BIOLOGY OF LECHWE FLIES MUSCA TEMPESTATUM BEZZI
WITH EMPHASIS ON THE NUTRITIONAL REQUIREMENTS
AS PROVIDED BY THE LECHWE ANTELOPE IN ZAMBIA.

A dissertation submitted in partial
fulfilment of the requirements
for the degree of Master of Science in
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Department of Biology.

by

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Abstract

Studies on the feeding behaviour of *Musca tempestatum* were carried out in order to investigate the biology of the fly and its relationship to the lechwe antelope. This was done by observing the fly's feeding activities on the antelope and its breeding activities on the lechwe faeces on which it oviposits. The larvae hatch out on the faeces and then migrate into the faeces. This is because, due to crust formation on the surface of the faeces, solidification of faeces and loss of water levels, there is left a small moist space in the middle of the faeces, into which the larvae congregate after making tunnels through which their posterior spiracles are exposed for air. The whole larval stage is accomplished within faeces and therefore larvae depend on faeces for food. The composition of the faeces and their variation was studied in the laboratory so as to investigate the effect of these variations on the survival of *M. tempestatum* dependent upon lechwe faeces. The detailed readings of moisture and nitrogen percent (dry weight percent of nitrogen) per month are tabulated in the appendices. The results showed that there were variations in the composition of faeces according to the months. This could have been due to seasonal changes in the composition of pasture grasses on which the antelopes feed which could have influenced the composition of faeces directly. Gorrod, (1959); Sen and Butterworth and Arias, (1965) c.f. Greenham, (1972) pointed out that differences in protein and fibre
content between grass species were much less important than the differences between immature and mature grass of the same species. Sizes and weights of emerged flies reared at different nitrogen percentages were taken to see whether these were affected by the composition of faeces. Results are shown in the dissertation.

Experiments were carried out on the effect of food substances such as sugar, fresh liver and fresh faeces with the combinations of water on the survival of *M. tempestatum* adults. The flies used for the experiments were collected from the field within faeces in the immature forms, (eggs, larvae, pupae) and then reared in the laboratory. The immature stages of the fly are being described for the first time, other works have shown the behaviour of the adult flies, Patton, (1936). The number of the surviving flies fluctuated between the treatments, with the highest being demonstrated by flies fed on sugar and water and the lowest was found among flies fed on fresh faeces and water.

Statistical analyses were done on the numbers of flies remaining alive at the end of the experiments to note whether there were any significant differences between treatments. The results of these experiments indicated that some of the foods given to the flies did not promote or increase survival; which meant that the food qualities obtained from these food substances were used for purposes other than survival (purposes such as reproduction). To this effect further experiments were done in the laboratory.
to investigate the effect of food quality on reproduction. Crude determinations of nitrogen content in the faeces which were done showed that there were variations which ranged from 2.5% to 6.25%. The highest nitrogen content was taken as a high quality and the lowest as a low quality type of food. The experiments started with varying nitrogen content. The effect of quality was interpreted by the number of eggs laid per larva present initially.

It has been shown that *M. tempestatum* oviposits on fresh lechwe faeces and that the faeces are suitable for oviposition only when they are fresh as soon as there is any crust formation the faeces cease to be attractive to ovipositing female flies. It has also been shown that the flies obtain moisture and food directly from the lechwe and so the flies have to be mobile and capable of following the lechwe from place to place and in this order the relationship is maintained between the two.
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1. General Introduction

Flies comprise one of the largest orders of insects including over 64,000 described species, Imms, (1951). When undescribed species are included they number at least 150,000, Colles and McAlpine in Insects of Australia, (1970). Almost all adult flies are immediately recognized by the presence of only one pair of functional wings. There are a few species which are apterous, but these bear other distinguishing characteristics of mouth-parts, thorax and abdomen that indicate their true relationships. These characteristics also distinguish them from the few other insects that have only two wings (some Ephemeroptera, male Coccoidea).

Adults of almost all the species of flies feed either on nectar or on decaying organic matter of various kinds. Considerable numbers of flies are predacious and others are parasites, living on or in various insects and vertebrates including man. Certain species have acquired sucking mouth-parts and others have lapping mouth-parts. Among the genera of Diptera, the genus Musca, has been considered as one of the most important group of the order Diptera from the medical, agricultural and veterinary point of view. The synanthropic forms, owing to their relationship to the human environment, have been studied in depth (Sacca, G. 1964). Musca domestica with its sub-species including members of the sorbens complex is widely known. The other group of the genus Musca comprises haematophagous species, having true blood sucking mouth-parts; these species are able to pierce the skin
of the host and suck blood, for example *Musca crassirostris* Stein; some are able to remove scabs and widen wounds which are almost healed, for example *Musca condudens* Walker. The other group of species is comprised of small flies which are said to be haematophagous. These flies have no blood sucking mouth-parts. Their mouth-parts have been modified into a long proboscis which is used for lapping up blood from exposed fresh wounds. Whether these species are obligatory blood-feeders is yet to be found out. The lechwe fly (*Musca tempestatum*) which is the subject of this dissertation has been identified as a member of this group. These species have been observed in some other African countries mostly in connection with cattle, for example, West and Peters (1929) reported their feeding activities on the wounds caused by blood sucking flies such as Tabanidae on cattle. Feeding by a number of muscid species on blood made available by biting flies is known to occur in the Old World (Hammer, 1941; West, 1951). Species in several genera are involved, more especially members of the genus *Musca*.

*Musca tempestatum* in Zambia has been observed in association with the lechwe antelopes, more especially the Kafue Flats lechwe (*Kobus leche kafuensis*). However, recently, *M. tempestatum* has been collected as adult feeding on faeces of the Black lechwe (*Kobus leche smithериану*) at Bangweulu; also the fly has been found feeding on a wound of a Zebra; (Howard, G. personal communication)

Biologically, flies as a whole are very efficient; (Oldroyd, 1964). They have evolved mechanisms for getting
food from sources that will always exist, thus securing their longevity, survival and reproductive performance and, as a whole, their future.
Plate 1.

The Kafue Flats lechwe (*Kobus leche kafuensis*).
The lechwe fly has not been recorded before, let alone studied in Zambia, so the flies require further detailed investigations on their biometrics and associations to lechwe, especially the Kafue Flats lechwe. The lechwe flies are well distributed throughout Africa and are mostly common with cattle.
1. Introduction

The lechwe fly has not been recorded before, let alone studied in Zambia, so the flies require further detailed investigations on their bionomics and associations to lechwe, especially the Kafue Flats lechwe. The lechwe flies are well distributed throughout Africa and are mostly connected with cattle.

Bezzi (1908) reported the presence of these flies in Ethiopia and recorded that they extended as far south as Natal (South Africa). West and Peters, (1929) in Sierra-Leone reported that lechwe flies had been observed in close association with cattle and that they caused injury to cattle by feeding on the wounds made by blood sucking flies, causing sores to cattle. In Sudan Musca tempestatum has been observed to be feeding on cow-dung, Lewis, D.J. (1954).

These observations reported from other African States provoke a thought of whether there are likely associations between Musca tempestatum and cattle in Zambia and this thought induces further detailed investigations in this field. In Zambia the flies have gained their name of the Lechwe fly because they have been observed to be following herds of the Kafue Flats lechwe, flying among them, settling on them, especially on some particular regions of the body, for example eyes, ears, nose, mouth, around the anal openings, and also on their droppings. The people found in the villages around the sampling areas refer to these flies
as 'Tuluunzhi', meaning small flies as compared to the house-flies which they call 'Baluunzhi'.

2. **Taxonomic Position of the Fly.**

The *tempestatum* species was first described by Bezzi (1908) and added them to the list of *Musca* species of the Ehtiopian Region. The classification of *Musca* species by Bezzi and other authors such as Malloch (1925) Curran (1928) Patton (1932) were assembled together by van Emden (1939) and used them in his key of *Musca*. Following van Emden's *Musca* key the lechwe fly which was identified by the British Museum, Entomology Department, from the batch of specimens sent to them may be classified as follows:

- **Genus** :- *Musca*
- **Subgenus** :- *Biomyia* Robineau - Desvoidy,
- **Species** :- *Musca* (*Biomyia R-D*) *tempestatum* Bezzi, 1908 (c.f. van Emden, 1939) Ruwenzori Expedition, Volume 2 No. 3

West in 1957 put *tempestatum* under the subgenus *Musca* and he, following Ch' 1 Ho's (1938) classification, recorded only three subgenera, *Musca*; *Viviparomusca* and *Eumusca*. 
3. **Morphology of the adult fly**

*Musca tempestatum* is generally grey in colour, smaller than *Musca domestica*. Using the head width, the sizes of the species vary. They are seen to be as small as .3mm and as large as 3.96mm. For identifying purposes only a few morphological features are pointed out. The most useful ones are: The vertex in the males is narrow and it looks silvery. The proboscis and the labella are long and this is said to be characteristic of this species, Patton, W.S. (1936). They are about as long as the third antennal segment. The proboscis and the labella are coupled with an extended mouth-area which gives flexibility to the proboscis. The mouth-parts take the form of a lapping - type proboscis, (Fig 2). At the free end of the proboscis on the surface of the labella are small invaginations looking like channels. These are the pseudotracheae into which the liquid flows when the labella lobes are set down and then its drawn up the gut, (Fig 3). On the thorax there are two longitudinal black bands (vittae). The vittae are well pronounced along the mesonotum. In both sexes the vittae unite in front of the suture ending up at the joint of the mesothorax and metathorax, (Fig 1). The hairs which are mostly distributed along the vittae and sides of the thorax are stunted and few. The abdomen of *Musca tempestatum* is bluish-grey. The 1st and 2nd terga appear darker almost black
with a greyish posterior border. The third tergum is bluish-grey with a black median stripe which extends posteriorly and anteriorly forming black bands, there are also narrow admedian stripes. The forth tergum is similar to the third tergum except that the stripes and bands are narrower. In the fifth tergum the median stripe is indistinct. The borders of the admedian stripes along the posterior ends are darker than along the anterior sides.
Figure 2.

Dorsal view of a whole fly showing the mesonotum pattern described in the text.
Figure 4.

Side view of a whole fly showing the proboscis as it is seen in situ.
Figure 4.

Enlarged proboscis showing the following:

a. - Fulcrum
b. - Clypeus
c. - Course of pharynx
d. - Maxillary palpi
e. - Labrum
f. - Hypopharynx
g. - Pseudotracheae
h. - Labellum.

Labelling after Imms, A.D. (1965).
4. Distribution of the Lechwe antelope and lechwe flies in Zambia.

