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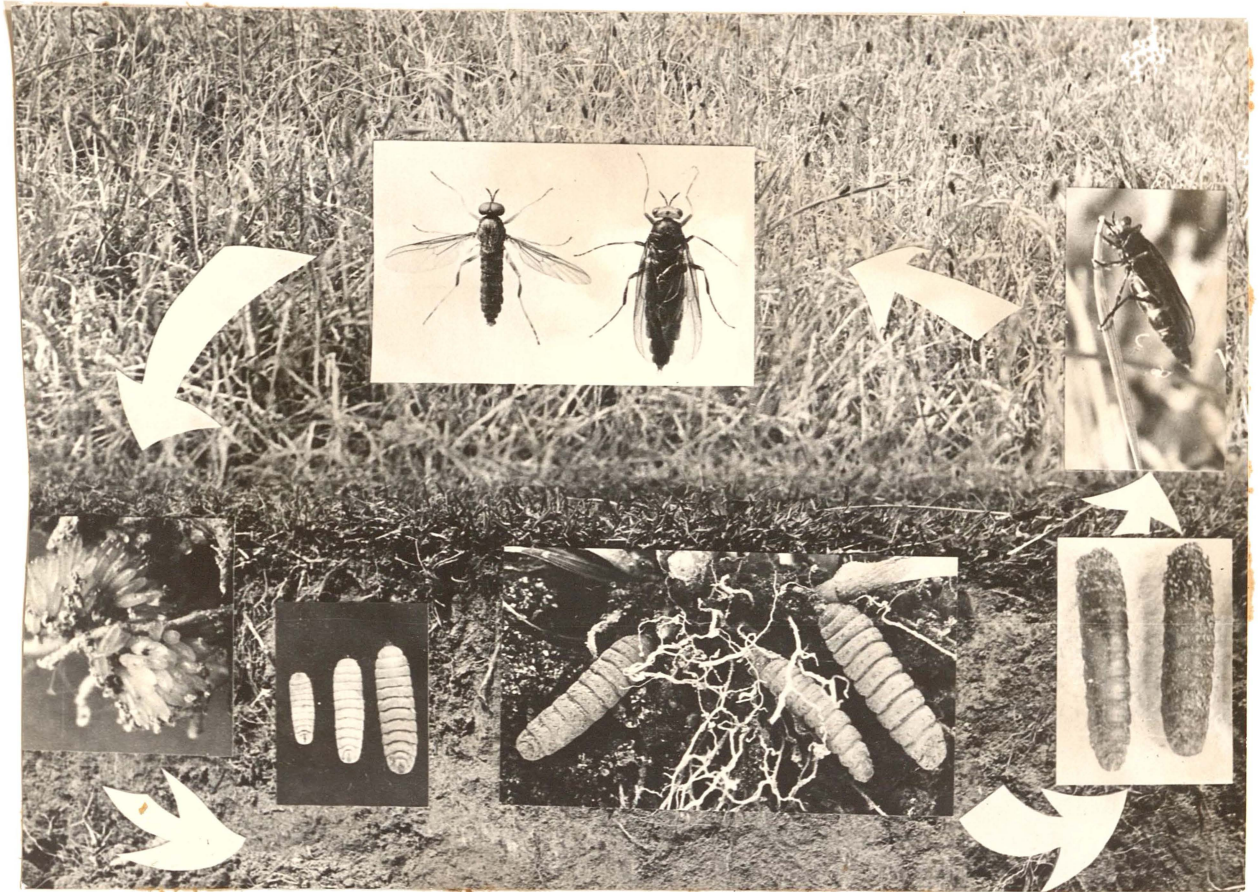
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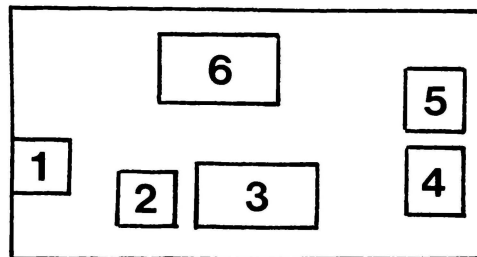
SOME OBSERVATIONS ON THE POPULATION DYNAMICS OF THE  
AUSTRALIAN SOLDIER FLY INOPUS RUBRICEPS MACQUART  
(DIPTERA : STRATIOMYIDAE)

Colin Richard Wilcocks

A thesis presented to the University of Waikato  
for the degree of Doctor of Philosophy, August 1973.



The life cycle of Inopus rubriceps (Macquart) NOT TO SCALE



1. An egg cluster
2. The larval stage
3. Larvae feeding
4. The pupal stage
5. A newly emerged female adult
6. Female adult on right, male adult on left.

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## PREFACE

Inopus rubriceps (Macquart) is an indigenous Australian stratiomyid, whose subterranean larval stage has been recorded as a pest of sugar cane and pastures in Queensland for some time (Saunders 1963 and Hitchcock 1970).

I. rubriceps has been known in New Zealand since the early 1940's (Muggeridge 1944), but it was not until the late 1960's that the N.Z. Department of Agriculture, under considerable pressure from the farming community, finally decided to initiate research work on this insect. The present writer was employed by the Department to commence work on the development of a pest management programme to be used in a pasture agro-ecosystem.

At that time, there was an almost complete lack of knowledge about any aspect of the insect's biology and ecology under N.Z. pasture conditions. The above, together with the failure to find a suitable chemical control from several insecticidal screening trials (Hewitt 1964) precluded, at least initially, any worthwhile work on direct control methods. Clark et al (1967) have argued that in those cases where no prior hypotheses can be made about an insect, the development of life tables provides much of the background biological and ecological information needed to put the development of control measures on a rational basis. Thus, the main aim of this work was to test the feasibility of developing life tables for the Australian soldier fly, under pasture conditions.

In the text of this thesis the following applies:

- (1) The term soldier fly refers to the Australian soldier fly Inopus rubriceps.
- (2) The mean  $\pm$  the 95% confidence limits are always given, unless otherwise stated.
- (3) The probability level of any test of significance has been indicated as:

*	significant	at	0.05
**	"	"	0.01
***	"	"	0.001

- (4) Ruakura refers to the Ruakura Agricultural Research Centre, Hamilton.

## THE SOLDIER FLY PROBLEM

Inopus rubriceps (Macquart), although indigenous to Australia (Irwin-Smith 1920), where it appears to be limited to the tablelands bordering the eastern coast (Osborn and Forteach 1972), also occurs in the North Island of New Zealand and in the San Francisco and San Mateo counties of California, U.S.A. (Campbell and Koehler 1971).

This insect was first recorded in the Opotiki district of New Zealand by Muggeridge (1944). Since then it has become well established in the Bay of Plenty, Waikato and South Auckland regions (Timlin 1969). According to Given (1970) an isolated infestation has recently been recorded close to Gisborne in the Poverty Bay region and Pert (Farmer, Karaka North Road, Karaka, 1972 pers. comm.) reported the insect at Massey, north of Auckland. Recently the insect has been found in the environs of Whangarei, in Northland (Hart, Farm Advisory Officer, Whangarei, 1973 pers. comm.).

The recognition of this insect as a pest, and the mainly qualitative assessment of its status are described below.

Methods of causing damage

Irwin-Smith (1920) was the first to report that the larvae of I. rubriceps fed on the sap of living plants by attacking their root systems. In a later paper (1921b) she described the larval mouth parts in detail and observed that they were well adapted for obtaining nourishment by suction rather than by biting and chewing.

Many workers (Mungomery 1926, Marryatt 1948, Dumbleton 1949, Saunders 1963, Hewitt 1969, and Timlin 1969) have described finding larvae attached by their head capsules to large roots, and that affected plants showed pitted roots where the larvae had fed.

Hitchcock (1970) described how the larva's two strong jaws can excavate cavities in the roots of maize plants, into which the larva inserts its head and sucks the sap. He also observed "second instar" larvae break off root hairs with their jaws and reported that in the laboratory, heavily excavated maize roots usually died distally from the damage.

Wilson (1958) found that the injection of a water extract of macerated bodies of soldier fly larvae adversely affected the germination and growth of sugar cane setts\* during a period of four weeks. Thus, Moller (1965) thought it probable that as well as causing mechanical root damage and removing sap from the plant, a growth inhibiting toxin was injected into the roots from the salivary glands during the feeding process.

#### Plants attacked

Attacks on sugar cane and pasture plants in Australia are well documented (Jarvis 1925, Mungomery 1926, Bell 1934, Moller 1961, Sturgess 1962, Mann 1962, Saunders 1963, Moller 1965, Wilson 1969, 1970, and Hitchcock 1970, 1971), as are attacks on a wide range of horticultural and fodder crops and pasture in New Zealand (Muggeridge 1944, Marryatt 1948, Dumbleton 1949, Hewitt 1964, 1969, and Timlin 1969).

Hewitt (1969) commented that there appeared to be little limit to the variety of host plants. He stated "Populations were found under permanent to semi-permanent vegetative cover ranging from that found in ornamental plants through to light scrub, weeds in waste areas

\* Sett: a stalk with two or three buds used to propagate sugar cane vegetatively.

and under pasture... Most, if not all, grasses are attacked and damaged to varying degrees".

#### Description of damage

Moller (1965) gave a good description of soldier fly damage to ratooning\* sugar. "Slow and variable ratooning... is the most obvious characteristic of affected ratoon fields. Where large populations of soldier fly larvae are involved the entire stool<sup>+</sup> may be killed, but it is more common for stool development to be retarded. Stalk numbers in length and thickness are reduced and stools tend to take on a somewhat grassy appearance".

Hewitt (1969) has given the most detailed account to date of the type and extent of damage to pasture and cereal crops. He commented that "Maize, barley, oat and millet crops very rapidly display damage from Australian soldier fly. Typical symptoms are yellowing, a scorched appearance of the leaf tips and a general withering of the whole plant. Many plants are killed at the germinating stage, while others collapse and die two to three weeks after emergence. Surviving plants remain stunted in growth, and yellow in colour, for many weeks. Single larvae appear to be able to cause the death of young plants by puncturing the stem just below ground level".

Regarding pasture damage, Hewitt, corroborated Saunders' (1963) observation that although there can be a rapid decline in vigour resulting in browning off and death of the sward, generally the damage to permanent pastures is of an insidious nature, indicated by the loss of better grasses such as ryegrass (Lolium perenne) from the sward, patchiness, clover dominance and weed invasion, all occurring

\* Ratooning: the formation of stools from the below ground level buds on the stalks left after harvesting.

+ Stool: an association of stalks which have developed from below ground level buds on a primary shoot of a sett.

over a number of years. It can take up to four years or more for pasture production to be noticeably reduced by soldier fly attack (Marryatt 1948).

While it is obvious that infestations result in pasture imbalance, there is little evidence which suggests there is selective feeding. Saunders (1963) commented that on the Atherton tableland kikuyu pastures appeared to be preferred by the insect, however, all grasses grown in the area are attacked to varying degrees. According to Hewitt (1969) some pasture species are probably able to withstand attack because of their ability to regenerate root systems.

Bloat and scouring are often a side effect due to soldier fly infestations, owing to the induced white clover dominance (Hewitt 1969).

#### Pest status

No accurate quantitative assessment relating number of larvae to damage caused has been made in monetary terms. Even in the case of sugar cane where figures are quoted for losses due to soldier fly attack (Wilson 1969, 1970, and Hitchcock 1971) no information has been given relating loss to number of larvae present. However, Sturgess (1962) has shown that increasing numbers of soldier fly larvae per sett caused a corresponding reduction in number of ratoon shoots. The qualitative estimation of damage due to soldier fly attack was readily recognised in horticulture and fodder crops, for as Hewitt (1969) commented "Cereal plants such as maize and barley show spectacular effects from larval damage". But, because of the more insidious nature of the insect damage to pasture, the insect was not readily recognised as a pasture pest. In New Zealand the pest status of soldier fly has increased considerably since the mid 1940's, for two main reasons. First, the fact that the insect has spread

during the last 30 years, from the Opotiki district throughout the Bay of Plenty, Waikato and South Auckland regions, and secondly, its recognition as an important pasture pest.

As I. rubriceps is a pest in three quite different agricultural systems, its pest status is considered under the following headings.

(1) Sugar cane in Australia

Jarvis (1925) first reported I. rubriceps as a pest to sugar cane in Queensland, and Mungomery (1926) confirmed this report with a description of larval damage to sugar cane roots. Dumbleton (1949) mentioned that, in Queensland the insect was regarded as only a minor pest of sugar cane, and this still seemed to be the case ten years later (Wilson 1958). However, this situation, or the recognition of I. rubriceps importance appeared to change relatively rapidly. For Moller (1961), Sturgess (1962) and Mann (1962) all stated that the insect was a major factor responsible for poor ratooning in cane. This view was supported by Wilson (1969, 1970), and Hitchcock (1971) several years later. Hitchcock (1970) stated that the pest status of soldier fly had changed from that of minor importance in the 1920's and 1930's to one of major importance in the 1950's and 1960's. He discussed how some changes in management practices, such as reduced cultivation and increased irrigation, could have been partially responsible.

(2) Fodder and horticultural crops in New Zealand

Both Muggerridge (1944) and Marryatt (1948) stated that soldier fly was a serious pest of first maize crops after grass in the Opotiki district. Marryatt (1948) estimated a 25% loss from such crops. Dumbleton (1949) presented evidence indicating that stunting in autumn sown oats was attributable to soldier fly larvae. Even light to moderate infestations can apparently reduce cereal

grain yields to such an extent that the farming enterprise becomes uneconomic (Hewitt 1969).

From reports to date (Muggeridge 1944, Marryatt 1948, Dumbleton 1949, Hewitt 1969, and Ray, Forest Research Institute, Rotorua, 1970 pers. comm.), it appears that soldier fly is only an important pest of horticultural and fodder crops during the first year when the crop is planted out of infested pasture. Following crops are generally free from infestation provided that there has been no carry over of larvae through poor grass growth control (Hewitt 1969).

### (3) Pastures

Irwin-Smith (1920) first recorded soldier fly larvae feeding on grass roots. However, she stated "... even where larvae are numerous, grass which harbours them shows no ill effects from their presence". Mungomery (1926) recorded larvae attacking bladey grass (Imperata cylindrica), paspalum (Paspalum dilatatum), and couch grass (Agropyron repens) in Queensland, Australia, but larvae were not thought to cause any serious damage to the pastures (Dumbleton 1949). However, Muggeridge (1944) observed that there seemed to be a correlation between the occurrence of high populations of larvae and pasture deterioration in the Opotiki district of New Zealand, but because deterioration took place over a number of years it was difficult to demonstrate clearly. This problem was accentuated by the larvae's high resistance to current insecticides (Marryatt 1948).

Evans (1952) recorded the larvae of I. rubriceps as a pest of lawns and pasture in New Zealand, but according to Hewitt (1964), Hoy (1961) in a D.S.I.R. report on the soldier fly problem in the Whakatane district, considered that no clear cut case had been established linking soldier fly larvae with pasture deterioration.

However, in Australia, Saunders (1963), reported that I. rubriceps larvae caused serious damage to pastures on some Atherton Tableland dairy farms during the 1961 to 1962 summer, attacking kikuyu (Pennisetum clandestinum), paspalum (Paspalum dilatatum), guinea (Panicum maximum) and molasses (Melinis minutiflora) grasses.

Apparently soldier fly have been known to occur on the Atherton Tablelands since 1925, and sporadic and intermittent damage to kikuyu grass has been recorded in the Queensland Agricultural Department records (Saunders 1963).

Hewitt (1964) reported that the deleterious influence of I. rubriceps on pasture production had been demonstrated by pot trials which showed that larvae reduced herbage yields. Both Campbell (1968), and Timlin (1969), substantiated the above. Hewitt also commented, that because there were often no obvious well-defined symptoms of this pest's depredations its presence was frequently overlooked. However, pasture damage by the Australian soldier fly has apparently had the effect of severely reducing the production of hay and silage crops, butterfat, wool and meat (Hewitt 1969). Infested farms in the Bay of Plenty region have had their hay crops reduced by up to 50%, and Hewitt (1969) mentioned how 25% and 33% drops in butterfat production had been recorded on two farms respectively over a period of three years. The economy of the soldier fly infested regions of New Zealand, in fact of the country as a whole, is very largely based on pasture production (Hewitt 1969, Cullen 1971). Thus, with increased farmer awareness of the damaging effects of this insect, its pest status, although not reliably quantified, has assumed considerable importance in the infested areas.

Within a number of years I. rubriceps could assume national

importance as a pasture pest in New Zealand. From its distribution, both within this country and overseas, there would appear to be no climatic or other environmental limitation to this insect spreading throughout much of the pasture based agricultural land of both the North Island and the upper part of the South Island.

In California, Campbell and Koehler (1971) reported I. rubricops larvae as a pest of lawns, and of the adults constituting a nuisance to home owners. However, the insect has assumed no importance as an agricultural pest there, since, at the moment, it appears to be limited to non-agricultural areas.

CONFIRMATION OF DAMAGE AND AN ASSESSMENT OF THE DAMAGING  
EFFECTS OF DIFFERENT NUMBERS OF SOLDIER FLY LARVAE

Introduction

Although several workers have shown that a certain number of larvae will stunt the growth of a variety of pasture grasses (Hewitt 1964, Campbell 1968, and Timlin 1969), no one has yet investigated the effect of different levels of infestation on grass production. The following experiment was designed to assess this effect over a short period and to confirm in general the damaging effects of the larvae on plant production.

