AN EXPERIMENTAL STUDY OF THE MORTALITY FACTORS OF LARVAL *MUSCA AUTUMNALIS* DeGEER[1]

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INTRODUCTION

THE APPROACH

The experimental approach to problems in insect population dynamics in the field has long been used but seldom has its full potential been exploited. Fuller (1934), in a now classic paper, reports on results of field manipulations of densities of blowfly larvae and available food, showing the importance of competition and predation. Additional mortality factors such as temperature, later shown to be of importance (Waterhouse, 1947), were not considered. Other attempts at constructing complete budgets of population mortality have been made since. One of the most notable is the work on the chrysomelid *Phytodecta olivacea* (Richards and Waloff, 1961). Those factors which could be measured directly from the populations, such as parasitism and egg inviability, were carefully studied. Only predation mortality was estimated independently using serological techniques. Although predation turned out to be the main factor contributing to mortality, competition and specific environmental factors could not be isolated and hence their importance remained unevaluated.

The studies of the mortality patterns of the cabbage aphid, *Brevicoryne brassicae* (Hughes, 1963) and the cabbage root fly, *Erioschia brassicae* (Hughes and Mitchell, 1960), are representative of other studies which used the correlative approach. Life tables were obtained and field population data were manipulated providing a partitioning of observed mortality into various components.

Probably the most ambitious effort at developing predictive schemes rather than merely descriptive models is the Canadian work on forest lepidoptera (Morris, 1963a, b; Embree, 1965).

Life tables were used extensively to evaluate overall mortality along with experimental evaluation of some of the mortality factors. Field populations were also examined using the key factor approach (Varley and Gradwell, 1960; Morris, 1963b). This approach is a form of logarithmic multiple regression which can be used to evaluate the contribution of mortality at each age interval to population change. Unfortunately, important mortality factors were evaluated using correlational techniques which inherently fail to provide a causal basis for conclusions. Further the large error in sampling budworm populations in particular and field populations in general, and the lack of accounting for all probable potential mortality factors are such that failure to find evidence for the

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action of a particular factor still does not allow the discarding of that factor as non-significant (Watt, 1963).

The need for experimental evaluations of the effect of mortality factors has been recognized by the workers involved in the forest lepidoptera study (Morris, 1963a; Embree, 1965). The life table and key factor approaches have provided good evaluations of mortalities. However, experimental partitions of the measured mortalities are necessary to allow the construction of predictive models or budgets with an empirical causal base which can be used to check against the demographic data.

Such an approach has been repeatedly recommended (Morris, 1963b; Hall, 1964; Kajak, 1964a; Henson, 1968 and others) and would demand as a prerequisite a sound knowledge of the natural history of the system to be studied; this would enable an intelligent selection of the main factors to be considered. Construction of laboratory and field life tables would then give evidence of the extant, overall population pattern.

Each potentially important factor could then be examined in the laboratory and, if possible, in field experiments in which manipulations should encompass the whole range of the factor in question under natural conditions.

The proper choice of experimental material and design can provide empirical equations or estimates that can be put together and may be used in a predictive fashion once all the factors under consideration have been evaluated. As a first approximation, each factor may be studied independently, but interactions merit a good deal of attention.

The combined estimates of the various factors should, when complete, predict a population effect that compares with the observed field life table estimates, given that the main variables have been monitored during the construction of the field life tables so that the experimentally obtained equations or estimates can be fitted to the observed demographic data.

Whenever possible, independent checks on the main experiments should be applied. Observations and smaller experiments using different techniques could provide such checks.

THE EXPERIMENTAL SUBJECT: *Musca autumnalis* DEGEER

The face fly, *Musca autumnalis* DeGeer, although a comparative newcomer to North America (Sabrosky, 1961), has received considerable attention. The basic facts of the life history of the face fly are well known (Hammer, 1941; Teskey, 1960; Fales *et al.*, 1961; Wang, 1964). Gravid females deposit eggs on freshly laid manure. The eggs hatch in 6-18 hr, passing rapidly through the first instar. By the 2nd day the larvae have molted into a 2nd instar and, if the temperature is warm enough, they reach the 3rd and last instar. In the 4-5th day of life, the whitish larvae become milky yellow and leave the dung, seeking a dry pupation site. The adults emerge after about a week in the pupal stage.

Although the natural history of the larvae can thus be sketched, nothing is known about the quantitative aspects of larval populations, even though dung pads seem particularly suited for quantitative studies. At least for the face fly, all eggs are laid within 2 to 3 hr after the dropping is deposited because oviposition is prevented after this period by the drying surface of the dropping; thus there are no overlapping generations. Further, not the least of advantages is the ease of replication enabled by the discreteness of dung pads.

The approach outlined in the preceding section was applied in this particular case by first estimating larval mortality in the laboratory. These results were then compared with estimates of mortalities in the field. Independent evaluations of the effect of various potential field mortality factors were carried out in an attempt to account for the difference between laboratory and field survival.

The potential mortality factors in the larval stages of face fly may be outlined as follows:

A. Non-Biotic Environmental Factors
   1. Temperature
   2. Moisture content of substrate (including effect of rainfall)
   3. pH of substrate
   4. Other conditions of the substrate (nutritive quality, site of deposition of dropping)

B. Biotic Factors
   1. Physiological mortality
   2. Pathogens
   3. Parasitism
   4. Competition for food
      a) Intraspecific
      b) Interspecific
   5. Predation
      a) By invertebrates
      b) By vertebrates

Estimates of the effect of the full range of each factor were obtained by means of laboratory and field experiments. From these estimates, predicted mortalities could be obtained by mimicking field conditions during the actual field survival measurements. The predicted and observed survivorships could then be compared. Fig. 1 provides a diagrammatic summary of the approach and procedures followed in this study.

Laboratory mortality has been described as physiological mortality, that mortality which occurs even under conditions as favorable as could be provided by the experimenter. As such, it comprises varied and unknown sources of mortality, being in effect a "background mortality" (Hughes & Gilbert, 1968) which cannot be dissected by the available experimental procedures. All the mortality factors listed were studied except site and substrate conditions, and pathogens. The experimental procedure, as will be seen, was such as to eliminate substrate and site variation. Pathogen action was not considered.

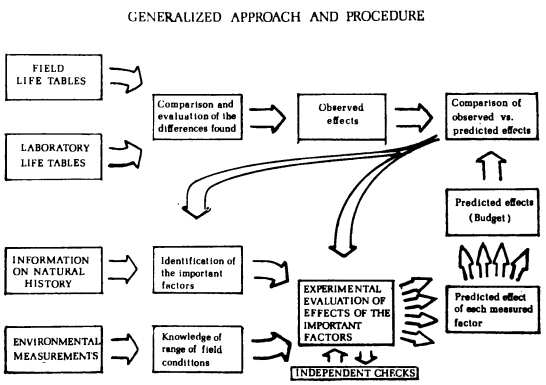

FIG. 1. Flow chart summarizing the main procedures suggested by an experimental approach and followed during this study. Titles in capitals indicate the steps in which data are collected.

EVALUATION OF EGG AND LARVAL MORTALITY: THE PROBLEM

INTRODUCTION

Few attempts have been made to evaluate mortality in field populations of immature diptera. In a long series of interesting reports, Kajak and his coworkers (1964a, b; 1965; Kajak & Rybak, 1966; Kajak *et al.*, 1968 and references cited therein) have described field populations of benthic dipteran larvae and experimentally obtained estimates of the effects of various mortality factors. Since the experiments were carried out in different sites over several years, no unified scheme could be produced for any one species.

For non-aquatic dipterans, probably the best known efforts are the already mentioned series of experiments with *Lucilia* in Australia (Fuller, 1934; Waterhouse, 1947). Variable but large mortalities were recorded. Competition seemed to be the most important mortality factor, followed by high temperatures and predation.

The mortality patterns of the eggs and larvae of the cabbage root fly, *Erioschia brassicae,* have been worked out in England (Hughes, 1959a, b). The main source of mortality was predation in the egg stage. Carabid and staphylinid predators apparently removed up to 95% of the eggs produced.

Research on face fly mortality has been limited mainly to a few inconclusive observations, so that no general statements can be made from available knowledge.

METHODS

Face flies were reared in a manner similar to Ode & Matthysse (1967). Manure, blood and sugar water were provided daily in paper cups half filled with vermiculite. Flies were kept in cages measuring 1 m^3 and illuminated by 200 watt bulbs. This light intensity was necessary to stimulate oviposition. The temperature in the rearing room was maintained at about 32°C.

To measure larval mortality in the laboratory, eggs were inserted into the surface of fresh manure in one-pint paper containers. Three replicates were followed by counting the survivors 1, 3, and 5 days later.

Measuring field mortality was somewhat more complex. To avoid heterogeneity due to diet (Treece, 1965), breed of cow, and habitat (Hammer, 1941; Mohr, 1943), a farm characterized by uniform herd and husbandry practices was chosen. This farm may be considered typical of dairy cattle establishments in New York state. All field experiments were performed in an open pasture within a wire-fenced enclosure measuring about 10 × 5 m.

Manure was collected while the cattle were being milked. The dung from 4 or 5 individual cows was mixed so as to decrease sample heterogeneity. The dung was then taken to the pasture and standard amounts put into 3 cm high cardboard hoops of about 20 cm in diameter. A round piece of fairly stiff plastic netting under the hoop prevented the manure from escaping under the cardboard. Sixteen such samples were prepared for each experiment, laid out about 30 cm apart in a square 4 by 4 pattern.

After each hoop was filled, the top surface was smoothed out. Since oviposition ends about 2 hr after the dung is deposited (Hammer, 1941), the eggs could be counted a few hours after the trial had been set up. Counting was feasible because of an interesting peculiarity of face flies: the eggs are inserted vertically into the dung, frequently leaving what is called a "mast" protruding above the surface. These masts could be seen on the flat surface.

To follow the cohorts, 4 of the samples were collected at random after 1, 2, 3, and 5 day periods. On the 3rd day, a pupal trap was placed under the remaining samples to collect the emerging larvae. These traps were made out of a sheet metal hoop 7.5 cm high with a wire mesh bottom. Since this large mesh allowed some larvae to escape, plastic netting of a finer mesh was secured to the interior of the trap with caulking compound. The larvae emerged from the dung and pupated in the provided vermiculite. The last sampling consisted of placing the vermiculite and pupae into plastic bags to await emergence. Field survivorship was measured in three such trials, each trial consisting of the sixteen individual experimental droppings.

The experimental pads produced were quite similar to natural droppings in regard to temperature, moisture content, and fauna (Valiela, 1968).

All samples were extracted with two sets of 4-unit Tullgren funnels provided with 200 watt lamps. Gasoline funnels with a maximum diameter of 30 cm allowed the comfortable placing of the 20 cm samples on the supporting wire. This large size also provided proper ventilation around the sample to avoid condensation on the funnel walls (Haarløv, 1947). A piece of organdy was fixed in place over the top of funnel to allow moisture to leave while retaining flying insects. The specimens were preserved in ¼ acetic acid and ¾ 75% alcohol with 5% glycerine.

Because both the egg counting and extraction procedures involved a considerable bias, correction co-

efficients were applied to the counts in order to give more accurate estimates.

A large bias in the egg counts was produced by eggs inserted so deeply in the dung that the mast was invisible. A correction coefficient for this bias was obtained by using a linear regression based on laboratory data. Manure was exposed to caged flies for varying amounts of time, producing different egg densities. The masts on the surface were then counted and this was followed by a thorough search of the manure. A simple linear regression was then calculated. This could only in a rough way yield a correcting coefficient, for this error is probably not a simple function of the total eggs present on a dropping. The highly contagious distribution of eggs within a particular pad produces great local differences in densities which might affect the number of submerged eggs. This complex distribution leads to difficult statistical and experimental procedures and was not considered further. The regression line of Fig. 2 was used to correct the egg counts. The appropriate corrected value for particular egg counts was located using the line and each value thus obtained appears in Appendix 1.

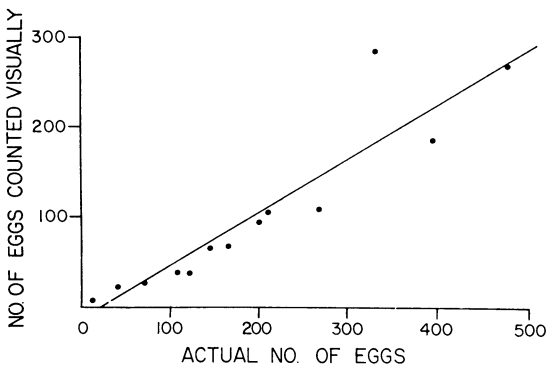

FIG. 2. Regression to correct errors in visual egg counts.

Many eggs were deposited beneath the surface. This posed a problem since conceivably submerged eggs may be subject to greater mortalities due to lack of oxygen (Hammer, 1941). However, Hinton (1960) has conclusively demonstrated that face fly eggs are capable of respiratory exchanges even when completely submerged. This problem may nevertheless be quite significant since laboratory life table experiments were based only on the survival of eggs arbitrarily placed at the surface whereas field studies included both eggs on the surface and submerged eggs.

The effect of manipulating eggs in setting up the survival experiments was measured by placing manure-filled containers into the colony cage, allowing normal oviposition and then carefully scanning the dung surface under a binocular microscope. This produced very accurate counts since ovipositing females leave a small orifice on the surface of the dung. Thus, even wholly submerged eggs could be counted. The survivorship of such eggs could then be measured. It was not feasible to carry out this procedure in the field.

The extraction technique was a compromise. Due to the rapid growth of the larvae it was necessary to extract as quickly as possible, yet prevent the heat gradients from becoming too severe. The conditions settled upon yielded excellent extraction of adult insects and large dipteran larvae but were deleterious to many smaller fly larvae. Therefore, it seemed that the size of larvae could be related to the efficiency of extraction. Larvae of various sizes were extracted to provide an estimate of the error involved. However, dung collected in the field is riddled by the activity of both larvae and burrowing beetles. The tunnels thus formed provide smaller individuals with avenues of escape. The only way to obtain a meaningful measure of the extraction efficiency was to collect as many species as possible, place them in samples with fly larvae, allow tunneling to take place and then extract. The small number of burrowers and the relatively short time allowed for burrowing prevented the production of a near-copy of a field dropping. Therefore, the error involved in the coefficient and the degree to which the coefficient corrects are both bound to be overestimated. Indeed this appars to be the case. The error shown by the data in Fig. 3 is quite large. Although each field-collected sample was searched seldom were many larvae found to have remained after extraction. This could be due to the difficulty in finding dried, small, soft-bodied larvae in the dry dung. Nevertheless, it was felt necessary to obtain the efficiency of extraction by using the regression in Fig. 3. Corrected values of extraction for each of three trials are presented in Appendix 1. Kempson *et al.* (1963) discuss more extensively the problem of the general technique of heat extractors.

