three specimens were reared from puparia of this fly collected in dung on August 2, 1931.

Phaenopria sp.

Host: P. haematobia has been recorded as a parasite of *Haematobia irritans* and others as from Diptera in general.

Successional Position: During February 1931, four specimens were reared from dung which contained puparia of *H. irritans, Paregle cinerella,* and *Sepsis violacea,* therefore evidently belonging in part at least to the first microseral stage.

Asobara lineata Viereck

Host: Probably dipterous larvae.

Only one specimen of this was reared from cow dung and from the first microseral stage.

Sarcophaga sueta V. d. Wulp

Successional Position: Females have been observed larvapositing in cakes exposed only five minutes and in cakes up to three hours old, but the peak of abundance on any one cake is usually reached in about half an hour. The representation on the surface is regular and usually continues, especially when the fly is common, as in the summer.

Breeding Media and Food: Larvae live in and feed on excrement of man (Greene 1926), sheep (Wilson 1932), and cattle. Since adult flies dip their proboscises into wet cow dung, they probably absorb dissolved nourishment from it.

Appearance and Activity: Adults are large tessellated gray flies with brick-red eyes. They vary in size from over six to about twelve millimeters in length. Females move slowly over the surface of dung occasionally dropping a white larva.

Numbers of Adults: Thirty-two have been observed on a single cake during midseason (June 20, 1932) but the average from twenty cakes is only eleven at population peak.

Numbers of Larvae: The greatest number found in dung exposed over twenty-four hours is one hundred and twenty. The average from twenty cakes exposed the same length of time during the summer months is ninety-four.

Pupation: Pupation takes place in the soil a few inches beneath or to one side of the dung.

Seasonal Activity: The species hibernates in puparia in the soil beneath droppings. Adults appear during warm weather of late April or early May and breeding is continuous from that time until the frosts of October or November. Larvae have been found alive in dung up to the time the frosts penetrate completely through the cake.

Life Span: Adults may commonly be reared in twelve or thirteen days, four or five of which are spent within the droppings as larvae before entering the soil during the summer months. These larvae, being larger, more abundant, and more regularly present than those of the horn fly, are more useful zoometers or indicators of the relative age of dung.

Sex Ratio: Forty-seven percent were females as determined from 399 individuals reared between June and November.

Xyalophora quinquelineata Say

Host: Sarcophaga sueta and probably other Sarcophaga.

Successional Position: This parasitoid wasp has been found to arrive at dung within several minutes and to be present intermittently during the entire first day, or, if the dung were dropped late in one day, to be present on it during part of the next day. Its representation on dung, though regular, is discontinuous.

Appearance and Activity: Only females have been observed at dung. They are black, compressed and large, attaining a length of five millimeters. Only one has been observed to oviposit into its host. Two *S. sueta,* to judge by their large size, had been larvapositing into a ten-minute-old cake late one morning while three adult Xyalophora walked slowly over the surface. As one of the newly dropped maggots of the fly was entering a female Xyalophora thrust her ovipositor into its back. The maggot, evidently pained, rose to the surface dragging its parasite almost an inch before a strong tug freed it. The maggot then burrowed into the dropping.

Most frequently, Xyalophora females work slowly over the surface of the dung, stopping to thrust in their ovipositors or to walk down the tunnel of a Sphaeridium or Aphodius beetle from which they emerge later with their wings smeared with dung.

Numbers of Adults: Six is the largest number observed on a single cake which was twenty minutes old on July 4, 1931. Three are frequently to be seen on cakes less than an hour old, but only a specimen or two are most commonly seen.

Seasonal Activity: Adults appear during the early days of May and breeding is continuous throughout the summer, ending during the latter weeks of October. The winter is passed in the puparia of its host.

Pupation: Pupae have been recovered from puparia of its host and some twenty adults were reared from the same stage.

Sarcophaga lherminieri Desvoidy

Successional Position: No adults of this variety have been distinguished in the field but circumstantial evidence indicates that larvaposition takes place during the first day if not while *S. lherminieri* is larvapositing. Great numbers of larvae have been found in a few cakes which had every appearance of being three or four days old and from which the larvae emerged to pupate in the soil a day after discovery. They were also associated with larvae of *Cryptolucilia caesarion* which emerged about the same time.

Breeding Media and Food: Cow dung is recorded as the breeding medium by Aldrich (1916). Dr. H. H. Ross and the writer reared this species from pig droppings in 1942. The larvae feed on the dung.

Numbers of Larvae: One hundred and twenty-nine were taken from a single dropping on September 20, 1932, and sixty-seven from another on October 15, 1933.

Appearance and Activity: According to Aldrich the adults average slightly smaller than those of *S. lherminieri* and are slightly more yellowish gray. It would be difficult to distinguish them from the larger species in the field. All known Sarcophagidae give birth to larvae. The larvae of this variety are white and similar to those of *S. lherminieri,* but differ in having dark caudal points.

Sarcophaga pusiola V. d. Wulp

Successional Position: This species has been found to occur so irregularly that no good idea of its successional position was established. It has been reared two times and observed larvapositing only six times and was each time found associated with the closely related *S. sueta.* The greatest number of adults observed on a cake was six, along with ten of the larger species, and the greatest number reared was seven along with sixty-three of the larger species. The average number reared per cake was six.

Breeding Media: Cow dung. Since only a small number of *S. pusiola* was reared the writer believes that this is not the preferred breeding medium. This was the only Sarcophaga found in cattle droppings in dense shade in southern Illinois.

Appearance and Activity: These are tessellated grey flies of about seven millimeters in length, not easily distinguished in the field from small individuals of the larger species, either by activity or general appearance. The above counts of adults were made on cakes which subsequently yielded a small number of larvae which were reared.

Sarcophaga ventricosa V. d. Wulp and *S. stimulans* Walker

During the summer of 1942, Dr. Ross and the writer reared both *Sarcophaga ventricosa* and *S. stimulans* from cattle droppings taken at Urbana. Both species have also been reared from human excrement

by Howard (1900) and Pratt (1912), under the names *S. assidua* and *quadrisetosa,* respectively.

Paregle cinerella Fallen

Successional Position: Females of this species begin ovipositing into dung within about five minutes after it is dropped unless it is exceptionally wet. They usually finish in an hour and a half or two hours, attaining their maximum abundance in an hour or less. Representation is generally regular and continuous.

Breeding Media and Food: Human excrement at Washington, D. C. and Virginia (Howard 1900), sheep dung (Wilson 1932), horse dung and fresh cow dung. Webster, 1900, recorded adults as emerging from wheat plants in Ohio, but his method of rearing seems unreliable. The larvae are scavengers and are known to ingest cow dung. Adults dip their proboscis into wet dung and probably absorb nourishment with moisture.

Appearance and Activity: Adults are gray flies similar in size and color to the horn fly, but easily distinguished from it in the field in being later visitors, and by moving about slowly over the surface of the dropping, without fluttering their wings, or resting quietly while ovipositing. The eggs are thrust singly and perpendicularly into the soft wet dung and when drying takes place their white upper ends are exposed, frequently studding the surface thickly. Larvae are whitish. Stigmal plates of the puparia resemble those of the larvae. The puparia are more slender than those of Haematobia.

Numbers of Adults: Sixty-three have been counted at the peak of abundance on a cake dropped June 20, 1933. The usual number is about half of this and often as few as a dozen during late summer, due possibly to repressive action of their parasite, *Idiasta* sp.

Numbers of Larvae: Two hundred and two, the greatest number recovered, were taken from a cake exposed forty-five hours by May 7, 1933. The average is forty-six from twenty-five cakes dropped between 9 a.m. and 4 p.m. Although hundreds of eggs are laid into each fresh cake during the spring a recovery of one hundred larvae is unusual, possibly due to parasitism, for *Idiasta* sp. is also abundant at that time.