Methods and Materials

This work was conducted on a pot basis under screen house conditions at Ruakura. The soil used was Hamilton clay loam and was assumed to be free of soldier fly larvae after being subjected to the extraction method described by Wilcocks and Oliver (1971). Plastic pots 16.5 cm in diameter and 20.3 cm deep were used. The drain holes were covered with a suitable size plastic mesh to prevent larvae escaping. Soil was added to these pots and lightly tapped to give some resemblance to normal pasture compaction. On 7 December 1970, Ariki ryegrass seedlings (Lolium perenne <sup>X hybridum c.v. Grasslands Ariki</sup>) were planted out at a rate of 10 per pot. Throughout the experiment pots were watered at frequent intervals and lightly cultivated to remove weeds and to prevent a hard surface crust developing.

On 5 January 1971 50 pots were divided into five groups of ten. Care was taken to see that as far as possible each group had the same balance between vigorously growing and not so vigorously

growing plants. The plants were then cut to a height of 2.5 cm and the pots arranged randomly in blocks of five (one from each group) on the bench in the screen house. A uniformity cut was taken on 20 January (Table 1).

The treatments, each one of which had ten replicates, were as follows:

- T.1 No larvae per pot (control)
- T.2 10 larvae per pot
- T.3 50 larvae per pot
- T.4 100 larvae per pot
- T.5 200 larvae per pot

The larvae were added to the pots between 21 and 25 January in a series of one replication from each treatment. Holes were made in the soil to a depth of about 2 cm near the grass plants and between 10 and 20 larvae were added per hole, then lightly covered up with soil. To start the experiment over a five day period the larvae were collected during the previous week and stockpiled in 10% moist sand. Middle sized larvae were used (approximately 10 months old) as it was wished to maintain a stable larval population during the course of the experiment from January to August. All the larvae were given a live test\* before being added to the pots. The grass was cut four times during the experiment (10 February, 10 March, 26 April, and 5 July) and the dry matter production for each pot was assessed at each cutting. A basal dressing of plant nutrients (Middleton and Toxopeus 1973) was added to the pots during the experiment.

\* Larval live test: a piece of 10cm diameter filter paper with a line drawn through the centre, was kept moist in a petri dish. Larvae were placed in a row with their head capsules resting on the line. Those that had not moved within a two hour period were classified as dead.

At the end of the experiment the number of larvae per pot was checked, and the number present during the experiment was taken as the mean of the initial and final number.

### Results

Despite the wide variation within each treatment, a definite reduction in the amount of dry matter produced corresponded with an increase in larval numbers (Fig. 1). Table 2 shows the percentage reduction in total dry matter produced by the different treatments when compared with the control. An analysis of variance showed that both T.4 and T.5 were significantly different from the control at the 5% level. Table 1 shows the summary of a series of analyses of variance carried out on each of the individual cuts.

### Discussion

The experiment has confirmed the damaging effects of soldier fly larvae and shown that, in the range of the experiment, increasing numbers cause increasing damage. The total dry matter produced by T.3 was not significantly lower than the control, but it probably represented the beginning of the reduction trend which reached significance in T.4 and T.5. The disappearance of the significant difference between T.4 and T.5 could possibly have been due to a combination of the seasonal effect on grass growth and a nitrogen deficiency appearing in the pots. Some yellowing of the leaves was noticed in some pots from all the treatments at the final cut (5 July 1971).

As this experiment was conducted on a pot scale and over a short time period, any conclusions drawn from the results are only indicative of the field situation. However, it is interesting to

FIGURE 1

The relationship between the total amount of dry matter produced during the experiment (Y) and the mean number of larvae present (X).

The regression equation was  $Y = 3.0959 - 0.0083 X$

$b = - 0.0083$  \*\*\*

$r = - 0.4832$  \*\*

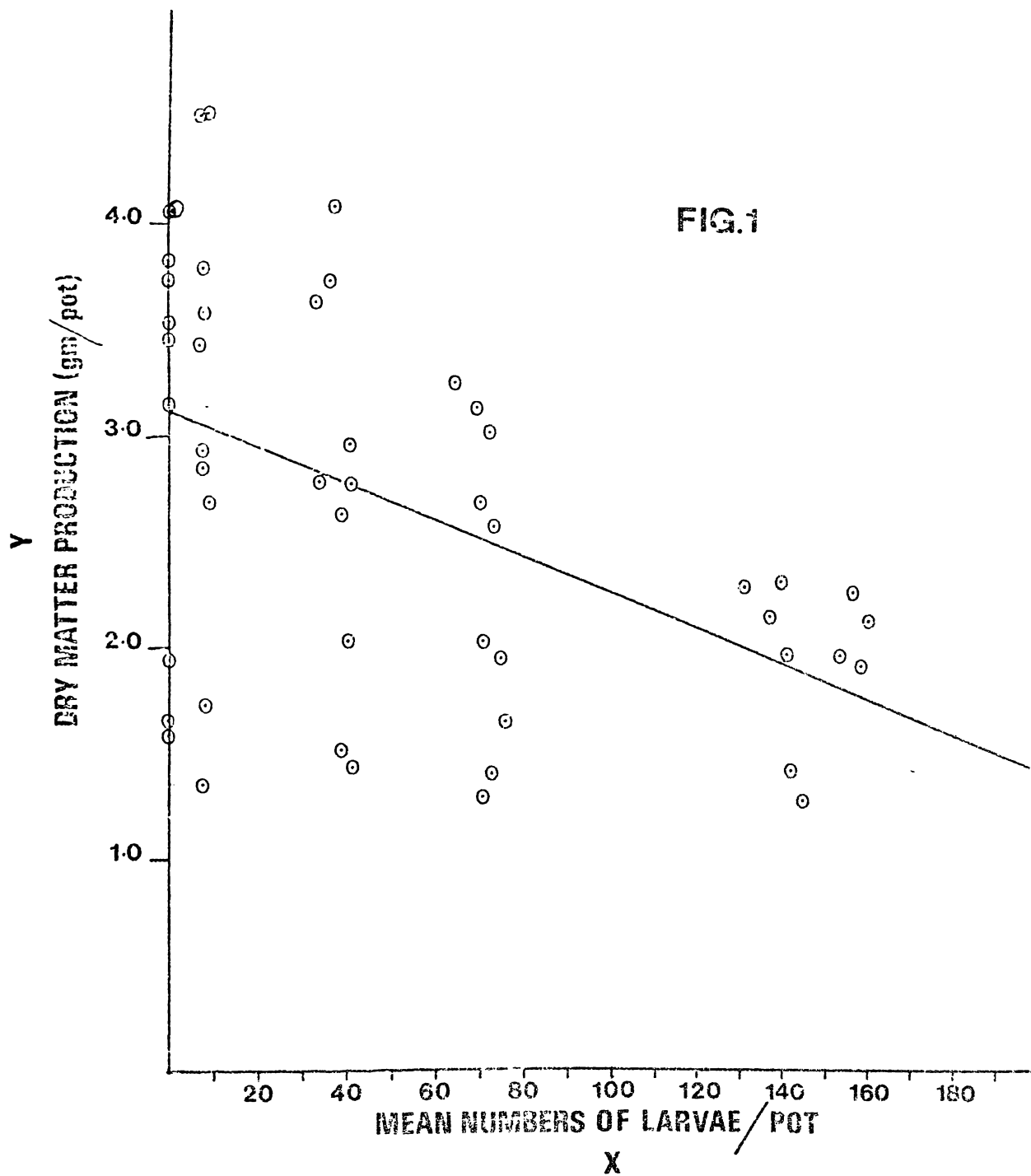


FIG.1

TABLE 1: A summary of analyses of variance carried out on each of the individual cuts.

Cutting dates	F test	L.S.D. test
20.1.71	Not significant at the 5% level	No significant difference at the 5% level between any two treatment means.
10.2.71	"	"
10.3.71	"	T5 significantly different from T1 at the 5% level.
26.4.71	Significant at the 1% level	T4 and T5 significantly different from T1, and T5 significantly different from T4 at the 5% level. T5 significantly different from T1 at the 0.1% level.
5.7.71	Significant at the 5% level	T4 and T5 significantly different from T1 at the 5% level.

TABLE 2: Percentage reduction in total dry matter produced from treatments T2 - T5 when compared with the control.

Treatment	% Reduction
T1	0.0
T2	-1.26
T3	10.97
T4	25.39
T5	35.94

consider the mean number of larvae per pot for each treatment on a number per square metre basis. These are as follows:

T.2 366/m<sup>2</sup>

T.3 1765/m<sup>2</sup>

T.4 3326/m<sup>2</sup>

T.5 6824/m<sup>2</sup>

It is not at all uncommon to find larval populations between 3000 to 8000/m<sup>2</sup> in the field, and populations between 12,000 and 15,000/m<sup>2</sup> have been recorded by the author. From the results of this experiment and field observations, the larval level at which damage begins to become noticeable is probably between 2,000 and 3,000/m<sup>2</sup>. Just how long pastures will tolerate larval levels of this range, before reaching the stage when it becomes economic to take some control action, is still unknown, and will undoubtedly vary greatly according to conditions of climate, soil, and pasture composition.

## THE DEVELOPMENT OF A RESEARCH PLAN FOR

I. RUBRICEPS

At this stage it is pertinent to briefly consider how an insect pest problem should be tackled in general, and specifically, to initiating a research plan for soldier fly.

Clark (1970) defines an insect pest as those injurious or nuisance species, the control of which, is felt to be necessary either for economic or social reasons. McGovran et al. (1971) give a wide range of examples of how insects can be pests, ranging from disease carrying mosquitoes to incidences of insect phobias, but from here on it is intended to restrict the discussion to those affecting agricultural plant production.

The first stage in any insect pest problem is usually the direct observation of damage, followed by identification of the insect causing it. The next step is that a decision has to be made of whether or not it is going to be a profitable operation to control the pest, and then the choice of control method has to be made.

In the majority of cases the decision as to the profitability or otherwise of a particular control method has been made on an intuitive or subjective basis. In fact, the extent to which man is prepared to tolerate the existence of a pest has never been evaluated in a strictly objective way (Ordish 1962, Clark et al. 1967). The tendency has been to exaggerate the danger of unfamiliar pests or on the other hand to regard as acceptable the damage which cannot be avoided by current control procedures. Waters (1963) states that many control actions are taken simply

because the insect is there and some damage might occur. The above situation reflects the extreme difficulties involved in making estimates of damage caused by insect pests (Strickland 1956). However, most authors agree (Waters 1962, Chant 1964, Clark et al. 1967, Rabb 1970, McGovran et al. 1971, to name a few) that it is important to assess insect damage in quantitative terms and to find out the levels of pest density which must be reached before plant production is affected significantly to make the control measure worthwhile.

It can be argued that the importance of assessing the problem in quantitative terms is very limited until some form of control method is available. Its only initial value is in deciding whether or not it is worth while developing a control method. However, it is important to realise that pest situations are usually political situations and thus, once damage has been clearly qualitatively demonstrated, it is often neither politically feasible nor logical to devote several years of research in proving in quantitative terms that there is in fact a problem. One must accept that a problem exists and start research work on developing a control method. Ideally work on the quantitative estimation of damage should be started concurrently with the work on developing the control methods.

In initiating work on the development of control methods for an insect, we have another political or socio-economic difficulty in deciding how one should attempt to tackle the problem. One can arbitrarily define two types of control methods:

- (a) completely dependent upon insecticides
- (b) making the minimal use of, or not using, insecticides.

There is a greater awareness now that pest control is not entirely a matter of controlling insect numbers (Cole 1966). The method adopted is important firstly, for making pest control as efficient as possible, and secondly for preserving a suitable environment for man to live in (Hurtig 1964 and Smith 1966). There are many disadvantages of a total reliance on insecticidal control. Smith and Bosch (1967) summarise these difficulties as follows:

"(1) Often the target pest species has become tolerant of the pesticides and no longer can be controlled economically with chemicals (pesticide resistance).

(2) The population of the target species may quickly recover from the pesticide action and for a variety of reasons, may rise to new and higher levels (pest resurgence).

(3) Often non-target insects may, following the pesticide treatment, increase in numbers to damaging levels (secondary pest outbreaks).

(4) The pesticide chemical may remain in, or on the crop or in the soil, drift to other nearby crop areas, flow into streams and drainages, and thereby create a hazard to man or his animals or produce additional side effects (residue problems).

(5) The pesticide chemical may create hazards to pollinators, wild life, and other beneficial forms (hazard to non-target species).

(6) Product contamination or environmental pollution can lead <sup>to</sup>~~at~~ legal action (legal problems)."

Perhaps, in fairness to chemicals, it has probably been their abuse rather than their proper use which has led to such an outcry against them (Smith 1970). Insecticides should not be used as an

insurance against pest attack (Cole 1966 and Smith 1966), but only when it is clear that (after the pest situation has been detected) if the pest is not controlled the damage it will cause will outweigh the cost, both short, and long term, of using the insecticide. Unfortunately, the information for making the above kind of decision is not very often available (Smith 1966).

The most successful alternative to a complete dependence upon insecticidal control is the development of an integrated control programme. This depends upon adopting an ecological approach to solving an insect problem. It should be remembered that the proper use of insecticides depends upon a detailed knowledge of the insect's biology and ecology, as much as any other method of control (Smith 1966).

As far as an ecological approach is concerned, there are two main methods of attack in developing control methods:

(1) An ecological empirical approach which examines all possible ways the agro-ecosystem can be economically modified to exploit some inherent weakness in the life history or ecology of the pest.

(2) An attempt to build a mathematical model describing the pest situation. This approach involves studying the population dynamics of the various stages in the life cycle of the pest, and relating the survival of these various stages to the survival of the pest population as a whole (or generation survival). It has been found from work done to date on several different pests that one or maybe two stages in the life cycle are critical, and their survival or changes in survival are mainly responsible for the changes in the population survival as a whole (Watt 1963, Morris 1969).

Once these key stages have been isolated, then a detailed study can be made of the factors that influence their survival (Clark et al. 1967). Thus, a model can be developed that will enable the projection of pest numbers into the future and will indicate the importance, to some degree, of already existing controlling factors. Ultimately, if the above approach is extended to a detailed study of density dependent relationships in the pest's life cycle, stabilising factors should be able to be identified and these together with the above, should allow realistic modelling of the insect pest population and thus, enable the testing by computer simulation of the effects of different management practices (Harcourt 1969).

The above two approaches overlap in many ways, but represent the two main lines of thought in developing sound pest management at the present time. The first method has been the most successful so far and incorporates both intuitive and mathematically based ideas. It is in fact the way that most successful integrated control programmes have been developed. It incorporates a thorough study of the biology and ecology of the pest as well as its target, but tends to restrict quantitative study to certain aspects of the pest situation. These particular aspects are usually chosen on the basis of a qualitative study of the whole situation, bearing in mind how much the agro-ecosystem can be altered while still serving its original function. The second approach is a more comprehensive one, and according to Clark et al (1967) "... it offers the prospect of providing the soundest possible basis for pest management and of yielding relative facts and ideas which are likely to be missed by a quasi intuitive

approach."

Concerning the development of a research programme aimed at developing control measures for soldier fly, the almost complete lack of information about any aspect of the insect's biology and ecology under New Zealand pasture conditions precluded, at least initially, any worthwhile work on direct control methods. The control measures which were available at the beginning of this research work were reviewed by Wilcocks (1971). At that time chemical control appeared to be too expensive for use under pasture conditions (Dumblaton 1949, saunders 1963, and Hewitt 1964, 1969), although now, one or two systemic insecticides have shown some promise in a recent screening trial (Dixon 1972 pers. comm.). The surface cultivation method proposed by Hewitt (1969) appeared to offer the most satisfactory form of control at that time and work carried out by Wilcocks and Hewitt (1971), and later by Dixon (1972 pers. comm.) substantiated its effectiveness in reducing larval numbers. However, this method was considered far from ideal because of the high cost involved. Also, it was only possible to evaluate its effectiveness in quantitative terms after research work on the life history and extraction procedures for the different stages had been started.

Thus, it was decided to carry out a comprehensive age-specific study, on a short term basis at least, to record and analyse the ecological events in the life system of the insect, and to detect critical age intervals and key influences that deserved detailed study (Clark et al. 1967).

The above programme was adopted so that the life table approach could be evaluated and at the same time gain information

on some of these aspects of the insect outlined in Phase I and Phase II of Clark's (1970) life systems approach to an insect pest problem.

THE LIFE HISTORY OF I. RUBRICEPS  
UNDER NEW ZEALAND CONDITIONS

Introduction

Morris (1955) commented that the nature of the life history and location of each stage of an insect often decided the feasibility of a particular sampling programme. As very little was known about the life history of I. rubriceps under New Zealand conditions, work was commenced on this aspect of the insect's biology, orientated towards developing a suitable sampling programme for an intensive population study.

The Adult Stage

1. Description

Hardy (1920a, 1920b, 1924), James (1960), and Nagatomi and Yukawa (1968) <sup>have given</sup> ~~gave~~ detailed descriptions of the adult stage. The following is a precis of a description given by Campbell and Koehler (1971).

Both the male and female are black except for the legs of the male, which are yellowish and the legs and head of the female which are reddish. The eyes of the male are contiguous and occupy most of the head, whilst they are widely separated in the female. In both sexes the antennae are simple, and shorter than the head, the wings are smoky with variable venation, the abdomen tapers from thorax to cauda and the mouthparts are vestigial. Mean total body length of 20 males was  $6.06 \pm 0.026$  mm; and of 20 females  $8.44 \pm 1.41$  mm.

Adults collected in the Hamilton district of New Zealand have been identified as Inopus rubriceps (Macquart) by Professor M.T. James of Washington State University, U.S.A.