RESULTS

The data obtained in the laboratory rearings are shown in Table 1 and Fig. 4. The total larval survival was about 76%. Killough & McClellan (1965) report that laboratory populations of *M. autumnalis* yielded an average survival of about 78.2%, in good agreement with the figures obtained here. Similar experiments with the closely related *M. domestica* showed mean survivals of 72.1% (Bøggild & Keiding, 1958) and 69% (Sullivan & Sokal, 1963). For comparison with the laboratory survival, a summary curve for the 3 field survival trials is also shown in Fig. 4.

Handling of the eggs did not affect survival, since survival of eggs which were not handled was 84.1%, 92.4% and 71.4% starting respectively with 44, 79 and 14 eggs. The mean hatching was 87.6% which agrees with 87.7% survival on the first day as shown in Table 1.

In the field survival trials each replicate was weighted according to its initial number of eggs while computing means and variances (Yates, 1960). The standard error of the means of the 3 field survival trials is not unduly large (Table 2, Fig. 4). When each survivorship trial is examined, however, the

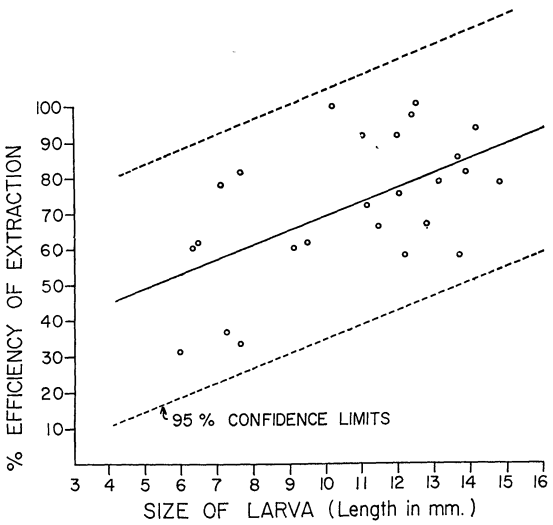

FIG. 3. Regression for correction of extraction bias of Tullgren apparatus.

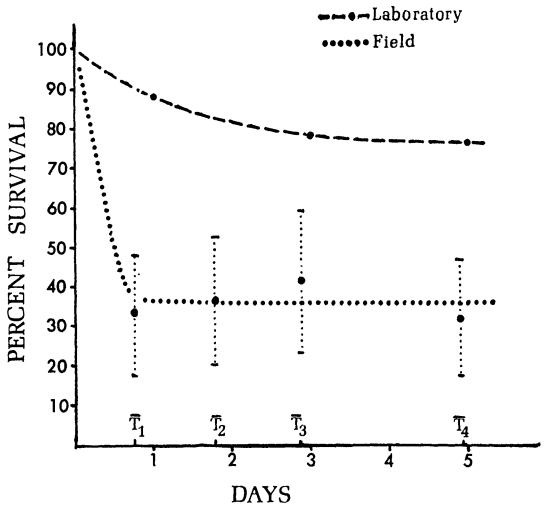

FIG. 4. Field and laboratory survival curves for larvae of *Musca autumnalis*. Curves are drawn by eye. Standard errors are shown about each field survival mean. Mean time intervals for the field samples are shown as T_1, T_2, T_3 and T_4.

notable variability becomes obvious (Appendix 1). The order of magnitude of this variability, interestingly, is similar to that found by Poorbaugh (1966) in his study of larval *Scatophaga*.

In each field trial there was one replicate that showed a survivorship greater than 100% (cf. Appendix 1). This may well be the result of undetected bias in the correction coefficients used. An alternate explanation for these deviant figures may be that sometimes the dung escaped somewhat from under the hoop, providing additional ovipositional surfaces after the egg counts had been completed. In any case, the aberrant values were included in all calculations.

TABLE 1. Survivorship for *Musca autumnalis* larvae under laboratory conditions. The values are numbers of individuals.

Days	Rep. 1	Rep. 2	Rep. 3	Mean % Survival ± 1 S.E.
0	50	49	48	100
1	44	42	43	87.7±0.36
3	39	37	39	78.3±0.23
5	39	34	39	76.2±1.90

Comparing the overall field and laboratory survival curves, 2 obvious differences emerge: 1) it seems that field mortality is about 40% larger; 2) most of the field mortality occurred during the 1st day. The survival rates after the first day are quite similar and the standard deviations of these means overlap so broadly as to make statistical tests superfluous at this point.

MORTALITY FACTORS FOR EGGS AND LARVAE OF FACE FLY: EXPERIMENTAL ANALYSIS

TEMPERATURE

INTRODUCTION

Temperature apparently has been shown to be most effective in lowering survival of most dipteran larvae at the extremes of field temperature ranges. Feldman-Muhsam (1944) demonstrated that housefly larvae died below −4°C. Eggs survived lower temperatures if the exposure times were short, but even at −8°C eggs survived for an hour. Larsen and Thomsen (1940-1) found that eggs of *M. domestica* hatched around 10-11°C, but that great larval mortality ensued. Housefly eggs showed a lower limit of development at about 12°C in Israel, while larvae were able to grow at 8°C (Feldman-Muhsam, 1944).

Eggs of *M. autumnalis* died when exposed to 11°C, while larvae endured such temperatures but growth was halted (Wang, 1964). Similarly, 3rd instars are more resistant to low temperatures than are earlier stages of *Haematobia irritans* (Bruce, 1964).

Since temperatures in the field rarely remain for very long at the apparently critical minima, it is to be expected that a temporary halt in development is not too harmful to face fly larvae. In fact, it probably is quite a regular event in Eurasian populations, judging from the temperature records of Hammer (1941).

Melvin (1934) found that eggs of *M. domestica* hatch up to 43°C, while those of *Haematobia irritans* hatched at 60°C. Viability of eggs of *H. irritans* was not affected by exposure to 48°C for 28 hr in North Carolina (Bruce, 1964).

Hafez (1941) showed that the first instar in the Egyptian housefly (*M. vicina*) is the most sensitive to high temperature. In Denmark, Larsen (1943) in a series of careful experiments, showed that for any length of exposure time, 1st instar larvae of *M.*

TABLE 2. Means and standard errors of percent survivals in field trials.

	T_1	T_2	T_3	T_4
Trial I	46.74±20.64	55.00± 5.98	44.86± 9.55	44.85±22.42
Trial II	24.24± 4.42	14.40± 1.54	48.29±19.47	36.93± 6.88
Trial III	28.66±14.35	39.50± 3.89	31.80±15.90	12.01± 6.01
Trial means ± 1 S.E.	33.2 ±14.1	36.3 ±16.3	41.7 ±17.3	31.3 ±14.0

TABLE 3. Percent larval survival at various constant temperatures.

Replicates	10°C	16°C	20°C	35°C	40°C	45°C	47°C	53°C
1	0	30	55	65	85	40	15	0
2	0	20	60	70	50	55	35	0
3	0	45	35	65	60	35	25	0
4	0	20	60	60	85	35	50	0
5	0	25	55	95	70	65	30	0
6	0	20	60	70	75	60	65	0
7	0	0	30	65	60	55	40	0
8	0	15	65	60	65	55	50	0
Mean	0	21.9	52.5	68.8	68.8	50.0	38.8	0
Std. dev.	—	4.1	4.1	3.6	3.9	3.7	4.2	—

domestica were more susceptible to high temperatures (49°C) than other larval stages, although not as sensitive as were eggs. At any one temperature and time of exposure 1st and 2nd instars are considerably more susceptible than the 3rd. There is probably some variation in housefly tolerance, since larvae of the tropical subspecies *M. d. corvina* may survive an hour's exposure to 60°C (Roubaud, 1911).

For *M. autumnalis* temperatures of up to 40°C may still be within the optimal range, but there is little critical evidence (Wang, 1964). However, on the basis of indirect evidence obtained mainly from the reviewed work with other muscoids, it would seem plausible to claim that immature *M. autumnalis* would be the most sensitive to heat during their first day of life.

METHODS

To obtain an independent estimate of the effect of different temperature regimes on larval survival, 20 eggs were placed on about 200 g of dung in a plastic-covered cardboard pint container. Eight replicates were subjected to each of 8 different temperatures in a constant temperature cabinet.

In the field, thermograph records were maintained during the course of the sampling. However, these temperatures refer to air temperatures 10 cm above the pasture floor. Using a probe thermograph, temperatures were recorded within the dung itself to obtain a relationship between air and dung temperature and to measure temperature gradients within droppings.

RESULTS

The data in Table 3 showing the response of larval survival at various temperatures are graphed in Fig. 5. There are several drawbacks to the use of constant temperature data to extrapolate to field conditions. Constant temperatures may not have the same effect as fluctuating temperatures. Also, no consideration is given to length of exposure to a particular temperature.

The evidence available in the literature suggests that temperature extremes should mainly affect eggs and 1st instar larvae. Therefore, temperature effects on mortality should be evaluated during that early period.

There is a further reason for considering temperatures only during the early life of *M. autumnalis*. There is a vertical gradient of temperatures in a field dropping (Hammer, 1941), and the greatest changes and extremes in temperature are to be found at the top of the dropping. It is almost the rule that if a high temperature is recorded at the top of a pad, the temperature at the bottom is more amenable to the larvae (Hammer, 1941; Valiela, 1968). Since larvae, especially mature ones, are quite active, it is to be expected that if temperatures become adverse at the top, the larvae would move to a more favorable part of the dropping. This is clearly not the case with eggs and newly emerged larvae, since they are limited to the top of the pad. Since we suppose that at this stage they are also most susceptible to temperature extremes, we have additional basis for suspecting that temperature extremes would be most important during the early stages.

Even though the mortality curve of Fig. 5 shows almost equivalent death tolls for both high and low temperatures, cold temperatures operated over a far longer time to produce their effect. In general, it is assumed that heat has a direct killing effect, while cold delays completion of the life cycle, and prolongs the exposure to various other death factors (Larsen, 1943).

A death rate can be obtained simply by dividing the mortality at each temperature by the span of time during which the larvae were exposed to that temperature. The results for the data are shown in Fig. 7. Since it is supposed that large larvae are inured to temperature extremes, only the span of time for eggs

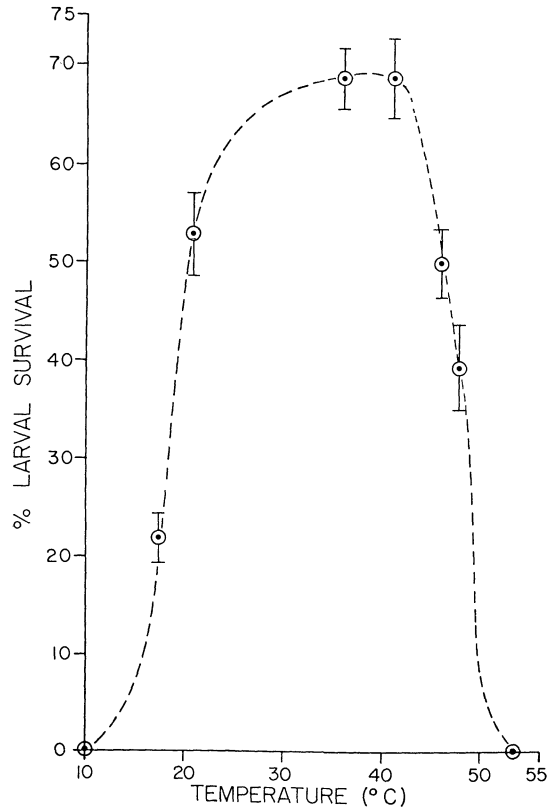

FIG. 5. Effect of constant temperature on larval survival in the laboratory. Means of eight replicates and standard deviations.

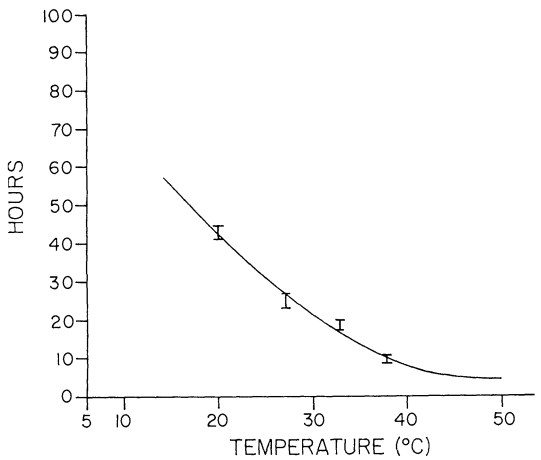

FIG. 6. Duration of the egg plus first instar stages at various constant temperatures. Adapted from Wang (1964).

plus 1st instar (Fig. 6, obtained from Wang, 1964) was used as the divisor rather than the duration of the full larval period. This evaluation assumes that death rates were uniform through the egg and first larval stages.

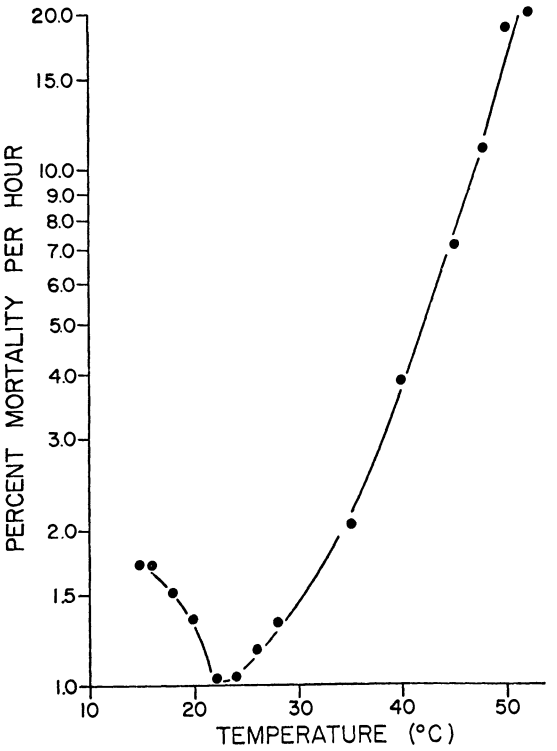

FIG. 7. Mortality rates at various temperatures. Curve drawn by eye.