Pupation: Larvae pupate in the dung.

Seasonal Activity: Hibernation takes place in the puparium in dung. Early adults have been observed March 27, 1931, April 1, 1932, and April 7, 1933. The latest have been observed October 15, 1931, October 23, 1932, and October 10, 1933. Breeding is continuous throughout the summer.

Life Span: About fourteen days, as determined from twelve adults reared out of doors from eggs laid May 1, 1931. The larval stage required five to six days of this time.

Idiasta (Phaenocarpa) sp.

Host: Paregle cinerella.

This parasitoid wasp emerged in numbers from puparia of *Paregle cinerella* between May 12 and 15, 1931. Many of the host flies were observed ovipositing into a newly dropped cake at 10 o'clock on May 1. During the afternoon of the next day about thirty *Idiasta* were collected on its surface as they moved slowly about ovipositing near the host eggs whose exposed ends studded the surface of the dung. This dropping was taken to the laboratory on the following day and yielded the above rearing records.

Hylemyia cilicrura Rondani

Successional Position: Hylemyia cilicrura, the seed-corn maggot, an economic pest, was found to be a very irregular visitor to cow dung and its position may only be guessed at from the rearing records. Ten specimens were reared on April 11, 1931, from a cake which had been dropped in the fall and which yielded six horn flies but no other Diptera. The presence of the horn fly and the fact that breeding was late that spring indicated that the *Hylemyia cilicrura* may have oviposited in the dung within a few days after the horn fly and that the larvae were associated in the same cake during their growth. It has been reared from fresh sheep dung in New Jersey by Wilson (1932), and from a wide variety of planted seeds and decaying vegetation by many other workers.

Aphaereta muscae Ashmead

Host: Hylemyia antiqua (Anthomyiidae). Reared by B. H. Walden according to "Hymenoptera, or wasp-like insects of Connecticut." Six were reared October 26, 1932, from cow dung which had dropped about a week before and which contained the puparia of *Paregle cinerella, Haematobia irritans,* and *Sepsis violacea.* It has been reared from some host in human excrement by Howard (1900).

Successional Position: This species evidently belongs to the first stage of the microsere.

Figites sp.

Host: Members of this genus are recorded as parasites in dipterous puparia.

Successional Position: Three males were reared from cow dung brought to the laboratory on February 21, 1932, and one female from cow dung of the first microseral stage brought to the laboratory on August 21, 1931.

Musca domestica Linnaeus

Successional Position: Adult houseflies are irregular visitors to droppings up to five hours of age, being slightly more common during dry or cool seasons, evidently taking moisture and food at all times and warming themselves during the cool season.

Numbers of Adults: The greatest number observed was three on dung slightly more than an hour old.

Numbers of Larvae: No larvae were taken during the present investigation. L. O. Howard (1911) recorded twenty specimens of adults reared from cattle dung, August 30, and September 3 and 4, 1889, but did not record the number, nature or age of the droppings studied. Comparison of rearing records with those for twenty-four species of flies on that author's

list indicates that the twenty individuals were from one or possibly two droppings, which suggests that breeding in this medium is naturally very rare. The writer wonders if these houseflies may not have been reared from a manure heap rather than from individual droppings.

Cochliomyia macellaria Fabricius

Activities of this flesh fly are similar to those of houseflies at cattle droppings. The odor of fresh droppings evidently attracts them but only a few, if any, individuals arrive. Adults have been observed to feed and rest on fresh wet droppings but to desert them within a few minutes without ovipositing.

Stomoxys calcitrans Linnaeus

Like the housefly and the false screw worm fly above, the adult stable fly frequently rests on moist cattle droppings, seemingly not purely accidental but attracted by warmth or odor. Unlike the other two flies however it has not been observed to feed.

Hydrotaea armipes Fallen

This fly was reared from droppings throughout the winter and up to April 18, having pupated there.

Sepsis violacea Meigen

Successional Position: Adult females begin ovipositing into the surface of dung when it reaches the uniformly moist brown condition, usually after exposure for fifteen minutes, and continue to do so until the surface becomes blackish brown after exposure for about seven days. During this time the surface is soft enough for them to run rapidly over it, thrusting their eggs in it singly and perpendicularly. After this they evidently continue laying eggs into moist crevices and beetle holes, for, though none have been observed doing so, more larvae may be recovered from cakes exposed thirty hours than from cakes exposed any lesser time.

Males and females are usually present in numbers long before and after dung is suitable for oviposition. They come almost immediately to the surface of dung which is dropped in a moist brown condition and remain for as much as a week until the cake becomes light brown and heavily crusted.

Breeding Media and Food: Human excrement and decaying vegetable material at Washington, D. C. (Howard 1900), sheep dung in New Jersey (Wilson 1932), and fresh cow dung in which the larvae are scavengers.

Appearance and Activity: Adult flies are slender, ant-like and shining black. They vary in size from slightly over one to slightly over two millimeters and are quickly distinguished by their habit of wig-wagging their wings as they run swiftly over the dung, meet their fellows face to face, mate, or lay eggs which they thrust endwise into the surface without more than a moment's pause. The puparium which is common in dung during summer and winter is slender, light tan and shows the bifurcations of the stigmal area which also characterize the larvae.

Numbers of Adults: The greatest numbers of adults observed on a cake was forty-five, on dung dried brown on June 21, 1931, after twenty-four hours of exposure. Forty were counted on another dried brown on July 5, 1931, after twenty-three hours. An average of twenty-five cakes in the same color range, all bearing Sepsis adults, at 10 a.m. July 4 of that year was twenty-three. Several bore as few as one fly and one bore forty-five.

Since the fly had been definitely observed to oviposit in dung varying from moist brown to blackish brown, a count was made of the numbers on thirty-eight cakes in this color range. The average, same day and time, was nine flies. The largest number of adults observed on any cake in this condition was thirty-three on dung dried blackish brown on August 13, 1933, after two hours of exposure.

Between the conditions noted above and at other times during the three-day period favored by Sepsis, there is much fluctuation in numbers, possibly due to its response to other conditions than those of the dung. This matter is worth a long and special study in itself, but is too long for this paper. Such a fluctuation is to be expected where daily rhythm and weather changes occur during a long period of relative stability of the dung.

Numbers of Larvae: The greatest number of adults reared from a single cake was a lot of 545 from dung of uncertain age; but less than five days old, on August 1, 1933. The average from fourteen collections of dung thirty hours old and collected during four summers is 436 and the lowest is 205. The number for any one cake gradually increases from the time the first females oviposit until thirty to thirty-six daytime hours have passed. Though the number of adults coming to the surface is greatest when dung is more than three hours old, there is no average sudden increase of larvae recoverable from cakes older than this, as might be expected.

Pupation: Larvae pupate in the dung in which they feed.

Seasonal Activity: Hibernation takes place in a puparium within the cake and emergence takes place during the first half week of very warm weather in late February, March, or early April. Breeding is continuous during a period of about six and one-half months, usually beginning during the first half of April and ending during the first half of October. Populations are, however, small and irregular before May 1 and after October 1. No larvae or adults have been found during the winter.

Life Span: About nine days from egg to adult as determined from twenty-two individuals reared in the field on July 12 from a cake dropped July 4, and thirteen reared September 28 from a cake dropped September 17. The presence of any growing stage in dung during the summer is good evidence that it is under ten days old.

Cryptolucilia caesarion Meigen

Successional Position: A few individuals may arrive at freshly dropped cakes almost instantly, but ovi-

position usually does not begin until the cake has passed its moist brown condition and ends in about six hours later.