## 2. Longevity

Irwin-Smith (1920) gave the length of adult life as between 3 and 10 days, and Wilson (1969) gave it as between  $\frac{1}{3}$  and 5 days. Both reports were based on work carried out under uncontrolled laboratory conditions in Australia. Campbell and Koehler (1971) recorded that, in the U.S.A., for adults kept at 20°C, females lived an average of 4.8 days (range 0-10), and males lived an average of 8.3 days (range 0-16). At a higher temperature of 25°C, females had an average life of only 2.8 days (range 0-5).

Adults reared from pupae, were maintained in moist individual containers at ambient field temperatures at Ruakura during the March/April period of 1970. (Mean maximum  $22 \pm 1.3^{\circ}\text{C}$ , mean minimum  $10.8 \pm 1^{\circ}\text{C}$ ). Females had an average life of 4.4 days (range 1-7), and males had an average life of 6.1 days (range 1-10), N = 17 in both cases. These results are in general agreement with those of Campbell and Koehler.

## 3. Emergence Pattern

### (i) Introduction

Irwin-Smith (1920, 1921a) reported two emergence periods for the adult fly in Sydney, New South Wales, Australia, one from mid October to early December, and a second one from early April to mid May. Further north in Queensland, although adults have been reported as being present from December through to the end of July (Moller and Mungomery 1962, and Moller 1964), and that the times of emergence varied from district to district, and from year to year (Wilson 1969), there seems to be a consensus amongst workers that there is only one peak flight which is usually in May (Jarvis 1925, Mungomery 1926, Moller and Mungomery 1962, Saunders 1963, Moller 1964, 1965, and Wilson 1969, 1970). The above visual observations

were supported by Elder's (1969) quantitative data which showed only one flight period a year from April to June, with a peak in early to mid May.

Campbell and Koehler (1971) reported that on the California peninsula, U.S.A., during 1964 and 1966 only an autumn flight was observed, whilst during 1965 in addition to the normal autumn flight, a very short spring flight occurred.

In New Zealand, Marryatt (1948) and Timlin (1969, and 1970 pers. comm.) reported that in the Opotiki-Whakatane districts, February and April were the two main periods of emergence, but flies were observed in the field from early November through till May. The above reports are either based on direct field observations, or on adult flight trapping figures. The following work was designed to determine the periods of adult emergence under New Zealand pasture conditions in the South Auckland, Waikato, and Bay of Plenty districts, by measuring the number of adults emerging per unit area of ground.

#### (ii) Methods and Materials

The emerging adult population was assessed on a per square metre basis as described in the adult sampling section (see p. 76 ), at the three study sites (see p. 68 ), Hamilton (Waikato), Whakatane (Bay of Plenty), and Karaka (South Auckland).

#### (iii) Results

##### (1) Hamilton (Waikato)

There were two main periods of emergence per season (Fig. 2), one in November-December and the other from mid March to the end of April. Emergence between these two main periods was low and spasmodic. The spring and autumn emergence periods each occupied 7-8 weeks, however the latter was the larger of the two and displayed a more pronounced peak of a 1 to 2 week duration.

There was no readily discernable trend between sexes in times of emergence during any one period. Overall, males dominated the autumn emergences of 1970 and 1972, and the spring emergence of 1971, whilst females dominated the autumn of 1971. The spring of 1970 approximated to a 50:50 ratio. Females predominated in the low-level emergences which took place between the two main periods. (Table 3).

(2) Karaka (South Auckland)

This was basically similar to the Hamilton pattern (Fig. 3), although the spring emergence began almost a month earlier. Also, the spring emergence tended to be more uniform from week to week than the autumn one. Thus, for Karaka the total number of adults emerging per square metre for the spring and autumn periods was fairly similar, 133 and 151 respectively. However, 85% of the autumn emergence occurred within a two week period whereas a similar proportion of the spring emergence occupied six weeks. Overall the spring emergence was <sup>♂</sup> male dominated, whilst the autumn period was ~~♂~~ female dominated. The emergence between the two peak periods consisted almost entirely of females. (Table 4).

(3) Whakatane (Bay of Plenty)

This was essentially the same pattern as at Hamilton (Fig. 4). During the main periods of emergence there was an approximation to a 50:50 sex ratio. (Table 5).

(iv) Daily Emergence Pattern at Hamilton

Moller (1965) commented that it was not uncommon for more than one major emergence to occur in any field, and from personal observations, emergence often seemed to occur in waves. This was shown to some extent in the weekly catches during the 1971 spring at Karaka, and the spring and autumn of the 1970-71 season at Hamilton. To investigate the above more fully, the day to day

FIGURE 2

The number of adults emerging at the Hamilton site.  
The black histogram represents the number of males, and  
the outlined remainder the number of females.

FIG. 2

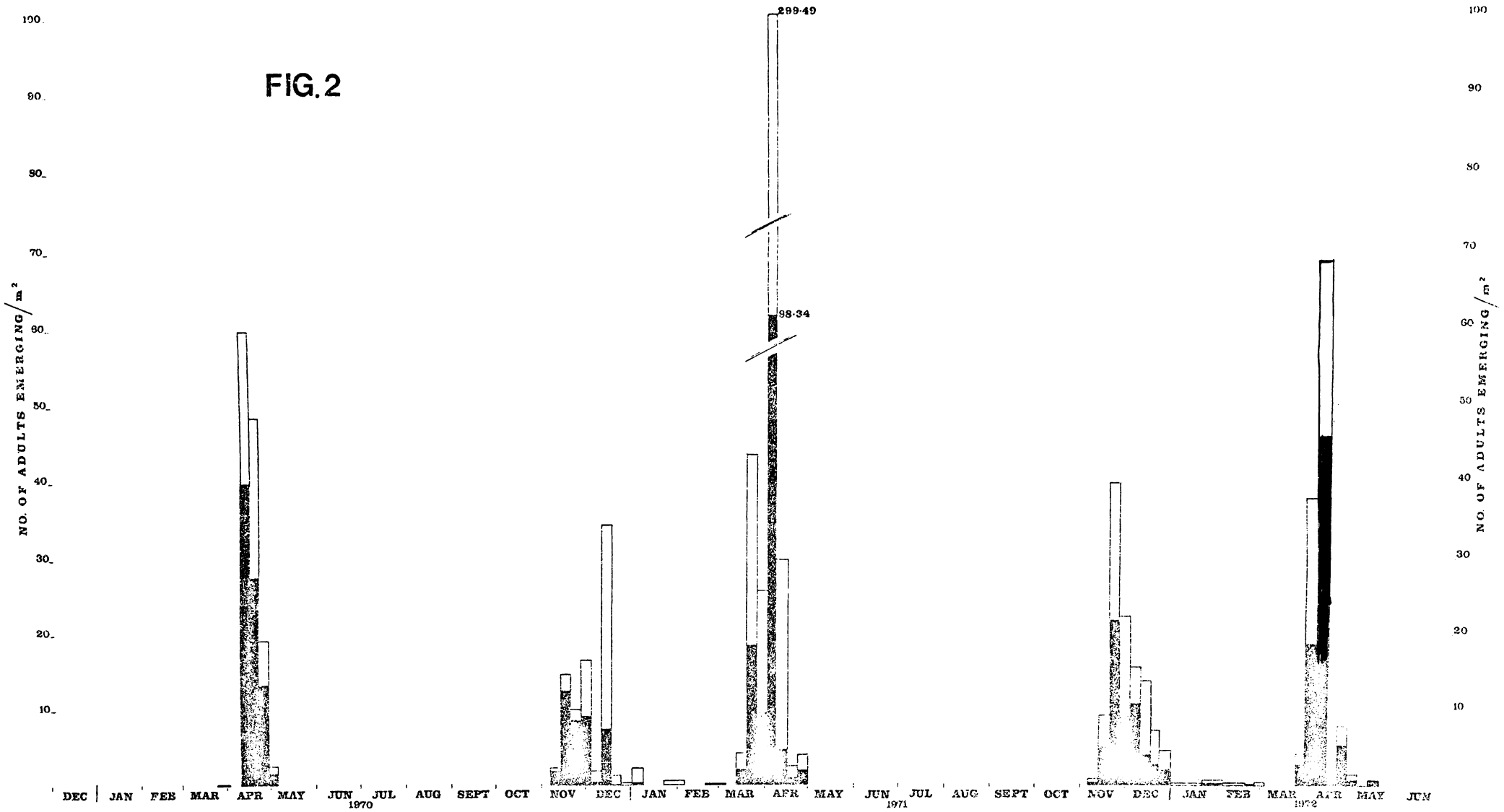


Table 3 The sex ratio of the emerging adult population at the Hamilton site. The results of a chi-square test for significant departure from a 50:50 ratio are included.

<u>Date</u>	<u>Sex ratio Male:Female</u>	<u>Significance of difference</u>
23. 3 - 2. 4.70	0 :100	
10. 4 - 16. 4.70	67 : 33	***
16. 4 - 22. 4.70	57 : 43	
22. 4 - 29. 4.70	69 : 31	*
29. 4 - 5. 5.70	60 : 40	
23. 3 - 5. 5.70	68 : 32	***
6.11 - 13.11.70	81 : 19	*
13.11 - 20.11.70	85 : 15	***
20.11 - 27.11.70	86 : 14	***
27.11 - 4.12.70	55 : 45	
4.12 - 11.12.70	23 : 77	
11.12 - 18.12.70	22 : 78	***
18.12 - 24.12.70	11 : 89	*
24.12 - 1. 1.71	0 :100	
1. 1 - 8. 1.71	13 : 87	**
6.11 - 8. 1.71	48 : 52	
22. 1 - 5. 2.71	0 :100	*
19. 2 - 5. 3.71	0 :100	
12. 3 - 19. 3.71	50 : 50	
19. 3 - 26. 3.71	42 : 58	*
26. 3 - 2. 4.71	37 : 63	**
2. 4 - 8. 4.71	33 : 67	***
8. 4 - 16. 4.71	16 : 84	***
16. 4 - 23. 4.71	39 : 61	
23. 4 - 30. 4.71	50 : 50	
12. 3 - 30. 4.71	33 : 67	***

Table 3 continued

<u>Date</u>	<u>Sex ratio</u> <u>Male:Female</u>	<u>Significance of</u> <u>difference</u>
12.11 - 19.11.71	61 : 39	
19.11 - 26.11.71	56 : 44	
26.11 - 3.12.71	59 : 41	**
3.12 - 10.12.71	69 : 31	***
10.12 - 17.12.71	29 : 71	***
17.12 - 23.12.71	38 : 62	
23.12 - 31.12.71	45 : 55	
12.11 - 31.12.71	54 : 46	*
31.12 - 21. 1.72	0 :100	
21. 1 - 4. 2.72	40 : 60	
4. 2 - 18. 2.72	0 :100	
18. 2 - 25. 2.72	0 :100	
25. 2 - 3. 3.72	0 :100	
24. 3 - 30. 3.72	67 : 33	
30. 3 - 7. 4.72	50 : 50	
7. 4 - 14. 4.72	67 : 33	***
14. 4 - 21. 4.72	48 : 52	
21. 4 - 28. 4.72	68 : 32	**
28. 4 - 5. 5.72	83 : 17	
24. 3 - 5. 5.72	61 : 39	***

FIGURE 3

The number of adults emerging at the Karaka site. The black histogram represents the number of males, and the outlined remainder the number of females.

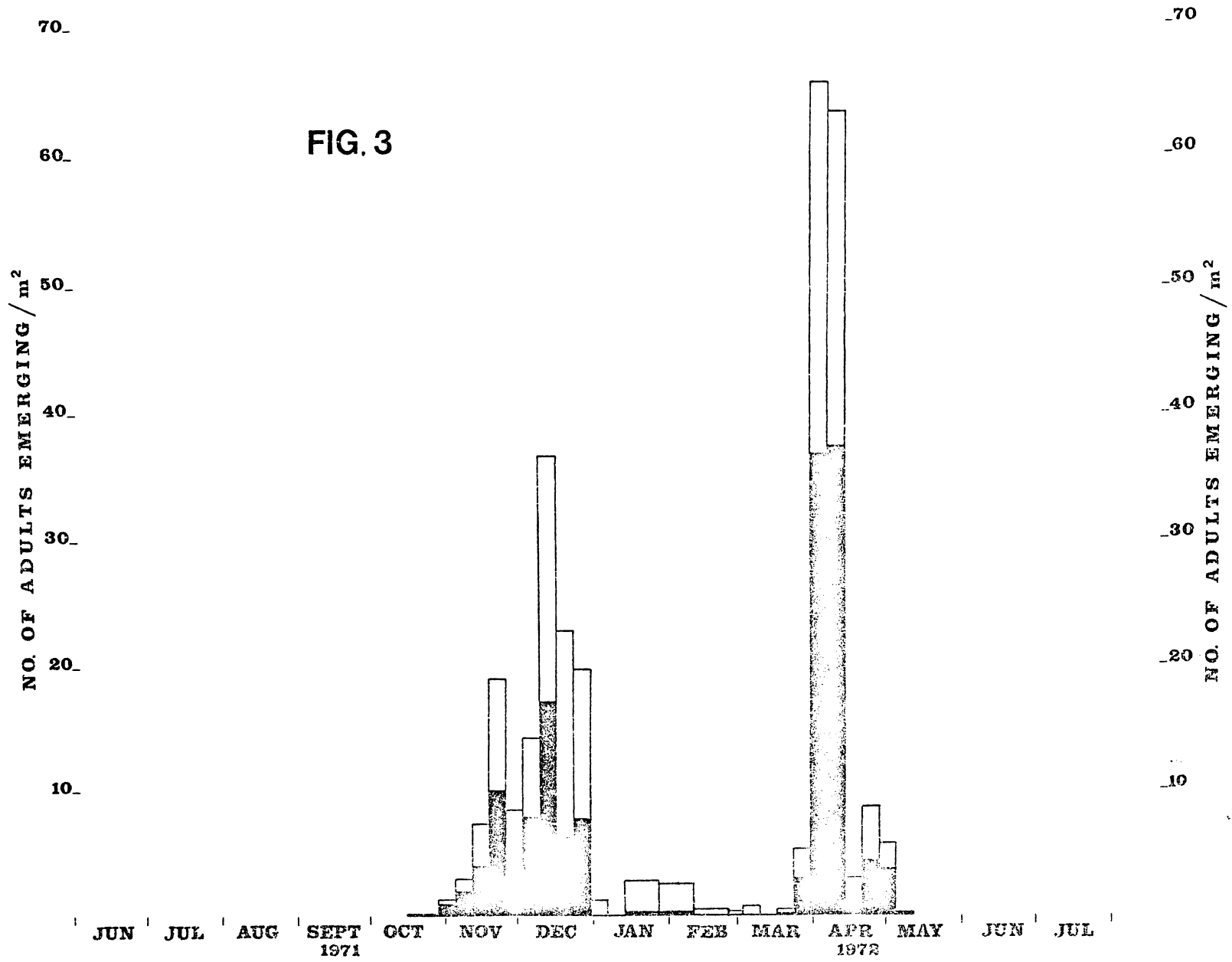


Table 4 The sex ratio of the emerging adult population at the Karaka site. The results of a chi-square test for significant departure from a 50:50 ratio are included.

<u>Date</u>	<u>Sex ratio</u> <u>Male:Female</u>	<u>Significance of</u> <u>difference</u>
15.10 - 28.10.71	100 : 0	
28.10 - 4.11.71	78 : 22	
4.11 - 11.11.71	67 : 33	
11.11 - 18.11.71	55 : 45	
18.11 - 25.11.71	53 : 47	
25.11 - 2.12.71	40 : 60	
2.12 - 9.12.71	58 : 42	
9.12 - 16.12.71	47 : 53	
16.12 - 23.12.71	27 : 73	***
23.12 - 30.12.71	39 : 61	
15.10 - 30.12.71	45 : 55	**
30.12 - 6. 1.72	0 : 100	**
13. 1 - 27. 1.72	10 : 90	**
27. 1 -10. 2 .72	11 : 89	**
10. 2 - 24. 2.72	0 : 100	
24. 2 - 2. 3.72	0 : 100	
2. 3 - 9. 3.72	0 : 100	*
16. 3 - 23. 3.72	33 : 67	
23. 3 - 30. 3.72	55 : 45	
30. 3 - 6. 4.72	57 : 43	**
6. 4 - 13. 4.72	60 : 40	***
13. 4 - 20. 4.72	33 :67	
20. 4 - 27.4 .72	51 : 49	
27. 4 - 4. 5.73	63 : 37	
4. 5 - 11. 5.72	100 : 0	
16. 3 - 4. 5.72	57 : 43	***

FIGURE 4

The number of adults emerging at the Whakatane site. The black histogram represents the number of males, and the outlined remainder the number of females.