The shape of the resulting curve, with a small tail in the low temperature range, indicates that for similar exposure times, low temperatures would exert much less effect than high temperatures. The thermograph records from the field were divided into hourly intervals as convenient time units; then the recorded air temperatures were converted to dung surface temperatures and applied to Fig. 7 to obtain a cumulative mortality budget due to temperature (Fig. 8). The right-most point of the curve for each survivorship trial was obtained by considering the mean temperature during the period and then using available data (Wang, 1964) to make an estimate of the total duration of the egg and first instar stages.

The predicted survival values for the 3 field trials on the basis of temperature are 77.2%, 73.2% and 47.0%. Only the last figure exceeds the mortality level set by laboratory survivorship in Fig. 5, a reflection of the higher temperatures during trial III.

MOISTURE CONTENT OF DUNG

The water content of manure presumably could become a limiting factor to larvae of face flies if the dung became too dry to allow feeding (Hammer, 1941; Mohr, 1943). Hafez (1939a) presents a graph showing a pronounced decrease in water content as time passed. However, these measurements of water content were performed on large masses of dung, including the dry outer layer. From the standpoint of a face fly larva, however, only the moist internal

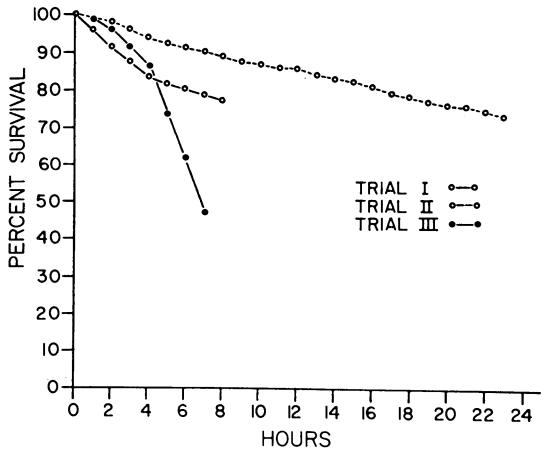

FIG. 8. Survival curves for the field trials predicted on the basis of mortality due to temperature. Physiological mortality was included in the calculations.

conditions have relevance. Measurements must therefore be made in the interior of the dropping if they are to reflect a situation affecting larvae.

METHODS

The changes in moisture content under field conditions were measured by sampling the interior of experimental droppings. Twelve standard experimental droppings were set up. Two replicates were then sampled at 1, 2, 3, 4, 5, and 7 days. Naturally deposited pads were labelled when deposited and sampled at some time afterwards. This gave a check on the experimental pads. The samples were dried at 80°C and the percent water content calculated by difference.

RESULTS

The changes in water content in the experimental pads are shown in Fig. 9. Replicate variability is so small that it is not shown. There is little if any change in moisture in the immediate environment of the larvae during the time that they are present in the pad. This remained true even in spite of the occurrence of rain (Fig. 9) during one of the trials.

The range of moisture percentages obtained is quite uniform and consistent with those water contents found in naturally deposited pads in New York (Valiela, 1968) and elsewhere (Hafez, 1939a; Hammer, 1941; Sobel, 1966). Natural pads older than 6 days do show a lowering of water content. However, face fly larvae have by that time migrated to pupation sites in the soil. If no changes occur during the time in which face flies are present, it is unlikely that the moisture level of dung affects larval survival.

There is a further reason for discarding water content as an important mortality source. Dowding (1967) found that larvae of higher muscids are in large measure filter feeders. Obviously, such a feeding method requires a semi-aqueous medium.

In the field, the clustered distribution of face fly

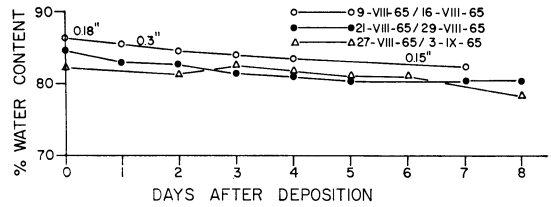

FIG. 9. Changes in moisture content of experimental droppings. Figures in inches between points indicate amount of rainfall between the points.

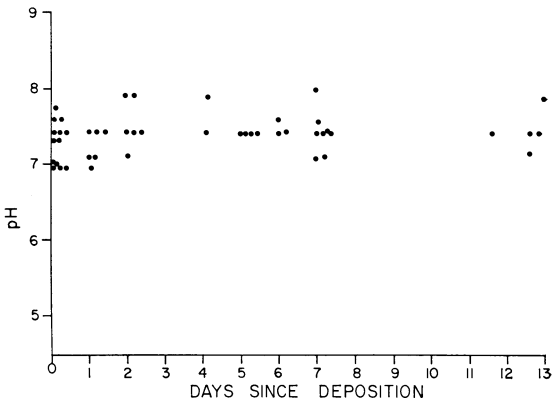

FIG. 10. pH determinations of natural droppings of various ages. All samples were collected during summer, 1964.

larvae within any one pad is striking. The ceaseless churning of the substrate by the aggregated larvae results in a notable increase in the fluidity of the dung. Thus, low water content of dung could hardly act as a factor limiting food availability since the clustering behavior of larvae may increase liquefaction to a level where feeding may take place.

pH

The relative acidity of the substrate could conceivably affect larval survival. Indicator paper was used to record pH in the naturally deposited pads that were sampled for moisture. Fig. 10 shows that pH does not seem to change as time passes. Dung seems to be effectively buffered between pH 7 and 8. Morgan and Schmidt (1966) show that larvae of the muscoid *Haematobia irritans* survived a pH range from 6.0 to 9.0. It would seem that the relatively constant pH range found in natural conditions has scant possibilities of producing significant amounts of mortality of face fly larvae.

COMPETITION FOR FOOD

INTRODUCTION

The food habits of many higher dipteran larvae have scarcely been studied. Some pertinent studies are those by Keilin (1912), Baumberger (1919), Muirhead Thompson (1937), and Dowding (1967). The main food of insects that occur in decaying organic matter is thought to be the microfauna and

microflora and not the substrate itself. Since a filtering mechanism seems to be a general occurrence in non-carnivorous, higher muscoid larvae (Dowding, 1967), competition for food can be expected, since in general only particle size can be used in food selection (Jørgensen, 1966). Of course, this would be true only if the competing species show no spatial isolation.

The reduction of pupal size and weight as an initial response to food limitation has long been known in fly larvae (Fuller, 1934; Waterhouse, 1947; Ullyett, 1950; West, 1951; Nicholson, 1954). In *Drosophila,* at least, this reduced individual size is accompanied by a protracted larval period (Robertson, 1960). However, if food deprivation is severe enough, reduction in the size of individuals or prolongation of larval life may no longer be sufficient to prevent larval mortality. Thus pupal size is a sensitive first indication of food shortage.

METHODS

To study the effect of intraspecific competition for food, rearings at varied larval densities were obtained by placing different numbers of eggs and known amounts of dung in pint cardboard containers, as outlined in Table 4. The resulting pupae from each treatment were counted and weighed soon after pupation was completed.

TABLE 4. Experimental design for food supply studies of face fly larvae. All weights in grams.

No. Larvae	No. Replicates	Wet Weight of Dung	% Dry Matter	Weight Dry Dung/Larva
20	3	300	15.6	2.340
60	3	300	15.6	0.780
100	3	300	15.6	0.468
120	3	300	15.6	0.391
110	2	200	16.2	0.324
150	2	200	16.2	0.216

Interspecific competition for food was studied by rearing larvae of *M. autumnalis* with larvae of other species. The rearing procedure was the same as described for intraspecific competition. Since *Sarcophaga* females are live bearers, first instar larvae were used instead of eggs. Only *Sarcophaga* sp. and *Orthellia caesarion* were available in large enough numbers to carry out competition experiments.

The length and width of pupae from the field survival experiments were recorded to obtain a measure of the level of competition to which the survivors were exposed.

In August 1967, naturally deposited droppings in which face fly larvae had reached the milky yellow stage were collected. The resulting pupae of the large dipteran species were then measured and weighed. Throughout the study, periodic checks on pupal size in natural pads were carried out. Collections were secured whenever pupae seemed small.

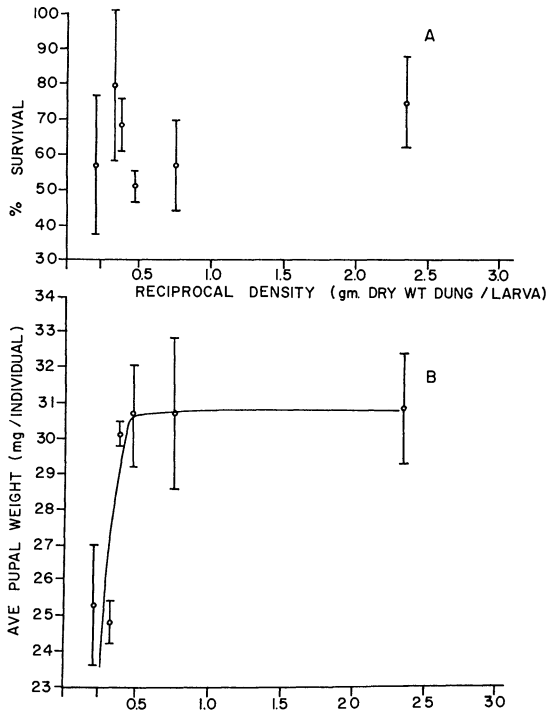

FIG. 11. Effect of food availability on a) % survival and b) pupal weight. Means and standard deviations from Table 5.

RESULTS

The data from the laboratory face fly crowding experiments (Table 5) are graphed as Fig. 11. The overlap of the standard deviations of the survival data suggests that there are no significant differences among treatment means. However, pupal weight decreased below a density of about 0.5 g dry weight of dung per larva. It would seem that competition can be expected to occur at densities above this threshold.

If all eggs laid in a dropping survived and shared in the available food, the resulting densities will be as shown in Table 6. Since mortality did take place, these estimates of substrate availability are quite minimal. Yet in only one out of 32 pads did the potential larval densities come under the threshold of 0.5 g dry matter per larva. It follows that intraspecific competition by itself could hardly account for any significant mortality. Apparently field oviposition by *M. autumnalis* rarely reaches the saturation point as defined by these experiments. Intraspecific competition, then, would seem to have little role in field survival.

If pupal size is a function of competition and if it is assumed that all large larvae of the various species found in dung use similar food, then pupal size should bear some relation to the total biomass that utilizes available food. The weights and sizes of large larvae obtained from natural droppings are shown in Table 7. These data yield the regression shown in Fig. 12. As occurred in the interspecific laboratory

TABLE 5. Results of intraspecific competition experiments with *M. autumnalis*.

	Density (Grams Dry Weight Dung/Larva)					
	2.34	0.78	0.47	0.39	9.32	0.22
Percent survival (3 replicates)	60.0	68.3	73.0	62.5	62.7	70.7
	85.0	41.7	68.0	65.0	93.6	41.3
	80.0	60.0	76.0	78.8	—	—
Mean:	75	57	72	68	79	56
Std. dev.:	13.2	13.4	4.0	7.1	21.9	20.8
Pupal weight (mg/individ.) (3 replicates)	31.70	30.90	31.46	30.81	25.38	24.43
	30.20	34.60	30.10	31.27	24.53	26.88
	33.50	31.60	32.98	—	—	—
Mean:	31.73	31.54	31.52	31.05	24.86	25.34
Std. dev.:	1.67	2.11	1 44	0.32	0.56	1.73

TABLE 6. Potential ratio between dry matter and larvae assuming no mortality in the field survivorship trials.

Replicate		Trial I		Trial II		Trial III	
		Correct. No. Eggs	Dry Matter per Larva (g)	Correct. No. Eggs	Dry Matter per Larva (g)	Correct. No. Eggs	Dry Matter per Larva (g)
T_1	r_1	35	3.89	135	1.01	87	1.57
	r_2	39	3.49	157	0.87	115	1.18
	r_3	35	3.89	400	0.34	183	0.74
	r_4	32	4.25	228	0.60	107	1.27
T_2	r_1	35	3.89	158	0.86	75	1.82
	r_2	25	5.45	49	2.78	65	2.09
	r_3	25	5.45	122	1.12	102	1.33
	r_4	25	5.45	39	3.89	120	1.13
T_3	r_1	135	1.01	177	0.77	52	2.62
	r_2	37	3.68	132	1.03	173	0.79
	r_3	25	5.45	153	0.89	163	0.84
	r_4	40	3.40	124	1.10	90	1.51
T_4	r_1	46	2.96	97	1.40	38	3.58
	r_2	46	2.96	148	0.92	52	2.62
	r_3	35	3.89	25	5.45	75	1.82
	r_4	67	2.03	36	3.78	168	0.81

TABLE 7. Total dry weight biomass in grams of fly larvae found in naturally deposited droppings. WxL is the product of the average width and length of the corresponding face fly pupae.

Sample	*Musca autumnalis*	*Sarcophaga* sp.	*Sarcophaga l'herminieri*	*Orthellia caesarion*	Total	WxL
1	4.12036	0.61250	0.24150	—	4.97444	17.29
2	11.75882	0.83010	0.03320	0.02405	12.64617	19.50
3	2.27529	1.11115	—	—	3.38644	18.14
4	0.61088	0.91042	0.13485	—	1.65616	17.11
5	2.32868	1.99799	0.11474	—	4.44141	12.68
6	8.22072	0.23613	0.05960	—	8.51645	18.18
7	2.30185	0.69760	0.13790	—	3.13735	18.79

experiments within the density range of these field data, pupal size increases as the biomass present increases. Apparently, some undercrowding effect may reduce pupal size.