The Geographical variations of lechwe in Zambia have been reported in detail by Howard, J.W. and Sidorowicz, J.A. (in press). There are three subspecies of lechwe reported to occur in Zambia (Ellerman et al., 1953; Ansell, 1964; 1969; Dorst and Dandelot, 1970): The three subspecies being:

Kobus leche leche Gray (the red lechwe)
Kobus leche smithemani Lydekker (the black lechwe)
Kobus leche (grandicornis) kafuensis Halternorth (the kafue lechwe).

Howard and Sidorowicz showed that the two subspecies namely the red lechwe (K. I. leche) and Kafue lechwe (K. I. kafuensis), that have previously been regarded as separate subspecies had no significant differences and therefore they suggested that subspecies Kobus leche (grandicornis) kafuensis Halternorth, 1963, be regarded as a synonym of the nominal subspecies Kobus leche Gray, 1850.

The lechwe are found in areas of inundated plains and shallow swamps that occur in the country. Most of the field work for this study was carried out at Lochnivar and Blue Lagoon National Parks, and also the samples used for the experiments were collected from the two parks. The Lochnivar and Blue Lagoon National Parks are located on the Kafue Flats (see Fig. 4). Lochnivar is in the Southern Province and Blue Lagoon is in the Central Province. Both these
Two parks are floraled by aquatic grasses and sedges covering the plain and rice grass is found in areas of deeper water. Lechwe are gregarious and aquatic antelopes, so these water - meadow pastures form the food for large herds of the lechwe (Vesey - Fitzgerald, 1965). Lechwe in large herds move seasonally according to the flood levels.

There are about 25,000 kafue lechwe in Blue Lagoon and about 35,000 in Lochnivar, Clarke and Loe, (1974).

At high water, the lechwe are seen along the upper flood line. As the floods recede the lechwe move northwards into the flood plain. The lechwe flies are seen following the herds of these antelopes having either direct contact with them or with their droppings. On the lechwe, M. tempestatum has been observed to be distributed around the eyes, nostrils, anal openings, ears and also around any fresh wound from which blood would be oozing.

On man the flies have been observed to settle themselves on the arms, the face, the back and also around the eyes, nostrils and ears. (see plate 2).
Plate 2.

*M. tempestatum* on human eyelid presumably getting moisture from around the eye.
Figure 1.

Map of Lochnivar and Blue Lagoon National Parks showing some places mentioned in the text.
1. Introduction

Observations on the biology of the egg, larval, pupal and adult stages of the lechwe fly (*Musca tempestatum*) are presented. Some aspects of the behaviour of the adult fly are easily observed, because the flies are attracted to large animals including man. Samples caught from the vicinity of lechwe (*Kobus leche kafuensis*) and man show a preponderance of female flies usually in the ratio of approximately four females to one male, so it is the behaviour of the female fly that is more easily studied.

In the field the flies showed two types of behaviour towards man and lechwe: (i) settling on exposed parts of the body, for example, bare arms and also on parts shielded from wind showing minimum movement, for example, the middle of the back, (ii) grouping around certain body regions actively seeking fluids, for instance, round the eyes, nostrils, ears, round the anal and genital opening and also at any exposed fresh wounds.

The first type of behaviour gives the fly an access to sweat (on man). Although sweat has been shown not to provide enough food for egg development in certain *Musca* species (Hughes and Greenham, 1972), it can supply water and perhaps essential salts; the second type of behaviour involves food-seeking, since tears, saliva, serum from sores and blood are protein-yielding substances.
E. tempestatum has also been observed to leave the body of the lechwe and alight on fresh faeces as soon as the antelope defaecates. Therefore this behaviour of the fly in following large animals seems to be for maintaining contact with sources of their major oviposition requirements—freshly dropped faeces. They appear to be strongly attracted upwind by the odour of fresh faeces. The gravid female lays her eggs in or under the faeces.

2. Life history and breeding site

When flies alight on fresh faeces, most of them settle while feeding on the pads and the gravid female fly then shows its characteristic behaviour. The male fly either sits still or flies off, but the female fly does neither. It moves rapidly over the surface searching for holes and crevices and exploring below the over-hanging edges. If the pad of faeces is suitable the fly backs into the hole or crevices or cracks under the edges of the faeces. (see plate 3). It compresses its abdomen and the ovipositor is extended. Then the ovipositor is pushed as far into the crevice as possible. Occasionally all eggs would be found deposited in a single mass but more often they are distributed in a number of locations. Usually the ovipositing period lasts between three to five minutes. Eggs found closely, packed together in any batch.

During the period the fly was laying eggs, even when disturbed, it rarely flew away; in some instances flies have been collected together with faeces.
Plate 3

Female lechwe fly searching for breeding site on a pad of lechwe faeces.
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During the period the fly was laying eggs, even when disturbed, it rarely flew away; in some instances flies have been collected together with faeces.
Plate 3

Female lechwe fly searching for breeding site on a pad of lechwe faeces.
Many of those collected with faeces were female flies. For example in September 1972, 30 samples of faeces were collected and out of those samples there were 3 females and only 1 male.

The presence of one female laying eggs on the pad was strongly attractive to other gravid females and they clustered round her, laying eggs together to make a larger mass. A favourable pad would be frequented by groups of female flies. This type of behaviour was also observed.
Many of those collected with faeces were female flies, for example in September 1974, 20 samples of faeces were collected and out of those samples there were 3 females and only 1 male.

The presence of one female laying eggs on the pad was strongly attractive to other gravid females and they clustered round her, laying eggs together to make a large mass. A favourable pad would be ringed by groups of female flies. This same type of behaviour was also observed by Browne, B. et al (1969) on Lucilia cuprina, Greenham (1970) (on Musca vetustissima). Browne demonstrated that this type of behaviour was due, in part, to the preference shown by gravid females for oviposition sites already occupied by ovipositing females. It was difficult to compare the favourability of different types of faeces by any female that started egg laying. Observations on the type of field faeces as a habitat for fly larval forms, (both personal and other sources) showed that freshly dropped faeces were suitable for oviposition. Once pads had formed even a very thin crust, pads became less attractive. Hammer, (1941) on cow-dung observed the same features and suggested that crust formation blocked the odour of the dung which attracted the adult flies. As the pads aged fairly rapidly and soon became unattractive to most adult flies for oviposition, the flies must be mobile and capable of following the herds about, from one place to another, to obtain fresh faeces. The fresh faeces also should be uniform, fresh droppings in the form of pellets were not suitable for egg laying.
In the field observations were made on three occasions to note the attraction of three types of faeces to adult flies. The types were:

(1) Freshly dropped faeces, which were collected as soon as the antelope defaecated to prevent any sort of intrusion before the observations.

(2) Pad of faeces which was allowed to dry for a short time. This was also carefully collected to avoid any intrusion.

(3) Pad of dry faeces.

Results are tabulated on table 1:

**TABLE 1.** Field observations on the attraction of three types of faeces.

<table>
<thead>
<tr>
<th>No. of observation</th>
<th>TYPES OF FAECES</th>
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<tr>
<td></td>
<td>Fresh</td>
</tr>
<tr>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>26</td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td>8.67</td>
</tr>
<tr>
<td><strong>Standard Error from means</strong></td>
<td>$8.67 \pm 0.675$</td>
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P value of less than 0.05 was considered significant.

P $< 0.05$ students-t-test.
On the basis of the results on table 1 a conclusion was made that flies prefer fresh faeces (26 against 17). When an attempt was made at collecting these flies, it was observed that most were female lechwe flies. For example at the first observation all the ten flies were collected from the first type of faeces and out of these eight were lechwe flies. Out of the five flies collected from the second type four were lechwe flies. On the whole the overall ration from subsequent observations was 4:1. These observations revealed therefore that ovipositing female flies show a preference for fresh faeces.
3. Egg

The female fly lays her eggs in the cracks and crevices of the faeces and in the space between the faeces and the soil. When the physical nature of faeces allows it, the fly crawls deep into the coarser crevices; sometimes it is out of sight while depositing the eggs, which are pearly white in colour. In common with other egg-laying Musca species such as Musca domestica West, L. (1951); Musca vetustissima Walker (Greenham, P.M. 1972) Musca tempesta-tum lays elongate - ovoid and slightly curved eggs. Both the posterior and anterior ends are bluntly rounded; the anterior end is more tapering than the posterior end. When closely viewed under the microscope a line extending along the concave side was seen, presumably a hatching strip, described by West, L. (1951) on Musca domestica. Greenham, P.M. (1970) on Musca vetustissima. Observed also was a pattern of small hexagonal markings, reflecting the cellular structure of the egg tube in which the ovum developed. On average the eggs measured .95mm (n = 20). When fully developed within the egg the larva struggles to rupture the chorion. The break occurs along the line of weakness at the edge of the hatching strip at the anterior end of the egg. As soon as the larva emerges from the egg it enters the faeces.
Figure 5.

Diagrammatic figure of the eggs of *M. tempestatum*.
4. Larva.

The larva of the lechwe fly is a typical Muscoid maggot, elongate and subconical, the body tapering towards the reduced head segments. There is a small structure on the side of the head in the form of a papilla, which corresponds to an adult antenna, but in the larva it is reduced. Due to reduced head capsule the mouth parts seem to be atrophied and represented by mouth-hooks. The maxillae and the labium which form up the lapping-proboscis of an adult-fly are recognized in a form of a papillae representing their palpi. Maybe the larva of Musca tempestatum, in common with other Musca species; for example Musca domestica, Muirhead-Thomson (1937); Imms, A.D. (1957), share the characteristic framework of articulated sclerites (mouth hooks or mandibular sclerites with their associated sclerites) which are known as a cephalopharyngeal skeleton (see fig. 6b).

Respiration of the larva is by spiracles seen externally as small finger-like processes (6-8 in number) anteriorly (see fig 6c). Posteriorly, the spiracles externally are seen as small oblique slit-like apertures. They lie within the circle on the face of the last segment. (see fig 6d). The larva passes through three instars in the maggot stage. Though the larva grows through three instars, its appearance remains almost the same. The main difference between the instars besides the size is in the occurrence and form of the spiracles. In the first instar, the larva, has two posterior spiracles. In the second instar larva the posterior spiracles become large and more conspicuous resembling a pair of eyes.
Third instar larva:

(a) Whole larva.
(b) Cephalopharyngeal Skeleton.
(c) Anterior spiracles with 6 - 8 finger-like processes.
(d) Last posterior segment of the larva with spiracular plates and the protuberances.
(e) Enlarged posterior spiracular plates with the peritremo which is well marked. Breathing slits long, each with 4 - 5 loops.
The posterior spiracles of the third instar larva have each three slits with a heavy ring around each slit (fig 6). The second and third instars have also the anterior spiracles which appear to be brown in colour.