Breeding Media: Larvae breed in and feed on cow dung. Adults have been observed to dip their proboscis into wet dung and possibly feed on the juices.

Appearance and Activity: The adults are shining, blue-green flies which measure around seven millimeters in length. They walk slowly over the surface when moving about, but the females stand quietly for long periods as they lay their eggs in large groups into natural crevices.

Numbers of Adults: The peak of abundance in one case was sixty-three. The average number found on fifteen cakes an even four hours old after being dropped in the morning in June, July, and August is twenty-two.

Numbers of Larvae: Twenty cakes between one and four days old in June, July, and August yielded an average of fifty-nine larvae, the lowest number being thirty-six and the highest being one hundred and thirty-two.

Pupation: Larvae pupate, along with those of *Sarcophaga lherminieri,* in the soil a few inches beneath and to one side of the cake in which they attained their growth. During the summer they leave the dung by the end of the fifth day.

Seasonal Activity: The adult evidently is the hibernating stage. One found beneath a drift of loose leaves at the mouth of a woodland cave near Murphysboro, Illinois, on February 22, 1933; three beneath burlap bands on apple trees on December 11, 1932 and many were collected on the wing in a sunny river-bottom pasture near White Heath, Illinois, on February 28, 1932. According to H. E. McClure, sunny days caused adults to take short flights from their hibernating quarters under the burlap bands.

Early larvae were found at Urbana on April 4, 1932. Breeding is continuous until the latter part of October, the latest larvae having been found at Urbana on November 5, 1932. After frosts, which were hard enough to freeze dung solid, no live larvae were recovered, but dead and blackened ones were common. It is a question as to how pupae fare in the soil during the winter, for, though its associate, *S. lherminieri,* has been found, no Cryptolucilia have. This is partially due to the fact that as weather cools Cryptolucilia breed less commonly on high spots, becoming restricted in sheltered places and are even there uncommon, but such places have been searched and the evidence, though negative, is strong that it does not winter in puparia.

Life Span: About eleven days, four or five of which are spent as larvae during the summer.

Sex Ratio: Forty-four percent are females as determined from one hundred and twenty-four individuals reared between June and September.

Myiospila meditabunda Fabricius

Successional Position: M. meditabunda has been found to reach its peak of abundance on cakes of about the same age required by *Cryptolucilia caesarion* during the summer. During spring and late fall it is commonly associated with *Scatophaga furcata,* reaching its greatest abundance a little later than that species.

Breeding Media and Food: Human (Howard 1900), cow (Howard 1901), pig (Keilen 1917), sheep (Wilson 1932), and rarely horse dung (Portchinsky 1910).

Larvae are scavengers during the first and second instars, and predaceous on larvae of flies associated with them during later instars. According to Portchinsky, several hundred larvae of *Phormia coerulea* R. D. were destroyed in several hours by eighteen larvae of *M. meditabunda.*

Appearance and Activity: This is a dull-colored fly about seven millimeters in length and similar to the housefly which, however, has a yellowish margined abdomen, rather than a plain olive gray one. The males of Myiospila have four distinct black spots on the abdomen which further distinguish them from the housefly. Both males and females come to the surface of cow dung where they walk slowly about or rest quietly, the females ovipositing occasionally. The eggs are said to be large, usually laid singly here and there into the dung, and are few in number. Each female is said to lay from twenty-four to thirty eggs (Howard 1900 and Keilin 1917).

The puparia, which are large, oval, and brown, bear stigmal plates that resemble those of the larvae.

Numbers of Adults: Twenty-five flies have been counted on a single dropping, May 17, 1933, at the height of desirability (about four hours). The average on twenty-three cakes at the height of desirability during the spring and fall is thirteen, but the number may be zero, and commonly does not run above six during midsummer.

Numbers of Larvae: The greatest number of immature flies taken from a single dropping is twenty-six, recovered in puparia on March 27 after passing the winter in that state. The average from thirty cakes dropped during the fall and examined at that time is thirteen.

Pupation: Larvae pupate in the droppings and according to Portchinsky, in the soil.

Seasonal Activity: This fly passes the winter in puparia in cattle droppings. All stages are common during the spring and fall but may be absent from many suitable droppings during the summer.

Life Span: A minimum of twelve days are required to produce adult flies from newly laid eggs. Fifteen days during the summer usually allows all adults to emerge, but cold, drought, and starvation will greatly prolong the time required. A minimum of four days are required to complete the larval stage.

Leptocera sp.

Successional Position: Leptocera, like *S. violacea,* usually arrive at cakes after fifteen or twenty minutes and gradually build up to a maximum population by the third day, after which the population falls gradually until, at the end of the eighth day, no individuals remain. The length of time during which both species

occupy individual droppings is greatly dependent upon drying characteristics of the weather.

Appearance and Activity: Adults are tiny black flies less than two millimeters in length, which run, flit, or hop actively over the surface of dung and spend much of their time in the crevices and galleries formed in it.

Numbers of Adults: Toward the end of the first day or early in the second day, during early summer, over one hundred individuals may frequently be observed on cakes in this age range. About as many more are likely to be hidden in crevices in beetle holes, or under the edge of the dung. Because of their small size, none have been observed actually ovipositing. They are most abundant, however, on cakes which are dry brown.

Numbers of Larvae: Evidence is very poor concerning the state preferred for oviposition and the number of larvae in dung; possibly due to the difficulty of rearing in laboratory cages. One cake, exposed twenty-one hours by 9 o'clock, July 5, 1931, yielded thirty-six adults, indicating that there were more than 36 larvae originally present. Another, exposed only three hours by May 7, 1933, yielded only six adults. One exposed ten days late in the year yielded only 8 by October 6, 1932. One exposed six and one-half hours September 17, 1931, yielded forty-one adults. Forty-five cakes taken during spring and summer months failed to yield adults. The average was about twenty-two.

Pupation: Larvae pupate in the dung in which they fed.

Seasonal Activity: Adults have been observed at all times of the year and are among the earliest flies to visit dung in the spring. Breeding is undoubtedly continuous from April until late in October.

Only adults have been taken during the winter.

Breeding Media: Leptocera (Limnosina) albipennis has been reared from human excrement and cow dung by L. O. Howard (1900, 1901). The writer's specimens were determined only to genus.

Life Span: Under ten days as determined from thirty-six individuals reared July 14 from dung taken to the laboratory for rearing on the morning of July 5 after exposure during twenty-one hours.

Coprophila equinus Fallen

Successional Position: Adults, apparently non-breeders in cow dung, are common visitors during spring and fall. They attain their greatest abundance on cakes which are about eight hours old; numbers gradually diminish during the greater part of the third day.

Appearance and Activity: Adults measure between three and a half and five millimeters from antennae to wing tip. They are very dark brown and quickly distinguished from the horn fly, which is about as long, by their darkness, squattiness, and prominent, thickened legs.

Numbers of Adults: Ninety-seven have been observed on a single cake during the first week of May, 1933. Between thirty and seventy are the usual numbers at this time of the year. The number falls to a few individuals toward the middle of June and increases again late in September. The adult fly is common on horse dung during the late winter and possibly winters in this stage, occasional individuals being found on cow dung as early as the middle of February.

No larvae of this species have been taken from cow dung.

Coprophila sp.

Specimens were determined by J. M. Aldrich in November, 1933.

Only fourteen individuals have been taken, all from cow dung, as follows:

5 on February 1, 1931,
1 on March 2, 1932,
2 on March 4, 1932,
1 on April 4, 1932, and
5 on April 7, 1932.