There now remains the matter of relating total biomass present to face fly survival. This was done by converting the data of both the intraspecific (Table 5) and interspecific competition experiments to biomass. All figures were then adjusted by multiplying by appropriate factors to make the amount of dung in each observation equal to that in an experimental pad. Fig. 13. shows the relation of survivorship and biomass present when the biomass values are classed into 1 g intervals (Table 8).

Some of the survival values from the controls in the interspecific competition experiments were low

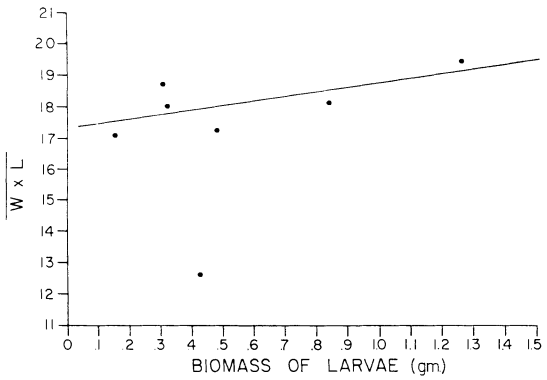

FIG. 12. Regression of size of face fly pupae on total biomass of larvae present in natural droppings. Pupal size is expressed as the mean product of width and length. The one very low value of WxL was rejected using a procedure from Bliss (1967) for dealing with outliers and was not included in the regression computations.

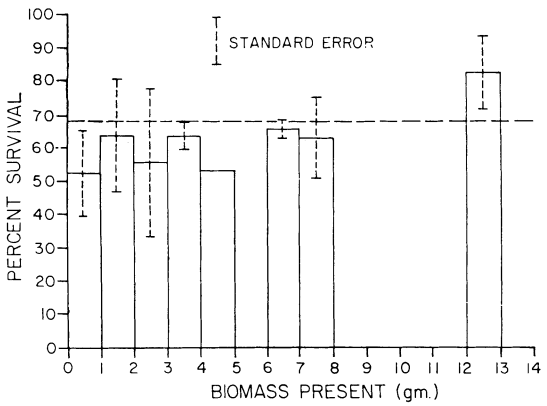

FIG. 13. Percent survival of face fly larvae in relation to the biomass of immature diptera present in the interspecific and intraspecific experiments. Dashed line represents control survival drawn from that portion of the curve of Fig. 11b in which competitive effects are minimal.

(Table 8 and details in Valiela, 1968). Fig. 13 includes these values, so that any predictions of mortality using this figure are probably too large.

The measurements of pupae from the experimental field survival samples are given in Table 9. Taking the values for the average product of length and width and using Fig. 12, rough predictions as to the biomass present in each of these field survival trials can be obtained (Table 10). These values of larval biomass, when applied to Fig. 13, indicate that larval densities did not greatly affect survivorship since all predicted survival values obtained (82%, 69%, 80%) equalled or exceeded control survivals (69%). A linear regression (not shown in Fig. 13) was used to obtain these rough mortality predictions.

TABLE 8. Biomass present and survival of face fly larvae in competition experiments. Both intraspecific and interspecific competition experiments are included.

Total biomass present (g)	% survival face fly larvae
0.555	60
0.167	60
0.674	70
0.452	30
0.422	46.7
	Mean ± 1 S.E.: 53.3±13.8
1.0507	65
1.3345	75
1.0540	53.3
1.8800	31.2
1.1860	60
1.6006	85
1.0710	80
	Mean ± 1 S.E.: 64.2±17.0
2.697	42
2.490	28.2
2.580	88.3
2.480	68.3
	Mean ± 1 S.E.: 56.7±23.2
3.950	68
3.479	60
	Mean± 1 S.E.: 64 ± 4.0
4.7595	53.3
6.3819	68
6.2616	65
	Mean ± 1 S.E.: 66.5± 1.7
7.1607	73
7.8152	76
7.2049	63
7.1139	41
7.8836	63
	Mean ± 1 S.E.: 63.2±12.3
12.575	71
12.950	94
	Mean ± 1 S.E.: 82.5±11.5

Competition, then, may take place, but within the density ranges studied its effect is to reduce individual size, rather than to affect mortality. Reduction of size can occur at very low densities, as in the field data shown in Fig. 12, and also at higher densities, as suggested by the results of the intraspecific competition experiments (Fig. 11b).

There is further independent evidence that competition is not of general importance. Of the many pads inspected throughout three summers, only on 2 occasions was notable size reduction found. Both of these occurred in 1967, the year of larger face fly populations. On July 31, 25 pupae out of a large collection averaged 25.237 mg. On September 4, 26 pupae averaged 23.011 mg. The latter lies just outside the range of Fig. 11b and may have shown a significantly different mortality due to competition. However, the rarity of this event merely points again to the improbable occurrence of mortality due to scarcity of food.

TABLE 9. Pupal sizes for the field survivorship trials expressed as the average product of pupal length and width.

Trial I		Trial II		Trial III	
r_1		r_1		r_1	
L	W	L	W	L	W
6.5	3.0	6.0	3.0	6.0	3.0
6.5	3.0	6.2	3.0	6.0	3.5
6.5	3.0	6.0	3.0	6.2	3.0
6.5	3.5	6.0	3.0	6.5	3.0
7.0	3.2	6.0	3.0	6.2	3.0
$\overline{WL}$=100.4/5=20.08		$\overline{WL}$=90.6/5=18.12		$\overline{WL}$=95.7/5=19.14	
r_2		r_2		r_2	
L	W	L	W	L	W
		6.2	3.0	6.2	3.0
		6.2	3.0	6.5	3.0
				6.5	3.0
				6.5	3.0
				6.0	3.0
		$\overline{WL}$=37.2/2=18.6		$\overline{WL}$=95.1/5=19.02	
r_3		r_3		r_3	
L	W	L	W	L	W
6.5	3.0	6.0	3.0	6.1	3.0
6.5	3.0	6.5	3.0	6.0	3.0
6.5	3.2	6.0	2.8		
6.5	3.0	6.5	3.0		
6.5	3.2	6.0	3.0		
$\overline{WL}$=100.1/5=20.02		$\overline{WL}$=91.8/5=18.36		$\overline{WL}$=36.3/2=18.15	
r_4		r_4		r_4	
L	W	L	W	L	W
		6.0	3.0	6.3	3.0
		6.0	3.0	6.0	3.0
		6.5	3.0	6.0	3.0
		6.5	3.0	5.5	2.8
		5.8	3.0	6.5	3.2
		$\overline{WL}$=92.4/5=18.48		$\overline{WL}$=91.1/5=18.22	
Mean $\overline{WL}$: 20.06		Mean $\overline{WL}$: 18.39		Mean $\overline{WL}$: 18.63	

TABLE 10. Predicted survival and mortality values based on undercrowding plus control mortalities for each field trial. Predicted mortalities have to exceed 31% to be significant.

	Trial I	Trial II	Trial III
Mean $\overline{WL}$	20.06	18.39	18.63
Predicted biomass present	2.0g.	0.76g.	1.2g.
Predicted % survival	>82%	69%	80%
Predicted % mortality	<18%	31%	20%

PARASITISM

The larvae of *M. autumnalis* are attacked by a number of hymenopterous parasites. The most prominent are *Aphaereta pallipes,* a braconid; *Xyalophora quinquelineata,* a figitid; and *Eucoila* sp., a chalcid (Blickle, 1961; Benson & Wingo, 1963; Treece, 1965). Except in a few instances, the percent parasitism reported is generally low. None of the pupae obtained from the field survival experiments seemed parasitized.

Staphylinids of the genus *Aleochara* also parasitize muscoids (Jones, 1967) but attack the pupal stage rather than the larvae.

A nematode parasite is also known to occur in face fly larvae (Stoffolano & Nickle, 1966; Jones & Perdue, 1967). However, the biology of this nematode requires completion of the life cycle in the adult fly, so that if the nematode causes any larval mortality of face flies, it does so at its own expense. Therefore, it can be expected that the host-parasite relation has evolved to minimize host mortality, at least while the host is in the larval stage. There is no published indication of a reduced viability of nematode-infected larvae.

PREDATION BY INVERTEBRATES

INTRODUCTION

Predation, of all the mortality factors considered, is the most complex and difficult to study independently. Therefore, a number of sometimes complex procedures are required to analyze this process. The main predators must first be identified. Second, their ability to deal with varied prey successfully must be ascertained.

Staphylinid beetles, mesostigmatid mites, and carnivorous fly larvae are the main groups of predators in dung communities. The ability of staphylinids to prey on face fly larvae has been mentioned (Drea, 1966; Jones, 1967) but not evaluated even though there are many references to their generalized predatory abilities (Voris, 1934; Hafez, 1939a, b; Mohr, 1943; Laurence, 1954; Sanders & Dobson, 1966).

Macrochelid mites have been shown to be active predators of muscid eggs (Axtell, 1963; Filipponi & di Delupis, 1963). These mites do have a certain predatory potential, since they may significantly reduce populations of *M. domestica* (Axtell, 1963; Singh *et al.,* 1966). However laboratory estimates of mite predation on *M. autumnalis* eggs, using arbitrarily selected predator and prey densities, are quite low, only about 1% of the exposed eggs being fed upon by mites (Singh *et al.,* 1966). Perhaps the peculiar manner in which face fly eggs are inserted into the manure serves as protection from mite predation.

Carnivorous muscid and anthomyiid larvae are prominent predators in Denmark (Hammer, 1941) and England (Laurence, 1954). They seemed more abundant in cooler, shadier locations as reported in Illinois (Mohr, 1943) and California (Poorbaugh *et al.,* 1968). Their overall prominence in Denmark and England is probably related to the cooler ambient temperatures of northern Europe.

In California (Poorbaugh, 1966; Poorbaugh *et al.,* 1968), the number of coprohagous fly larvae present in field droppings was correlated with the density of the larvae of the fly *Myospila meditabunda* and the hydrophilid *Sphaeridium scarabaeiodes.* It was concluded that virtually all larval fly mortality was due to predators. The limited analytical ability of such a correlational approach has been mentioned. Further, this California study dealt mainly with *M. meditabunda,* a fly that appeared very seldom in the open

pasture samples obtained in the present work. In addition, in New York the larvae of *S. scarabaeoides* became prominent in dung succession only after the larvae of face fly had reached such a large size that they were free from predators, particularly such sluggish ones as *S. scarabaeoides*.

It seemed, then, that staphylinids should be the best choice as an experimental predator, not only because of predatory potential, but also because of their local abundance.

Once the main predators were known, a representative species out of this spectrum was selected for experimental use. Field experiments were then performed to evaluate the overall effect of the selected predators.

However, it was not sufficient to consider only direct predator-prey relations, for there are other members of the community that may have an indirect effect on predation. For instance, Hammer (1941), and indirectly Mohr (1943), argue that dung-burrowing scarabaeids and hydrophilids favor predators by their tunneling action. Predatory beetles, in general lacking fossorial adaptations, could use the tunnels made by burrowers to reach and feed upon otherwise unavailable larval diptera.

Further, natural conditions are hardly constant. Two of the most obvious variables—prey and predator densities—are bound to affect the degree of prey mortality. Lastly, there is what Solomon (1949) calls a functional response, a rather complex process (Holling, 1965; 1966) by which the rate of predation varies as prey density varies.

Each of these steps is potentially important in affecting field mortality due to predation and hence must be considered before that mortality can be evaluated.

METHODS

Nine sets of samples were obtained throughout the summer of 1966 exactly as described for the field survival study. In fact, 3 of the 9 sets of samples were also involved in the field survival trials. The extraction of these field samples provided not only face fly larvae but also all the other species found in the droppings. All specimens extracted were identified as far as possible and counted. However, the large number of species made further analysis awkward. Since many of the species were uncommon, it seemed that they would contribute little to the study. Therefore, a modified application of a procedure described by Hairston and Byers (1954) was followed to specify and eliminate the more uncommon species in the censuses. Species which occurred in fewer than 6 out of 27 samples for each of the 4 time intervals were considered uncommon and eliminated by this method (Appendix 2).

The food habit determinations consisted of confining a likely predator with possible prey in a petri dish containing a layer of agar and suspended manure. Additional information was obtained by similar types of field and laboratory observations.

Philonthus cruentatus was chosen as the experimental predator for the estimation of overall effects of predation in the field. This species was the most aggressive predator, showed the widest spectrum of prey (Appendix 3), and was one of the most prominent predators both numerically and in terms of biomass.

Screen-bottomed pupal traps were converted into field cages by attaching vertically 70 cm lengths of 3 cm metal rods to the traps and soldering a wire loop to the tops of the rods. These frames were covered with fitted organdy covers whose bottom edge could be secured against the vertical walls of the traps using heavy rubber bands. Standard experimental droppings and known numbers of predators and larvae were introduced into the field cages.

To evaluate predation in the field, as well as to test the effect of burrowers (*Sphaeridium scarabaeoides* was the most abundant burrower at the time) in the predator-prey interaction, the following experiment was carried out using the field cages:

Treatment	PBL:	6 *Philonthus*	10 *Sphaeridium*	50 *M. autumnalis* eggs	
"	PL:	"	—	"	
"	BL:	—	10 *Sphaeridium*	"	
"	L:	—	—	"	

Each treatment was replicated 3 times.

Observations on the outcome of predatory attacks suggested that only early stages of face fly development would be subject to predatory mortality (Appendix 2). Although *Philonthus* and *Aleochara* are shown as predators of second instar larvae, repeated observations showed that success of attack on larvae of this size was infrequent.

An experiment to pinpoint more rigorously the effect of larval age (or size) on predatory mortality was feasible only in the laboratory. The predator treatments are the same as just described for the field experiments. However, 5 individuals of *Philonthus* were used instead of 6 and 20 prey individuals rather than 50.

The effect of age was partitioned by exposing larvae of different ages to the predators. A large number of eggs were obtained from the laboratory face fly colony, separated, counted and assigned to the proper predator treatments. The following day, 1st instar larvae of the same egg cohort were similarly disposed. The 3rd day the same procedure was followed using 2nd instar larvae. Each of 3 sets of such experiments was allowed to continue until the larvae in each entered pupation, at which point the survivors were counted. This procedure was repeated 3 times, each block having 2 replicates. Within each block the stock of larvae had to be stored in cooler conditions (about 21°C) to space out the instars to allow enough time to set up the proper treatments.