Towards the end of the third instar, the larva stops feeding and there is no food in the gut. It is a uniform pale yellow in colour. The ultimate size of the larva is strongly influenced by the conditions under which it is reared. At the end of the third instar, the larva contracts within its own integument to form a cylindrical puparium.

The only medium in which larvae have been noticed to develop in the field is animal faeces more especially lechwe faeces, but on one occasion cattle dung collected from the same locality (Howard, G. 1975; personal communication). Observations showed that larvae eat liquid and soft - parts of the faeces, leaving only a loose, dry and fibrous residue. If the pad of faeces dries up rapidly due either to its texture or disturbance, the larvae leave the pad and if fully grown form small pupae. If not fully-developed, they dry and die.

The behaviour of the larvae once they enter faeces is probably governed by the need for air and moist areas. At first larvae feed near the surface and in moist areas that are aerated by tunnels made by the dung beetles and larvae themselves. As the faeces shrink due to moisture drainage and larvae eating up the food sources, the wet part shrinks and a small space is formed below the crust. Ultimately, the larvae are confined to a central position near the lower surface of the faeces.
Plate 4.

Larvae on top of faeces before migrating into faeces. Note the plastron network, clearly seen in the larva on the top plate.
In the field the prepupa either buried itself in the narrow air space in which they remained congregated. In the laboratory experiments were carried out to investigate the effect of larval density on survival.
In the field the prepupa either buried itself in the soil adjacent to the faeces or remained in the interspace between faeces and soil, the heap of faeces acting as a shield against sun rays. In the laboratory it pupated in the sand on the enamel dish on which faeces had been put in cages for rearing purposes. The observed factors, therefore, which might have affected the survival of the larvae were:

(i) Physical environment of faeces which might have coincided with seasonal conditions.

(ii) The favourability of food found in the faeces in which they were reared.

(iii) Competition for that food, air and moisture in the narrow air space in which they remained congregated.

In the laboratory experiments were carried out to investigate the effect of larval density on survival.

**Description of cages used for rearing flies.**

For rearing cages, soft wood was used for the framework. The cages were 16cm x 12cm. The top and two opposite sides were covered with fine wire gauze. The other side was completely covered with a piece of soft wood. The other side which was also covered with a piece of wood had a whole in the middle in which was pinned a piece of mosquito net left hanging on the outside in the form of a handglove. The bottom of the cages was left open. The cages were put on the laboratory benches, and the handglove was used for feeding purposes and also for taking out any flies needed for experiments, (see fig 7).
Fig 7.

Diagrammatical rearing cage used in this study.
Technique and method.

Some three-day old female flies were fed on blood squeezed from fresh liver and allowed to mate with males from the same culture, of the females fed thirty-six were introduced into nine cages, four in each cage, and into each cage was placed fresh lechwe faeces on enamel dishes on which the flies oviposited. Of the fresh hatched larvae 450 were collected from the pooled larvae from all the nine cages. This 450 was then put into three lots of 200, 150, and 100 larvae. Then each lot was subdivided into 4 replicates so that in the first experiment each of the four cages contained 50 larvae in the second experiment each of the four cages contained 37/38 larvae; and the third experiment had 25 larvae in each cage. In each of these cages was placed a rearing medium of fresh lechwe faeces put on enamel dishes which had sand about 1mm from the bottom and the respective larvae were then inoculated in their respective media. Pupae resulting from each replicate were recorded, also the number of emerging flies were counted.

Results

These are tabulated on tables 2,3 and 4. They showed that larval mortality was in part affected by the numbers; the density of larvae used; thus, 200 larvae/400g faeces/74% survival; 150 larvae/400g/82% survival and 100 larvae/400g. faeces/56% survival. Converting
the remaining percents into mortality percent, for example 26%, 18% and 4% respectively show that larval mortality in these experiments was high at 200 density. Density-dependent larval mortality seemed to be the mechanism causing population regulation within faeces; this agrees with Nicholson, A.J. (1950); also with Lack, D. (1954a); Hughes and Walker, (1970) c.f Hughes et al (1972). Mortality could have been the result of intraspecific competition by larvae to get at food, oxygen or even moisture. Due to the normal levels of water loss caused by the effects of tunneling larvae, chemical change and solidification of faeces, there was only a small air space left in the middle of the faeces into which all the larvae had grouped.
**TABLE 2**

Larval survival at 200 larvae/400g. of faeces.

**REPLICATES**

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>Total</th>
<th>( \bar{x} \pm S.E. )</th>
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<td>50</td>
<td>50</td>
<td>50</td>
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<td>Resulting Pupae</td>
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<td>36</td>
<td>40</td>
<td>35</td>
<td>153</td>
<td>38.35 ± 1.65</td>
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<td>Emerging Flies</td>
<td>40</td>
<td>36</td>
<td>38</td>
<td>34</td>
<td>148</td>
<td>37 ± 1.29</td>
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<tr>
<td>Total % of survival 74</td>
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### TABLE 3
Larval survival at 150 larvae/400g.

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<th></th>
<th></th>
<th>( \overline{x} \pm \text{S.E.} )</th>
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<tbody>
<tr>
<td>Initial No. of Larvae</td>
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<td>2</td>
<td>3</td>
<td>4</td>
<td>Total</td>
<td>150</td>
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<tr>
<td>Resulting Pupae</td>
<td>37</td>
<td>38</td>
<td>37</td>
<td>38</td>
<td></td>
<td>35 ± 0.41</td>
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<tr>
<td>Emerging Flies</td>
<td>36</td>
<td>35</td>
<td>35</td>
<td>34</td>
<td>140</td>
<td>30.75 ± 0.48</td>
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<tr>
<td>Total % survival</td>
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<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
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<td>25</td>
<td>100</td>
<td></td>
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<td>25</td>
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<td>24</td>
<td>97</td>
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<tr>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>96</td>
<td></td>
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</table>

Initial No. of Larvae
Resulting Pupae
Emerging Flies

Mass = 400g
### TABLE 5

Analysis of Variance of Resulting Pupae of all three experiments

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<th></th>
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<th>d.f</th>
<th>M.S.</th>
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<tbody>
<tr>
<td>Between treatment</td>
<td>429.5</td>
<td>2</td>
<td>214.75</td>
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<tr>
<td>Within treatment or Residual</td>
<td>37.5</td>
<td>9</td>
<td>4.17</td>
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<tr>
<td>Total</td>
<td>467</td>
<td>11</td>
<td></td>
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</tbody>
</table>

\[ F = 51.4988 \]
\[ = 51.5 \]

\( F(5\%) = 4.26 \) \( \text{As } F = 51.5 > 8.02 \text{ the null hypothesis is rejected} \)

\( F(1\%) = 8.02 \) \( \text{is rejected & the population means are not equal. This result is highly significant.} \)
### TABLE 6

Analysis of Variance of emerged adult flies of all three experiments

<table>
<thead>
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<th></th>
<th>SS</th>
<th>d.f.</th>
<th>m.s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between treatment</td>
<td>338.167</td>
<td>2</td>
<td>169.0835</td>
</tr>
<tr>
<td>Within treatments or Residual</td>
<td>24.75</td>
<td>9</td>
<td>2.75</td>
</tr>
<tr>
<td>Total</td>
<td>362.917</td>
<td>11</td>
<td>/</td>
</tr>
</tbody>
</table>

F(5%) = 4.26 As F = 61.48 > 8.02, this result is F(1%) = 8.02 highly significant. The null hypothesis can be rejected, and the population means are not equal.
5 Puparium.

The puparium is subcylindrical with rounded ends. It is shorter and broader than the prepupa from which it has developed. Averagely, the puparium measures 9mm to 3.3mm. The colour of fully-tanned puparium is brown and the conjunctival folds are clearly seen. Externally, the puparium retains most of the characteristics of the prepupa cuticle from which it is formed. This agrees with observations made by West, (1951); on Musca domestica; Hughes; Greenham, (1972); on Musca vetustissima. The plates of the posterior spiracles are the same but they are not functional. Respiration is maintained by means of pupal spiracles in the form of small spine-like projections between the fifth and sixth segments of the puparium. A few observations were made on the natural pupation sites in the field. Those prepupa located were typically near the pad about 10 to 15mm below the soil surface. But mostly, puparia were found in the pads. In the laboratory a few were found in the sand which was put below the rearing faeces. The duration of the pupal stage is between seven and eighteen days.
Figure 8.

Puparium.
When the transformation of the pupa into a fly has been fully completed, the fly pushes out by the anterior end of the puparium by the use of the ptilinum. There is a circular slit and the detached cap is slit into two parts by longitudinal fissures in line with the anterior spiracular processes. Once the head is free the fly withdraws the ptilinum and then crawls out of the puparium. The adult fly works its way through the debris of faeces. The mouth-parts take the form of a lapping type proboscis, normally held retracted below the head. Maxillae have been reduced and there is an increase in the membranous areas which give flexibility to the proboscis which consists of a proximal cone-shaped basal part which corresponds to the rostrum and a distal portion which corresponds to the haustellum of other Cyclorrhapha species. The rostrum carries a structure corresponding to the fulcrum, the haustellum is strengthened by the prementum on the posterior side. Diagram of the proboscis is shown on figs 2 and 3.
When the fly is not feeding the proboscis is withdrawn into the head capsule and is extended again when feeding. The behaviour of flies towards the exposed liquid is interesting. Many of them congregated around the fresh exposed wound as soon as it was inflicted. Over a hundred flies were seen concentrated on a small wound on the antelope made by a gun shot. Each fly was trying to get at the exposed blood, burrowing its head in the wound as shown in plate 5a. Some flies had congregated round ears, nostrils and mouth exudations.

I collected flies from all these areas. Plate 5b shows collection of flies from a gun shot wound, the small structures looking like-globules, are flies. The sex ratios of flies collected from various areas varied. On blood the ratio was 1:1; from ears it was 3:1 in favour of females.

When fresh faeces were put on the ground as near the wound of the lechwe as possible to note any fly migration, it was observed that for the first sixty seconds no fly alighted on faeces. Then one fly alighted and started foraging, then a few more did; in the end about 15 flies stationed themselves on the faeces. Putting fresh faeces there seemed to unsettle some of the flies, so that they started flying from the wound to faeces and back again.

All the fifteen flies which had settled on faeces were collected and all of them were females. This indicated that female flies are more attracted to fresh lechwe faeces than the males. The female fly
Plate 5.

Top-plate.

Flies feeding on a fresh wound of the antelope inflicted by a gun shot.

Bottom-plate.