The four cakes from which these were taken had been dropped during the previous fall, and it is possible that this fly breeds in such cakes. No immature stages of the species have been discovered.

Borborus geniculatus Macquart and *Borborus marmoratus* Beck

Successional Position: These two species are discussed together because of the difficulty of distinguishing them in the field. *B. geniculatus* has been collected in October and *B. marmoratus* in April, May, and October. Together, they reach numbers around fifty in three or four hours and zero in the next two days. They probably have specific differences in taste for age classes of dung, but these may be detected only by long and careful collecting and note making. None have been reared from cow dung under circumstances which would definitely settle their position.

Appearance and Activity: Adults are squat and prominent-legged like *Coprophila equinus*. Large individuals of *B. geniculatus* may not be distinguished readily from small *C. equinus* in the field and the difficulty of counting is further increased by the close resemblance of the smallest Borborus, namely *marmoratus,* to the large Leptocera.

Scatophaga furcata Say

Successional Position: Adults appear on dung within a few minutes after it is dropped and numbers gradually diminish for about twelve hours.

Breeding Media and Food: Sheep dung, according to Wilson (1932), human excrement, according to Howard (1900), and cow dung, the larvae being scavengers. Adult flies have been observed to capture adult *Myiospila meditabunda* from which they suck fluids. Adult *S. furcata* have a wide range of prey species.

Appearance and Activity: Adults are large, hairy, yellowish brown flies about one centimeter long. While on the surface of dung, they slowly, frequently

tussle in pairs while copulating; often rest quietly while injecting an egg here and there into the dung; and occasionally seize and suck body juices from an associated species of fly which usually is a Myiospila. The larvae are whitish and are caudally truncate in their later instars.

Numbers of Adults: Fourteen have been observed on a suitable cake during the fall but the average number observed on eighteen cakes between one and four hours of age between September 15 and October 15 is eight.

Numbers of Larvae: Fifty-eight larvae were recovered from a two-day-old cake. The average number from the above eighteen cakes is twenty-five.

Pupation: Larvae pupate in the dung.

Seasonal Activity: Winter is generally passed in the puparial stage; these overwintering puparia are in a sufficiently advanced state that adult emergence will take place if brought into the laboratory. Early adults have been observed soon after the first warm days in middle February and it is therefore possible that adults also overwinter. Breeding continues until the middle of May, and after a lapse in the summer begins about the middle of September to continue until the end of October.

Scatophaga sterocoraria Linnaeus

Successional Position: Very small numbers of adults were found irregularly on cow dung within a day of age in April, early May and again in late September and October, always in the company of *S. furcata.* None were found breeding in cow dung in open pastures during the course of this study.

Breeding Media and Food: Human, poultry, sheep, cattle, and horse excrement, all of sufficient consistency for the larva to complete its life in England without being dried out, according to Cotterell (1920). Cattle and sheep excrement are preferred and that of horses rarely used for oviposition. Sludge from septic sewage tanks was found to contain an enormous number of the growing larvae. This fly bred rarely, if at all, in droppings in open pastures at Urbana, Illinois during the period of this study. Excrement is the larval food according to Cotterell. Food of the adults is body juices of many flies and especially those which are common about the breeding media. These include *Coprophila equinus* Fallen which breeds abundantly in horse dung and passes the winter as an adult; the housefly, *Musca domestica* Linnaeus; blow flies, Calliphora and Lucilia; and, in Urbana, *Myiospila meditabunda* and *Sarcophaga lherminieri.*

Seasonal Activity: Cotterell found large numbers of adults about on warm sunny days in winter, 90 percent of which were males, and judged that the majority of individuals which hibernate do so as adults, but might do so in puparia.

Breeding, according to this author, takes place from April to October and results in probably five broods a year. In summer the whole surface of a deposit of cow dung may be covered with wing-like extensions of the eggs.

Pupation: In England, pupation occurred mainly in the soil, very few pupae being found in the dung.

Life Span: Seventeen to thirty-one days were required for the development of adults from freshly laid eggs and adults were found to live from eleven to twenty-two days in the laboratory but great dryness of food prolonged the larval stage greatly. Accordingly to Cotterell, no females were observed to lay more than one hundred and twenty eggs and it is probable that one female is capable of laying from one hundred to one hundred and fifty eggs, after which she dies.

Sphaeridium scarabaeiodes Linnaeus

Successional Position: Adults have been observed arriving at dung as soon as it is dropped until about three hours have passed, when the dung becomes dark brown. Most of them arrive during the first half hour, run excitedly over the surface, plunge inside and come out again to repeat the performance many times. An adult or more may be found in dung as old as two days but the greater number leave after the first half day.

Breeding Media and Food: Fresh cow dung. This species is commonly said to feed on dipterous larvae. During the course of this study one grub, over half grown, was collected with its mandibles fastened into the body of a large *Sarcophaga lherminieri* maggot which was lately killed and shriveled. Another grub of this species was collected with its mandibles fastened into a live larva of *Geosargus cuprarius* which was about half grown and which died in a few minutes after collecting. A third grub dug accidentally out of a cake had its mandibles fastened into the body of a horn fly larva, *Haematobia irritans.*

Appearance and Activity: Adults are short, flattened beetles about six millimeters long, mostly black but having whitish tips on each elytron and a reddish spot near each humeral angle. While on the surface of dung they rush actively over it but soon plunge inside only to break through at another place. They are mainly responsible for the many holes in dung between May and September.

The larvae are maggot-like in shape but may be quickly distinguished as being of the present beetle, by their short thoracic legs and distinct head. Four, instead of only two, fleshy protuberances at the caudal end of the body distinguished this species from the closely related *S. bipustulatum.*

Numbers of Adults: As many as four or five may occasionally be seen on the surface at one time, but more than two or three is unusual. Thirty adults is the greatest number taken from a single cake, which, on July 5, 1931 had been exposed twenty-one hours. Four other cakes, dropped at various places in the same pasture and within an hour of this one, contained fifteen, twenty-three, twenty-four and twenty-seven adults, giving an average of 22.25. Field examination of sixteen cakes dropped during June and July but varying in age from a half to one day gave an average of eleven adults present inside.

Numbers of Larvae: Field examinations of twenty-

seven droppings, deposited during June and July of four summers and between two and three days old, yielded an average of thirteen larvae. The maximum number was twenty-seven.

Pupation: Larvae pupate in the soil an inch or so beneath or beside the cake.

Seasonal Activity: The earliest adults were observed April 8, 1933. Breeding is continuous, beginning early in April and ending late in October. The latest observed was a single specimen November 3, 1932. Full-grown larvae have been collected as early as May 19, in 1931, and as late as September 18, in 1932.

Life Span: As little as five days are required to complete the larval stage in the field during summer. The larvae enter the soil along with those of the flies *Cryptolucilia caesarion* and *Sarcophaga sueta* and pupate with them. In as little as seven more days the adults emerge, about the time the adult flies emerge.

Grubs of *S. scarabaeoides* are, however, present in dung more than five days old. They are evidently more resistant to drying of dung than are the two flies mentioned above and are commonly found with *G. cuprarius* larvae four or five days after the two muscoid flies have entered the soil to pupate. This is possibly due to a requirement which will not allow complete development until sufficient food has been eaten, this food being furnished by young *G. cuprarius* larvae.

Sex Ratio: Sixty-five percent are females as determined from eighty-one collections totaling three hundred seventy-five individuals during four summers.

Platystethus americanus Erichson

Successional Position: Adults arrive singly soon after dung is dropped and commonly reach their greatest abundance during the period selected by *Sarcophaga sueta* for its oviposition, or, if during the spring before this fly is active, at about the same period. They move slowly over the surface until they find a crevice or beetle hole by which they enter the cake.