A 2nd field experiment was carried out to study the effect of varied predator densities on the mortality of face fly larvae. The number of prey and predators used encompassed the range found in natural situations.

A measure of food consumption rate was obtained by placing 2 *Philonthus* in a petri dish with fragments of wetted paper towel and then adding a suitable prey, in this case the small staphylinid *Oxytelus*. Measurement of the initial prey biomass and that remaining at the conclusion of the experiment yielded the dry weight of *Oxytelus* consumed by *Philonthus*.

RESULTS

Overall Effects of Predation

The experiment to evaluate the overall effect of predation produced the data in Table 11. Logarithmic transformations homogenized the variances and allowed the computations summarized in Table 12. Duncan's new multiple range test for significance of differences among means was used, in spite of its drawbacks (McNemar, 1962), to group means as shown by the line beneath the body of Table 11. This follows the standard usage of underlined means being similar.

The evidence shows that face fly mortality is greater when predators are present, particularly so when, as occurs in field conditions, both predator and burrower are present (PBL). Since burrowers alone (BL) do not cause a mortality different from the control (L), burrowers seem to act only indirectly in increasing mortality. There must be a synergistic effect of burrowers on the effectiveness of predators.

The control (pooled BL and L) mortality can be subtracted from the predator plus burrower (PBL) mortality. The result measures the effect of the predators when burrowers are present. This value, 38.3 $\pm$ 3.6%, is the first evaluation of field predatory mortality.

Effects of Varying Prey and Predator Densities

The prey and predator density experiments did not yield significantly different treatment effects and are not shown here. However, this is not evidence against density effects. During the course of the experiment, an invasion of large numbers of the small staphylinid *Oxytelus* took place. The organdy mesh of the field cages was not small enough to exclude these beetles and as a result, the *Philonthus* had an almost inexhaustible food supply since *Oxytelus* is an acceptable prey (Appendix 3). Therefore, in the presence of an abundant alternate prey, in addition to food available as manure, it could be expected that predator pressure on face fly larvae was considerably lessened and any density treatment effects would be obscured.

This is interesting, since coupled with the relative lack of prey selection (except on the basis of prey size (Appendix 3)) this suggests that *Philonthus* would prey on a species as a function of the density of that particular species within the community. That is, predation on a species would be minimal when other numerous prey were available.

TABLE 11. Percent survival of larval face flies under various predation treatments. Means tested using Duncan's multiple range test with a 0.01 protection level.

Replicate	PBL	PL	BL	L
1	20	26	48	70
2	22	28	66	68
3	24	30	54	56
Mean $\pm$ 1 S.E.	22.0$\pm$1.2	28.0$\pm$1.2	56.0$\pm$5.3	64.7$\pm$4.4

TABLE 12. Analysis of variance for face fly survival under various predation treatments for data of table 11.

Source	d.f.	M.S.
Treatments	3	0.1557**
Error	8	0.00286
Total	11	

**Significant at 0.01 level.

Table 13a gives an idea of the rate of predation of *Philonthus*. By supplying the predator with surplus food, the consumption over a known period of time can be calculated. There is a suggestion of a functional response: the more food available, the greater the rate of consumption. However, since the range of prey availability in the experiment is smaller than that found in the field, this set of data is of little use in elucidating the import of such a response. As a first approximation it can be assumed that the effects of functional responses on the part of the predator are small. Given this simplifying assumption these data can be used to furnish an extremely rough, but independent prediction for face fly loss due to predation. A number of manipulations are necessary, as outlined below.

There are repeated indications that the mortality occurred mainly between T_0 and T_1 in the field trials. Since the number of predators at T_1 is known from the extracted insect census, the total predator biomass at T_1 can be calculated. Then the total predicted biomass to be consumed by the predator biomass per unit time can be obtained using the rate from table 13a. This assumes that *Oxytelus* is representative of all prey, that all predators are similar to *Philonthus*, and that the predator biomass at T_1 is a valid estimate of the presence of predators during the interval T_0 to T_1.

Since the time intervals between samplings in each survivorship trial are known, by assuming that predation is constant through time, the total prey biomass that the predator biomass present can consume can be calculated.

The weight of *M. autumnalis* consumed by the predator biomass can also be computed, knowing the percent of face fly biomass out of the total available prey biomass during the period in which *M. autumnalis* is subject to predation. Since predators seem

TABLE 13a. Feeding experiments with *Philonthus* as a predator consuming *Oxytelus;* two predators per replicate; 19.5 hrs of exposure. All weights are in mg dry weights.

Rep.	No. Prey Available	Biomass Available	No. Prey Remaining	No. Prey Attacked	Biomass Attacked	Biomass Remaining	Biomass Consumed
1	80	8.408	17	63	6.62	0.94	5.68
2	67	7.042	24	43	4.52	2.11	2.41
3	63	6.621	21	42	4.41	1.46	2.95
4	75	7.881	33	42	4.41	0.47	3.94
						Mean:	3.75

$$\frac{3.745 \text{ mg. consumed} \times 2(2.289 \text{ mg./predator})}{19.5 \text{ hrs.}} = 0.04195 \frac{\text{mg. prey consumed}}{\text{mg. pred./hr.}}$$

TABLE 13b. Calculations using data obtained in table 13a to obtain predicted values of predatory mortality for each field trial. All weights in mg.

Trial	Predator Biomass	Predicted Biom. Prey Consumed/Hr	No. Hr. of Exposure to Predators	Predicted Tot. Biom. Consumed by Predators	Total Prey Biomass Present
I(T_1)	8.79	0.3687	21.72	8.019	784.73
II(T_1)	3.33	0.1397	9.17	1.282	8.44
II(T_2)	5.64	0.2366	28.50	6.743	20.33
III(T_1)	6.56	0.2752	26.50	7.293	18.85

Minimal estimate of mortality:

Trial	Total biomass *M. autumnalis*	Biom. *M. aut.* / Tot. Prey Biom. × 100	Min. Predicted *M. aut.* Biom. Consumed	No. Eggs *M. aut.* Eaten	Min. % Mortal.
I(T_1)	0.809	0.11	0.0882	1.01	2.86
II(T_1)	5.38	63.74	0.8171	9.42	2.94
II(T_2)	5.25	13.73	0.8988	10.37	11.27
III(T_1)	6.34	33.63	2.4530	28.29	23.00

Maximal estimate of mortality:

Trial	Predicted Frey Biom. Consumed	Biom. of *M. aut.* Available	% Biom. *M. aut.* Consumed	% Mortality	Midpoint of Mortal. Range
I(T_1)	8.019	3.056	100	100	51.4
II(T_1)	1.282	19.940	6.431	6.4	3.3
II(T_2)	6.743	7.976	84.54	84.6	47.9
III(T_1)	7.293	10.664	68.39	68.4	45.7

to have low prey selectivity, it can be expected that they will consume a given species of prey in proportion to the density of that species in the community.

Since most predation takes place during the egg stage, the weight of *M. autumnalis* consumed by predation can be divided by the weight per egg and the number of individuals of *M. autumnalis* eaten by predators calculated. From this, knowing the number of eggs in each survivorship trial, a predicted percent mortality due to predation can be obtained. The figures from these manipulations and the results appear in Table 13b. The mortalities predicted on this basis are 2.9% for trial I, 11.3% for trial II (note that this is for T_2, the more comparable set of samples due to the shorter duration of T_1), and 23.0% for trial III.

These predictions are probably minimal predictions. Early in the dung succession, face fly eggs probably make up the bulk of available biomass, since face flies are among the first visitors to fresh manure (Hammer, 1941). Since eggs are not able to escape, they would fall easy prey to roving predators. A maximal estimate of predatory loss could be obtained by supposing that predators would take as many eggs as they find in a particular pad. The rest of the predation biomass demands would, if necessary, be supplied by other species.

If the prey biomass demanded by the predators present is known, together with the prey biomass present in a dropping, these maximal losses can be computed. Such manipulations for each of the three trials are included in Table 13b.

The upper and lower limits of predatory loss are then approximately defined. The nature of survival

for an individual is essentially binomial, that is, an individual survives or does not. As the number of trials (predator-prey encounters) increases, this would approximate a doubly truncated normal distribution. Roughly, then, the midpoint between the minimal and maximal values approximates the expected value for the mean of this distribution (Table 13b). This second evaluation of predatory mortality yields values of 51.4% for trial I, 47.5% for trial II and 45.7% for trial III. These would be approximations to predatory mortality if it merely depended on predator abundance and consumption and prey abundance. Quite clearly, these values are of dubious consequence due to the assumptions needed to obtain them. They can only be used as tenuous, but nevertheless independent, checks on the previous estimate of predatory mortality.

Effect of Prey Age and Size on Predation

The laboratory study of predation on various larval ages yielded the data of Table 14. A square root transformation was used prior to the computations of an analysis of variance. The nonsignificant terms were pooled into the remaining error term using the criterion suggested by Storm (1962) and tabled values made available by Dr. J. L. Gill. Table 15 is the result of this procedure.

The significant predation mean square is studied on the right-most column of Table 16. The presence of predators (PBL and PL) produced greater mortalities than those observed under treatments lacking predators (BL and L), in agreement with previous results.

Although the presence of predators and burrowers produced a greater mortality than predators alone, the difference is not significant. The lack of statistical difference may be related to the smaller surface area of dung in this laboratory experiment. The predators could have merely found all their prey on the smaller surface, damping out effects due to burrowers and perhaps providing too high an evaluation of predatory mortality.

For some unknown reason, larval survival reacted differently under the 3 blocks (Table 15). As a result the effects of larval age must be interpreted within blocks, as shown on the bottom row of table 16. The first block shows that survival for L_1 differed from that of L_2 and L_3. In the second block all the larval age treatments differ, while there are no differences in the third block. However, even if significance is not always present, there is a consistent trend of decreasing larval mortality as the individuals age.

A closer scrutiny of Table 16 suggests interactions between predation and larval age treatments in spite of the non-significance of this term in the analysis of variance. Only where predators are present does differential mortality of any magnitude take place. This is especially true when exposure of egg and first instars are involved. It can be shown using orthogonal comparisons that only 2 cells in block 1 (PBL-L_1 and PL-L_1) differ from the others, while a single cell in block 2 (PBL-L_1) significantly differs from the rest.

TABLE 14. Laboratory survival of face fly larvae of different ages under different predation treatments. Numbers are survivors out of 20 individuals.

Block 1	L_1		L_2		L_3	
	r1	r2	r1	r2	r1	r2
PB	1	1	15	13	16	17
P	1	3	13	9	12	18
B	6	15	13	16	17	16
L	13	14	14	9	14	15
Block 2	L_1		L_2		L_3	
	r1	r2	r1	r2	r1	r2
PB	1	5	5	11	14	16
P	2	11	10	12	12	17
B	13	8	7	14	16	16.709*
L	12	15	15	13	16	16
Block 3	L_1		L_2		L_3	
	r1	r2	r1	r2	r1	r2
PB	9	9	7**	12**	11	16
P	15	14	16	16	12	14
B	11**	14**	12**	14**	15	10
L	12	12	15	14	13	18

*Missing value estimated
**_Aphodius fimetarius_ were used as burrowers instead of _Sphaeridium sarcabaeoides_.

TABLE 15. Analysis of variance for the survival of larvae of different ages in the laboratory under different predation treatments.

Source	d.f.	M.S.
Predation	3	1.9568**
Larval age	2	6.483 N.S.
Larval age x Blocks	4	1.2380*
Remaining error	49[1]	0.3756
Total	70[1]	

[1]One degree of freedom subtracted for missing value estimate.
*Significant at the 0.05 level.
**Significant at the 0.01 level.
Note: The remaining error was used to test the mean square for predation and the larval age x blocks interaction; the larval age mean square was tested with the larval age x blocks term.

The effect of the few significant cells was probably obscured in the calculations by the large number of unresponsive cells.

Assuming that the effects of mortality factors are merely additive across time, a number of manipulations can be performed on the percent mortality values obtained from the data of the laboratory experiment just discussed to arrive at rough estimates of the predation mortality during each larval instar. Since this manipulation will merely provide an approximate value, the differences among blocks will be disregarded and the overall percent mortalities will be used. First, row L can be subtracted, member by member, from each of the other rows (PB, P, B) on Table 16. The results are an evaluation of the mortality due to a particular predator treatment. Second, for each value in the resulting column, the sum of entries to its right within a row was subtracted yielding values corre-

TABLE 16. Mean percent mortalities for the data of table 14. Means joined by lines are not significantly different at or below the 0.05 protection level using Duncan's multiple range test. The values shown are percents calculated from the original data; all tests were performed on square root transformations.

	Block 1			Block 2			Block 3			Mean Mortality for Predation Treatments
	L_1	L_2	L_3	L_1	L_2	L_3	L_1	L_2	L_3	
PBL	95.0	30.0	17.5	85.0	60.0	25.0	55.0	52.5	32.5	50.3
PL	90.0	45.0	25.0	67.5	45.0	27.5	27.5	20.0	35.0	42.5
BL	47.5	27.5	17.5	47.5	47.5	18.2	37.5	35.0	37.5	35.1
L	32.5	42.5	27.5	32.5	30.0	20.0	40.0	26.5	22.5	30.6
Mean mortality for larval age treatments	66.3	36.3	21.9	58.1	46.6	22.8	40.0	33.8	31.9	

sponding to mortality at each instar. The last column comprises the toll of third instars as well as second instars. However, the feeding experiments suggest little predatory loss once the third instar is reached, so that second instar mortality should be the main mortality component at L_3.

The data thus reorganized are shown in Table 17. The mortality due to predation within the treatment PBL is most pronounced during the 1st age interval. The total mortality for this treatment, summed over all larval stages, is 43.3%. This total, in spite of the obviously artificial conditions of the experiment, is close to the value obtained in the field experiment.