Collection of flies from the same fresh wound. All these dots are flies.
adult stages. Infact, it was observed that majority of the flies started showing mating tendencies after three
days. Observations done on the emerging activities
developed quickly through the larval and pupal stages.
lays her eggs in faeces and preparatory to oviposition, the genitalia are extended in the form of a thin ovipo-
sitory tube as long again as the abdomen at rest.

7. Emergence

At emergence neither sex is mature for mating purposes. They still contain a variable amount of pupal fat body cells, which are found lying loose in the body cavity, and the testes of male flies are bright orange in colour, changing to dark-brown after a few days. These changes parallel those in other calyptrate flies, Hori, (1960). The development of ovaries is influenced by the nutrition of both the larvae and adult stages. Infact, it was observed that majority of the flies started showing mating tendencies after three days. Observations done on the emerging activities revealed that there were some changes in the sex ratios of emerging flies in most cultures. For example, larvae which were reared at the room temperature of maximum 24 ± 20°C and minimum 20 ± 20°C had their first emergence after 8 days. The first emergence consisted of 39 males: 131 females: The second emergence occured 5 days later, with 120 males: 109 females. A day later there was an emergence of 47 males and 17 females; then the next emergence was 27 males; 14 females. Overall, in most cultures the sex ratio averaged 1:1. This type of development suggested that probably females developed quickly through the larval and pupal stages.
Size

The ultimate size of the fly depended directly on the quality of faeces on which larvae were reared. Using the head width measurements the sizes of the flies at emergence were from 1.08 to 3.01mm with a mean of $1.7 \pm 0.069$.

Longevity.

In most Musca species, the individual life span is affected by temperature; Tyndale-Biscoe and Hughes (1969); Greenham, (1972); Hewitt, (1914); West, L. (1951). The longevity of Musca tempestatum might have been affected by the temperature; this needs further detailed studies. When flies were exposed to sugar and water under the varying room temperatures of $25 \pm 10^\circ$ maximum and $20 \pm 20^\circ$ minimum, the life span was high. After 7 days most of the flies that had died were smaller in size, in the range of 1.6 to 2.1mm (head width).
8. Reproduction

At emergence, both sexes are not mature enough for mating. Male flies show mating tendencies earlier than the females. Saccá, G. (1964) on Mueca domestica showed that male flies were ready to mate by 10 to 12 hours after emergence. The females take a little longer, preferably on about the third day.

Even if the flies mate the fertility of the ovum depends on the intake of protein. Flies fed on carbohydrates, for example sugar can mate and fecundate. A fertilized female fly is able to produce fertile eggs during its entire life time; but in order to produce fertile eggs, it is necessary for it to absorb a diet that is sufficiently rich in protein, (Ascher and Levinson, 1956; Saccá and Benetti, 1960). This behaviour seems to be characteristic of female Dipteran flies; for instance, it is widely known that the egg of many haematophagous species can not develop their eggs completely if the female does not feed on blood, (Imms, A.D. 1957). Protein is an essential requirement for flies. It has been shown that flies reared in laboratories on a water and sugar diet, can produce mature eggs, only if they feed on the body of a fly in the cage, (Saccá, G. 1964). Indicating that even small quantities of proteinaceous substances are likely to be sufficient. So, the female lechwe flies need good quality food both during the larval stage and the adult life to allow complete egg development.
9. **Natural Enemies**

Most of the species given here as natural enemies of *Musca tempestatum* are those general predators and parasites of the genus *Musca*, given by various authors and are quoted accordingly. Some of these species have been observed during the course of this study. Natural enemies of *Musca* belong to numerous groups and only a few will be mentioned here.

**Fungi**

Many species of fungi have been described as being parasites of flies, Saccá, G. (1964); *Empusca Muscae* Cohn. and *Entomophthora Muscae* Cohn infested flies reared in the laboratory especially during the rainy season. *Empusca Muscae* has been described as attacking and killing *Musca domestica*, Saccá, (1964). Walker, et al (1972) write that Norris, reported the infestation of *Entomophthora Muscae* on the Australian bushfly collected from Tasmania. Among other recorded fungi attacking *Musca* species which could involve *Musca tempestatum* if investigated are: *Aspergillus parasiticus* Speare; *Empusa american Thaxter Fusarium tricinctum* Corda; Hewitt, C.G. (1914); West, L. (1951); Steinhaus, E.A. (1963).

**Bacteria**

*Bacillus thuringiensis* Berliner was, described as originating from diseased larval of *Anagasta kühniella* Zeller. It was also found to prevent the development of the larvae of *Musca domestica*. 
Further studies have shown that *R. thuringiensis* can be added to the food of cattle and poultry to prevent larval development in the faeces of the animals themselves (Briggs, G.D. 1960). Among other recorded bacteria are: Bacterium delendae - *muscae* (Rouband and Descazeaux, 1923). *Staphylococcus muscae* (Glasser 1924b, 1926a) c.f. West L. 1951.

**Insects and other Arthropods.**

Hammer, (1941) and Hafez,, (1948, 1949) recorded some other species of insect acting as predators on larvae and eggs in cow-dung (c.f. Laurence B.R. 1954). The fly *Anaclysta flexa* Wiedemann feeds on full grown larvae of *Musca* species for example *Musca domestica*, Muir head - Thomson, (1947). The larvae of *Musca lucoria* Wiedemann have been reported as predacious and these larvae have been noted to be inhabiting lechwe faeces (Howard, G.W, personal communication). Beetles (Coleoptera) which are general predators of *Musca*; Hewitt, (1954; Laurence, 1954; Hughes et al, 1972, have been found inhabiting the lechwe faeces but whether these are natural enemies of *Musca tempestatum* is yet to be seen. The larvae of mites have been seen attached to the bodies of flies in the cages in the laboratory. Hewitt, (1941) reported that the larvae of mites were observed sucking up juices of the host by means of their thread like mouth-parts. The presence of mites on the bodies of the lechwe fly may indicate that the acarin suck up the juices from them.
10. **Discussion**

Behaviour of the female adult fly was more easily studied than that of the male, because flies collected from the field were mostly females. Lechwe flies were among the first of the coprophagous species of insects to reach a faecal dropping. They normally started arriving at the dropping as soon as it was being deposited. Oviposition, however, did not occur immediately, it occurred several minutes later. The interval between alighting of the fly and first oviposition might have been spent on feeding on the fluids of faeces. Gravid female flies wandered randomly over the pad of faeces looking for suitable sites in which to lay their eggs. When the faeces were still fresh the flies did not take long in finding suitable sites, such as cracks, crevices or on top of the faeces. As the pad formed a hard crust, the flies looked for any moist depressions. When the eggs hatched the larvae migrated within the faeces and all the three larval instars were passed through in faeces. Results of the experiments done on larval density showed that there was a high survival percent at a lower population density: 200 larvae/400g: 74%; 150 larvae/400g: 82%; 100 larvae/400g: 96%. This indicated that the competition between larvae feeding on faeces given as food had some direct effects on larval survival. Experiments done under more closely controlled conditions on one of the *Musca* species, *Musca vetustissima* have confirmed that larval survival is greatest at lower population densities; Hughes *et al.* (1972).
4. Food Requirements

1. Introduction

Flies collected from the field were dissected to examine the gut contents so as to try to establish as nearly as possible the types of foods that flies feed on in nature. When the flies were dissected the guts were opened up and their contents examined with the aid of a microscope. The contents of the guts in some of the flies recognized were dark patches which looked dark green indicating that the flies had taken meals of faeces, in some flies the gut contents had pink patches indicating that those flies had taken blood meals. (c.f. Tyndale-Biscoe M. 1971). These two colours (dark-green and pink) were easily recognized in the mid-gut. The crops of the flies were also opened up to note the types of food substances they contained. It was noted that the crops of flies in which the gut content showed dark-green had green substances and in the others, the crops revealed contents spotted with red colour. Observations in the field on the distribution of the fly on lechwe and man showed that the flies were seen congregating on certain parts of the body, for example, eyes, ears, nostrils and mouths and when these flies were closely observed on a freshly killed animal, it was noted that they were feeding on the exudations from these regions. These substances were not noted in the gut and crop contents of the dissected flies caught from the field, due
maybe to their being colourless. Blood, faeces and exudations from the mentioned body regions contain proteins (though exudations such as saliva, tears etc. were not recognized in dissected field flies) Sacca, D. (1963); Sirigardene, et al. (1966); Tyndale - Biscoe, M. (1971). The question of flies feeding on proteins was studied in the laboratory using blood (in the form of fresh chopped liver) and fresh lechwe faeces.

**Method used**

Method used followed Tyndale - Biscoe, (1971). Flies in two sets of two-hundred each that were three days old from a fly culture were put in two separate cages. One set of flies was presented with a petri-dish of very fresh sliced liver and the other with a petri-dish of fresh lechwe faeces. Day prior to the experiment flies were given only water. Their feeding activities were noted after two hours, they were allowed a further hour of feeding and then all the flies from the two cages were killed to note gut contents.

**Results.**

Results showed that in the first cage only 56 male flies, had fed on liver compared to the 116 female flies, (red crop and pink gut). 27 male flies and 1 female had not fed (crop and gut colourless) as shown on table 7. In the second cage 83 male and 91 female flies had fed on faeces (green crop and gut). 23 male and 3 female flies
had their crops and guts colourless indicating that they had not fed as shown on table 8. On the basis of these results deductions were made that female flies feed more on proteinaceous substances, and also that where proteinaceous foods were presented to starved males, they fed on them, though not in high numbers as female flies.

### Table 7

Response of flies fed on fresh liver.

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<th>%</th>
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<td>56</td>
<td>28</td>
<td>116</td>
<td>58</td>
</tr>
<tr>
<td>Unfed flies</td>
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<td>13.5</td>
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<td>0.5</td>
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<tr>
<td>Total</td>
<td>83</td>
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<td>117</td>
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### Table 8

Response of flies fed on fresh faeces.