Numbers of Adults: Sixteen have been observed on a cake in July and the average during the summer and at the height of succession is five.

Numbers of Larvae: One hundred and sixty-four were reared August 10, 1933 from a cake which was removed from the field after being deserted by larvae of the first microseral stage but containing no *Geosargus cuprarius.* An average of forty-two have been reared from six droppings late in the first stage during June, July, and August. The beetle appears to be an irregular breeder in cow dung.

Appearance and Activity: The adults are tiny, subrectangular, blackish, rove beetles nearly three millimeters long, which walk slowly over the surface of the dung as they search for holes in the surface into which they enter immediately.

Aphodius distinctus Mueller

Successional Position: This beetle, a non-breeder, illustrates conspicuously the relation of numbers available close at hand, and successional position. When abundant, during spring and fall migration, *A. distinctus* is one of the very earliest arrivals at newly dropped cow dung. It is no uncommon occurrence to see one or more flying beetles arrive before the dung is completely dropped or to see half a dozen on a cake within the minute and a half, a degree of freshness demanded only by the horn fly. Unlike the horn fly, however, they remain in dung for several days and sometimes as long as a week.

Breeding Media and Food: So far as the writer has been able to discover, no breeding media are recorded for this beetle.

Appearance and Activity: Adults are sub-cylindrical beetles, about four millimeters in length, with dark brown or black prothorax and dull, brassy colored elytra irregularly marked with dark brown. They walk slowly over the surface of dung and soon enter. During spring and fall they are mainly responsible for the shot-holed appearance of dung of cattle, horses, sheep, pigs, and man.

Numbers of Adults: Their peak of abundance during the fall occurs on cakes which are from half an hour to an hour old, when as many as fifty-eight have been observed milling around on the surface, digging in, coming out, arriving by wing, and flying away. As the cake grows older more and more remain inside and fewer on the surface until at the end of three hours only an occasional individual or pair may be seen above.

The interior population of a cake, two hours old on October 13, 1933, on which only an occasional adult was to be seen was one thousand and ninety-seven adults. The average from fifteen cakes between three and ten hours old was eight hundred fifty-three.

Spring populations during four years were found to be much less than that of fall populations, the maximum number of adults observed on the surface being eighteen and beneath being two hundred thirty-two. The average for interior populations during spring obtained from twelve cakes between three and seven hours old was one hundred and seven adults.

Interior populations, both in spring and fall, decline gradually until at the end of five days no adults are likely to be found.

Seasonal Activity: Spring dispersal periods have been found to begin during the warm days of the latter half of February, to reach their height irregularly toward the last of April, and then to decline gradually toward the first of June.

Fall dispersal periods begin rather suddenly during the latter weeks of September and decline irregularly with cooling weather early in November.

No adults have been found in cow dung during the summer months and only three during the winter, two alive an inch or two in the soil beneath, and one in the dung.

Aphodius femoralis Say

Successional Position: Adults, non-breeders like the last, are early arrivals at newly dropped cow dung during spring and fall migrations but probably be-

cause of their lesser abundance average later than *A. distinctus*. Individuals have been observed to arrive within two minutes but a quarter of an hour may elapse before the first arrives, and during this time *A. distinctus* usually arrives by dozens. Others straggle in at intervals during the next three or four hours, most of them entering the cake to remain for about a week and usually longer than does *A. distinctus*.

Breeding Media and Food: The writer has discovered no record of breeding media for this species.

Appearance and Activity: Adults are sub-cylindrical beetles about five millimeters long, with black or brownish prothorax and dull brassy colored elytra, differing from *A. distinctus* in being larger and in having unspotted elytra. During the short time each individual spends on the surface of dung, it moves slowly.

Numbers of Adults: The same droppings from which population counts were made for *A. distinctus* yielded the following counts for *femoralis:*

One interior population for a cake three hours old on October 10, 1932 yielded a maximum of fifty-three adults and the average from ten cakes between two and four days old was thirty-nine. No spring counts were taken.

Aphodius bicolor Say

Successional Position: This species has been collected little more than a dozen times and in numbers less than eight except in one case. September 20, 1930, one hundred twenty-three were taken from a single cake. On removal from the field it bore signs of having been deposited either the night before, or early in the morning being visited by *Cryptolucilia caesarion* flies in numbers.

The other collections, smaller in number, were made from cakes up to two days old, and only during the fall months.

No larvae of this species have been discovered in cow dung.

Breeding Media and Food: The writer has no record of breeding media of this species.

Appearance and Activity: Adults are sub-cylindrical beetles about five millimeters long, black above and reddish beneath. Like other Aphodius they are slow and spend little time on the surface.

Other Aphodius collected

Small numbers of the following Aphodiinae were taken from cow dung of the first and second stages but were not found breeding:

Aphodius terminalis Say
Aphodius granarius Linnaeus
Aphodius sterocorosus Melsheimer
Aphodius vittatus Say
Ataenius strigatus Say

Mites, *Parasitus* sp.

Mites were found commonly during this study but were not investigated in detail. It is possible that more than one species of mites were involved. Usually mites appeared on the surface of droppings as soon as beetles arrived, at least some of the mites having been carried by the beetles to the dropping. Inside the dropping, mites were frequently found clustered in great numbers around any scarab larvae or adults. About a week after their first appearance on the dropping, great numbers of mites emerge and run rapidly over the surface of the dropping for a day or so giving the impression that they had multiplied in the dropping during that period. This is suggestive that the mites may be predators or external parasites on the beetles.

SPECIES COMPONENTS OF THE SECOND MICROSERAL STAGE

Geosargus cuprarius Linnaeus

Successional Position: Adults appear so uncommonly on the surface of dung as to allow only citation of incidents. At 2:35 p.m. June 21, 1931, two adults were seen resting quietly for several minutes on the edge of a cake dropped at 3:30 p.m. of the previous day. Other dipterous indicators on this cake, which was dried brown, were forty-five *Sepsis violacea* and twenty-seven *Leptocera* sp. At 11:15 a.m. May 28, 1933, one *G. cuprarius* alighted on a dry brown cake deposited four hours earlier and remained only an instant. At 2:00 p.m. another was seen at the same cake along with three *C. caesarion,* ten *S. violacea,* forty-five *Borborus* sp. and a half dozen *Leptocera* sp.

Breeding Media and Food: The larvae are scavengers in cow dung, and horse dung.

Appearance and Activity: Adults are slender, metallic green flies about eight millimeters long, easily distinguished from the other metallic fly, Cryptolucilia by their slenderness. The activity of the few observed individuals is described above.

Numbers of Adults: Not more than two have been observed together on a cake.

Numbers of Larvae: Larvae of this species are among the most common insects in cow dung and afford the greater part of the evidence of this fly's place in the succession. Four hundred and forty-eight were recovered from a ten-day-old cake on June 21, 1931. The youngest cake to yield larvae was four days old on August 23, 1931 and contained only twenty-four of this species, along with larvae of horn flies and *S. lherminieri,* which is an unusual association, since early succession flies usually complete their development and leave the dung before *G. cuprarius* oviposits. The average number of larvae recovered from fifty cakes between five days and eight days of age is one hundred and thirty-five. One contained as few as thirteen and many between thirty and fifty.

Pupation: Larvae pupate in the dung and under it but not in the soil.

Seasonal Activity: Breeding is continuous during the summer. The earliest adults were active during the first weeks of April and the latest during the first weeks of October.

Hibernation takes place in puparia in the dung and between it and the soil.

Life Span: Twenty days as determined by fifty reared May 7, 1933. They remain in the cake the entire time.