FIG. 4

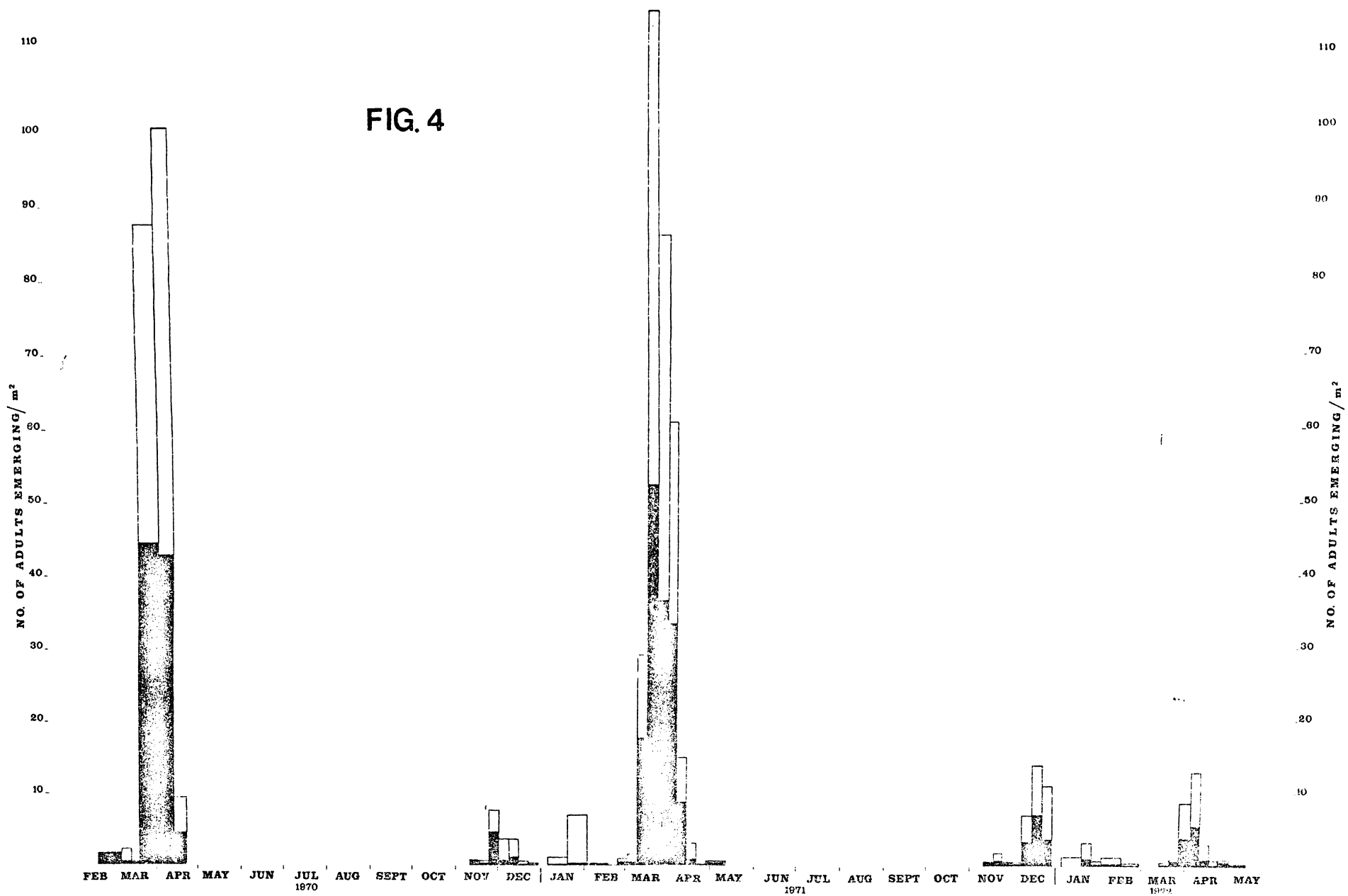


Table 5 The sex ratio of the emerging adult population at the Whakatane site. The results of a chi-square test for significant departure from a 50:50 ratio are included.

<u>Date</u>	<u>Sex ratio</u> <u>Male:Female</u>	<u>Significance of</u> <u>difference</u>
18. 2 - 6. 3.70	100 : 0	
6. 3 - 13. 3.70	25 : 75	
13. 3 - 19. 3.70	100 : 0	
19. 3 - 2. 4.70	51 : 49	
2. 4 - 13. 4.70	41 : 59	*
13. 4 - 22. 4.70	50 : 50	
6. 3 - 28. 4.70	46 : 54	
10.11 - 17.11.70	100 : 0	*
17.11 - 24.11.70	50 : 50	
24.11 - 1.12.70	58 : 42	
1.12 - 8.12.70	36 : 64	
8.12 - 15.12.70	57 : 43	
15.12 - 22.12.70	25 : 75	
22.12 - 29.12.70	0 : 100	
10.11 - 29.12.70	53 : 47	
5.1 - 19.1.71	13 : 87	*
19. 1 - 2. 2.71	4 : 96	***
2. 2 - 9. 2.71	0 : 100	
9. 2 - 16. 2.71	100 : 0	
23. 2 - 2. 3.71	50 : 50	
2. 3 - 9. 3.71	27 : 73	
9. 3 - 16. 3.71	61 : 39	**
16. 3 - 23. 3.71	46 : 54	*
23. 3 - 30. 3.71	43 : 57	**
30. 3 - 6. 4.71	55 : 45	*
6. 4 - 13. 4.71	53 : 47	
13. 4 - 20. 4.71	33 : 67	

Table 5 continued

<u>Date</u>	<u>Sex ratio</u> <u>Male:Female</u>	<u>Significance of</u> <u>difference</u>
20. 4 - 27 4.71	100 : 0	
27. 4 - 11. 5.71	75 : 25	
9. 3 - 20. 4.71	48 : 52	
10.11 - 17.11.71	75 : 25	
17.11 - 23.11.71	42 : 58	
23.11 - 30.11.71	75 : 25	
30.11 - 7.12.71	50 : 50	
7.12 - 14.12.71	49 : 51	
14.12 - 21.12.71	51 : 49	
21.12 - 28.12.71	33 : 67	**
10.11 - 28.12.71	45 : 55	
4. 1 - 18. 1.72	0 : 100	
18. 1 - 25. 1.72	30 : 70	
25. 1 - 1. 2.72	40 : 60	
1. 2 - 15. 2.72	22 : 78	
15. 2 - 28. 2.72	33 : 67	
13. 3 - 20. 3.72	33 : 67	
20. 3 - 27. 3.72	83 : 17	
27. 3 - 4. 4.72	44 : 56	
4. 4 - 11. 4.72	42 : 58	
11. 4 - 18. 4.72	29 : 71	
18. 4 24. 4.72	20 : 80	
24. 4 - 2. 5.72	67 : 33	
2. 5 - 14. 5.72	50 : 50	
13. 3 - 14. 5.72	43 : <sup>5.</sup> <del>47</del>	*

emergences were recorded during the spring of 1971 at Hamilton and the results (total number of adults caught in 32 cages) graphed in Fig. 5.

### Results

There were two definite emergence peak days, on the 23 November and the 10 December. Initially the emergence pattern consisted of a series of definite peaks at 2-3 day intervals up to the 6 December (including peak 23 November). This was followed by a three day lull before another peak emergence (10 December) after which emergence remained reasonably uniform for two weeks.

#### (v) Discussion on Emergence Patterns

At each of the study sites there were two main periods of emergence per season, one during the months of November and December, and the other during March and April. The latter was usually the greater of the two. The variation in time of emergence from season to season and from place to place was probably due to a complex of climatic and topographical factors. Within the immediate environs of Hamilton, the times of adult emergence have been observed to vary by a week or so from one area to another, often for no obvious reason.

The late beginning to the autumn emergence of 1970 at the Hamilton site was probably due to the drought conditions which occurred from December 1969 to late February 1970.

Why the emergence per week during the spring should be more uniform than during the autumn period is not clearly understood. Possibly the decreasing soil temperatures during the autumn period has the effect of concentrating most of the emergence into a shorter time interval. Whereas, during the spring period when soil temperatures are generally rising, temperature possibly does not play such an

FIGURE 5

Total number of adults emerging per day during the 1971  
spring at the Hamilton site.

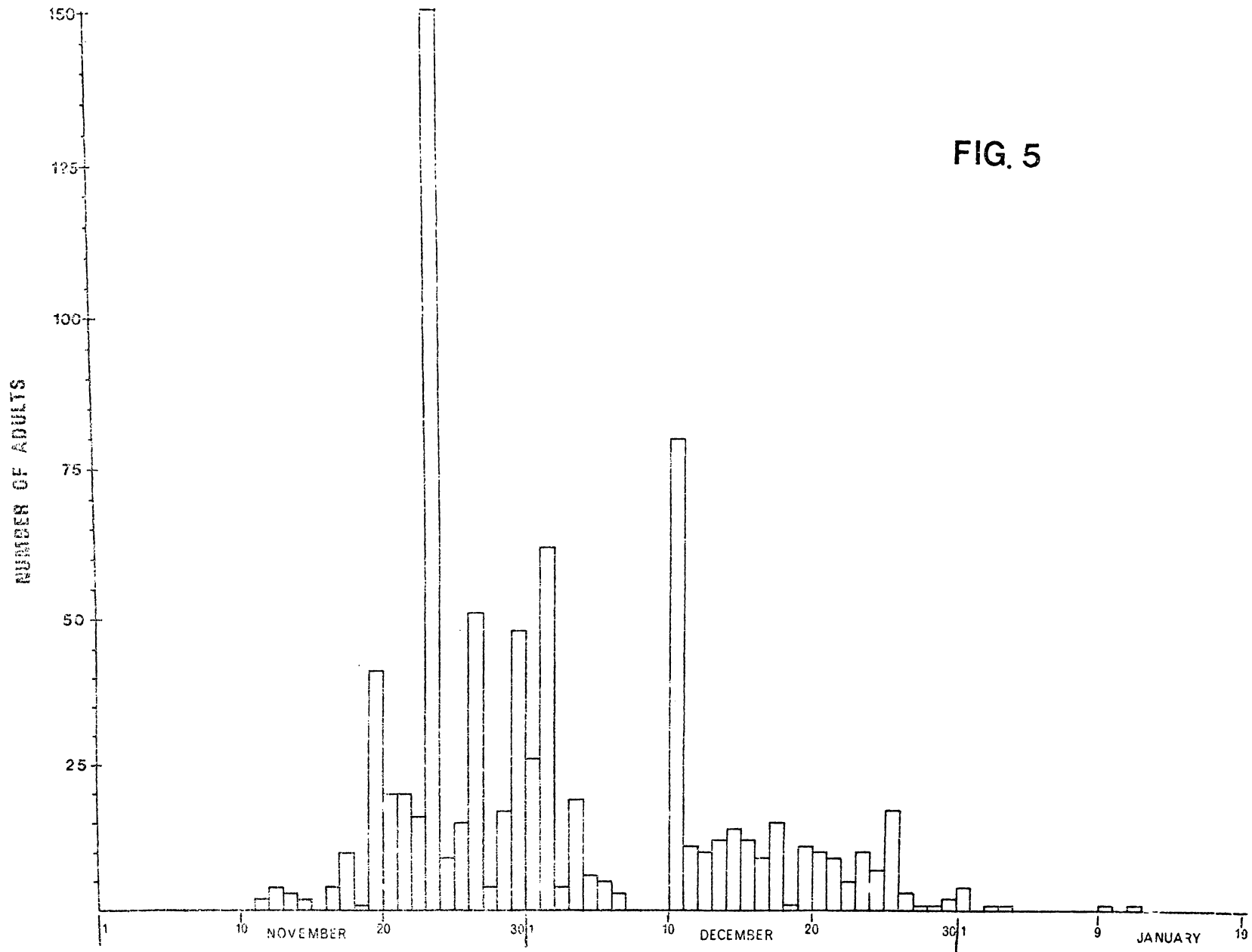


FIG. 5

important co-ordinating role on the individual insect's biological clock (Figs. 6 & 7).

Within both spring and autumn emergence periods there was a definite tendency for adults to emerge in waves. At Hamilton during the 1971 spring, the actual waves did not appear to be influenced by either soil temperature or moisture. This emergence pattern may act as a survival mechanism against possible bad weather conditions preventing flight and mating activity at any one time.

Although there were differences from week to week in the sex ratio there was no definite pattern related to time of emergence. It is likely, considering the relatively short lives of both, that the sexes emerge at the same time. Any variation in the above is probably due to chance or some mortality factor which has upset the sex ratio of either the larval or pupal stage.

The spring and autumn emergence periods probably represent distinct generations, however, whether they are genetically isolated from each other is open to doubt (see larval life history section). The emergence which takes place during the summer months probably represents individuals which owe their origin to either a spring or autumn emergence approximately two years previous. It would seem unlikely that they represent a distinct generation, but rather are indicative of the variability in the length of the life cycle of a percentage of the population. The fact that the majority of adults emerging in this period are females is rather inexplicable.

Campbell and Koehler (1971) have proposed a theory to explain the variation in the number of emergence periods per season as reported by various authors. They suggest that the spring flight initially represented a hold-over of individuals which failed to emerge for various reasons during the previous autumn. If this

FIGURE 6

Weekly mean maximum and minimum soil temperatures recorded at a depth of 1.3 cm at the Hamilton site. Weekly means were calculated from daily recordings.

FIG. 6

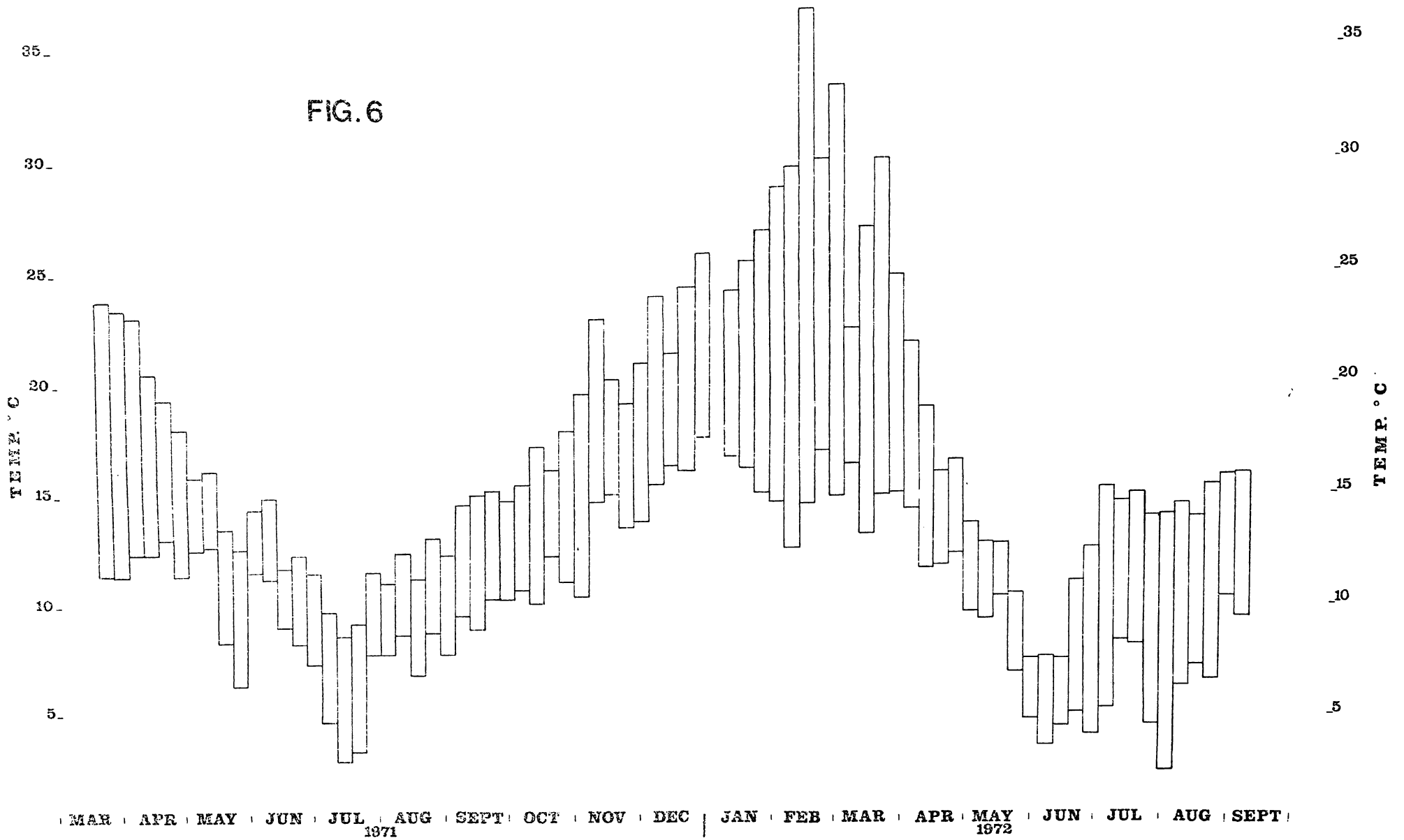
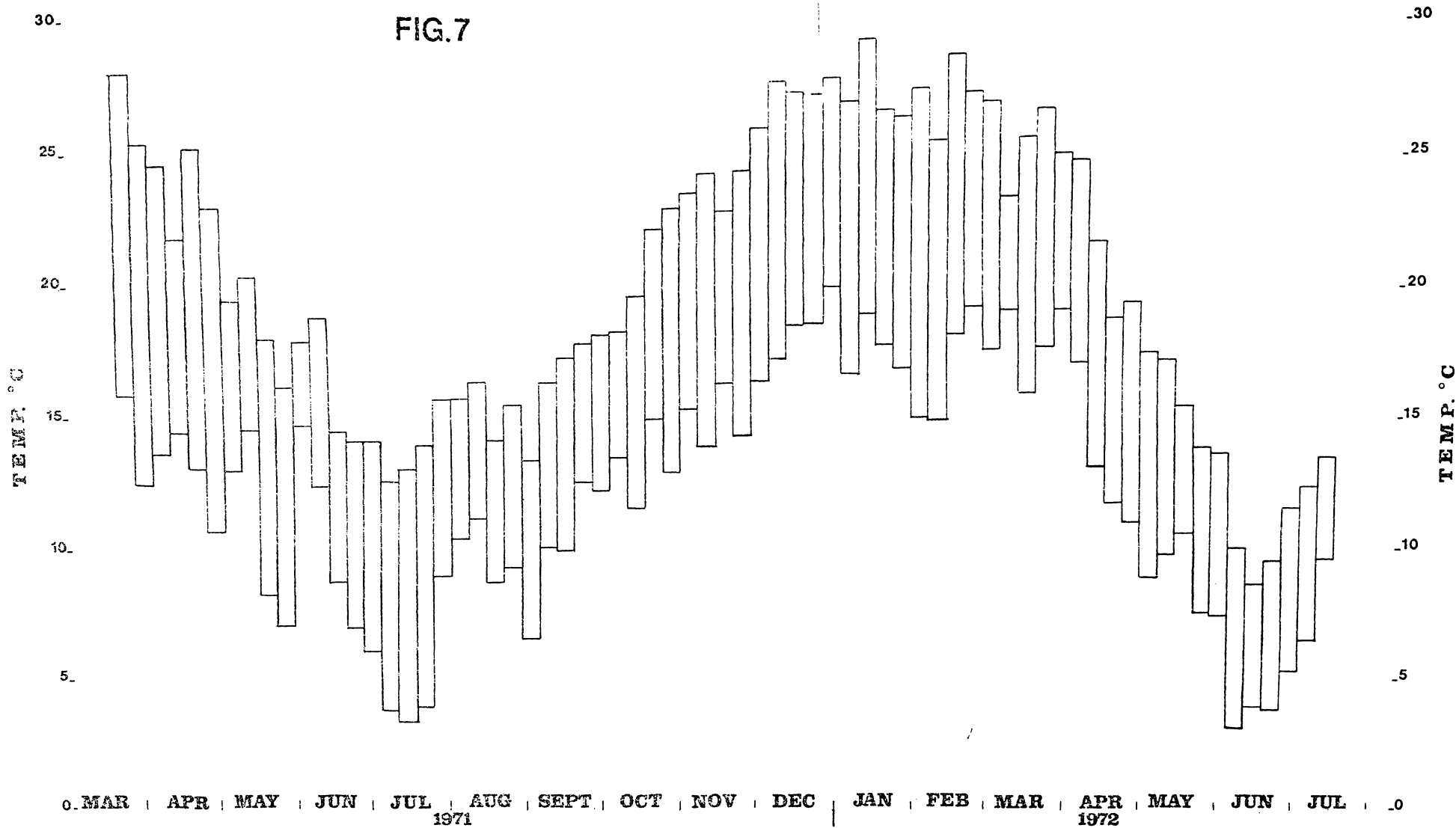


FIGURE 7

Weekly mean maximum and minimum soil temperatures recorded at a depth of 1.3 cm at the Whakatane site. Weekly means were calculated from daily recordings.