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<th>%</th>
<th>0</th>
<th>%</th>
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</thead>
<tbody>
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<td></td>
<td>83</td>
<td>41.5</td>
<td>91</td>
<td>45.5</td>
</tr>
<tr>
<td>Unfed flies</td>
<td>23</td>
<td>11.5</td>
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<tr>
<td>Total</td>
<td>106</td>
<td></td>
<td>94</td>
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</table>
Larval food material

Basic requirements for a satisfactory breeding and rearing of most Musca species are suitable food, high humidity, sufficient oxygen and water, some protection from direct impact of rain and actinic light; Boddamou, (1901); Portchinsky, (1910); West, (1951); Redshaw, (1965). All these conditions are available in lechwe faeces for the larvae of Musca tempestatum. Musca tempestatum has been observed to lay its eggs on lechwe faeces and sometimes on cattle-dung (c.f. breeding sites). When the larvae hatch out they migrate in the faeces and depend on faeces for food. It is observed that after eclosion the 1st instar larvae remain near the surface of the faeces with their posterior spiracles exposed. Once they are disturbed they disappear into faeces, but reappear after a short-time at the same place. When there is a light crust formation, they maintain numerous tunnels in the crust to which they return to expose their spiracles. The larvae depend on faeces for food; in this connection the composition of the food is important. Seasonal changes which may affect the composition of pasture plants on which the antelopes feed may be expected to influence the composition and texture directly; (c.f. Greenham, 1972). The main components of faeces are undigested food residues, including plant cell, walls and lignified tissue, products of the gut muoosa and the excretory products of the hosts metabolism; Greenham, (1972) Handlos, D (personal
communication). Faeces therefore are the residue of pasture after it has interacted with the digestive processes of the host and its micro-organisms. This type of digestion (common to all ruminants) is characteristically aided by symbiotic micro-organisms which break down dietary cellulose and, to a lesser extent, proteins. When mature herbage is ingested, the relatively higher proportion of cell-walls and lignified tissue impedes enzyme activity so reducing further digestion of fibrous materials and proteins and as a result there is an increase in the size of solid particles in the faeces and a decrease in available nitrogenous materials. The composition of the faeces and their variation were studied in the laboratory so as to investigate the effect of these variations on the survival of *M. tempestatum* depended upon lechwe faeces.

**Collection of faeces**

Every effort was made to collect fresh faeces in plastic bags to prevent loss of moisture. This was done by following the lechwe up to the high flood line (refer to the map) during the dry season. During the wet season, herds of lechwe were found even near the lodge (see the map) so collections were done around there.

Each sample was made up of 4 pads of faeces. These were put in plastic bags transported to the laboratory and analysed within twenty-four hours.
In the laboratory each sample was sub-sampled for moisture, nitrogen and the remainder used for rearing flies to observe the effect of changes in faecal quality on larval survival.

**Method and material used for nitrogen determination.**

10g of each sample was weighed and transferred into Kjeldahl flask adding 10g of copper sulphate as a catalyst. The samples were then digested in sulphuric acid over the Kjeldahl digestive accelerator for 2 hours before being made up to standard volume of 250ml with distilled water. The nitrogen content in the samples was determined by using the Markham distillation apparatus using the following reagents; 40% sodium hydroxide; 1% Boric acid solution containing 25ml/litre of 2 parts 0.2% Methyl red + 3 parts 0.2% Bramo cresol green. These contents were titrated using the receiving flask with N/100 Hydrochloric acid. The determinations were done for 8 months from May to December inclusive; in May determinations were done twice so that the number of determinations became nine.

**Method and material used for moisture determination.**

The method used for moisture determination followed Greenham, (1972). For each sample four porcelain dishes of known weight were filled with faeces, reweighed and then heated for 48 hours at 95°C. After that the dishes were weighed again and the weight loss converted to percent moisture content. Each sample was done in replicates of four.
Results of both nitrogen and moisture determinations

These showed that there was $2^{±1}\%$ difference between the replicates; and the means which are shown on tables 9 and 10 showed that there was a range from $2.48\% - 5.43\%$ nitrogen content and from $4.25\% - 7\%$ moisture content. There was a difference of about $1\%$ between the means of the samples determined for nitrogen. In moisture content the difference varied. For example, there was a difference of $0.2\%$ between the months of June (21/6/74) and July (24/7/74). Whereas, between the months of September (26/9/74) and October (23/10/74), there was a difference of $8.75\%$. August samples had the highest percentages ($5.43^{±0.42}$ nitrogen and $74.9^{±1.71}$ moisture). October had the lowest ($2.48^{±0.31}$ nitrogen and $64.25^{±1.03}$ moisture); $P < 0.01$, students-t-test for both. These results also revealed that moisture and nitrogen contents follow the same pattern. For both contents the highest occurred in August (means of $5.43\%$ nitrogen and $74.9\%$ moisture) - and the lowest in October ($2.48\%$ nitrogen and $64.25\%$ moisture) (see also fig 9 for nitrogen and moisture content). For the full results of percentages determined in the data collected between May 12th and December 12th 1974 for nitrogen and moisture are shown in the appendices I and II.

Responses of flies to variation in faeces were measured by the survival of larvae to adult, also by the size and weights of emerged flies (weights are given on table 11). It was observed that variations in nitrogen content could
Figure 9

Moisture and Nitrogen content determined in data collected between 12th May and 12th December 1974.
affect fly survival. The percentage survival from larvae is shown on fig 10. At 2.48% nitrogen content survival was 40% and at 5.43% survival was high. At emergence the flies were measured head width and weighed. At 40% survival the measurements ranged from 1.5mm - 2.6mm (n=50) and at 80% they were from 1.8mm - 3.91mm (n=50). Average weight for the month of August which had the highest nitrogen content was 10.31mg (n=50) and for October with the lowest nitrogen percentage the average was 5.6mg (n=50).

Discussion

Variations in the contents of nitrogen and moisture were observed and the means taken as shown on tables 9 and 10. These indicate with near certainty that in samples collected between May 12 and December 12 1974, moisture content followed the same pattern with nitrogen (highest in August and lowest in October P < 0.0.01, students-t-test). Nitrogen percentage was high in the second week of May (12.5.74), then declined towards the end of May (24.5.74). There was a steady rise in the months of June and July so that in August there was a peak and then a decline in September and October, a rise in November and December. Fly survival is presented on fig 10 and this demonstrated that the highest percentage was demonstrated by flies reared at 6.25% nitrogen content. That sizes and weights of flies also followed same pattern with nitrogen content was demonstrated with some near certainty as shown on lables 11 and 12. The content of nitrogen might not have affected
Figure 10

Effect of nitrogen on the survival of flies fed on it.
EFFECT OF NITROGEN CONTENT ON FLY SURVIVAL

Percent of Fly Survival (Larvae-Adult)

Percent of Nitrogen in Samples
fly survival severely, due to the fact that there are some other contributing factors to fly survival (refer to section III). But nitrogen content contributed to the final size of the emerged flies. When nitrogen content was from 1.9 - 3.1%, the sizes were in the range of 1.01 - 2.01mm and when the range was from 3.5 - 6.25%, the sizes were between 1.64 - 3.96mm.

In the month of October, nitrogen content was comparatively low, with the mean of 2.48% and the percentage of fly survival was 40% (fig 10) and at 5.43% survival was high. At emergence the flies were measured (head width) and weighed. At 40% survival the measurements ranged from 1.5mm - 2.6mm (n=50) and at 80% they were from 1.8mm - 3.97mm (n=50). Average weight for the month of August which had the highest nitrogen content was 10.31mg (n=50) and for October with the lowest nitrogen percentage the average was 5.6mg (n=50).
### TABLE 9

Mean numbers, standard error from the means and the range of nitrogen content

<table>
<thead>
<tr>
<th>Date Data collected</th>
<th>$\bar{x}$</th>
<th>S.E. of $\bar{x}$</th>
<th>Range</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>12/5/74</td>
<td>3.95</td>
<td>±0.17</td>
<td>3.2-4.5</td>
<td>6</td>
</tr>
<tr>
<td>24/5/74</td>
<td>3.35</td>
<td>±0.14</td>
<td>3.1-3.8</td>
<td>4</td>
</tr>
<tr>
<td>21/6/74</td>
<td>3.7</td>
<td>±0.27</td>
<td>2.5-4.9</td>
<td>6</td>
</tr>
<tr>
<td>24/7/74</td>
<td>4.03</td>
<td>±0.23</td>
<td>3.2-4.8</td>
<td>4</td>
</tr>
<tr>
<td>22/8/74</td>
<td>5.43</td>
<td>±0.64</td>
<td>3.7-7</td>
<td>10</td>
</tr>
<tr>
<td>26/9/74</td>
<td>4.5</td>
<td>±1.06</td>
<td>2.5-6.9</td>
<td>6</td>
</tr>
<tr>
<td>23/10/74</td>
<td>2.48</td>
<td>±0.27</td>
<td>1.9-3.1</td>
<td>4</td>
</tr>
<tr>
<td>6/11/74</td>
<td>4.2</td>
<td>±0.29</td>
<td>3.06-4.75</td>
<td>4</td>
</tr>
<tr>
<td>12/12/74</td>
<td>4.19</td>
<td>±0.15</td>
<td>3.5-4.75</td>
<td>4</td>
</tr>
</tbody>
</table>

$\bar{x}$ = Means; S.E. = standard error; N = size of replicates.
<table>
<thead>
<tr>
<th>Date</th>
<th>Data collected</th>
<th>$\bar{X}$</th>
<th>S.E of $\bar{X}$</th>
<th>Range</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>12/5/74</td>
<td>66.5</td>
<td>±1.26</td>
<td>61 - 69</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>24/5/74</td>
<td>64.75</td>
<td>±1.03</td>
<td>62 - 67</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>21/6/74</td>
<td>72.25</td>
<td>±1.65</td>
<td>68 - 76</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>24/7/74</td>
<td>72.23</td>
<td>±0.41</td>
<td>67.4 - 79</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>22/8/74</td>
<td>74.9</td>
<td>±1.71</td>
<td>67.4 - 79</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>26/9/74</td>
<td>73</td>
<td>±2.74</td>
<td>67 - 79</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>23/10/74</td>
<td>64.25</td>
<td>±1.02</td>
<td>62 - 67</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>6/11/74</td>
<td>71.01</td>
<td>±0.82</td>
<td>68 - 76</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>12/12/74</td>
<td>69.88</td>
<td>±0.68</td>
<td>68 - 72</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Date Data collected</td>
<td>X</td>
<td>S.E</td>
<td>Range</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>--------------------</td>
<td>-----</td>
<td>------</td>
<td>----------</td>
<td>----</td>
<td></td>
</tr>
<tr>
<td>12/5/74</td>
<td>8.25</td>
<td>8.25±2.21</td>
<td>4-10.25</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>24/5/74</td>
<td>6.36</td>
<td>6.36±2.91</td>
<td>3.75-9.25</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>21/6/74</td>
<td>7.39</td>
<td>7.39±3.61</td>
<td>4-11.1</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>24/7/74</td>
<td>9.79</td>
<td>9.79±3.64</td>
<td>4.7-14.1</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>22/8/74</td>
<td>10.31</td>
<td>30.31±141</td>
<td>4.7-17.2</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>26/9/74</td>
<td>8.65</td>
<td>±.5</td>
<td>3-14.1</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>6/11/74</td>
<td>7.24</td>
<td>5.6±3.34</td>
<td>1.5-9.25</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>12/12/74</td>
<td>8.34</td>
<td>8.35±5.1</td>
<td>1-13.1</td>
<td>50</td>
<td></td>
</tr>
</tbody>
</table>
TABLE 12