Sex Ratio: Fifty-two percent females as determined from seven hundred and eleven individuals reared from February through October.

Geosargus viridis Say

Successional Position: Adults of this species were observed on cow dung only once. At 10:30 p.m. of May 28, 1933 one *G. viridis* alighted on a dry brown cake deposited three hours earlier. It left after resting there only an instant.

Numbers of Larvae: Larvae of this species were recovered only three times as follows:

8 on June 21, 1931
2 on July 4, 1931
5 on October 23, 1932.

In each of these cases they were associated with a large number of *G. cuprarius* larvae.

Sphaeridium bipustulatum Fabricius

Successional Position: This species was found to be too rare to give any general statement about its successional position. An occasional adult may be found on or in dung in which *C. caesarion* and *S. sueta* have attained from 1/3 to 2/3 of their growth, indicating that dung is suitable to the beetle over a number of days. It has been found very uncommonly in dung less than 1½ days old.

Breeding Media and Food: Cow dung is a breeding medium. No larvae of this species were observed as were those of *S. scarabaeoides,* with mandibles sunk into maggots, but they are said to be predaceous like that species.

Appearance and Activity: Adults resemble those of *S. scarabaeoides* in behavior and form. They differ in being entirely dark and in being more common in and on dung over a day old.

Numbers of Adults: Five adults have been found in a single cake, but even as many as three have been found unusual.

Numbers of Larvae: The greatest number of larvae found in a single cake is twenty-seven for May 30, 1933. An average from fifty cakes between five and eight days old is 15.3. All these cakes contained *G. cuprarius* maggots with which these beetle grubs are associated.

Pupation: Larvae pupate in the soil a few inches beneath or slightly to one side of the cake.

Seasonal Activity: The earliest adults were collected April 13, 1932 and the latest on October 1, 1933. Larvae have been taken throughout the summer between early May and late September.

Hister abbreviatus Fabricius

Successional Position: Early adults have been found to arrive singly at droppings into which Cryptolucilia and Myiospila have all but finished ovipositing. The largest numbers of adults have been found associated with well-grown larvae of those two flies and later with the young larvae of Geosargus and Aphodius.

Breeding Media and Food: Blatchley (1910) wrote that adults occur especially beneath dead fish and turtles along sandy margins of lakes and ponds; also rarely in fungi and cow dung. During the course of the present study it was found to be a regular breeder in cow dung over three days old.

Appearance and Activity: The adult beetle is flat, shining black, slightly over five millimeters in length and almost as broad. When on the surface it walks very slowly and soon enters the dung. The larva is maggot-like in general form, but, like the larvae of the Sphaeridium, has a small, distinct head. It may be quickly distinguished from those grubs by its segmented cerci.

Numbers of Adults: The greatest number of adults discovered in a single dropping was fourteen on August 12, 1932. These were found associated with larvae of Geosargus nearly half grown. Eight similar cakes were examined during the same month and in August a year later, yielded an average of five.

Numbers of Larvae: Twenty-three were reared from a dropping in which they were associated with completely grown larvae and pupae of Geosargus. Sixteen is the average number found in seven similar droppings.

Pupation: Those larvae which were reared pupated in the dropping which, however, was not placed over soil in the rearing cage for a real test of their preference. The larvae seemed to be familiar with the possibilities of the dung for they gathered the larger fibers about them to form a bristly-coated capsule with the loose ends of the fiber directed forward.

Hister americanus Paykull

Successional Position: Adults were collected twice, first on April 17, 1931 and again on April 19, 1932, each time from droppings between three and five days old. They reach four millimeters in length and are therefore distinctly smaller than *H. abbreviatus.*

Cercyon quisquillius Linnaeus

Successional Position: These beetles have been observed at dusk during October hovering in great numbers over dung dropped earlier in the day, individuals coming now and then to the surface beneath which they soon penetrate. Small numbers of *Aphodius distinctus* visited the same cakes, but preferred fresher ones. During the day, adults have been observed coming only occasionally to young cakes into which *Paregle cinerella* have nearly completed oviposition and adults are commonly found in cakes bearing barcophagid maggots from one-third to one-half grown.

Breeding Media: Cow dung.

Appearance and Activity: Adults are small and bicolored, having the prothorax blackish and the elytra straw colored. They are about two and a half millimeters in length, nearly as broad and, during the short time they may be seen on the surface, they walk slowly over it. The immature stages are not figured

because the beetle's niche is in the second stage of succession.

Cercyon haemorrhoidalis Fabricius

Successional Position: Small numbers of *C. haemorrhoidalis* have been found in cakes within the age range of this study, and in one case a dozen were found in a cake containing maggots of *C. caesarion* and *S. lherminieri.* It evidently breeds in those older cakes. It has not been reared, though it is undoubtedly a breeder in cow dung.

Cercyon pygmaeus Illiger

Successional Position: This Cercyon, like *C. quisquillius* and *C. haemorrhoidalis,* is found as adults in cakes within this age range but evidently breed in the older cakes. It has not been reared.

Philonthus tetragonocephalus Notman
and
Philonthus varians Paykull

Successional Position: Adults of both species arrive singly at dung within five or ten minutes after it is dropped and continue to call during the next three or four days, reaching their internal population peak about the time Sarcophaga and Cryptolucilia maggots enter soil to pupate.

Appearance and Activity: These adults are slender rove beetles about five millimeters long, which, as soon as they alight on dung, run wildly over its surface searching for entrance holes into which they dash. When dung is so fresh that the drying process, or other beetles, have not yet provided entry, they either fly away or work beneath its edge. Larvae are cursorial and bear jointed cerci about one quarter as long as the body.

Numbers of Adults: Sixteen have been found at the peak of abundance (August 12, 1933) but only ten in any cake coming within the age limits of this study. The species were unfortunately not distinguished and counted separately.

Numbers of Larvae: None have been reared from any cake within the age limits of this study but a maximum of five have been collected from those slightly older cakes containing pupari of Sepsis and Haematobia. Older cakes undoubtedly bear more.

Six staphylinid beetles of the genera Quedius, Tachyporus, Metaxaya, Dimetrota, Falagria and Baryodma were found on or in droppings of the same stages occupied by Philonthus, described above. They are generally not numerous and apparently largely predaceous and appear to be dependent upon the galleries made by the beetles Sphaeridium, Aphodius and by flies for entry into the dropping. Most of them appear on fresh droppings, even within several minutes of deposition, and remain well into the period during which the droppings are occupied by large Geosargus and Aphodius larvae. It is probable that some breeding is continuous as long as any larvae of any of the characteristic dung insects are present in their usual numbers. They appear to be less affected by the state of the dung than by the state of a prey population in that dung.

SPECIES COMPONENTS OF THE THIRD MICROSERAL STAGE

Aphodius fimetarius Linnaeus

Successional Position: Although an occasional adult may arrive at cow dung dropped within a half day, this species is a feeder and breeder in cow dung over three days old. It does not figure largely in surface populations, partly because of the fact that conditions desirable for it are developed slowly and last many days, and partly because adults soon enter the dropping. Three-day-old dung attracts adults and such a cake continues to attract for about a week during the spring and fall.

Breeding Media and Food: Cow dung during the spring and fall. Breeding undoubtedly takes place in other media and even in cow dung during the summer, where it is shaded, but this phase of the history could not be investigated for lack of time. The larvae feed on the dung.

Appearance and Activity: Adults are sub-cylindrical beetles about seven millimeters long with coppery colored elytra and shining black prothorax and head. They move slowly and spend little time on the surface, preferring to burrow into the cake. The eggs are rounded, pearly and almost one millimeter in diameter. The grubs resemble those of the well-known June beetles.