The differences between PBL and PL at the L_1 and L_2 treatments may be construed as the effect of burrowers exposing otherwise unavailable submerged prey; this is mere speculation, however. The mortality values for the controls (L) have a trend contrary to what may be expected from the life table study (cf. Fig. 4). No explanation is available for this discrepancy. The one negative value ($PL-L_2$) is a reminder of the error involved in these manipulations.

There are available, then, a field estimate and two rough independent checks of the import of predators of face fly survival. In the presence of burrowers, predators in the field trials reduced the larval population by $38.3 \pm 3.6\%$. Under laboratory conditions, the predator-burrower treatment produced a larval mortality of 43.3%, a result similar to that of the field data. The closeness of these results is all the more remarkable in view of the different numbers of predators, prey and amounts of dung used in the experiments.

The precedures used to obtain the predictions for each of the 3 survival trials (51.4%, 47.5% and 45.7%) are undoubtedly weak. They are included because they provided some insight into the predatory process and because they provide the only predictions that can be assigned to each trial. The fact that they are as close as they are to the other predatory mortality values is pleasing but perhaps deceptively reassuring.

PREDATION BY VERTEBRATES

Laurence (1954) remarks on the activity of jackdaws (*Corvus monedula*) in destroying dung pads while seeking insect prey. Starlings (*Sturnus vulgaris*) and rooks (*Corvus fragilegus*) exhibit similar behavior in Denmark (Hammer, 1941). A similar phenomenon can be documented for New York.

Starlings, meadowlarks (*Sturnella magna*), cowbirds (*Molothrus ater*), killdeer (*Charadrius vociferus*), and crows (*Corvus brachyrhynchus*) were repeatedly seen tearing apart droppings toward the end of each summer of study, after the end of their breeding season.

Dung-inhabiting insects, mainly beetles but including some mature dipteran larvae, were found in the stomachs of starlings, meadowlarks, and killdeer in this late summer period. However, not many birds were examined. Nevertheless, similar observations are to be found in a very long series of reports of bird stomach analysis from journals published by the U. S. Dept. of Agriculture (Farmers' Bulletin, Bulletin of the U. S. Bureau of the Biological Survey, and Departmental Bulletin).

Table 18 shows a summary of dropping damage due to birds in various pastures on the farm used throughout the study. Each observation was obtained by counting and classifying as to the degree of injury each dropping encountered along a 100 by 10 yard strip.

Damaged pads, as noted by Hammer (1941), particularly those here labelled "completely destroyed," dried up rather quickly and ceased to hold insects. Thus, the action of birds had a catastrophic effect from the standpoint of one particular dropping. Undoubtedly, bird activity is of note in regard to overall face fly mortality. However, since the experimental unit for all the preceding discussions was a single dropping, it does not seem possible to consider bird-caused mortality as part of the process of larval mortality in specific pads. The catastrophic nature of bird-inflicted mortality would require that the experimental unit be expanded to include whole pastures including a large number of pads such that a probability could be assigned to mortality in any specific pad from the action of birds.

Therefore, although bird-caused larval mortality may be of importance at certain times, it cannot be included in the present study.

TABLE 17. Percent mortalities during various larval periods exposed to the predation treatments.

	L_1	L_2	L_3	Specific Predator Treatment totals	Total Mortality	% Survival
PBL	29.1	12.5	1.7	43.3	78.3	21.7
PL	25.0	−4.2	5.9	26.7	61.7	38.3
BL	5.8	2.3	1.1	9.2	44.2	55.8
L	1.7	10.0	23.3	35.0	35.0	65.0

TABLE 18. Percent of bird-damaged droppings in 100 × 10 sq yard strips in several pastures and years.

Date	Pasture number	Condition of dropping*				Total no. droppings
		Undamaged	Slightly damaged	Moderately damaged	Completely damaged	
8/11/65	2	20.0	16.7	10.0	53.3	30
8/4/66	1**	23.5	17.6	16.4	42.6	28.3
	2**	16.5	20.0	23.7	39.7	13.7
	3**	22.1	32.7	20.8	24.4	8.3
8/22/67	2	22.2	18.5	14.8	44.4	27

*Slightly damaged pads had $<\frac{1}{4}$ of the top surface broken up. Moderately damaged pads had $<\frac{1}{2}$ of the top surface broken up. Completely damaged were those pads with over $\frac{1}{2}$ of the top surface broken.
**Mean of 3 strips.

TABLE 19. Remainder percent mortalities after subtracting physiological mortalities for the field survivorship trials.

	T_1	T_2	T_3	T_4	Mean ± S.E.
Trial I	35.8	27.5	29.6	29.7	30.7±1.8
Trial II	58.1	68.1	26.2	37.6	47.5±9.5
Trial III	53.8	35.0	42.7	62.5	48.5±6.1
Mean ± S.E.	49.2± 6.8	43.5±12.5	32.8±5.0	43.3±10.0	42.2±18.0

TABLE 20. Analysis of variance for data of table 19.

Source	d.f.	M.S.
Trials	2	402.37 N.S.
Times	3	140.17 N.S.
Error	6	191.83
Total	11	

LARVAL MORTALITY IN THE FIELD: THE SYNTHESIS

The predicted mortality components can now be integrated and the results compared to field survival. It has been suggested repeatedly that the bulk of predatory mortality suffered by face fly larvae takes place in the egg and first instar stages. Therefore, every mean obtained in the field trials is an estimate of predation mortality for T_1 plus whatever other components may have later contributed to overall mortality. Further, if physiological mortality estimates (Table 1 and Fig. 4) are subtracted from the field survival curves, the remainder is an evaluation of mortality caused by the various environmental factors (Table 19). This is possible using Appendix 1 to determine larval size, from this get an approximate age and then using Fig. 4, obtain an estimate of physiological mortality for that particular age.

Remainders thus obtained can be shown to be part of the same population (Table 20). There are no significant differences among the remainder mortalities either in regard to field trials or times. There is some justification, then, for pooling the 3 field trials (Table 2, Fig. 4) and obtaining the overall survival curve for field conditions.

Looking again at Table 19, there is a strong resemblance between the remainder mortalities (particularly the overall mean, 42.2 ± 18.0%) and the estimates obtained for predatory mortality. However, before going further, it would be informative if it were established that the predicted and observed mortalities did indeed share a similar historical pattern.

Fig. 14 shows the field and laboratory survival curves from Fig. 4. In addition, the horizontal lines indicate the approximate span in time of the various immature instars of the face fly in the field trials. Varying environmental factors, such as temperature, caused differential growth rates in the laboratory and field populations. Since the mortalities from the laboratory predation experiment (treatment PBL) were determined approximately at the end of each molt, these end points can be used to synchronize the laboratory values with the other curves in the graph. The adjusted laboratory predation curve fits nicely with the observed field results. The result of the predator-burrower treatment of the field predation

TABLE 21. Cumulative mortality budget for each field survivorship trial. Observed values show mean percent survival ±1 standard error.

	Mortality source	Trial I		Trial II		Trial III		Means	
		Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed
T_1	Predation	38.3		38.3		38.3			
	Physiological	9.0		15.0		14.0			
	Temperature					21.8			
		47.3	53.3±20.6		75.8± 4.4	74.1	71.3±14.4	60.7	62.7±31.6
T_2	Physiological	11.0				7.0			
		58.3	45.0± 6.0	53.30*	86.6± 1.5	81.1	60.5± 3.9	64.2	65.8±37.4
T_3	Physiological	3.0		6.0		3.0			
		61.3	55.1± 9.6	59.3	51.7±19.97	84.1	68.2±15.9	68.2	61.5±39.34
T_4	Physiological	2.0		2.0		2.0			
		63.3	55.1±22.4	61.3	63.1±15.9	86.1	88.0± 6.0	70.2	69.9±26.7

*T_1 and T_2 are pooled together since predation took place in both periods.

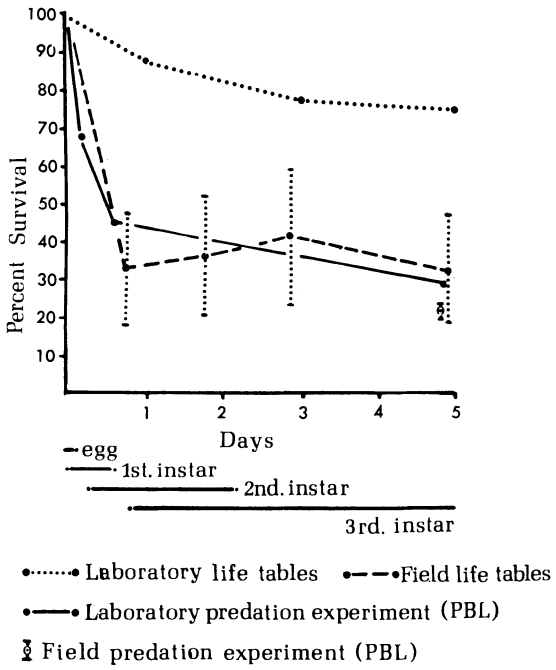

FIG. 14. Comparison of field and laboratory survival curves with the results of field and laboratory predation experiments.

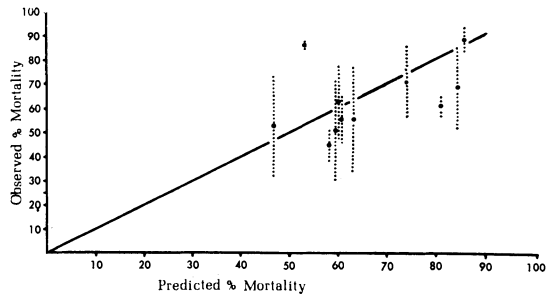

FIG. 15. Comparison of observed and predicted mortalities for the field trials. Means and standard errors from Table 21. The diagonal line indicates the trend if the predicted were exactly equal to the observed values. Appendix 2. Frequency of occurrence of dung arthropods for four time periods. (T_1, T_2, T_3, T_4) for 9 sets of experimental droppings.

experiment also falls within the standard error of the field trial mean.

It would seem, then, that both the magnitude and the pattern of field mortality are similar to that produced by predation plus physiological mortality.

However, the study of temperature as a mortality factor predicted a 21.8% mortality due to temperature during the first interval of trial III. It is a measure of the error in field measurements that so large a discrepancy in one of the compared values was not detectable with standard statistical techniques (Table 20).

The predictions for all significant factors can be integrated into a cumulative mortality budget that compares the predicted with the observed cumulative mortalities for the 3 field trials through the 4 time intervals (Table 21). Similar budgets for field situations have been prepared by Hughes & Mitchell (1960), Berryman (1967) and Waloff (1968).

If the agreement between the observed and predicted survival values of Table 21 were perfect, a diagonal would result if the observed survivals were plotted against predicted survival (Fig. 15). Even though the standard errors of all but three observed mortality means overlay the line of perfect fit there are sizable discrepancies in the means.

There are at least 2 possible reasons why disparities should be found. Up to now, the problem of interactions between mortality factors has been assiduously avoided. However, such interactions are a notable part of the population dynamics of any species. For example, predator activity could be influenced by temperature. The number of eggs laid and length of larval development (and therefore competition) and exposure to predation could depend on temperature. These and other interactions among

factors are potentially of importance but were not evaluated.

There is a second kind of possible interrelation between mortality factors. Predation, heat kill and physiological death can overlap. For example, an egg with a lethal physiological deficiency can be killed by heat and eaten by a predator, since a deficient egg that has just died is just as acceptable a prey as a live one. Besides this, dead eggs remain exposed for a longer period, and probably have a greater chance of being found by a foraging predator.

Since mortalities are expressed in percents, these can be converted directly into probabilities and the overlap can be calculated. For 2 factors A and B, the total mortality P(AUB) can be expressed as

$$P(AUB) = P(A) + P(B) - P(AB).$$

If factors other than physiological mortality are considered, the addition of mortalities can be represented as

$$P(A) + P(B) = P(AUB) + P(AB).$$

We take the right hand term as an estimate of the total mortality. Rigorously, a term P(AB) should be subtracted from the total to obtain the true value of P(AUB), the total mortality.

Suppose, however, that factor B is physiological mortality. Both P(AUB) and P(B) have been measured. Then to estimate P(A), the procedure was

$$P(AUB) - P(B) = P(A) - P(AB).$$

Thus, whatever factor A was, the procedure always underestimated it by P(AB). Fortunately, since physiological mortality was relatively small, the product AB was also small. This was particularly so since the overap occurred only during the early stages. Physiological mortality *after* larvae grew past the critical length of about 9 mm cannot be included since these larvae were not available to predators and probably were inured to mortality due to temperature. However, this level of analysis seems fatuous in light of the magnitude of the error in the observed measurements.

Unmeasured interactions and overlaps may be responsible for whatever disparities occur between observed and predicted mortalities. However, in general the fit is good. The predicted values account for all the observed mortality since predicted values are as large as (in fact, somewhat larger than) those observed in the field. In addition, since the adjusted field mortalities cannot be shown to differ, a mean for all trials can be calculated. The mean predicted values on the right hand column of Table 21 show an excellent coincidence with observed survivals.

Unfortunately, the relationship between predicted and observed values cannot be evaluated using a regression technique. The predicted values do have an error term (not shown in Table 21), and although these variances are small relative to those of the observed values, they preclude the use of a regression.

A combination of predatory and physiological mortality, along with that due to temperature, seems sufficient to account for the magnitude and pattern of observed field death rates in larval face flies.

SOME PROBLEMS AND COMMENTS ON THE EXPERIMENTAL APPROACH AS APPLIED IN THIS STUDY

Throughout this paper there has been concern with large variabilities and their interpretation. There are 2 sources for such variabilities. First, the system under scrutiny may itself provide some intrinsic variance. Second, the methods of measurement themselves could contribute to the error.

Replication could reduce sampling error but only to a certain constant minimal level characteristic of the system. In small systems, such as the one dealt with here, random effects can be expected to be prominent, producing large variances. The problem becomes one of evaluating this error within reasonable limits of time and effort. The proper experimental design, once the basic natural history of the system is known, should be able to provide the balanced error control which can be used to estimate natural variability. In the present study, for example, the experiments on predation seemed to provide good estimates of the level of intrinsic variation.