Sizes of flies in mm that emerged from faeces collected between 12th May and 12th December 1974

<table>
<thead>
<tr>
<th>Date Data collected</th>
<th>$\bar{x}$</th>
<th>S.E. of $\bar{x}$</th>
<th>Range</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>12/ 5/74</td>
<td>1.66</td>
<td>1.66±0.096</td>
<td>1.01-2.98</td>
<td>25</td>
</tr>
<tr>
<td>24/ 5/74</td>
<td>1.61</td>
<td>1.61±0.147</td>
<td>0.36-3.1</td>
<td>25</td>
</tr>
<tr>
<td>21/ 6/74</td>
<td>1.7</td>
<td>1.7±0.9</td>
<td>1.08-3.01</td>
<td>25</td>
</tr>
<tr>
<td>24/ 7/74</td>
<td>1.9</td>
<td>1.9±0.064</td>
<td>1.02-3.06</td>
<td>25</td>
</tr>
<tr>
<td>22/ 8/74</td>
<td>2.52</td>
<td>2.52±1.33</td>
<td>1.64-3.96</td>
<td>25</td>
</tr>
<tr>
<td>26/ 9/74</td>
<td>2.4</td>
<td>2.4±0.2</td>
<td>1.96-3.91</td>
<td>25</td>
</tr>
<tr>
<td>26/ 10/74</td>
<td>1.6</td>
<td>1.6±0.064</td>
<td>0.25-2.01</td>
<td>25</td>
</tr>
<tr>
<td>6/11/74</td>
<td>1.71</td>
<td>1.71±0.11</td>
<td>1.09-3.06</td>
<td>25</td>
</tr>
<tr>
<td>12/12/74</td>
<td>1.7</td>
<td>1.7±0.07</td>
<td>1.08-3.01</td>
<td>25</td>
</tr>
</tbody>
</table>
3. **Food for Imago**

Food for adult flies is important in two ways:-

(i) To supply energy.

(ii) To enable the immature female flies to start the development of their eggs.

Glasser, R.W. (1923 a – 1924 a) studied the physiology of *Musca domestica* and found that certain foods that serve adequately for the purpose of sustaining life of these flies did not induce the maturation of the sex organs of female flies. Sugar or assimilable starch proved necessary for the normal longevity of adult individuals. In addition a protein-yielding food was required for the production and deposition of eggs.

In the field, *Musca tempestatum* probably obtains carbohydrates from the vegetation. It obtains proteins from the faeces of the host and from any other exudations, blood included. Flies which were collected from the field were dissected to note the gut contents and these contents showed the presence of blood and faeces (ref. 4.1).

Feeding experiments were carried out in the laboratory to investigate:-

(i) The effects of proteins and carbohydrates on the survival of flies,

(ii) The effects of the quality of food on reproduction and survival.
Effects of proteins and carbohydrates on survival.

The flies used in these experiments were from a laboratory culture, started with the immature stages (eggs, larvae, and pupae) collected within the pads of faeces from the field. In order to get adequate results of the effect of (i) and (ii) the experiments were done in replicates of 4 each, so the sampling plan was designed to give estimates of within-treatments and between-treatments variability.

**Materials and method**

800 flies were exposed to 4 feeding regimes of

(i) Fresh liver and water (referred to as Treatment I = $t_1$)

(ii) Sugar and water ($t_2$) (sucrose)

(iii) Liver, water and sugar ($t_3$) (sucrose)

(iv) Faeces and water ($t_4$)

**Design**

Each feeding regime was tested on 200 flies in 4 replicates of 50 each. The flies were put in cages designed for rearing (c.f. section 3). The experiments were carried out for 7 days and dead flies were removed from the cages daily by using a very fine brush through the hand glove of the cage. The surviving flies were counted and recorded for the calculations and estimations at the end of the 7 days. In cages in which liver was used as food, fresh
material was given daily so as to ensure the supply of blood. Lechwe faeces were also replaced daily with faeces stored in the fridge in air-tight plastic bags. The experiments were done on dates shown below.

<table>
<thead>
<tr>
<th>Treatment - No.</th>
<th>Dates of Sampling</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7th - 13th August 1974</td>
</tr>
<tr>
<td>2</td>
<td>6th - 12th August 1974</td>
</tr>
<tr>
<td>3</td>
<td>8th - 14th August 1974</td>
</tr>
<tr>
<td>4</td>
<td>7th - 13th August 1974</td>
</tr>
</tbody>
</table>

Results

The results varied. The highest number of survival was demonstrated by flies exposed to \( t_2 \) (sugar and water) appendix IV. Then \( t_3 \) (liver, sugar and water) appendix V; \( t_4 \) was the next (liver and water) appendix I and lastly \( t_4 \) (faeces and water) appendix VI.

Treatment 2 and 3 in combination with water, allow measurements of comparative effect due to liver and sugar. The observations revealed that the flies can and do assimilate carbohydrates.

Analysis of Variance.

Analysis of variance was done on the numbers of surviving flies from each treatment to test the
significance due to replicates and also due to treatments. Table 14 shows the analysis of variance. The "F" test is the ratio of the mean square between-treatments and the mean square within - treatments (replicates). The latter variance was not greater than residual so a more accurate variance ratio was calculated with residual as a denominator. The results were significant at 5% and at 1% level, indicating that population means were not the same between treatments in the four comparisons. In the sixteen replicates (4 replicates for each treatment), there were no significant differences within each treatments, A highly significant difference appeared in the means of treatment 1 (7th - 13th August) and treatment 2 (6th - 12th August). Also in the means of treatment 3 (8th - 14th August) and treatment 4 (7th - 13th August) and in treatment 2 and treatment 4. The mean of treatment 2 is the greatest with treatment 4 being the lowest.

**TABLE 13**

Mean numbers of surviving flies of treatments 1-4

<table>
<thead>
<tr>
<th>Treatment-No.</th>
<th>Mean and standard error</th>
<th>Variance</th>
<th>σ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment 1</td>
<td>30.0 ± 1.4</td>
<td>8</td>
<td>2.83</td>
</tr>
<tr>
<td>Treatment 2</td>
<td>38.25 ± 1.26</td>
<td>6.33</td>
<td>2.25</td>
</tr>
<tr>
<td>Treatment 3</td>
<td>37.75 ± 1.03</td>
<td>4.25</td>
<td>2.06</td>
</tr>
<tr>
<td>Treatment 4</td>
<td>26.5 ± 1.7</td>
<td>11.65</td>
<td>3.42</td>
</tr>
</tbody>
</table>
TABLE 14

Analysis of variance for surviving flies from the four treatments,

<table>
<thead>
<tr>
<th>Source of Variations</th>
<th>d.f</th>
<th>ss</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between treatments</td>
<td>3</td>
<td>415.69</td>
<td>138.56</td>
<td>8.66</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Between replicates</td>
<td>3</td>
<td>30.85</td>
<td>10.28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>9</td>
<td>144.15</td>
<td>16.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>580.69</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Note:*

\[ F = 3.86 \text{ at } 5\% \text{ level of significance} \]

\[ F = 6.99 \text{ at } 1\% \text{ level of significance} \]

\[ F = 13.9 \text{ at } 0.1\% \text{ level of significance}. \]
Analysis for differences between treatments

The number of flies remaining alive after seven days under four different treatments is tabulated in the appendices III to VI. They show the collected data under the four different treatments. Table 14 shows the analysis of variations between treatment, that is, the difference between treatments and the residual treatments. With an F-value of 8.66, there is a significant difference between the four treatments. The t-values were calculated between pairs of treatments. These values were found in order to identify where the variation lay. There was no significant difference between treatments 2 and 3.

The model of these analyses is shown in table 15.

The formula used for the calculations of t-values was expressed in units of standard deviation,

\[
\frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{N_1 S_1^2 + N_2 S_2^2}{N_1 + N_2 - 2}}} = \sigma
\]

\(\sigma\) standard deviation of the population.

\(\bar{x}_1, \bar{x}_2\) are means

\(S_1, S_2\) standard deviation of each treatment

\(N_1, N_2\) number of replicates.
TABLE 15

$t$-Values between pairs of treatments 1, 2, 3 and 4.

<table>
<thead>
<tr>
<th>Difference between treatments</th>
<th>Value of $t$ d.f 6)</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatments 1 and 2</td>
<td>3.86</td>
<td>$P &lt; 0.01$</td>
</tr>
<tr>
<td>Treatments 2 and 3</td>
<td>0.266</td>
<td>NS</td>
</tr>
<tr>
<td>Treatments 3 and 4</td>
<td>5.66</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>Treatments 1 and 3</td>
<td>4.45</td>
<td>$P &lt; 0.002$</td>
</tr>
<tr>
<td>Treatments 1 and 4</td>
<td>1.59</td>
<td>NS</td>
</tr>
<tr>
<td>Treatments 2 and 4</td>
<td>5.42</td>
<td>$P &lt; 0.001$</td>
</tr>
</tbody>
</table>

Note: $t$-values of $3.71 = P 0.01$
$2.45 = P 0.05$
$5.96 = P 0.001$
$5.21 = P 0.002$. 
Protein foods as sources of other food requirements

An experiment was set up to see whether proteins could act as sources of carbohydrate or water. Three-day-old flies starved a day before the experiment were put in 4 cages of 60 each and allowed to feed on various combinations of sugar, water and fresh faeces. Dead flies were removed daily and fresh liver was supplied everyday. Lechwe faeces were replaced with faeces kept in a tied plastic bag kept in the fridge; due to the fact that the lechwe are found in Lochninvar and Blue Lagoon which are far from Lusaka, the faeces could not be collected everyday to ensure their freshness. Pattern of survival is shown on table 15.

On the basis of these results an assumption could be made that wet faeces could replace water satisfactorily but could not replace sugar. The early mortality suggests that faeces are inadequate direct sources of available carbohydrate for energy.