Numbers of Adults: More than two adults on the surface of a cake is an uncommon sight. The largest number found inside a single cake is twenty-six, which were taken from a cake January 1, 1932. The average number of adults taken for four winters from forty-two cakes during December and January is twelve.

Dung dropped the fall of one year usually retains similar numbers of adults until the middle of March or the first of April when the days become warm enough to permit flight and general dispersal. The number then falls rapidly as the number of flight hours increases until during the latter part of April such cakes contain only eggs and larvae of the species.

Dung dropped during the spring dispersal receives these adults and the number varies greatly, depending upon the number of new cakes available. During four springs twenty of such cakes were found to contain a maximum of thirteen beetles and an average of seven. This number is included here only to illustrate what was found true of each spring: that the average population in spring-dropped dung was less than the average population in late fall dung. Both dispersal and normal death rate probably account for the falling off.

Dung dropped during late June, July, and August usually contains no adults, but sometimes, one, two, or three after it attains attractive conditions. After this time the population gradually gains its midwinter height.

Numbers of Eggs: Two hundred and forty eggs were taken from a cake January 1, 1932 which also contained twenty-six adults. The average number estimated from cakes containing eggs during December and January of four winters is one hundred ninety-five from thirty-six cakes, most of which contained adults and were used in obtaining an average for the adult winter population above.

It is possible that some of these eggs are laid during warm winter days but most of them are laid during the fall and are in condition to hatch in a few days during the warm weather between the first and middle of April. While they are hatching the adults lay a few more eggs in the same cakes before dispersing and the result is a large variety of stages and instars in a single cake that passed the winter full of eggs and adults.

Eggs were found in increasing numbers from the middle of September onward.

Numbers of Larvae: Since the numbers of eggs have been given and since the numbers of larvae roughly correspond to them, as well as being difficult to count, only a general history will be given here rather than a numerical one. They begin hatching in overwintered cakes about the first of April and finish by the end of April. During this time there is a steady decline in the numbers of eggs and the numbers of larvae which is at first retarded by early additions of spring-laid eggs. Between the end of April and the latter part of May, the number of larvae in overwintered cakes remains about the same, though undoubtedly decreasing because of adverse ecological conditions.

During the latter part of May there begins a decline in the number of larvae and a corresponding increase in number of pupae, and about the middle of June, especially if the season is dry, a greater decrease in young larvae, due to death from dryness. During the years of this study few larvae hatching from eggs laid during the spring in overwintered cakes were found to attain adulthood, mainly because the cakes become bone dry before the long life history became complete.

On the other hand, many but not all of the eggs laid in cakes dropped in early spring yielded adults before rapid drying took place. Those laid in late spring, or in very thin cakes, did not fare so well. No larvae have been found in cakes of any age between the middle of June and the end of September. Those which hatched at that time, few in number, were not observed to complete their life history nor were any larvae found after the end of Otcober.

Seasonal Activity: Eggs, and adults which would lay eggs during the spring, were found overwintering in the dung. A few adults spend the winter some inches beneath the cakes. Adults have been found throughout the year but were uncommon or rare during the latter part of June and in July and August. Neither eggs nor larvae have been found in cow dung during the summer months. Eggs are laid in increasing numbers about the beginning of September, some of them hatching but none of the larvae completing their development in the dung nor apparently surviving the winter.

Pupation: Larvae pupate in the cake.

Life Span: The minimum time required to rear adults from eggs is as follows:

42 days from 448 eggs collected January 4, 1933. Reared in laboratory.

40 days from 213 eggs collected April 7, 1931. Reared in laboratory.

44 days from 320 eggs collected May 1, 1930. Reared in field.

Aphodius haemorrhoidalis Linnaeus

Successional Position: Small numbers of adults have been found in cakes more than a day old. Only one breeding record is available to indicate more. On May 28, 1933 eighty-five larvae were found in a cake bleached white and containing no Sarcophaga, Cryptolucilia, Sepsis or Geosargus maggots and, therefore, probably older than two weeks. On June 7 Leptocera adults emerged from the cake and on June 12 the adult beetles emerged in great numbers.

Numbers of Adults: No adults were found in this cake at the time of collection. An occasional adult is not seen on dung and the small maximum number of seven have been collected in cakes.

Numbers of Larvae: On discovering the eighty-five larvae recorded above, a search of above thirty similar cakes was made during the next two days without discovering more.

Seasonal Activity: Adults have been taken only in April, May, and June at Urbana.

Aphodius ruricola Melsheimer

Five adults were reared from the pupal stage in a dropping brought to the laboratory on April 19, 1932 from which *Geosargus cuprarius* adults had already emerged.

Euphoria inda Linnaeus

Successional Position: This beetle has been reared from cow dung only two times, the larvae having been found at Oakwood, Illinois on May 24, 1931 in their first instar and having yielded adults on July 20. In both cases the dung showed weathering which indicated that it had been dropped during the previous fall.

Numbers of Larvae: Seven and five were found in the two cases.

Seasonal Activity: Adults are known to fly commonly on the first warm days of spring, to disappear during the summer and to appear again in September.

Breeding Media: The larvae are said to live in rotten wood, beneath chips and other woody debris (Blatchley 1910). Those reared during the course of the present study were found in cow dung and made it their food, since, during their second and third instars there was nothing else in the cage available for food.

Life Span: Fifty-seven days were required to rear adults in the laboratory from well-grown first-instar

larvae. All had reached their second instar in fourteen days.

IRREGULAR INFLUENTS

Onthophagus hecate Panzer

Though adults are commonly found in cakes they do not occur there in large numbers. A maximum number of four has been found. They remove fresh dung to burrows underneath the cake but not in large amounts.

Onthophagus pennsylvanicus Harold

Habits of *O. pennsylvanicus* resemble those of *O. hecate.*

Pinotus carolinus (Linnaeus)

Successional Position: Though this species does not breed in droppings it definitely belongs to its earlier stages, the adults visiting it during its first few days.

Activity: During spring and fall adults dig their holes beside or beneath cakes from which they remove great amounts of the interior, frequently leaving nothing but a quick-drying shell in which maggots and grubs perish early.

Copris tullius Oliver

The habits of this beetle are similar to those of *P. carolinus,* but it removes considerably less dung from each cake and is therefore less destructive to insects dependent on breeding there.

Geotrupes splendidus (Fabricius) and *blackburni* (Fabricius)

The influence of these beetles is similar to that of *C. tullius.*

Ligyrus gibbosus Degeer

The habits of *Ligyrus* beetles are somewhat like those of *C. tullius,* but differ notably in that old or overwintered cakes are chosen.

Canthon laevis (Drury)

This scarab, like Pinotus and Copris, removes such large mounts of dung that the shell which remains frequently dries so fast as to prevent most or all of the flies from maturing in many droppings.

At Urbana it is relatively uncommon and its effect is accordingly not great, but in southern Illinois its influence is marked.

MISCELLANEOUS INSECTS

The Collembola, *Achorutes maturus* and Proisotoma; the minute feather-winged beetle *Acrotrichis aspera;* the crane fly *Tipula bicornis;* the moth fly *Psychoda cinerea;* fungus flies of the families Sciaridae and Scatopsidae; and gnats of the families Lonchaeidae and Drosophilidae were collected irregularly in old droppings.

As noted before, droppings in the later stages acquire a larger and larger fauna which is not strictly characteristic of dung but rather of decaying vegetable matter or rich soil. The species recorded above are largely of this general type.

The midge, *Smittia sterocorarius* appeared more regularly as a larva in droppings of the third microseral stage and is probably a more strictly dung-inhabiting species.