FIG.7



happened fairly regularly there would eventually develop a spring brood as distinct from an autumn one. Thus, the three different conditions now existing over the range of the species possibly represents:

1. The original condition with an autumn emergence only
2. An early transitional condition with an autumn emergence and a transitional spring emergence
3. An advanced transitional condition with a major autumn emergence and a small spring one.

In time, a fourth condition could develop with emergences of equal magnitude in both autumn and spring. Alternatively, they suggest that a two brooded condition was the original one, and that because of factors not yet understood, the spring brood is gradually disappearing.

Both of the above suggestions could be evaluated in a new light if it was known for certain what part of Australia the insect originated from; whether in the Atherton Tablelands of Queensland where it appears to have only an autumn emergence, or further south in New South Wales where it appears to have regular spring and autumn emergence periods.

Another possible explanation of the variation in seasonal emergence pattern is that of the interaction between climate and the innate variability in the length of the life cycle (see larval life history section). The two emergence periods have obvious survival value as a safeguard against unsuitable weather conditions preventing either flight or mating activity during one particular emergence period. Thus, in generally favourable climatic circumstances as found in New South Wales and New Zealand, where the rainfall is

relatively evenly distributed throughout the year and soil temperatures are suitable for both spring and autumn emergences, the apparently innately variable length of the life cycle could have led to the development of the spring emergence (assuming one emergence was the original condition). However, in Queensland, with its summer monsoons and dry winter and spring conditions, one period of adult emergence is probably all that is possible. But it is interesting to note that Moller (1964) mentioned that adults have occasionally been seen in the field during December in Queensland. Thus, it is possible that in certain areas, variations in the climatic conditions from year to year are responsible for the occasional spring emergences.

## The Egg Stage

### 1. Description

The eggs are ellipsoids which are opaque white when newly laid, but change to light amber as eclosion approaches (Campbell and Koehler 1971). Their length varies between 0.8 and 0.88 mm, and their width between 0.22 and 0.27 mm (Irwin-Smith 1920).

### 2. Location

The eggs are laid in clusters (Irwin-Smith 1921a, Moller 1965, Campbell and Koehler 1971) at shallow depths in the soil (Saunders 1963).

As mating and oviposition occur shortly after emergence (Campbell and Koehler 1971), eggs are present in the field over approximately the same time as adult emergence is taking place.

### 3. Hatching time

Irwin-Smith (1921a) recorded that eggs took 17 days to hatch at room temperature. Mungomery (1932) found that eggs hatched in 15 days at a mean temperature of 16.1 °C, and both Dumbleton (1949) and Saunders (1963) reported that eggs took two to three weeks to hatch under field conditions at Opotiki in New Zealand and on the Atherton Tablelands of Australia respectively.

In the sugar-cane belt of Queensland, with presumably a higher mean temperature than that encountered by previous authors, Moller (1965) stated that provided there was adequate moisture, eggs hatched within seven days. Moller's statement was substantiated, with respect to the moisture requirement, by Campbell and Koehler (1971) who found that all eggs subjected to ambient humidity shrivelled and died. However, they recorded the following for eggs kept on moist towelling:

<u>Temperature</u>	<u>Comments</u>
10 °C	No development after 3 weeks
15 °C	Most eggs hatched on day 15
20 °C	A few hatched on day 11 and the remainder on day 12
25 °C	Three dead larvae were found on day 11 and all other eggs darkened and decomposed by day 15
30 °C	All eggs darkened and decomposed with no evidence of hatching

(Number of eggs in each case was 500).

In view of the differences between the findings of Moller (1965) and Campbell and Koehler (1971) with regard to the effect of temperature on hatching time, the following experiment was carried out to check the timetaken for eggs to hatch at different temperatures, when moisture conditions were kept optimal.

Two hundred eggs were kept on 2% agar in an incubator at each of the following temperatures: 15°, 20°, and 25°C. All eggs were laid on 27.4.72 by previously mated females and were placed in their respective incubators on the following day. During the experiment the eggs were checked daily.

#### Results ( Table6, Fig. 8).

At 25°C the majority of the eggs hatched in seven days, at 20°C in 10 days, and at 15°C in 22 days. An experiment carried out earlier showed that eggs hatched in seven days at 28.5°C.

At the lower temperature of 15°C , there was more variation in the individual length of hatching time than at the higher temperatures. The percentage of successful hatchings decreased with increasing temperature.

During the autumn of 1970, 100 eggs on agar were placed out in

FIGURE 8

Relationship between temperature and the rate of development  
of the egg stage.

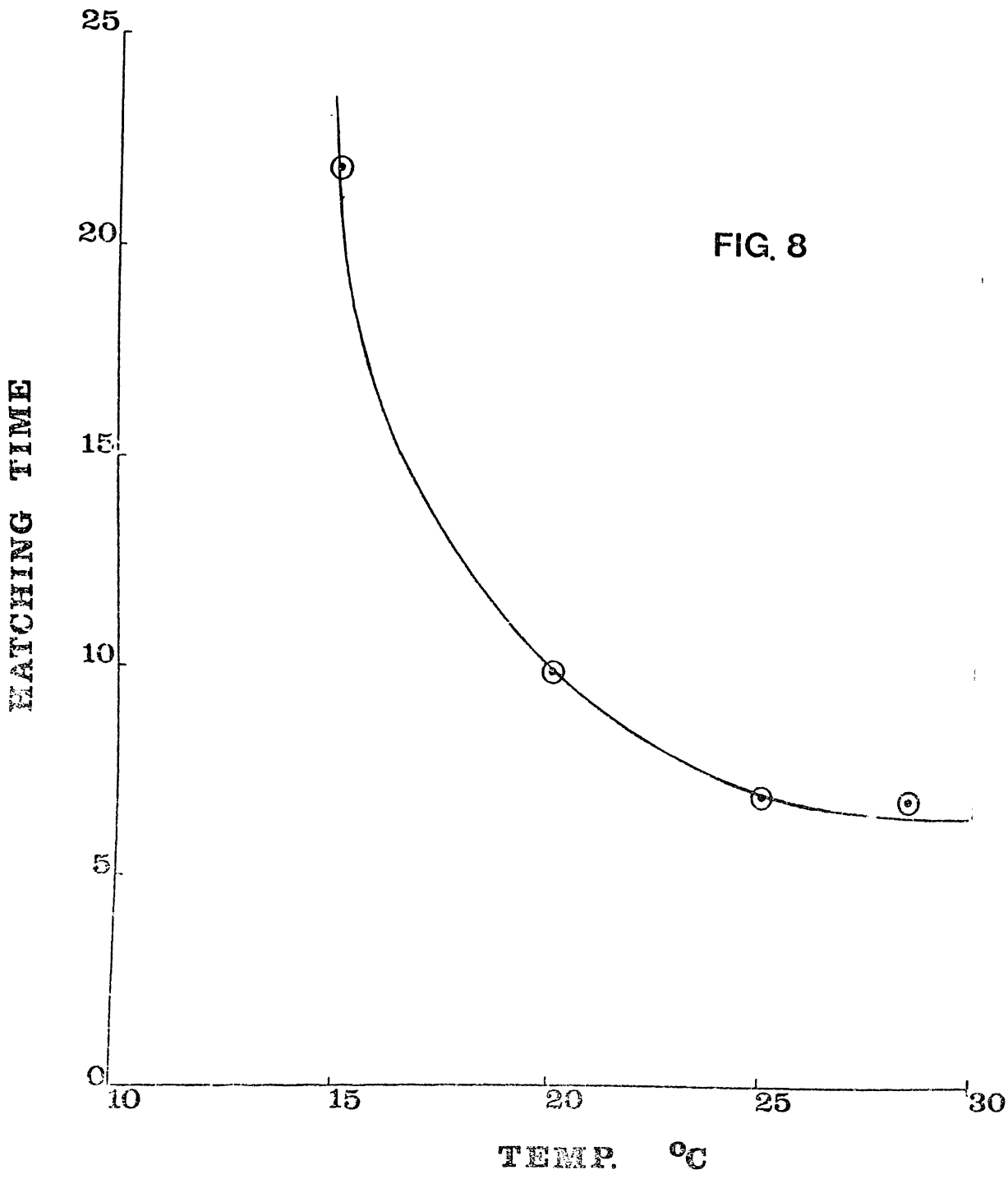


FIG. 8

Table 6 The rate of development of the egg stage at three temperatures. n = 200 at each temperature.

<u>Age of eggs</u> <u>in days</u>	<u>Numbers of eggs hatched</u>		
	<u>15 °C</u>	<u>20 °C</u>	<u>25 °C</u>
6	0	0	0
7	0	0	117
8	0	0	2
9	0	0	0
10	0	116	0
11	0	20	0
12	0	0	0
13	0	0	0
14	0	0	0
15	0	0	0
16	0	0	0
17	0	0	0
18	0	0	0
19	0	0	0
20	0	0	0
21	34	0	0
22	89	0	0
23	29	0	0
24	4	0	0
25	3	0	0
26	0	0	0
27	0	0	0
28	4	0	0
29	0	0	0
30	0	0	0
<u>% hatched</u>	81.5	68	59.5

the field at the beginning of April (mean maximum daily temperature  $22.5 \pm 1.0$  °C, mean minimum  $11.6 \pm 1.2$  °C). All eggs that hatched did so in 13 days (53) or 14 days (19).

### Dissussion

The above work supports Dumbleton's (1949) observations, and under pasture conditions in New Zealand eggs should take approximately two weeks to hatch. The results indicate that contrary to Campbell and Koehler's (1971) observations, eggs are capable of successful hatching at 25 °C and above, although 25 °C appears to be near their optimum. Since temperature has a large influence between 15 and 20 °C, fluctuating daily temperature must be taken into account when estimating hatching time under field conditions.

The effect of moisture has not been investigated, but from general observations it is possibly a critical factor, and lack of moisture could play an important role in egg survival. Hitchcock (1970) has observed that provided there is some surface moisture at the time of oviposition, subsequent complete drying out of the soil did not affect the viability of the eggs. However, the present author has observed, as have Campbell and Koehler (1971) that eggs left exposed in the laboratory soon shrivel and die.

### The Larval Stage

#### 1. Description

The following is a summary of Irwin-Smith's (1920, 1921a, 1921b, and 1923) detailed description of the larval stage:

Newly hatched larvae are 0.8 to 0.96 mm long, and fully grown male larvae are 7-8 mm and female 10-11 mm. The new larval skin is

a delicate white or creamy colour, flecked with glistening particles. This typical stratiomyid type cuticle consists of large hexagonal plates separated by granular areas, and is strongly impregnated with calcium carbonate. As the age of the instar increases, the cuticle assumes a grey-brownish colour. Larvae have twelve post cephalic segments, which are all much broader than long, and are of uniform width from the second to the tenth; the terminal segments are slightly narrower. Each segment bears a series of stiff black bristles. In transverse section the segments are biconvex, with the lateral edges expanded into tumid ridges marked off from the main body on both surfaces by a shallow groove. Between the segments, the body is slightly constricted and in contraction the segments are imbricated, overlapping from behind forward in front of the fourth segment and in the reverse direction from the fourth backward. Situated at the anterior extremity is the dark brown strongly sclerotized head which can be retracted into the first thoracic segment. The mouth opening is terminal and the mouth parts are well adapted for obtaining nourishment by suction. The smallest larvae are similar to the fully developed ones, except in size and the relative length of the bristles.

The majority of larvae are found in the top 10 cm of soil (see section on vertical distribution).

## 2. Chronological Classification and Length of Larval Period

### (i) Introduction

The most detailed work on the length of the larval period reported to date is that being carried out by entomologists of the Bureau of Sugar Experimental Stations, Queensland. Wilson (1969) reported that a small proportion of larvae hatched (1967) and reared

in a laboratory where the temperature was regulated to correspond with field conditions, emerged as adults in one year (by May 1968). The majority of the larvae, whether field collected or laboratory reared, remained in the larval stage in the second year. Unfortunately these subsequently died. Wilson (1970) reported that from eggs hatched in 1968 some larvae were reared to adults in one year, while the remainder reached the adult stage after two years. One and two year life cycles were observed in both sexes.

Owing to the pattern of adult emergence, a variable larval developmental rate (Wilson 1969, 1970, Hitchcock 1970), the presence of overlapping generations (Hitchcock 1970), and the difference in sizes between the sexes (Hitchcock 1970, Campbell and Koehler 1971), there is a wide range of larval sizes present at any time during the year. Irwin-Smith (1920) noted that size appeared to be the only external age criterion. In fact, according to Campbell and Koehler (1971), there appeared to exist a continuous gradation in size from small to large larvae, with no readily observable morphological differences between instars. Hitchcock (1970) stated that a key had been worked out to separate the various instars, but commented that determination of individual larvae was often not easy. As the above classification method has not yet been published, it is difficult to comment on its practicality. Thus, at the start of this project no method was available for classifying larvae on a chronological basis.

It was necessary to adopt some method of larval classification to determine the possibility of sampling particular larval groups of known age at the times of their peak occurrence. To determine if and when these peaks existed, and how long it took for the larva to

develop from one such point to the next, two approaches were adopted. The first was to rear larvae individually in the insectary under conditions as close to those in the field as possible, and by monthly inspections, to monitor their growth. The second was to take field samples at monthly intervals, and by using some larval classification method, follow the course of the individual groups.

(ii) Development of larval classification method

Any method of classification adopted had to leave larvae undamaged to allow monitoring of the life cycle work in the insectary to continue.

Head capsule width and larval weight were both considered as the basis for a classification system, and the latter was finally adopted for the following reasons. The head capsule, because of its curvature, could not be measured reliably, so the distance between the bases of two posterior dorsal bristles was used. However, often one or even both of these bristles was missing, preventing a measurement being made. Also, the head capsules, particularly those of older larvae were often covered by calcareous deposits which had to be removed before measurements could be made. Larvae received less handling during weighing, and as a result were much less susceptible to damage.

The disadvantages of such a classification method were that weight is not always highly correlated with instar number, and often larvae lose weight either during a particular instar or in changing from one instar to another (Wigglesworth 1965). However, accepting the assumption that there existed in general a correlation between the age of a larva and its state of growth, expressed in terms of body

weight, a classification based on weight should give the required information necessary for the formulation of the larval sampling programme.

An additional problem was that weight could vary not only with age, but also with water balance, the latter reflecting the variable moisture state of the soil. This was assumed to be offset to some degree by the extraction process (Wilcocks and Oliver 1971), and also by keeping the larvae in standardised well moistened conditions for between 24 and 48 hours before being weighed.

Larvae were collected from the field at Hamilton ( 16.4.69, 26.11.69, 10.2.70 and 17.6.70) and were weighed on a five figure Mettler balance. The weights were subjected to a probability paper analysis (Cassie 1963a) to see if any naturally occurring groups were present. Both the male and female pupal weight data, when graphed on arithmetic probability paper, formed curved lines which approximated straight lines when plotted on log probability paper. Thus, a log transformation was used in the larval weight analysis.