Comments

All these experiments mentioned in the text were done to investigate the effects of proteins and carbohydrates on the survival of flies. The results indicated that the feeding of flies on fresh liver and fresh faeces did not increase the life span of the individuals as compared to the flies fed on sugar. Also results indicated that the types of food substances had different effects on flies (significant differences between 4 treatments, table 14). On the basis of these results an assumption was made that the flies fed on liver and faeces might have used the proteins obtained from these substances for purposes other than promoting the life span of the
<table>
<thead>
<tr>
<th>Days</th>
<th>Sugar &amp; Water</th>
<th>Faeces &amp; Water</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day 1</td>
<td>60</td>
<td>60</td>
</tr>
<tr>
<td>Day 2</td>
<td>60</td>
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<td>Day 3</td>
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<td>Day 6</td>
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<tr>
<td>Day 10</td>
<td>58</td>
<td>48</td>
</tr>
</tbody>
</table>

Survival of flies when faeces is substituted for sugar or water.
individual. For this purpose further experiments were done to note the effects of food quality on reproduction.
5. **Effects of food quality on reproduction and survival.**

Observations on the effect of proteins and carbohydrates on fly survival showed that flies did not depend on protein yielding foods for survival, even though they feed on proteinaceous foods, for example, blood (sliced fresh liver) and fresh lechwe faeces. This behaviour indicated, therefore, that the flies were not obligatory blood feeders but can and do feed on other foods such as sugar and maybe other assimilable starch, for example, flies in the field may depend on vegetation for carbohydrates; such vegetation as the sweet from nectar of flowers.

Probably in common with many insect species, for example, *Musca domestica* Ascher, and Levinson, (1956); Sacca and Benetti, (1960); and *Musca vetustissima* Tyndale-Biscoe and Hughes, (1969); Walker, Tyndale-Biscoe, (1971), flies feeding on carbohydrates and water can mate and fecundate, but in order to produce mature eggs, it is absolutely necessary for the female fly to absorb a diet that is sufficiently rich in protein. It has been proved that flies reared in laboratories on a water and sugar diet can produce mature eggs only if they feed on the body of a dead fly in the cage (Monroe, Kaplanis, and Robins, 1961). Therefore even small quantities of proteinaceous substances are likely to be sufficient. Experiments were done to observe the effect of the quality of food on reproductive performances. Quality of food was based on the nitrogen content in material used as food, as in Hughes and Walker, (1971).
Fresh lechwe faeces varying in quality were used. Crude determinations of nitrogen content revealed that variations ranged from 2.5% to 6.25%. For these observations lowest and highest nitrogen contents were used as controls. Observations were done in 4 replicates starting with 300 newly hatched larvae from the same populations. The observations were carried out side by side at the same time. These three hundred larvae were directly innoculated into 400g of fresh lechwe faeces. The numbers of each subsequent developmental stage of the fly were recorded, as were the numbers of emerging females and their egg complement after being fed on slices of fresh liver. The sizes of emerged flies were also measured, (head width).

Results

These are tabulated on tables 17 and 18. They showed that the total number of the resultant pupae from high nitrogen content was 692 and the emerged flies were 633, out of these 439 were females. The number of eggs after two days was 15,365, which meant that probably each female fly had laid about 35 eggs. Resultant pupae from food with low nitrogen content was 458 with the emergence of 386 adults and out of this total 119 were females. The number of eggs was 2580, therefore each female must have laid about 22 eggs. This showed the difference of 11, which was quite a large enough difference to show that good quality food (high nitrogen content) promotes fecundity.
**TABLE 17**

Effect of poor quality on *M. tempestatum*

**REPLICATES**

<table>
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<tr>
<td>Eggs</td>
<td>2580</td>
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### Effect of good food quality on *M. tempestatum*

#### Replicates

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<th>Total</th>
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<tbody>
<tr>
<td>Larvae</td>
<td>300</td>
<td>300</td>
<td>300</td>
<td>300</td>
<td>1200</td>
</tr>
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<td>300</td>
<td>300</td>
<td>300</td>
<td>300</td>
<td>1200</td>
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<tr>
<td>Pupae</td>
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<td>154</td>
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<tr>
<td>Adults</td>
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<td>143</td>
<td>160</td>
<td>166</td>
<td>633</td>
</tr>
<tr>
<td>♀ Adults</td>
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<td>108</td>
<td>84</td>
<td>126</td>
<td>439</td>
</tr>
<tr>
<td>Eggs</td>
<td>15365</td>
<td></td>
<td></td>
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</tbody>
</table>
Summary on the effect of food quality on flies reared on high and low nitrogen content.

<table>
<thead>
<tr>
<th></th>
<th>% Nitrogen</th>
<th>Survival % to Pupae</th>
<th>% Emergence</th>
<th>Mean Oviposition</th>
<th>Mean Head size (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>HIGH PROTEIN FOOD</strong></td>
<td>6.25</td>
<td>57.67</td>
<td>52.75</td>
<td>35</td>
<td>2.5</td>
</tr>
<tr>
<td><strong>LOW PROTEIN FOOD</strong></td>
<td>2.5</td>
<td>38.17</td>
<td>32.17</td>
<td>21.68</td>
<td>1.77</td>
</tr>
</tbody>
</table>
When flies from both culture were measured (head width) it was found that the flies from low quality food were smaller in size as compared to flies from the high quality food. The average size of flies from the poor quality was 1.7mm (n=50), the range of sizes being from 1.01mm - 3.01mm. The average size of flies from good quality was 2.5mm (n=50), the range being from 1.64mm - 4.01mm.

The results, therefore, indicated that the quality of food affects oviposition, final size of the adult fly and also fecundity of the adult female flies. It would seem that the reduction of fecundity with food quality during the larval stage was associated with the reduction in the average size (head width of emerging flies, thus: good 2.05mm and poor 1.07mm). It seems possible therefore, to assume that larvae reared on food of poor quality reduces body size and food reserves in the adult females, causing a reduction in the number number of active ovarioless per ovario.

The progeny of these females was ascertained after flies had fed on liver, which was considered to be an optimum source of protein, by Hughes and Walker, (1971). If these flies were fed on suboptimal protein sources such as faeces, of low quality instead of liver, a further reduction of egg numbers would probably result. For example, when a set of 12 gravid female flies were allowed to feed on fresh liver and fresh faeces, it was observed
that fecundity (fecundity was measured by number of eggs laid and head sizes of emerged flies). Of those flies fed on liver was 85% as compared to 70% of those fed on fresh faeces. The reduction in the resulting numbers might have been due to the large numbers of the initial larvae used. It has been shown already in this study that when the faeces solidify, there is a small moist-place in the middle of the pad of faeces in which the larvae congregate with their posterior spiracles pointed upwards. The physical effect of funnelling by larvae cause more than normal levels of water loss, so that each larva in this small space tries to get at the available food, oxygen water etc. To investigate the effect of larvae density on survival of flies in connection with the quality of food, two experiments were carried out at the same time. Experiment 1 started off with 600 larvae reared from a known nitrogen percent inoculated in 800g of fresh faeces. The larvae were put in 2 separate cages of 300/800g each. Concurrently, two more cages were set up with the same weight of faeces (800g,) doubling the population density (method used followed Hughes and Walker, 1970). Results of these observations are shown on fig 12. The number of eggs produced after feeding on faeces are expressed as a percentage of the number usually produced after feeding on liver. There seems to be a reduction in number of eggs produced by flies
reared at higher density the general linear relationship of egg numbers to the quality of faeces seems to be apparent. Similar experiments on some other *Musca* species carried out under more closely controlled conditions have confirmed that larval survival is greatest at lower population densities. (Greenham, P.M. and Tyndale-Biscoe, 1972).

These results in conjunction with those on tables 17 and 18 indicated that the differences in quality of faeces used resulted in some difference in the potential rate of increase of the flies expressed here by the number of eggs produced per larva present initially. When best conditions are provided (quality of food) the increase would be five to sixfold, when there is poor quality food, the emerged small flies could be prevented from developing any eggs so that there would be a severe population decrease, These observations, therefore, indicated that even in the field situations, during the months of the year when there is a decline of food quality a subsequent decrease in fly numbers is likely. Further experiments were carried out to investigate the effect of food quality on survival. Three - day old flies were put in two separate cages, having sugar and water in one cage and the other cage a dish of fresh liver and water. The initial number of flies were 200 in each cage. The observations were carried out for 7 days and everyday, dead flies were removed from the cages and liver was exchanged.
Figure 11.

Relation between fecundity and percent nitrogen used as adult food at two larval densities.
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Figure 11.

Relation between fecundity and percent nitrogen used as adult food at two larval densities.
Relation between fecundity and % nitrogen used as adult food at two larval density

- 600 larvae / 800g mass.
- 300 larvae / 800 g mass.
Results

The experiment revealed that the survival percentage of liver-fed flies after 7 days was less than the percentages of sugar fed flies (fig. 12). When after a day of feeding a dish of fresh lechwe faeces was put in each cage, it was noted that female flies in liver-cage laid some eggs on faeces; whereas this was not the case with the sugar fed flies. Thus, this experiment also revealed that, the adult life span did not depend on protein or on the quality of food, probably, this because, a liver meal, enough to induce egg development reduces the life span of the flies, presumably food reserves are used for purposes other than staying alive. Carbohydrates seemed to promote the longevity or life span of individual flies of both sexes.

Discussion

It seems that all the experiments carried out on the food requirements of the fly reveal that inadequate food during either larval or adult life of the female can reduce the number of eggs produced in the ovarian cycle. The smallest flies that developed from larvae reared on favourable faeces produced up to 20% more eggs than similar flies given the same adult food but reared from unfavourable faeces. In the laboratory the number of eggs produced by female fly can be reduced by limiting the intake of protein-rich food or by feeding on protein
Figure 12.

Compared results on the survival of flies under two feeds.
COMPARED RESULTS ON THE SURVIVAL OF FLIES UNDER TWO FEEDS
(P 0.002 STUDENTS-T-TEST)

- - Liver fed
- - Liver starved

NUMBER OF SURVIVING FLIES

NUMBER OF OBSERVATIONS IN DAYS

0 1 2 3 4 5 6 7
poor food. For example, flies fed on faeces produced much less than half the eggs that similar flies produced when fed on liver. The results revealed that proteinaceous food stuffs did not promote survival as much as the carbohydrates did, but that the ultimate size of the flies, their weights and also fertility of the female flies depended on the quality of food they had been reared on. Where as food quality and quantity (quantity refers to observations on larval density) seemed to have similar effects on mortalities. The effects of quality differences on subsequent stages to the larval stage seemed to persist more strongly. Presumably the natural lasting effects of the differences in food quality lie in the nature of the reserves involved. Recent works done on the biochemistry of the metamorphosis of the fly *Lucilia cuprina* (D'costa and Birt, 1966; Crompton and Birt, 1967; Birt and Christian, 1969); showed that during the pupal stage, fat metabolism was the only source of energy used. Slight changes in the carbohydrates and the stability of the reserves of nitrogen compounds present, suggest a mechanism to account for the relative persistence of quality effects beyond the larval stages. Therefore, whereas only larval mortality is affected by numbers of larvae used on the quantity of food, food quality showed marked effects on larval and pupal survival and also on the fecundity and fertility of the emerging adults.
5. DISCUSSION

1. **KOBUS LECHÉ KAFUENSIS AS A HABITAT FOR M. TEMPESTATUM.**

Reports by West and Peters (1929); Lewis, (1954) on *M. tempestatum* showed that the fly could also be associated with cattle. It has been mentioned in this dissertation that at one time lechwe flies were reared from cow-dung collected from Lochnivar (Howard, personal communication). But the actual behaviour of flies on cattle has yet to be investigated. For the time being an attempt was made in this study to demonstrate the possible factors contributing to the association of the fly with the lechwe.