RELATIVE ABUNDANCE OF LARVAE OF THE FIRST MICROSERAL STAGE

A consideration of numbers is important because the actual position in succession is here considered to be measured, not by the earliest arriving individuals, nor the latest staying, though these facts are important in measuring range of preference, but by the peak of abundance, which marks the individuality of the species rather than of members of it. Grubs of *Sphaeridium scarabaeoides* may, for example, be found in dung which has been deserted by maggots of Sarcophaga and Cryptolucilia, but most of them attain their growth and enter the soil to pupate with the maggots. Again, grubs of this beetle are frequently found in equal numbers with grubs of the closely related beetle *S. bipustulatum,* of the second microseral stage, though the latter species is a little later breeder and reaches its full growth somewhat later.

The larger number of individuals of the species in this list complete their feeding and pupate, either in the dung, or in the soil beneath it, during the fourth or fifth day.

It was found, during the course of this study, that great diversity existed in the relative numbers of associates, prey, and predators, due partly to differential seasonal activity; partly to differential daily activity; and probably partly to differential selection of breeding materials. Few of the species are obligatory inhabitants of cow dung and some not even of dung of any kind.

Relatively large and small numbers may be the expression of a number of factors in the life history of any species.

Two species, *Scatophaga furcata* and *Myiospila meditabunda,* have been found in uncommonly low numbers and then only during spring and fall. Three species: *Sarcophaga peniculata, Paregle cilicrura,* and *Geosargus viridis* evidently are only occasional breeders in dung of open pastures, preferring other media or other situations. One species, *Sepsis violacea,* finds dung suitable for oviposition during a number of days, therefore may lay enormous numbers of eggs into it. The predators, *Sphaeridium scarabaeoides,* and *M. meditabunda,* have been found in much lower and almost equal numbers, as might be expected, than the total of their likely prey.

ECOLOGICAL POSITIONS OF LARVAE

Since scavenger flies in cow dung are very probably dependent in some way upon microorganisms, these are probably the dominant organisms in that microhabitat in the sense that they control it.

If this is true, it leaves the secondary position of subdominance to two or more maggots which are characteristic, conspicuous and effective in influencing

succession. Such maggots, during early succession in summer months, are those of *Cryptolucilia caesarion,* obligatory breeder in cow dung, and *Sarcophaga lherminieri,* a constant but selective breeder. Both are numerous; together closely approximating the numbers of the most common of the maggots, *Sepsis violacea,* which they greatly out-bulk; and exceeding those of any other maggot or grub. Both are large, closely approximating the bulk of all other maggots and grubs, therefore perhaps passing through their digestive tract and modifying a relatively larger amount of the habitat. Both furnish flesh in large amounts to the predators and, perhaps most important, leave entrance chambers and galleries in ever-increasing number and size as they grow.

These galleries are used by *Xyalophora quinquelineata,* parasite of Sarcophaga, and by the gradually increasing number of late-succession staphylinid adults. In the case of Xyalophora, somewhat more than half of its parasitism seems to be accomplished through its activities in these galleries, and in the case of the staphylinid beetles it seems that these galleries must be used, for they make ready use of any openings to the surface of fresh dung, but have not been observed to make their own entrance.

Dung which is dropped before the middle of April and after the middle of October differs widely in its large, early-succession fauna for, during the growing season before and after those dates, *Scatophaga furcata* and *Myiospila meditabunda* replace the two large summer flies. Maggots of Sepsis usually outnumber those of Scatophaga and Myiospila combined, but rarely out-bulk them. The other fly present, *Paregle cinerella,* does not attain considerable numbers except in late April and May. For these reasons and because of the gallery-forming capacity, it is likely that *S. furcata* and *M. meditabunda* are subordinants at this time.

There comes a time later in the season when Scatophaga ceases to breed in cow dung in open pastures, and only small numbers of Myiospila are found breeding while Cryptolucilia, first, and Sarcophaga, later, gradually replace them, and when perhaps their position as subdominants is assignable for the four and measurable by the relative numbers of each.

Sepsis violacea being common in large numbers in both spring- and fall-dropped dung, and furnishing at least supplementary food to predators, undoubtedly has sufficient force in this mircohabitat to be classed as an influent along with *Sphaeridium scarabaeoides* grubs which, evidence goes to show, are predatory at least on *Sarcophaga lherminieri* and, late in their development, on *Geosargus cuprarius.*

BOVINE DUNG AS A STRUCTURAL UNIT OF THE PRAIRIE

Hayes, 1928, wrote of the place of bovine dung in natural prairie as follows: "One of the most interesting groups of prairie insects is the scavenger group which originally derived its sustenance from droppings of the buffalo, but now thrives on the excrement of domestic cattle and horses which have replaced the buffalo on the prairies."

Seton (1929) estimated that natural, undisturbed prairie was inhabited at the rate of one buffalo to twenty acres and that the plains were inhabited at the rate of one to forty acres.

It would be necessary to make a study of the number of new droppings left by each buffalo in order to gain an idea of the numbers of insects inhabiting their droppings. One may however, get a rough idea from feeding experiment of cattle. According to Henry and Morrison, 1923, beef cattle produce 52 pounds of dung per each 1000 pounds of live weight daily. Buffaloes average somewhere between a thousand and two thousand pounds and probably produce dung in amounts somewhat resembling that of cattle. If so, each individual has an output of about ten droppings each day or one to every two or three or four acres daily.

The number of individual species of flies to be observed on bovine droppings therefore runs into the hundreds for the larger, early succession species and into the thousands for the smaller and late succession species which can tolerate wider age-range in droppings. The numbers of individual flies to be found on all kinds of droppings, bovine and others, is therefore enormous.

Unless the ecologist who samples an area, actually sweeps over a dropping, or otherwise samples it, few or no coprophilous insects will be netted. Most of them are in or on the dung even when winged but their numbers can be estimated by certain observation suggested above.

Shackleford, 1929, found and estimated *Sepsis violacea* as being a "vernal and estival influent" on Illinois prairie. This insect is a general dung scavenger. Adams, 1915, found no dung-inhabiting insects but these authors had studied prairie which was far from normal, having lost its large mammal population for one thing.

Dung inhabiters are apparently not as common as general feeders on grass, weeds, or shrubs, but are probably more common than many insects more often caught, but dependent on some specific grass, weed or shrub. Only attention to a structural evaluation of the prairie can reveal the true relative numbers.

SUMMARY

Insect succession in and on cattle droppings in open pastures began with one or two species of flies and ended as the dropping disintegrated, with a possible population of several score species of various orders of insects. However, despite increasing acceptability of the older droppings to a greater number of species, any given dropping was actually likely to be inhabited by fewer species as it grew older. The greatest number of species inhabiting it at a given time occurred during the early middle stages.

Those species which were obligatory breeders in dung, especially cow dung, occurred early in the suc-

cession while those which were facultative breeders in dung tended to occur in later stages.

Those species which were earliest in the succession tended to have (1) the shortest life histories and (2) the shortest periods of representation either in or on the droppings. Those species which occurred latest, tended to have the longest life histories and to be represented longest in or on the dropping. Succession, in other words, moves faster during early stages and slower during later stages.

The environment in which dung is dropped, has a profound effect on the composition of its fauna. Droppings in densely shaded woods have a different set of dominant insects than those in sunny, open pastures. Some species which are common in and on droppings in sunny pastures, are completely absent under dense shade.

Physical properties of droppings and, to judge by differences in odor and color, chemical or bacteriological, were decidedly different in the two environments noted above.

The degree of light on droppings in open pastures had a noticeable effect. Some of the early succession species failed to oviposit in dung dropped early at night.

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