Each of the methods used here had its share in introducing variability. The egg counts with the necessarily large correction coefficients can lead to increased variation, particularly since it turns out that most mortality occurs at the egg stage. Further, even the correction coefficient has its source of error, since the regression was calculated mainly from points with high egg counts. Trial I, for example, had very low egg counts, yet that same linear regression was used to obtain corrected egg counts. Egg counts of zero occur; these, when corrected, can give rise to considerable error and therefore trial I may show survivorships which are entirely spurious. Thorough examination of the counting error made over the whole possible range of egg abundance would reduce the error considerably.

All eggs were assumed to be equally viable, regardless of whether they were on the surface or submerged. The corrected egg counts were based on those eggs which were visible above the surface. Since the majority of eggs was submerged, this may lead to errors if indeed there was a difference in viability.

The large error involved in the extraction procedure must be responsible for a large proportion of the observed variances. Even with the very best funnel extractors available, there are great differences in the efficiency with which quite similar organisms are extracted (Macfadyen, 1953, 1955, 1962).

There is a unfortunate lack of published evaluation of the variability of funnel extractors, but in view of the large variation among very similar groups of arthropods and among different reports, variances of the order of magnitude found here should not come as a surprise. It is obvious that further studies must find improved methods of extraction.

The fact that the egg counts and the extraction techniques have errors adds to the total variance when both these measures are combined to provide survival percents. The direction of errors, increas-

ing or decreasing one of the estimates, would be important in affecting the variability of the estimates. If replication is inadequate, these biased effects may not be cancelled out, adding variability to the estimates.

It seems clear that improved techniques are necessary before further field work of this nature is attempted. Assuming that these are available, it may be fruitful to design more controlled experiments to evaluate field phenomena. Notably, error became a problem in this study when measurements of field survival were attempted; experiments such as the one to evaluate overall predation effects in the field produced quite manageable variances. Thus one avenue of attack would be to control starting conditions for any field evaluation. This was attempted in the case at hand by standardizing the size and composition of the droppings, among other things. In spite of this, large error emerged. This may suggest that there is no guarantee that improved techniques and controlled experiments will significantly reduce variances since the intrinsic variance will not be removed by such means. Variability seems to be a pervasive property of field studies (Richards & Waloff, 1961; Morris, 1963a, for example). However, there is no question that an attempt to reduce methodological error should be made first.

Not only is large error a problem analytically, but it can also be troublesome on the synthetic stage of a field study. As in the case of the 21.8% mortality assigned to heat in trial III, large errors may mask a seemingly important mortality factor. In addition, cumulative errors in the field estimates may have produced an artificial mortality which, due to the method of analysis, has been assigned to predation. Granted that the coincidence of the value for predatory mortalities in the field estimate and the independent checks is good; nonetheless, not enough is known about density effects and functional responses. In these circumstances this constancy of mortalities under various conditions is suspicious. In addition, it may be that these mortality levels are only an artifact produced by singling out two organisms and carrying out the analysis partly outside the context of their community. This problem must be solved by studying predator activity in the context of all other prey and predator species.

There is yet another problem in the synthesis. How should estimates and corresponding errors from experiments dealing independently with different mortality sources be combined into a final mortality budget? This is a very difficult area which merits further study and which was essentially ignored in the present work by assuming that mortalities from different sources were additive. Once methodology and design reduce error terms, the problem of both instantaneous and cumulative overlap and interaction would become prominent and would need to be taken into account.

In any event, the mean predictions obtained in this study are, in general, satisfactory estimates of the observed survivorships. A study of predations, competition, and other biotic mortality factor interactions through time and in response to environmental stresses could yield more realistic and accurate estimates, but the present results could be used profitably in a model similar to that presented by Hughes & Gilbert (1968) for predictive purposes.

In general terms, stochastic effects and the accuracy of field methods limit the degree of detail to which a field analysis can be taken. The important decision to be made is whether the limits in any particular case are such as to warrant the study. Proper design can to a degree minimize error, but only to the limit of natural variability and measurement methods. Field ecologists must first eschew simplistic models. Then the problem becomes one of treading a narrow path between very complex experiments to encompass and dissect the complexity of biological systems, and the very real limits imposed on the subsequent analysis by natural variability and methodology.

Along with progress on the perhaps more appealing investigations of biological mechanisms, there is a great need to seek more satisfying ways to handle large errors, since there is now sufficient evidence that field studies will show large variances.

SUMMARY

Larvae of *M. autumnalis* reared under optimal conditions in the laboratory showed a $76.2 \pm 1.9\%$ survivorship. In the field, face fly larvae suffered a larger mortality. For 3 sets of field measurements only 44.9 ± 22.4, 36.9 ± 6.9 and 12.0 ± 6.0 percent reached the pupal stage. Most of this field mortality took place very early in the larval development.

Potential mortality factors were then independently evaluated in an attempt to account for the field mortality. Temperature appeared to act as a lethal factor only in the high temperature range. A consideration of natural history and physical properties led to the assumption that high temperatures as found on the top surface of droppings could exert their effect only on the egg and first instar stages. The temperature regimes of each of the field trials led to predicting heat mortalities only in 1 (21.8%) out of 3 trials.

Moisture content and pH of dung were quite constant. An examination of the biological properties of face fly larvae showed that these variables were dubious contributors to the mortality budget.

Competition for food led to a reduction in pupal weight when larval densities were high, regardless of whether the competitors were other face fly larvae or other species. At lower densities, pupal weights also decreased, but in this case mortality increased, perhaps because a critical minimal density is needed for the proper liquefaction of the substrate to make available enough food for the filter-feeding larvae. This effect of undercrowding was not large enough to cause significant mortality in the field trials.

Parasitism was unimportant as far as face fly larvae were concerned.

Predators (*Philonthus cruentatus*) in the field experiments caused $38.4 \pm 7.7\%$ larval mortality if bur-

rowing beetles (*Sphaeridium scarabaeoides*) were present. Predatory mortality was reduced if the burrowers were absent, indicating some sort of synergistic interaction. A rougher second estimate based on prey consumption rates suggests that predators could have reduced face fly populations by 51.4, 47.9 and 45.7 percent in the field trials. Laboratory experiments showed that the bulk of predation occurred during the egg and first instar stages. The laboratory predation experiments provided a third corroborative mortality prediction of 42.3% with burrowers present.

Predatory actions by birds, though possibly important, were discounted since they were outside the scope of this study.

When an estimate of physiological death at each of 4 time intervals was removed from field survival, the remainders estimated true field mortality for each trial. These remainders for the 3 trials can be shown to be similar. Further, the overall mortalities for the field trials were quite close to the results of both field and laboratory predation experiments.

The addition of all the mortality components furnished a predicted set of mortalities that tended to be somewhat larger than the observed values. However, the overall fit between predicted and observed survival rates was good.

The independent experimental evaluations of potential mortality factors furnished an adequate manner with which to judge the relative importance of each factor and yielded a good overall mortality prediction. Interactions and overlaps between mortality factors were not accounted for in this study. A study of these factors could provide better and more realistic prediction and models. However, the variability intrinsic to the system and the errors of measurement may limit the detail of the analysis even if the proper experimental design is used. Better evaluation of these sources of error is needed before further field work is attempted.

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LITERATURE CITED

AXTELL, R. C. 1963. Effect of Macrochelidae (Acarina: Mesostigmata), on house fly production from dairy cattle manure. J. Econ. Entomol. **56**: 317-321.

BAUMBERGER, J. P. 1919. A nutritional study of insects, with special reference to microorganisms and their substrata. J. Exp. Zool. **28**: 1-81.

BENSON, D. L., & C. W. WINGO. 1963. Investigations of the face fly in Missouri. J. Econ. Entomol. **56**: 251-258.

BERRYMAN, A. A. 1968. Development of sampling techniques and life tables for the fir engraver *Scolytus ventralis* (Coleoptera: Scolytidae). Can. Entomol. **100**: 1128-1147.

BLICKLE, R. L. 1961. Parasites of the face fly, *Musca autumnalis* in New Hampshire. J. Econ. Entomol. **54**: 802.

BLISS, C. I. 1967. Statistics in biology. Vol. 1. McGraw-Hill Book Co., New York. 558 pp.

BØGGILD, O. & J. KEIDING. 1958. Competition in house fly larvae. Experiments involving a DDT-resistant and a susceptible strain. Oikos **9**: 1-25.

BRUCE, W. G. 1964. The history and biology of the horn fly, *Haematobia irritans* (Linneaus), with comments on control. North Carolina Ag. Exp. Station, Tech. Bull. No. 157.

DOWDING, V. M. 1967. The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclorrhaphous Diptera. Parasitol. **57**: 371-388.

DREA, J. J. 1966. Studies of *Aleochara tristis* (Coleoptera: Staphylinidae) a natural enemy of the face fly. J. Econ. Entomol. **59**: 1368-1378.

EMBREE, D. G. 1965. The population dynamics of winter moth in Nova Scotia, 1954-1962. Mem. Entomol. Soc. Can. **46**: 1-57.

FALES, J. H., O. F. BODENSTEIN & J. S. KELLER. 1961. Facefly laboratory rearing. Soap and Chem. Spec. **37**: 81-83.

FELDMAN-MUHSAM, B. 1944. Studies on the ecology of the levant housefly (*Musca domestica vicina* MacG.). Bul. Entomol. Res. **35**: 53-67.

FILIPPONI, A. & G. D. DI DELUPIS 1963. Sul regime dietetico di alcuni macrochelidi (Acari: Mesostigmata), associati in natura a muscidi di interesse sanitario. Riv. di Parassit. **24**: 277-288.

FULLER, M. E. 1934. The insect inhabitants of carrion: a study in animal ecology. Counc. for Sci. and Ind. Res. Bull. **82**: 1-62.

HAARLØV, N. 1947. A new modification of the Tullgren apparatus. J. Anim. Ecol. **16**: 115-121.

HAFEZ, M. 1939a. Some ecological observations on the insect fauna of dung. Bull. Soc. Fouad 1er Entomol. **23**: 241-287.

———. 1939b. The life history of *Philonthus quisquiliarius* Gyllh. Bull. Soc. Fouad 1er Entomol. **23**: 302-311.

———. 1941. Investigations into the problem of fly control in Egypt. Bull. Soc. Fouad 1er Entomol. **25**: 99-144.

HAIRSTON, N. G. & G. W. BYERS. 1954. The soil arthropods of a field in southern Michigan: a study in community ecology. Cont. Lab. Vert. Biol. **64**: 1-37.

HALL, D. J. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology **45**: 94-112.

HAMMER, O. 1941. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. Bianco Lunos Bogtrykkeri A/S. Copenhagen. 257 pp., or: 1942. Vidensk. Medd. Fra Dansk Naturh. Foren. **105**: 1-257.

HENSON, W. R. 1968. Some recent changes in the approach to studies of climatic effects on insect populations, pp. 33-46 in T.R.E. Southwood (Ed.), Insect abundance. Symp. Roy. Ent. Soc. Lond. **4**. Blackwell Sci. Pub. 160 pp.

HINTON, H. E. 1960. The structure and function of

the respiratory horns of some flies. Phil. Trans. B **243**: 45-73.

HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population. Mem. Entomol. Soc. Can. **45**: 1-60.

———. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. **48**: 1-86.

HUGHES, R. D. 1959a. Natural mortality of *Erioschia brassicae* (Bouche) (Diptera, Anthomyiidae) during the immature stages of the first generation. J. Anim. Ecol. **28**: 231-241.

———. 1959b. The natural mortality of *Erioschia brassicae* (Bouche) (Diptera, Anthomyiidae) during the egg stages of the first generation. J. Anim. Ecol. **28**: 343-357.

———. 1963. Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (G.). J. Anim. Ecol. **32**: 393-424.

———, & E. MITCHELL. 1960. The natural mortality of *Erioschia brassicae* (Bouche) (Diptera, Anthomyiidae): life tables and their interpretation. J. Anim. Ecol. **29**: 359-374.

———, & N. GILBERT. 1968. A model of an aphid population—a general statement. J. Anim. Ecol. **37**: 553-563.

JONES, C. M. 1967. *Aleochara tristis*, a natural enemy of face fly I. Introduction and laboratory rearing. J. Econ. Entomol. **60**: 816-817.

———, & J. M. PERDUE. 1967. *Heterotylenchus autumnalis*, a parasite of the face fly. J. Econ. Entomol. **60**: 1393-1395.

JØRGENSEN, C. G. 1966. Biology of suspension feeding. Pergamon Press. Oxford. 357 pp.

KAJAK, Z. 1964a. Experimental investigations of benthos abundance on the bottom of Lake Sniardwy. Ecol. Polska **12**: 12-31.

———. 1964b. Remarks on conditions influencing the appearance of new generations of *Tendipedidae* larvae. Ecol. Polska **12**: 173-182.

———. 1965. Remarks on the scarcity of benthos in Lake Lisunie. Ecol. Polska **13**: 24-32.

——— & J. I. RYBAK. 1966. Production and some trophic dependencies in benthos against primary production and zooplankton production of several Masurian lakes. Verh. Int. Verein. Limnol. **16**: 441-451.

———, K. DUSOGE & A. STANCZYKOWSKA. 1958. Influence of mutual relations of organisms, especially Chironomidae, in natural benthic communities, on their abundance. Ann. Zool. Fenn. **5**: 49-56.

KEILIN, D. 1912. Structure du pharynx en fonction du regime chex les larves des Dipteres cyclorhaphes. C.r. hebd. Seanc. Acad. Sci., Paris **155**: 1548-1550.

KEMPSON, D., M. LLOYD & R. GHELARDI. 1963. A new extractor for woodland litter. Pedobiol. **3**: 1-21.

KILLOUGH, R. A. & E. C. MCCLELLAN. 1965. Face fly oviposition studies. J. Econ. Entomol. **58**: 716-718.

LARSEN, E. B. 1943. Problems of heat death and heat injury. Experiments on some species of diptera. K. Danske Vidensk. Selskab. Biol. Medd. **19**: 1-52.

———, & M. THOMSEN. 1940-1. The influence of temperature on the development of some species of Diptera. Vidensk. Medd. fra Dansk. Naturh. Foren. I København **104**: 1-75.

LAURENCE, B. R. 1954. The larval inhabitants of cow pats. J. Anim. Ecol. **23**: 234-260.