(iii) Initial classification adopted (Fig.9 )

The initial classification adopted was based on the probability analysis shown in Fig. 9 . The log probability paper used only represented 96% of the data. Thus, the lower 2% was grouped to allow representation and the upper 2% was not included in the analysis. The nine normal distributions obtained were set up as representing nine larval classes.

The error introduced into the classification system by disregarding the terminal 2% of each distribution, was considered acceptable and also contributed to keeping areas of overlap of the various distributions to a minimum. However, there still existed a

FIGURE 9

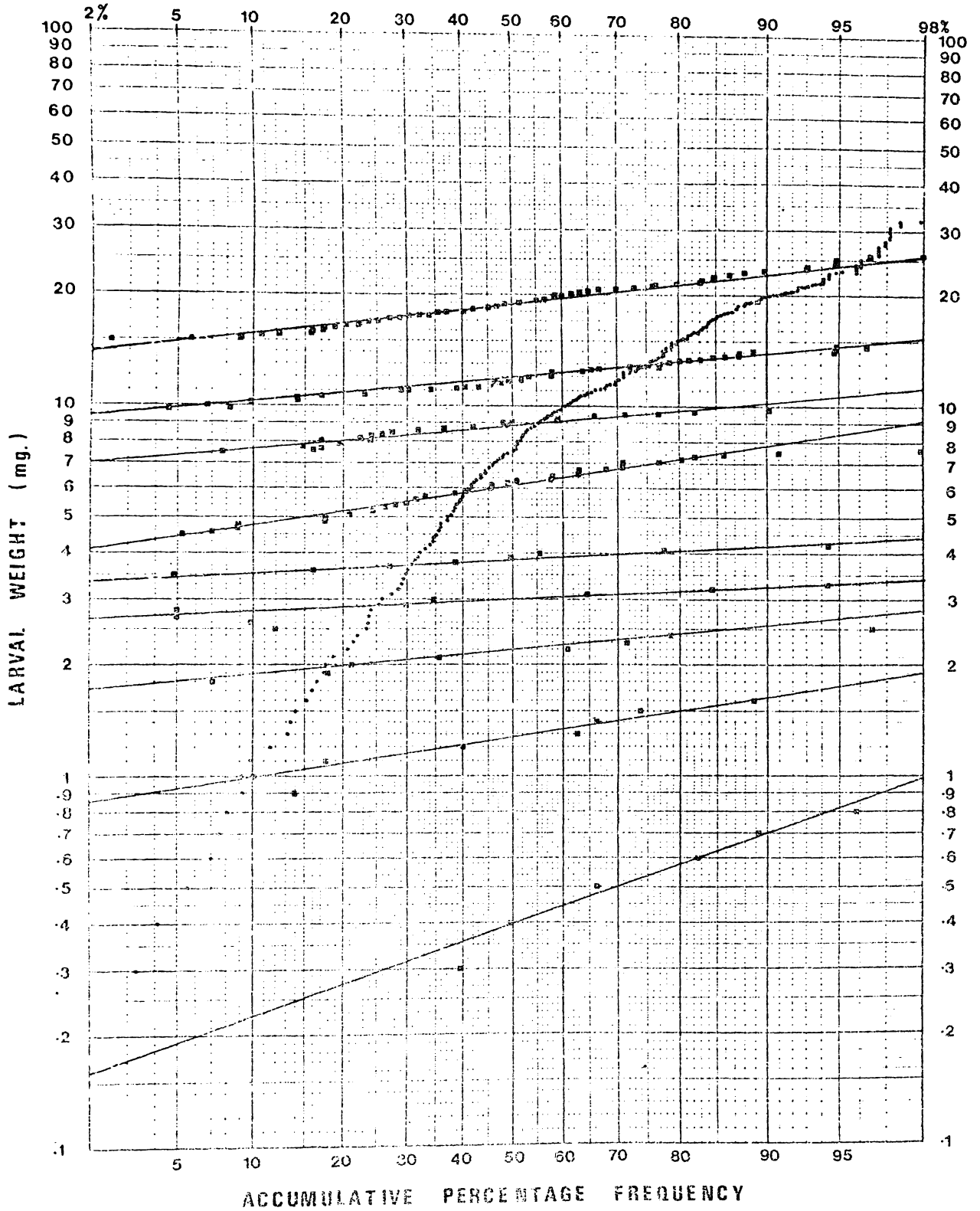
A probability paper analysis of larval weight.

The points of inflexion chosen were: 8.5, 16, 23.85, 29.5, 34.5, 50.5, 61, 80, and 97.

Total number of larvae = 357.

	<u>Mean <math>\pm</math> S.E. of each distribution</u> <u>in mg</u>	<u>No. in each distrib-</u> <u>ion</u>
1	0.04 $\pm$ 0.04	30
2	1.28 $\pm$ 0.05	27
3	2.19 $\pm$ 0.05	28
4	3.02 $\pm$ 0.04	20
5	3.86 $\pm$ 0.06	18
6	6.18 $\pm$ 0.17	57
7	8.80 $\pm$ 0.18	37
8	12.00 $\pm$ 0.18	68
9	19.00 $\pm$ 0.38	61

FIG. 9



considerable amount of overlap between some of the classes. The following classes were set up, representing the non-overlapping areas of each distribution:

<u>Class</u>	<u>Weight range in mg</u>
0	0.0000 - 0.1599
1	0.1600 - 0.8600
2	1.0000 - 1.7000
3	1.9000 - 2.6500
4	2.8000 - 3.3500
5	3.4000 - 4.1000
6	4.4000 - 7.0000
7	9.1000 - 9.4000
8	11.2000 - 13.9000
9	15.3000 and above

Thus, the areas of overlap were:

<u>Between classes</u>	<u>Weight range in mg</u>	<u>Ratio</u>
1 & 2	0.8601 - 0.9999	2 : 8.5
2 & 3	1.7001 - 1.8999	4.5 : 11.5
3 & 4	2.6501 - 2.7999	3 : 10
4 & 5	3.3501 - 3.3999	5 : 1
5 & 6	4.1001 - 4.3999	16 : 3
6 & 7	7.0001 - 9.0999	21.5 : 58
7 & 8	9.4001 - 11.1999	28 : 26
8 & 9	13.9001 <sup>- 15.2999</sup> <del>and above</del>	8 : 5.5

Larvae falling into one of the above "between class" groups were classified on the following basis:

From Fig. 9 it can be seen that the region of overlap between classes

1 and 2 represents 2% of class 1, and 8.5% of class 2. Thus, larvae falling into this region were divided between class 1 and class 2 in the ratio of 2 : 8.5. Larvae falling in the other intervals were divided on a similar basis as detailed in the ratio column above.

The size difference between male and female pupae was probably reflected back through several of the later instars, and thus, each class probably did not represent an instar. Also, it is unlikely that larvae progress from one class to the next in an orderly fashion, nor all the classes contain equal numbers of males and females. The field and insectary work were designed to test whether these broad growth classifications could be invested with any sexual or chronological meaning.

#### The Insectary Study

Larvae were reared individually on maize plants grown in black sand under screen house conditions. The use of artificial diets was not attempted because of the difficulties in developing a suitable one (Dr. Singh, Entomology Div., D.S.I.R. Nelson, 1970 pers. comm.). and the wish to rear the larvae under as near natural conditions as possible. Black sand was chosen because the light coloured larvae were clearly visible against it. Maize was used in preference to ryegrass because it more rapidly developed a root system that was capable of supporting a larva for a month. Also, the root system was much less fibrous and this facilitated larval extraction.

Black sand, collected from dunes near Raglan, was washed, sieved, and then oven dried. 10% moist sand was prepared and 100ml poured into each individual ( 23 x 6 cm) plastic maize tube. Maize seeds, incubated at 25 °C for 6-7 days on agar, were planted out in the tubes and left for approximately 10 days at room temperature to become

established. Larvae were then added, one per numbered tube, care being taken to bury them 2-3 cm below the surface. The tubes themselves were buried in a 10 cm deep tray of soil in the screen house. The maize tubes were inspected daily and the sand maintained at approximately the 10% moisture level. (Temperatures Fig. 10).

After a month, the contents of each tube were gently washed into a sieve ( mesh size 0.8 mm). Often the larva, particularly when over one year of age, was obvious at once. If, not, the sand was gently washed through the sieve and the maize root examined until the larva was found. With small larvae (less than 1 mg at their previous weighing) the above sieve was placed over a finer sieve (mesh size 0.2 mm). If the larva could not be found in the top sieve, the contents of the fine mesh sieve were examined under a microscope.

Each larva was gently washed to remove surface sand and kept moist in individual containers until weighed on a Riic L.M. -500 electric micro-balance. Surface moisture was removed before weighing. Larvae were then returned to prepared maize tubes and left for another month.

During the emergence periods the top 2 cm of the maize tubes were plugged with cotton-wool to prevent emerging adults escaping.

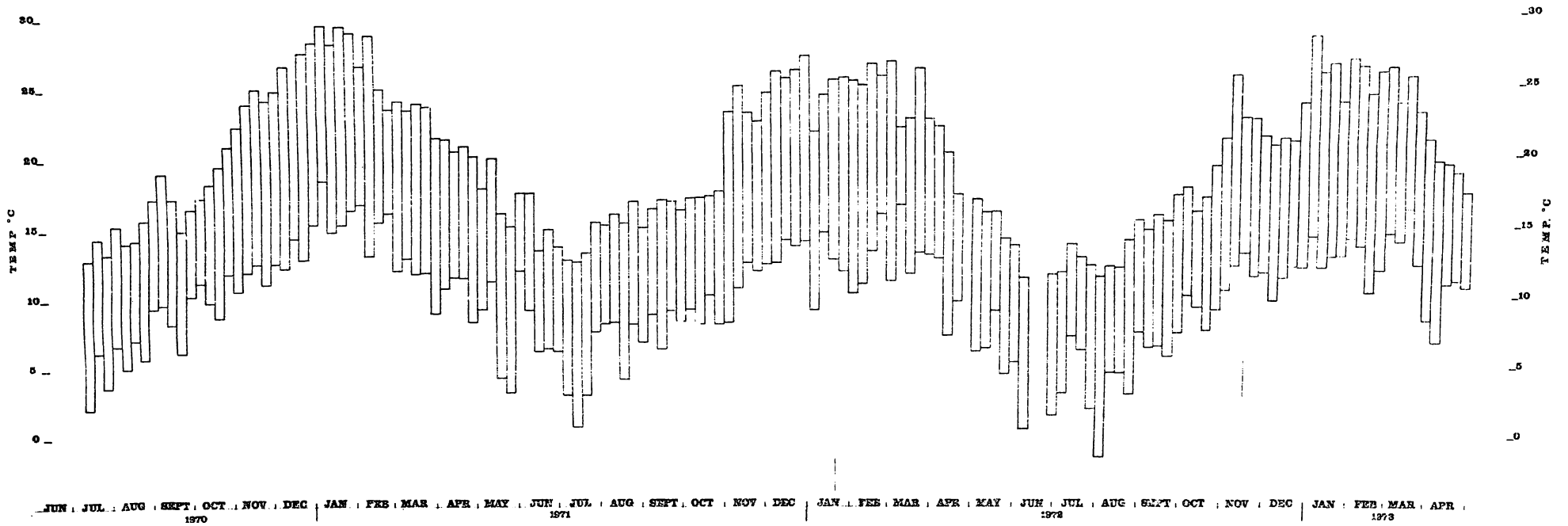
An attempt to start the life cycle from eggs during the autumn of 1970 failed due to inadequately developed larval handling and rearing techniques. Hence, 100 small larvae were collected from the field at Hamilton and initially reared on ryegrass plants grown in plastic tubes of black sand. However, considerable difficulty was encountered in extracting individual larvae from the fibrous root mat and so a change was made to maize.

The larvae, particularly those under 2 mg, often did not withstand

FIGURE 10

Weekly mean maximum and minimum temperatures at which larvae were reared in the screenhouse. Weekly means were calculated from daily recordings.

FIG. 10



the monthly inspections, and replacements from the field were necessary. Larvae were occasionally killed outright by handling, but bacterial and fungal diseases appeared to cause the highest mortalities in all groups. Whether these diseases were primary or a result of larvae being damaged by handling was not known.

The decision of whether a larva was dead or not was based on its general appearance, dead larvae being either extremely flaccid or discolored. Marginal cases were given the benefit of the doubt, since larvae approaching ecdysis often appeared the same as those in the early stages of bacterial or viral disease.

The life cycle was successfully started from eggs during the autumn of 1971. Eggs were collected from impregnated females and incubated on agar at 25 °C. One hundred newly hatched larvae were placed individually in maize tubes. These were not inspected for two months to reduce the high mortality of the young larvae through initial handling. Another group of newly hatched larvae were weighed, and then kept at room temperature for approximately a week in plant nutrient agar supporting ryegrass seedlings, before being weighed again.

So that losses amongst the original 100 larvae could be replaced, a reservoir was set up consisting of 100 plastic tubes each with two ryegrass plants supporting 50 newly hatched larvae. Grass was used in this case because it was envisaged maintaining the reservoir for as long as possible.

## Results

### Life cycle commenced early winter 1970

Only four of the original 100 larvae started ( 15.7.70) were still alive after one year. 92% died during the first six months; thus during this period dead larvae were replaced, and an additional 30 larvae were started on 18.8.70.

The weights of those larvae which lived for approximately six months or longer were plotted against time (Figs. 11 & 12). They were separated into two arbitrary groups based on the shape of their growth curves, Fig. 11 representing larvae which exhibited a faster rate of growth than those represented in Fig. 12.

Larva no. 115 (Fig. 11) was started during August 1970 and reared to become a female pupa in March 1972. With a weight of 1.89 mg in mid August it was debatable whether it hatched from an egg laid during the March-April emergence 1970 or the November-December emergence of 1969. Since no individual was recorded as weighing over 1 mg by late August from larvae hatched from eggs at the beginning of April 1971 ( Fig. 13) it was probable that the larva hatched from an egg laid during the spring emergence of 1969. There was a period of rapid growth from mid October 1970 through the summer months to the beginning of April. During early winter a loss of weight occurred, which was quickly recovered one month later to be followed by a three month period of relative stability. Another rapid increase in weight occurred during October, followed by an overall small increase through to pupation in March. This larva exhibited at least a 24 month life cycle and could possibly have had approximately 28 months.

This pattern of rapid growth during the summer months, a maintenance of body weight during the winter and a resumption of growth the following spring was by no means rigidly adhered to, and larvae recorded in Fig. 11 exhibited a considerable amount of variation in both the time and amount of growth.

Considering the difference in mean weight between male and female pupae ( 12.9 and 24.3 mg respectively) it seemed probable that

FIGURE 11

Changes in larval weight with time. All larvae were collected from the field. Termination of a line represents the death of an individual except where indicated to the contrary.



those larvae that exhibited a faster rate of growth were mainly females.

Considering Fig. 12, this group on the whole did not show periods of such rapid growth as characterised the larvae recorded in Fig. 11, and were probably mainly males.

Larva no. 40 showed a similar growth pattern to those of Fig. 11 up to the beginning of April, after which it lost weight. Then over the following year it grew very slowly to become a male pupa in March. No. 36 exhibited quite a different growth pattern, increasing in weight almost uniformly to become a male pupa in March 1972. Both nos. 40 and 36 showed at least a 24 month cycle. No. 111 increased in body weight reasonably uniformly to become a male pupa at the beginning of March 1971.

Nos. 8 and 80 are examples of larvae which maintained an almost constant body weight over considerable periods of time. No. 80 barely increased in weight after a year. No. 102 is of particular interest since its weight at starting in December of 1970 indicated that it most probably came from the March-April emergence period in that year. The larva lived between 31 and 32 months.