It was observed that the distribution of the lechwe fly on the antelope was concentrated more around the eyes, mouths, noses, ears and also around the anal opening especially if and when there were any exposed faecal matters. Also the flies were seen to congregate themselves at any exposed wound. When this behaviour was closely observed on a freshly killed lechwe, it was seen that the flies were feeding on the exudations from all these regions. Also they were seen feeding vigorously at the blood from the exposed wound.

So, in this connection the association would be that the flies obtain food and moisture directly from the lechwe.
2. M. TEMPESTATUM AND LECHWE FAECES.

Laurence, B.R. (1954) reported that it had been recorded for over 200 years that certain flies may be bred from the dung of mammals, and that there were some old records purporting to these reports, for example, Reamur, (1740) described the life history of flies in cow-dung, giving details of the egg, larva and the duration of the development. He reported that some flies which as larvae feed on the dung may use the dung also as food in the adult forms. Some other flies may frequent the dung as adults only for the purpose of oviposition. Portshinsky, (1885, 1910) described as members of a complete ecological community the inhabitants of the dung. He distinguished between larvae which fed on dung and those which fed on coprophagous members of the community. He also considered that the competition within the dung was higher than the competition between members of the carrion community, showing that viviparous flies were more successful in a rapidly ageing habitat than were the oviparous flies.

In this study an attempt was made to demonstrate the use of lechwe faeces by M. tempestatum as a habitat. M. tempestatum is oviparous and lays its eggs on lechwe faeces. The larvae hatch out on the faeces and the whole larval stage is accomplished within faeces, so that larvae depend on faeces for food.
It was also demonstrated that adult flies use faeces as food. Lechwe faeces are suitable for oviposition when they are still fresh. When the lechwe defaecates the faeces are liquid, but the surface soon dries and a crust is formed. This crust blocks the odour of the faeces which attract adult flies. As the faeces age fairly rapidly, and soon become unattractive to most ovipositing flies, the flies must be mobile and capable of following the herds of lechwe from place to place to obtain fresh faeces. Thus: the two main contributing factors towards relationship between lechwe and *M. tempes-tatum* are:

(a) To obtain food and moisture directly from the antelopes.

(b) To maintain contact with sources of their major requirements (freshly dropped faeces).

3. NON-BITING FLIES AND DISEASES.

Patton (1926) reported the haematophagous habits of the genus *Musca*. He reported that the species which were wild were only seen in the open on large animals feeding on blood discharged from cuts, bites of other biting flies and wounds also on eyes, nostrils etc., which would be diseased. He observed this behaviour in *Musca pattoni* Austen of which both sexes were seen greedily feeding on blood on the sores on the bellies
of calves. Bearing in mind the nature of the food for *Musca* species and remembering that they are intermittent feeders, flying about from one large animal to the other, it is easy to understand that they would be considered as potential carriers of many kinds of pathogenic organisms. It may be that some of the facultative haematophagous species of this genus in Africa are mechanical carriers of trypanosomes in those parts where *Glossina* is absent and other biting flies are rare. (Patton, 1926). Some members of this genus have been connected with transmission of the causative agents of many cases of enteric bacterial infections of all types than are the biting flies. Their feeding and breeding habits make them vectors for many diseases such as poliomyelitis, dysentery, diarrhoea, cholera, infective-conjunctivitis. York and baker, (1957) cited the transmission of a virus which cause "Miyagawanella bovis" which produces symptomatic disease and lack of weight in young animals especially cattle. *Musca* species have been connected with the transmission of a bacillus causing bovine tuberculosis, (Watson, 1965). Rankin and McDirmid, (1969), reported that the disease can be transmitted from wild animals to domestic animals such as cattle and vice-versa.

Zumpt, (1965) published, a comprehensive monograph on Myiasis in man and large mammals in Africa caused by most of the larvae of *Musca* species. Watson, (1965) pointed out that Musca species can even spread leishmaniasis and
trypanosomiasis by licking the blood drops from interrupted vector feeds, (for example, Tabanids).

4. A NOTE ON MUSCA TEMPESTATUM IN CONNECTION WITH DISEASES. 

M. tempestatum has so far been associated with the lechwe antelopes and also with Zebra, (Howard, G. personal communication). It has also been associated with cattle and man who is invariably associated with cattle.

It has been observed during this study that the adult lechwe fly depends on the antelopes for food and moisture which is obtained either directly from them or from their droppings. It has also been established that the adult ovipositing female flies lay their eggs on the fresh faeces, the hatched larvae depend on faeces for food, as a result of this behaviour the fly is always found in close associations with the antelopes feeding on either fresh wounds or the exudations of this and that antelope, in so doing the fly is enabled to transmit pathogens from one diseased animal to the other animal, just like some of the Musca species such as M. domestica and M. pattoni. A few diseases will be cited here for which M. tempestatum would in part be suspected of transmitting. Brucelloses in man and domestic animals are caused by Brucella species. The infection in man of caprine origin is referred to as Malta fever and that of bovine origin as undulant fever. In cattle the disease is known as contagious abortion, in ewes as bovine abortion and in rams as infectious infertility. The Brucella
species are said to be transmitted in part by *Musca* species such as *M. domestica*, (Wellman, 1952). McCaughey, (1969) reported that this disease could also be spread from wild animals to herds of cattle and flocks of sheep by flies that are always in close associations with both wild and domestic mammals. Satchel and Harrison, (1953) studied the transmission of Yaws and pointed out that the spirochaetes of the disease are transmitted by the wound-feeding flies such as *M. domestica* and other small flies. Diptera are the only insects that regularly infest the bodies of vertebrates; this type of infestation is termed myiasis. Myiasis can be either facultative or obligatory. Several species of Muscidae exhibit facultative myiasis. The subject of myiasis is comprehensively reviewed in a monograph by Zumpt, F.,(1965). In his work only species from the Old World were considered, and 63 were listed as causing facultative myiasis or pseudo-myiasis. Among the *Muscidae*, the genus *Musca* is listed as causing facultative myiasis. He pointed out that musci-form flies oviposit or larviposit on vertebrate faeces, occasionally even as faeces leave the anus. Eggs hatch out around the anus in the remaining faecal matters; the larvae then migrate inside the rectum causing rectal myiasis; *Musca domestica* has been recorded as causing rectal myiasis.
Though such habits of ovipositing round the anus have not yet been observed in M. tempestatum, the habit of concentrating round the anal opening especially if and when there are any faecal matters have been observed, so the possibilities of M. tempestatum causing rectal myiasis can not be ruled out.

Foot-and-mouth disease, which is prevalent in Zambia is a virus infection disease. The viruses are passed out in faeces, saliva and nasal excretions. Hugé-Jones, M.E. (1967) reported that, many possible means of spread of the virus of foot and mouth disease have been suggested. It is believed that the virus can be carried by any of the following agents: infected or incubating animals, bones, or meat or milk from such animals, by fomites such as birds, insects, rats, vehicles or people and by wind. It has been established during this study that adults of M. tempestatum feed on faeces as well as on exudations from the mouth, nose and fresh wounds. In so doing, it would be suggested that the flies could take in the viruses and introduce them to the next susceptible animal they feed on, but the authenticity of this suggestion should be investigated in details.

The spread of Ephemeral fever, referred to as three day disease is prevalent in Zambia. Murray, M.D. (1970) suggested that active transportation of the virus is done by wind for major dispersal then insects for local spread.
In summary, Patton's reports, (1936) showed that *M. tempe-
statum* is considered a species of medical and veterinary impor-
tance, which means that even though its early stages were not
yet known the feeding and breeding habits of the adult fly
enable it to be a potential vector of disease.

5. **SUGGESTED AREAS WHERE RESEARCH IS NEEDED.**

The diverse findings shown in this study indicate a
need for systematic studies of *M. tempestatum* for example on:-

1. Its position in connection with cattle as it had
   already been reared in the cow-dung collected
   from Lochnivar National Park.

2. Its capabilities of transmitting pathogens
   among the lechwe and between lechwe and cattle.

3. The effect of both faeces and environmental
temperature on the fly should be closely
investigated, so as to be able to establish
whether the fly is affected by any adverse
conditions offered by the temperature. In
doing so we can trace out the relationship
between the incidence of fly populations,
the temperature and the epidemics of certain
infectious diseases such as tuberculosis which
affects both antelopes and cattle. Also the
relation of weather and fly, to the spread of
foot and mouth disease.
4. To continue with the studies on its distribution in the country, its associations with any other mammals and to try to assign whether in the areas where the fly is found, there are any incidences of the same type of diseases, so as to establish its authenticity as a potential vector of infectious diseases.
APPENDIX 1. Monthly determination of nitrogen for data collected between May 12th and December 12th

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<tr>
<th>Date data collected</th>
<th>% Nitrogen Content of replicates (dry wt.)</th>
<th>Size of replicates</th>
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<tr>
<td>August</td>
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<td>September</td>
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<tr>
<td>October</td>
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</tr>
<tr>
<td>November</td>
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</tr>
<tr>
<td>Dec.</td>
<td>4.5, 3.5, 4, 4.75.</td>
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APPENDIX 2. Monthly determinations of Moisture Content for data collected between 12th May and 12th Dec.

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<tr>
<td>May</td>
<td>67, 65, 65, 62.</td>
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<tr>
<td>June</td>
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<td>July</td>
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<td>October</td>
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<tr>
<td>November</td>
<td>69, 70, 70, 68, 72, 74, 68, 76, 71, 72.5.</td>
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<tr>
<td>December</td>
<td>68, 70, 71, 70, 72, 68.</td>
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Treatment I

APPENDIX 3. The survival of flies fed on liver and water for 7 days

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<th>No. of replicates</th>
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APPENDIX 4. The survival of flies fed on liver, sugar and water for 7 days.

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Total survival
Survival % 77
Treatment 3.

APPENDIX 5. The survival of flies fed on liver, sugar and water for 7 days.

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Total survival
Survival % 75.5
Treatment 4.

APPENDIX 6. The survival of flies fed on faeces and water for 7 days.

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