MACFADYEN, A. 1953. Notes on the methods for the extraction of small soil arthropods. J. Anim. Ecol. **22**: 65-77.

———. 1955. A comparison of methods for extracting soil arthropods. pp. 315-332 in D. K. McE. Kevan, ed., Soil Zoology, Butterworth, London.

———. 1962. Soil arthropod sampling. pp. 1-24 in J. B. Cragg, ed., Adv. in Ecol. Res. 1. Academic Press, New York.

MCNEMAR, Q. 1962. Psychological statistics. 3rd ed. John Wiley and Sons, Inc. New York. 451 pp.

MELVIN, E. 1934. Incubation period of eggs of certain muscoid flies at different constant temperatures. Am. Entomol. Soc. Amer. **34**: 406-410.

MOHR, C. O. 1943. Cattle droppings as ecological units. Ecol. Monogr. **13**: 275-298.

MORGAN, N. O. & C. D. SCHMIDT. 1966. The pH tolerance of horn fly larvae. J. Econ. Entomol. **59**: 222-223.

MORRIS, R. F., ed. 1963a. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. **31**: 1-332.

———. 1963b. Predictive population equations based on Key factors. Mem. Entomol. Soc. Can. **32**: 16-21.

MUIRHEAD THOMPSON, R. D. 1937. Observations on the biology and larvae of the anthomyiidae. Parasitol. **29**: 279-358.

NICHOLSON, A. J. 1954. An outline of the dynamics of animal populations. Aust. J. Zool. **2**: 9-65.

ODE, P. E. & J. G. MATTHYSSE. 1967. Bionomics of the face fly, *Musca autumnalis* DeGeer. Cornell Univ. Agr. Exp. Stat. Mem. 402. 91 pp.

POORBAUGH, J. H. 1966. Ecological studies on the insect community utilizing undisturbed cattle droppings. Ph.D. Thesis, Univ. of California, Berkeley. 168 pp.

———, J. H. ANDERSON & J. F. BURGER. 1968. The insect inhabitants of undisturbed cattle droppings in Northern California. Cal. Vector Views **15**: 17-36.

RICHARDS, O. W. & N. WALOFF. 1961. A study of a natural population of *Phytodecta olivacea* (Forster) (Coleoptera, Chrysomeloidea). Phil. Trans. B **244**: 205-257.

ROBERTSON, F. W. 1960. The ecological genetics of growth in *Drosophila*. 3. Growth and competitive ability of strains selected on different diets. Genet. Res. **1**: 333-350.

ROUBAUD, E. 1911. Sur la biologie et la viviparite poecilogoniques de la mouche des bestiaux (*Musca corvina* Fab.) en Afrique tropicale. Compt. Rend. Acad. Sci. Paris **152**: 158-160.

SABROSKY, C. W. 1961. Our first decade with the face fly, *Musca autumnalis*. J. Econ. Entomol. **54**: 761-763.

SANDERS, D. P. & R. L. DOBSON. 1966. The insect complex associated with bovine manure in Indiana. Ann. Entomol. Soc. Amer. **59**: 955-959.

SINGH, P., W. E. KING & J. G. RODRIGUEZ. 1966. Biological control of muscids as influenced by host preference of *Macrocheles muscadomesticae* (Acarina: Macrochelidae). J. Med. Entomol. **3**: 78-81.

SOBEL, A. T. 1966. Physical properties of animal manures associated with handling. Proc. Nat. Symp. on Animal Waste Management. Amer. Soc. Ag. Eng. Pub. No. SP-0366, pp. 27-32.

SOLOMON, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. **18**: 1-35.

STOFFOLANO, J. G. & W. NICKLE. 1966. Nematode parasite (*Heterotylenchus* spp.) infecting face fly in New York State. J. Econ. Entom. **59**: 221-222.

STORM, L. E. 1962. Nested analysis of variance: review of methods. Metrika **5**: 158-183.

SULLIVAN, R. L. & R. R. SOKAL. 1963. The effects of

larval density on several strains of the house fly. Ecology **44**: 120-130.

TESKEY, H. J. 1960. A review of the life-history and habits of *Musca autumnalis* DeGeer (Diptera: Muscidae). Can. Entomol. **92**: 360-367.

TREECE, R. E. 1965. Research on *Musca autumnalis* Deg. in the United States. Proc. XII Int. Cong. Entomol. London, 1964 (Sect. 12): 785.

ULLYETT, G. C. 1950. Competition for food and allied phenomena in sheep-blow fly populations. Phil. Trans. B **234**: 77-174.

VALIELA, I. 1968. An experimental study of the mortality factors of larval *Musca autumnalis* DeGeer. Ph.D. Thesis, Cornell Univ. 99 pp.

VARLEY, G. C. & G. R. GRADWELL. 1960. Key factors in population studies. J. Anim. Ecol. **29**: 399-401.

VORIS, R. 1934. Biologic investigations on the Staphylinidae (Coleoptera). Trans. Acad. Sci. St. Louis **28**: 233-261.

WANG, C. H. 1964. Laboratory observations on the life history and habits of the face fly, *Musca autumnalis* (Diptera: Muscidae). Ann. Entomol. Soc. Amer. **57**: 563-569.

WATERHOUSE, D. F. 1947. The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly *Lucilia cuprina*. Council for Sci. and Ind. Res. Bull. 217. 31 pp.

WATT, K. E. F. 1963. How closely does the model mimic reality? pp. 109-111 in R. F. Morris, (ed.). The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. **31**: 1-332.

WEST, L. S. 1951. The housefly. Comstock Pub. Co. Ithaca, New York. 584 pp.

YATES, F. 1960. Sampling methods for censuses and surveys. Hafner Publ. Co., New York. 440 pp.

APPENDIX 1a. Survival under field conditions, trial I. Begun 7 July 1966, 2:30 p.m.

Time of Collection	Replic.	No. of Eggs	Corrected No. of Eggs	Number of Larvae Extracted	Corrected No. Larvae Extracted	Size (mm)	Extraction Efficiency	% Survival
T_1 (8 July 10:45 a.m.)	r_1	3	35	13	19.5	9.37	66.5	55.7
	r_2	6	39	19	41.3	4.1	46.0	105.9
	r_3	3	35	1	2.2	3.8	45.0	6.3
	r_4	2	32	2	2.9	10.0	68.5	9.1
T_2 (9 July, 2:50 a.m.)	r_1	3	35	23	31.5	11.0	73.0	90.0
	r_2	0	25	1	1.4	10.5	71.0	5.6
	r_3	0	25	13	18.1	10.7	72.0	72.4
	r_4	0	25	7	9.5	11.2	73.5	38.0
T_3 (10 July, 8:50 a.m.)	r_1	65	135	47	57.3	13.1*	82.0	42.4
	r_2	5	37	23	29.5	12.3	78.0	79.7
	r_3	0	25	0	—	—	—	—
	r_4	7	40	7	8.3	13.92	84.0	20.8
				Number of pupae				
T_4 (12 July, 11:00 a.m.)	r_1	10	46	34				73.9
	r_2	10	46	20				43.5
	r_3	3	35	0				0
	r_4	23	67	33				49.3

*Values estimated from other replicates in same time period.

APPENDIX 1b. Survival under field conditions, trial II. Begun 2 August 1966, 10:00 a.m.

Time of Collection	Replic.	No. of Eggs	Corrected No. of Eggs	Number of Larvae Extracted	Corrected No. Larvae Extracted	Size (mm)	Extraction Efficiency	% Survival
T_1 (2 Aug. 5:10 p.m.)	r_1	64	135	18{16, 2}	27.4{23.4, 4.1}	{9.9, 5.0}	{68.5, 49.0}	20.3
	r_2	77	157	12	26.1	4.3	46.0	16.6
	r_3	223	400	53{49, 4}	112.1{103.8, 8.3}	{9.5, 4.5}	{66.5, 48.0}	28.0
	r_4	120	228	28	57.7	4.8	48.5	25.3
T_2 (3 Aug. 12:30 p.m.)	r_1	78	158	3	5.7	5.7	52.5	3.6
	r_2	12	49	12	22.0	6.3	54.5	44.9
	r_3	56	122	12	17.5	9.9	68.5	14.3
	r_4	6	39	5	7.9	8.5	63.0	20.3
T_3 (4 Aug. 2:45 p.m.)	r_1	89	177	33	43.7	11.6	75.5	24.7
	r_2	62	132	117	170.8	9.9	68.5	129.4
	r_3	75	153	52	67.5	12.1	77.0	44.1
	r_4	58	124	1	1.3	11.5	75.0	1.1
				Number of pupae				
T_4 (6 Aug. 11:00 a.m.)	r_1	41	97	24				24.7
	r_2	72	148	81				54.7
	r_3	0	25	5				20.0
	r_4	4	36	3				8.3

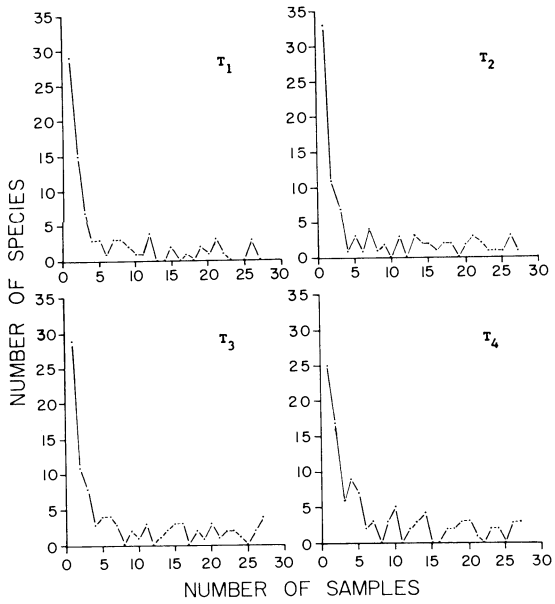
Note: in 2 replicates larvae of different sizes appear. These are bracketed together.

APPENDIX 1c. Survival under field conditions, trial III. Begun 7 August 1966, 8:30 a.m.

Time of Collection	Replic.	No. of Eggs	Corrected No. of Eggs	Number of Larvae Extracted	Corrected No. Larvae Extracted	Mean Size (mm)	Extraction Efficiency	% Survival
T_1 (8 Aug. 11:00 a.m.)	r_1	34	87	51 {49 2	72.4 {68.5 3.8	{10.6 5.5*	{71.5 52.0	83.2
	r_2	52	115	12	24.0	5.1	50.0	20.9
	r_3	93	183	16	30.0	5.8	52.5	16.4
	r_4	47	107	8	13.5	7.5	59.0	12.6
T_2 (9 Aug. 10:30 a.m.)	r_1	28	75	15	20.7	10.9	72.5	27.6
	r_2	22	65	59	79.7	11.4*	74.0	122.6
	r_3	44	102	27	37.5	10.6	72.0	36.8
	r_4	55	120	4	5.1	12.7	79.0	4.3
T_3 (10 Aug. 11:45 a.m.)	r_1	14	52	4	5.5	11.0	73.0	10.6
	r_2	87	173	50	64.1	12.4	78.0	37.1
	r_3	81	163	7	9.1	12.0	77.0	5.6
	r_4	37	90	60	74.0	12.9	81.0	83.0
				Number of Pupae				
T_4 (12 Aug. 11:45 a.m.)	r_1	5	38	26				68.4
	r_2	14	52	6				11.5
	r_3	28	75	2				2.7
	r_4	84	168	6				3.6

*Values estimated from other replicates in same time period.
Note: in one replicate larvae of different sizes appear. These are bracketed together.

APPENDIX 2. Frequency of occurrence of dung arthropods for four time periods. (T_1, T_2, T_3, T_4) for 9 sets of experimental droppings.



APPENDIX 3. Food habits of the prominent members of the dung community. Summarized from feeding experiments and laboratory and field observations. Adults are involved unless otherwise specified. Code numbers following names are merely labels used during this study.

Potential prey \ Potential predators	Sphaer. scar.	" " lar.	Sphaer. bip.	" " lar.	Philonthus	Platystethus	Falagria	Oxytelus	Hyponigrus	Aleochara	Atheta	Aleocharine B65
Sphaeridium scarabaeoides	4		4	4	5	5		5	4	5	4	4
" " larva	4		4	4	5	5		5	4	4	4	4
Cercyon	5		4		1	5		4	4	4		
Philonthus	5		4	4	1	5		5	5	5	4	4
Platystethus	5		4		1			5	1	2	4	
Falagria	5		4		2	4		5	2	2		
Oxytelus	5		4		1	4		5	2	2		
Hyponigrus	5		4	4	3	4		5	2	3	4	4
Aleochara	5		4	4		4		5	4	3	4	4
Atheta	5		4		1	4		5	2	2		4
Aleocharine B65	4		4		2	4		4	2	2		
Acrotrichis	4		4			3						
Aphodius	5	5	5	5	5	5	5	5	5	5	5	5
Musca autumnalis eggs	5		4		1	5	5	4	2	1		
" " first instar	5	5	5		1	4	5	4	2	1		
" " second instar	5	5	4	5	1	4		5	1	1		4
" " third instar	5		4	4	5	4	5	5	5	5	4	4
Sarcophaga sp. first instar	4		4		1			4	2	2		
" " second instar	4		4		5	5		5		1		4
" " third instar	5	5	5	5	5	5	5	5	5	5	4	4
Ravinia l'herminieri first instar	4		4		2	4		4	2	2		
" " second instar	4		4		5	5		5		2		4
" " third instar	5	5	5	4	5	5	5	5	5	5	5	4
Saltella sphondylii larva	4		4		1	5		4	1	1	5	
Sepsis sp. larva	4		4		1			4	1	1		
Sepsid B larva	4		4		2				2	2		
Leptocera	4		4		2				2	2		
" larva	4		4		2				2	2		
Sargus larva	4		4		5				4	4		
Psychoda larva	4		4		2				2	2		
Diptera B66	4		4		2				2	2		
" C66	4		4		2				2	2		
Collembola	4		4		2	3			2	2		
Macrocheles	4		4		1	3			2	2		
Parasitus	4		4		1	3			2	2		
Dung	1		1		1	1	1	1	1	1		

Number code: 1: known to feed; 2: presumed to feed; 3: feeding possible; 4: presumed not to feed; 5: known not to feed.