#### Life cycle commenced autumn 1971 (Fig. 13)

The life cycle was started with larvae hatched from eggs on 5 and 6 April 1971. Again, extremely high mortalities were recorded during the first few months, and out of 5,100 larvae started from eggs during April, only 25 were still alive one year later. The mean weight of newly hatched larvae was  $0.0305 \pm 0.0011$  mg (n = 40). After approximately three months (30.6.71) there was a very wide distribution in the actual weight attained by different larvae (range

FIGURE 12

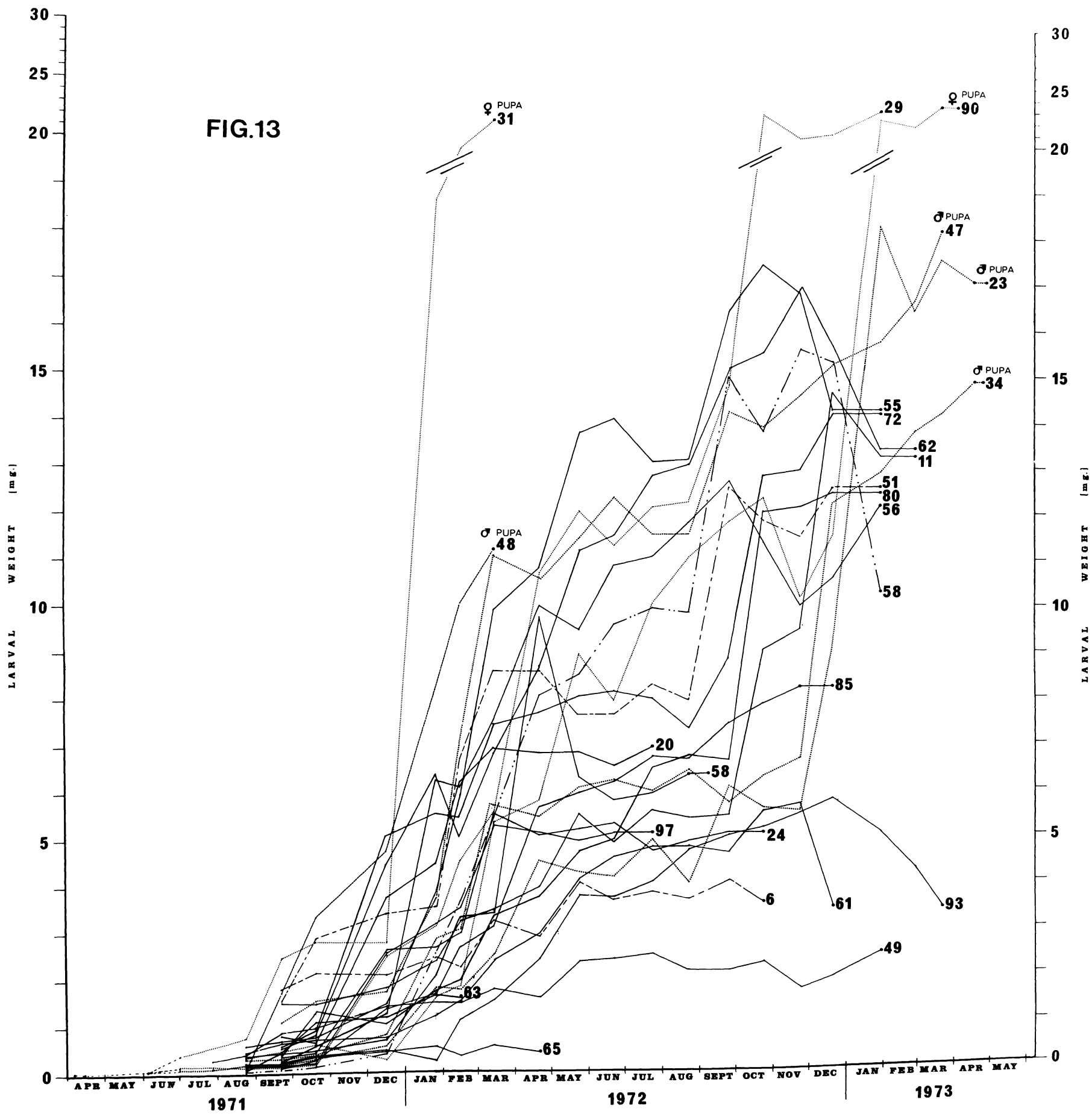
Changes in larval weight with time. All larvae were collected from the field. Termination of a line represents the death of an individual except where indicated to the contrary.



FIGURE 13

Changes in larval weight with time. All larvae hatched from eggs during April 1971. Termination of a line represents the death of an individual except where indicated to the contrary.

FIG.13



0.0545 to 0.5850 mg. n = 100).

One female and one male came through from egg to adult in one year, emerging during April 1972. These two represented 8% of the surviving larvae after a one year period.

There was a considerable variation in the rate of growth and the times at which growth occurred. The greatest increases in body weight occurred between October and May, with the late summer and autumn months usually showing the greatest increase. In general, periods of rapid growth were preceded by, or interspersed with, slower growth periods, and weight increases were not so marked during the winter. The majority of the surviving larvae entered into their second larval year, and three males and one female emerged during the March-April period of 1973.

#### Summary of liveweight gains (Figs. 11, 12, & 13)

1. A wide range of growth rates was recorded both in time of increase and actual weight gains, even from larvae which hatched within hours of each other.
2. The majority of large weight increases tended to occur during the spring, summer and autumn months. There was a marked tendency for weight to be maintained or gained slowly during the winter.
3. There appeared to be a sexual difference in growth rate, those larvae which exhibited prolonged periods of rapid increase were probably mainly female larvae, whereas those which exhibited a slower increase were probably mainly males.
4. The majority of larvae appear to have a 24 to 28 month life cycle, 24 months being the most common. It is conceivable that some larvae could reach the pupal stage in 20 months i.e. from autumn to the spring 20 months later. Some, up to 10% of the

population (based on the survival shown in Fig. 13) came through from egg to adult in 12 months, whilst one larva was recorded as still being alive after 31 months, probably indicating a 36 month life cycle.

5. A few larvae exhibited an extremely slow growth pattern, either maintaining a stable body weight or increasing very slowly over a period of between 12 and 18 months.

6. Increases in body weight, even during the active growing periods, were usually broken by periods of a month or more of weight stability or much slower increase.

(iv) Remodification of the Larval Classification Scheme

From the insectary work it was found that all the larvae did not stay in all the class groupings long enough to be recorded at the regular monthly inspections. Whilst all larvae were recorded in classes 0, 1 and 6, only some were recorded in serial succession in 2,3,4 and 5. Some larvae were not recorded in classes 7 or 8, while others pupated as males before reaching class 9. All larvae were recorded serially in either classes 2 or 3 and then either classes 4 or 5. Hence, the initial number of classes was reduced by combining classes 2 and 3, 4 and 5, and 7, 8 and 9 into three distinct groups respectively.

(v) The Application of the Larval Classification Scheme to Field Studies

Introduction

To investigate the change in larval class structure with relation to time at the Hamilton and Whakatane study sites, the larval population was sampled at approximately monthly intervals. A sub-sample, which usually comprised every fourth core, was set aside

for the assessment of the larval class structure of the field population. All larvae extracted from these cores (using the method described by Wilcocks and Oliver 1971) were weighed on a Riiic LM -500 electric micro-balance, and classified by weight as in the modified scheme. An assessment of the number per square metre for each class was made by multiplying the total sample estimate by the percentage present in each class as estimated from the sub-sample.

The confidence limits of each class were quite large (Appendix 1), but were considered acceptable as it was the general trend of the different classes which was of main interest. One large error that was not noticed initially was the low percentage recovery of the class 0 larvae. Even after this had been noted, it was not until June 1972 that the percentage recovery of this group was improved from below 20% up to approximately 80%. In the interpretation of the following data the above should be borne in mind.

Results     Hamilton study site (Fig. 14)

( See p. 108 - 112 for discussion of individual class trends with relation to overall population trend )

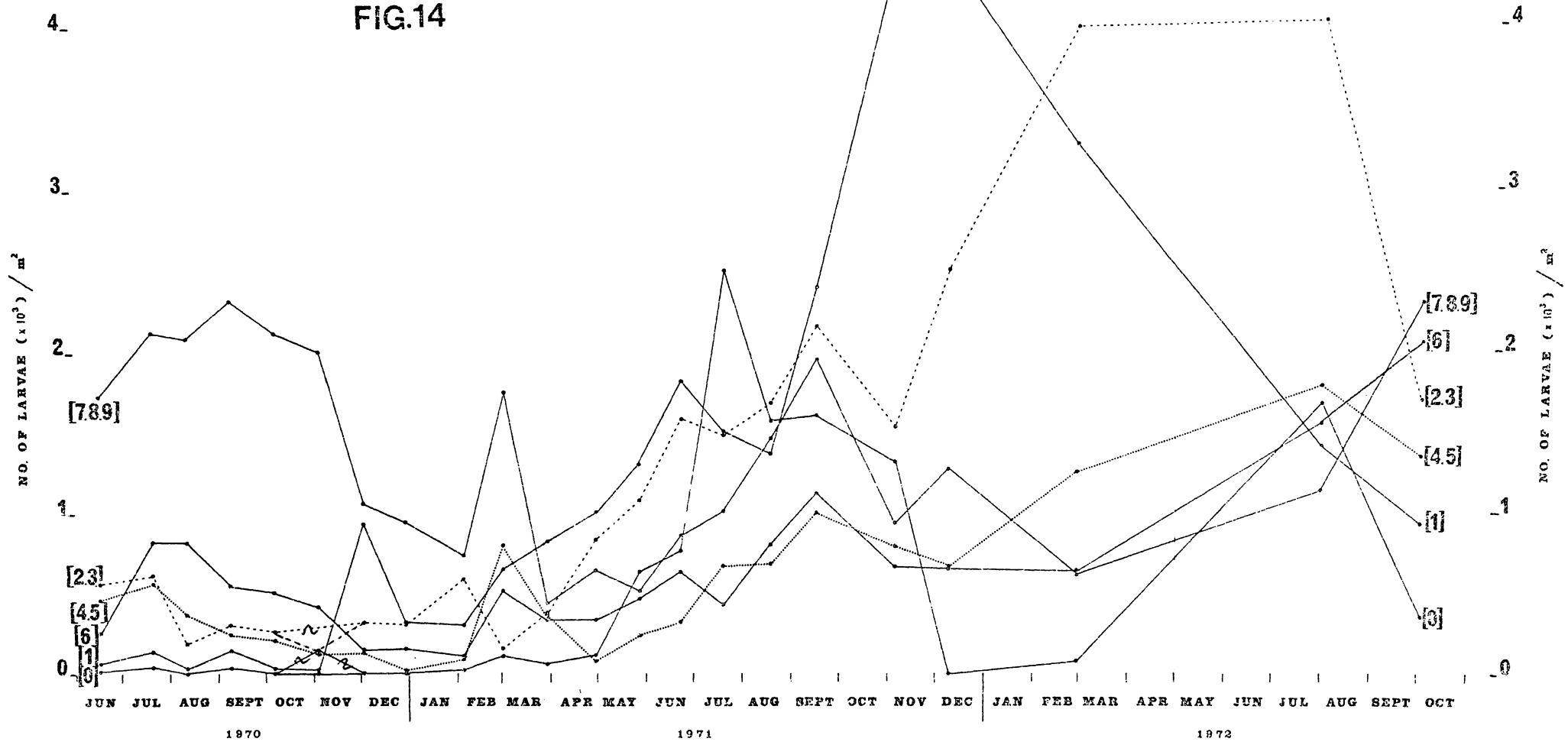
Class 0 had a small March (1971) peak. This probably represented those larvae which hatched during the previous spring emergence period. Another peak occurred at the end of July ( 1971 & 1972 ) which probably represented larvae which hatched during the previous autumn emergence. The delay in picking up the peak numbers after the conclusion of the emergence period from which the larvae had come was due to the inefficient extraction of this class.

The time taken from the emergence period, to which the larvae owed their origins, to their peak numbers being recorded, was the same for both spring and autumn periods ( 3 months ).

FIGURE 14

Changes of the individual larval classes at the Hamilton site.

FIG.14



Class 1 had two well defined peaks per year, one at the beginning of December, and the other at the end of June. These probably corresponded to autumn and spring emergences respectively. The time taken to develop to these peak periods was the same for larvae from both the autumn and spring emergence periods, approximately seven months.

Class 2.3 had a February and a September (1971) peak, probably representing larvae from the preceding autumn and spring emergences respectively. This represented a period of nine months in each case. However, a considerable proportion of the larvae contributing to the February peak may well stay in this class through until July (see p. 57 ). During the early winter and early summer periods classes 1 and 2.3 increased almost at the same rate, with class 2.3 lagging one to two months behind class 1.

Class 4.5 exhibited a similar pattern to 2.3, but at a much lower level and with some indication of lagging a month behind.

Class 6 reflected at a much lower level the pattern of class 7.8.9.

Class 7.8.9 had a September and late summer (probably February) peak. The rapid decline during November and February-March represented larvae pupating for the spring and autumn emergences respectively.

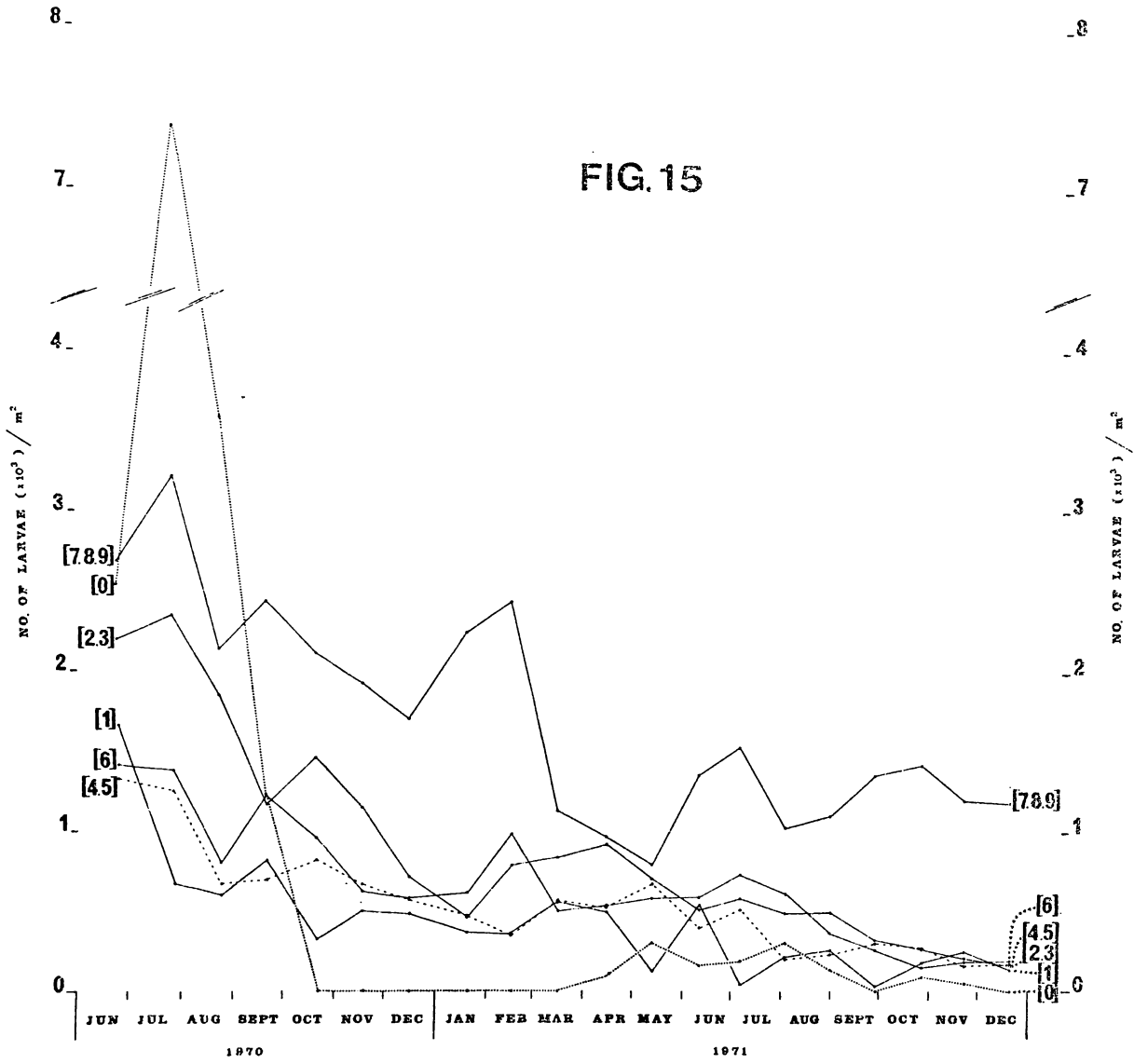
#### Whakatane study site (Fig. 15)

Heavy mortality and a continuously declining total larval population masked the individual class trends at this site (see p.117 for discussion).

FIGURE 15

Changes of the individual larval classes at the Whakatane site.

FIG. 15



(vi) Discussion on Larval Classification

Because of the size difference between the sexes and the variable rate of development within each, the larvae within any class were not necessarily the same age. To explain the movement of the larvae through the class system the following assumptions were made:

1. Larvae which hatched from eggs laid in spring developed at the same rate as those from eggs laid in autumn.

2. The life cycle started during the autumn of 1971 in the screenhouse at Ruakura consisted of a 50 : 50 ratio of males and females.

3. During the course of the experiment both sexes suffered the same degree of mortality.

4. The female larvae grew at a faster rate than the males.

With reference to the life cycle work commenced in early April (Table 7) (1971) all the larvae were still in class 0 by the beginning of June, although even by this stage there was a wide variation in actual body weight (see p. 50). At the end of August, 49% of the population had moved into class 1. This probably represented the point where the majority of the female larvae had entered into class 1, whilst the majority of the male larvae still remained in class 0. Assuming that this trend continued, by 21.4.72, the majority of the female larvae had probably entered into class 7.8.9 with some still being present in class 6, while the males were approximately equally divided between classes 4.5 and 6, with some still occupying classes 1 and 2.3. Five months later (25.9.72), approximately 90% of the surviving population had reached class 6 or above, the majority of female larvae probably being in class 7.8.9 and the majority

Table 7 The estimated percentage of surviving larvae in each class throughout a two year period based on the life cycle work commenced autumn 1971. Projected figures for larvae hatched at the beginning of December are also presented (underlined), assuming a four month interval between the middle of the spring and autumn emergence periods. The percentage figures refer only to the larvae coming from one particular emergence period, and are not representative of the population percentage of the larval groups.

<u>Date commenced</u>	<u>% in each larval class</u>						<u>No. of Larvae weighed</u>		
	<u>Spring '70</u>	<u>Autumn '71</u>	<u>0</u>	<u>1</u>	<u>2.3</u>	<u>4.5</u>		<u>6</u>	<u>7.8.9</u>
4 . 2.71			<u>100</u>						
1.. 3.71			<u>63</u>	<u>37</u>					
27. 3.71			<u>62</u>	<u>38</u>					
23. 4.71			<u>51</u>	<u>49</u>					
21. 5.71			<u>19</u>	<u>67</u>	<u>14</u>				
	4 . 6.71		100						100
18. 6.71			<u>10</u>	<u>65</u>	<u>19</u>	<u>6</u>			
	30. 6.71		63	37					100
	27. 7.71		62	38					50
16. 8.71			<u>7</u>	<u>34</u>	<u>47</u>	<u>5</u>	<u>7</u>		
	23. 8.71		51	49					100
	21. 9.71		19	67	14				100
26. 9.71			<u>0</u>	<u>10</u>	<u>46</u>	<u>23</u>	<u>15</u>	<u>6</u>	
15.10.71			<u>0</u>	<u>11</u>	<u>34</u>	<u>21</u>	<u>28</u>	<u>6</u>	
	18.10.71		10	65	19	6			75
14.11.71			<u>0</u>	<u>4</u>	<u>19</u>	<u>19</u>	<u>34</u>	<u>24</u>	
	16.12.71		7	34	47	5	7		42
21.12.71			<u>0</u>	<u>4</u>	<u>9</u>	<u>17</u>	<u>35</u>	<u>35</u>	
24. 1.72			<u>0</u>	<u>0</u>	<u>5</u>	<u>17</u>	<u>43</u>	<u>35</u>	
	26. 1.71		0	10	46	23	15	6	30
	15. 2.72		0	11	34	21	28	6	28

Table 7 continued

<u>Date commenced</u>		<u>% in each larval class</u>						<u>No. of</u>
<u>Spring '70</u>	<u>Autumn '71</u>	<u>0</u>	<u>1</u>	<u>2.3</u>	<u>4.5</u>	<u>6</u>	<u>7.8.9</u>	<u>Larvae</u>
								<u>Weighed</u>
22. 2.72		<u>0</u>	<u>0</u>	<u>5</u>	<u>13</u>	<u>45</u>	<u>37</u>	
	14. 3.72	0	4	19	19	34	24	26
24. 3.72		<u>0</u>	<u>0</u>	<u>5</u>	<u>10</u>	<u>45</u>	<u>40</u>	
	21. 4.72	0	4	9	17	35	35	23
23. 4.72		<u>0</u>	<u>0</u>	<u>5</u>	<u>9</u>	<u>44</u>	<u>42</u>	
	24. 5.72	0	0	5	17	43	35	22
25. 5.72		<u>0</u>	<u>0</u>	<u>5</u>	<u>5</u>	<u>40</u>	<u>50</u>	
	22. 6.72	0	0	5	13	45	37	22
24. 6.72		<u>0</u>	<u>0</u>	<u>5</u>	<u>5</u>	<u>28</u>	<u>62</u>	
23. 7.72		<u>0</u>	<u>0</u>	<u>6</u>	<u>0</u>	<u>25</u>	<u>69</u>	
	24. 7.72	0	0	5	10	45	40	21
21. 8.72		<u>0</u>	<u>0</u>	<u>7</u>	<u>0</u>	<u>7</u>	<u>86</u>	
	23. 8.72	0	0	5	9	44	42	20
	25. 9.72	0	0	5	5	40	50	19
30. 9.72		<u>0</u>	<u>0</u>	<u>9</u>	<u>0</u>	<u>9</u>	<u>82</u>	
	24.10.72	0	0	5	5	28	62	19
28.10.72		<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>100</u>	
22.11.72		<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>100</u>	
	23.11.72	0	0	6	0	25	69	17
	21.12.72	0	0	7	0	7	86	16
	30. 1.73	0	0	9	0	9	82	13
	28. 2.73	0	0	0	0	0	100	6
	22. 3.73	0	0	0	0	0	100	5

of male larvae in class 6. During the spring and summer (1972-1973) more and more probably male larvae moved into class 7.8.9. Assuming that larvae hatched during the spring emergence (beginning of December taken as the middle of the emergence period) developed at the same rate as the above, they would pass through the above classes approximately four months earlier. This assumption was supported to some extent by the approximate four month period <sup>two peaks of both classes 0 and 1 respectively which occurred</sup> between the ~~class 0 and class 1 peaks~~ at Hamilton during 1971.

Larvae that hatched between the spring and autumn emergence period would occupy a position intermediate between the two described above.

The end of June would appear to be a suitable time to separate the larvae into age groups of under (0+) and over (1+) one year of age (Table 7). However, the field data suggests that at the end of July 1972 there was still a large number of class 2.3 larvae present which hatched during the 1970-1971 season. The number of eggs laid during the spring of 1970 and 1971 were very similar (see p. 112), thus, the big difference in numbers of class 2.3 larvae between July 1972 and July 1971 was probably due to the autumn emergence of 1971 being much larger than that of 1970. The above explanation was supported by the drop in numbers in this class during the following few months with a corresponding increase in classes 6 and 7.8.9. The discrepancy between the field and insectary data on the above point could possibly be attributed to the very high mortality which was experienced in rearing the larvae, and this may have been biased towards the smaller larvae. Thus, early September, although not ideal, was selected as the time to divide the larval population into those under (0+) and over (1+) one year of age. Classes 0, 1, and 2.3 were classified as 0+ larvae and

classes 4.5, 6 and 7.8.9 as 1+ larvae at this date.

The above classification had certain anomalies. With reference to Table 7, during September, classes 2.3, 4.5, 6 and 7.8.9 all have larvae which were incorrectly classified. Assuming that both spring and autumn emergences contributed the same number of new members to the larval population, and ignoring mortality factors, in September approximately 45% of the previous spring population were classified as 1+ compared with approximately 5% of the autumn 1+ population classified as 0+. There was a discrepancy of 40%. Probably by September a negligible number of larvae from the spring emergence, approximately 22 months earlier, were still in classes 2.3 and 4.5.

When considered together with the autumn emergence of the same season, the above discrepancy amounted to 20% of the 0+ larval population being classified as 1+. Fluctuations in the relative sizes of the spring and autumn emergences (all other things being equal) will cause some variation in the above percentage, but there will <sup>usually</sup> be some bias towards underestimating the 0+ group. But, in the light of the differences between the field and insectary data commented on earlier, the actual percentage underestimation was probably very much less than the figure previously mentioned, and compared with sampling and extraction errors, was probably not of much practical significance.

Hitchcock (1970) has reported that the particular instar a larva was in, did not necessarily reflect its correct age. Some larvae reached the sixth instar in five months, whilst others took twelve months. Thus, there appeared no easy way of classifying the larvae by age, and the proposed division based on weight, although by no means perfect, did allow some assessment of the larval age structure

to be made. Unfortunately the complexity of the lifecycle made it impossible to accurately sample for any particular class at its peak, (since larvae of different ages would be present).

The larval work reported from Queensland, Australia is based on one emergence period per season occurring in autumn. With the two emergence periods which occur per season in New Zealand the larval population has a considerably more complex age structure. However, in most other respects the larval life history resembled that reported for the insect in Australia.

## The Pupal Stage

### 1. Description

Pupation occurs within the old larval skin, which assumes a dry, rigid appearance (Irwin-Smith 1921a). There is a basic size difference between male and female pupae, male pupae measuring 7-8 mm in length, and female pupae 10-11 mm (Irwin-Smith 1920). The above also shows up as a difference in weight, the female weighing on an average almost twice as much as the male, i.e.  $24.3 \pm 1.39$  (n = 90) and  $12.9 \pm 0.67$  (n = 60) mg. respectively. However, there was a considerable degree of overlap in weight and it was necessary to dissect the pupae to definitely determine their sex. Irwin-Smith (1923) has described in detail the morphological changes which occur during pupal development.

Pupae occur just beneath the soil surface.

### 2. Length of the Pupal Period

Irwin-Smith (1920) recorded that the pupal period lasted for at least 18 days (Australia), and Campbell and Koehler (1971) showed

that at 20 °C the length was between 23 and 29 days (U.S.A.). There was no apparent difference between the sexes.

As the onset of pupation is not marked by any outward change in the form of the larva the exact time that a larva enters the pupal stage is difficult to determine (Irwin-Smith 1920). However, larvae were considered to have entered the pupal stage when the skin had become more dried and leathery, and abdominal puckering was becoming noticeable. Thus, the decision as to when pupation commenced was partly subjective. However, with some experience a reasonably consistent estimate could be made, though possibly underestimating the length of the pupal stage by one or two days.

Pupae were kept individually on moist filter paper under insectary conditions (mean maximum  $22.0 \pm 1.3$  °C; mean minimum  $10.8 \pm 1.0$  °C) during the autumn of 1970. The mean length of the pupal period was  $28.2 \pm 1.9$  (n = 41) days, which agreed reasonably well with Campbell and Koehler's (1971) data. Under New Zealand pasture conditions the pupal period lasts approximately a month.

### 3. Time of Occurrence

Pupae occur in peak numbers during October - December and February - April corresponding with the two major emergence periods.

### Summary of the Life History under New Zealand Conditions

There are two adult emergences each year, one in spring (November - December) and the other in autumn (March - April), the latter usually being the larger of the two. The adults only live for a few days. The eggs take approximately two weeks to hatch. The time spent in the larval period is variable, with a small percentage

remaining approximately 11 months, the majority taking between 19 and 27 months, with 23 months probably being the most usual. A very small number probably took 35 months. The pupal stage lasts approximately a month.

The above type of life history probably confers a considerable survival advantage on the insect. With four generations present at the same time there is a good chance that unless a certain mortality factor acts equally on all age intervals, some larvae will survive any natural catastrophe that might occur.

MATING AND OVIPOSITION BEHAVIOUR OF THE ADULT  
SOLDIER FLY

Introduction

Flight activity occurs during the day, and usually reaches a peak towards late morning. The adults are slow and weak fliers, and even for stratiomyids, sluggish in their habits (Irwin-Smith 1920 and Mungomery 1926). They rest for long periods on the grass blades. There is a distinct difference between male and female flight (Kessel 1948 and Campbell 1968). The males characteristically fly in clusters in a zigzag fashion just above the level of the grass, whereas the females tend to fly less readily and have a generally, higher, longer and more directional flight.

Mating occurs on the vegetation (Kessel 1948, Campbell 1968, and Wilson 1969 pers. comm.), and according to Campbell, females were often mated several times. Irwin-Smith (1921a) noted that immediately after emergence adults would climb to the top of a grass blade and rest there. She also described a courting dance where a male followed a female in a rapid jerky flight. However, Campbell (1968) did not observe such a dance, and commented that it appeared that the males in their flight over the grass tops were attracted to females resting in the grass below. Both Kessell (1948) and Campbell (1968) noted that frequently two or more males attempted to copulate simultaneously with the same female, and Campbell observed that mating can occur among newly emerged teneral adults before their wings have hardened sufficiently to permit flight.

According to Wilson (1969 pers. comm.) oviposition can occur at any time from less than half an hour up to several hours after

mating. However, females which emerge later than mid-day seem to wait till the next day to oviposit. From observations of caged females, Irwin-Smith (1920) noted that ovipositing occurred rapidly and that eggs were laid irregularly on the top of one another in one or two clusters. Campbell and Koehler (1971) have observed females walking about on the soil surface, both in the field and the laboratory, probing into crevices with their ovipositors. They concluded that a thigmotactic response was associated with oviposition.

#### Mating and Oviposition Behaviour Under New Zealand Pasture Conditions

The account below is based on field observations made over a two year period (1970 to 1972) on the Ruakura Agricultural Research Centre station.

Generally it would appear that on emergence, females climb to the top of the nearest grass blade and wait there to be mated. The males tend to fly in clusters in a slow, sometimes hovering, zigzag fashion over the pasture. On locating a waiting female they will attempt to copulate with her. There appeared to be no preliminary to mating, and on location of the female the male mounted and commenced copulating. Mating lasted for one to eight minutes and usually the male would then fly away. Occasionally, the female ended copulation by walking down the grass blade, into the grass mat until the male was brushed off. On several occasions non-gravid looking females were observed being mated, thus, many females were probably mated more than once. However, just mated females usually did not immediately copulate with another male.

Male flight to locate the resting females was the most common method observed. However, when flight activity was high several females were observed to be mounted by males while both were in

flight. Immediately they fell to the ground where mating continued.

On two occasions a female was observed hovering about 15cm above the ground, then taking a short jerky flight forwards for 2-3 cm, hovering, then moving forward again. A male followed behind with a similar flight pattern, and when the female landed, copulated with her. This may have been the 'dance' described by Irwin-Smith (1921a).

When very few males were present, occasionally whole clusters of up to a dozen females were observed to hover just above the grass for a minute or more and then to resettle. This was repeated several times and may have been to attract males.

The mechanism by which the male located the female was not clear. Usually newly emerged females were mated quite rapidly in the early morning just after the commencement of flight. However, on one occasion a newly emerged female sat for 25 minutes on top of a grass stem without being mated, while several males flew past. It was not until a male flew within 2-3 cm that she was mounted. Males were frequently observed trying to mate with other resting males and even ribgrass (Plantago lanceolata) seed heads. Occasionally one female was besieged by up to a dozen or more males, and a tight cluster of adults was formed at the top of a long grass blade or seed head. In forming the above, there was initially a considerable amount of movement among the outer males, presumably to try and mate with the central female. But, as the group grew in size the whole cluster tended to sit still. Such groups were observed intact for up to 10 minutes, then usually either the grass stem toppled over, or the outer males slowly started to leave the cluster and the group dispersed. The above was also observed to centre around two males

attempting to copulate.

Newly emerged females were observed to elongate their abdomens slightly, and turn the tip upwards; this might provide some visual or chemical stimulus to the male. The red head of the female, or her gravid abdominal silhouette when newly emerged, or any combination of the above, could play a part in helping the male locate the female. Perhaps several step sequences are involved, the first of which is chemical, and then when within a certain range visual and tactile mechanisms come to the fore. This could explain the almost chaotic way males attempted to mate with other males or objects against the skyline, if by chance they happened to pass within a certain distance of them. Another possibility is if the male behaves similarly to Habrobracon (Murr 1930), which is attracted to the female by scent, but will also attempt to mate with other males if they have recently copulated.

Immediately after mating all newly emerged females move down into the grass mat and search for suitable oviposition sites. Although difficult to follow when moving amongst the bases of the pasture plants, one female was followed for over 20 cm before being lost. However, most only moved five to seven cm before locating a suitable oviposition site. The females rummaged around in the grass mat, initially using their head receptors to seek for suitable cracks in the soil surface or a small gap between the soil surface and a plant stem. When a possible site had been located the female turned her body around and extended her abdomen into the possible site and thoroughly explored it with her mobile tactile cerci and elongated abdomen. The female often forced her way back into the crack as far as she could, to the extent of crumpling up her wings

in the process. The above was often repeated several times before a suitable site was chosen. When a place had been selected she laid a cluster of eggs (about 40 per cluster), and then climbed to the top of a grass blade and rested. On an average each female was capable of laying three to four clusters (see fecundity section). After laying the first cluster close to where she copulated, or after searching for an initial oviposition site, she usually took a short unidirectional flight of between 1 and 30 m. On landing she either rested and then searched for another oviposition site or rested and then took another short flight before searching for a suitable site. Females often had long rests before flights, and one female was recorded resting for well over two hours before moving.

Moisture and the physical closeness of the sides were probably the critical factors in the choice of the oviposition site. However, under stress females appeared to deposit their eggs almost anywhere, although when held in containers they tried to deposit them in a corner if possible.

Females kept in captivity would lay eggs without first being mated. Whether, or how often this happens in the field is not known. Moller (1965) has commented that when females emerge in standing sugar cane in Queensland they do not move far from the point of emergence. However, on emerging in a fallow field he reported them being able to move 'considerable distances', usually in the direction of the prevailing wind. Thus, if no suitable oviposition sites were close at hand, females would probably attempt to disperse as far as possible, but as death approached would probably lay their eggs in the best place they found.

THE DEVELOPMENT OF A POPULATION TABLE  
FOR I. RUBRICEPS

The Mechanics of Sampling

1. Introduction

Life tables systematically record those facts basic to understanding population change throughout the life cycle of the species (Allee et al 1949, Harcourt and Le Roux 1967). The terms 'life equation' (Leopold 1939) and 'budget' (Richards 1961) have also been used.

Deevey (1947) discussed the meaning of life tables and the different types which could be constructed. However, the term 'life table' and the type as outlined by Morris and Miller (1954) and developed for the Spruce budworm have been accepted as the working norm by the majority of workers in the field of insect population dynamics and system modelling.

Life tables are not an end in themselves (Richards 1961, Clarke et al 1967, and Harcourt 1969), and one or two will only reveal the type of survivorship curve for the particular insect. A sequence of tables is required, replicated in time and space, to develop a population model. The purpose of this model is twofold, first to project the generation to generation changes in insect population density, and second to project the average level about which these changes take place. According to Varley and Gradwell (1970) no models have yet been published which accomplish both of the above.

The population table of Beaver (1956) is of the same general form as a life table, but is modified to deal with the presence of overlapping generations, incomplete mortality and different immature

stages occurring at the same time.

The basic aim of the following work was to evaluate the feasibility of developing life tables, population tables, or some modified form of the above for soldier fly under pasture conditions.

## 2. Description of Study Sites

The sampling universe was an arbitrarily defined area of soldier fly infested pasture as representative as possible of the district in which it was located.

The size of the study areas were arbitrarily chosen hopefully large enough to allow eventual monitoring of any predator population and to make the amount of soil removed for soldier fly assessments during the course of the work negligible relative to the total area of the site. Yet small enough to ensure as much as possible, uniform conditions as far as microclimate, aspect, soil type, pasture composition and grazing pressure were concerned on the soldier fly population being monitored.

There were three study sites; at Hamilton, Whakatane, and Karaka respectively (Map references: N.Z.M.S.I., N. 65/822488, N. 69/382281, and N. 47/411317). A description of the site and of the work carried out at each is given below.

### (i) Hamilton (Central Waikato)

The study site was situated in an approximately 2 ha paddock on the Ruakura Agricultural Research Station. The soil type was Hamilton clay loam. The exact age of the pasture was unknown, but was at least ten years old. The pasture composition, as estimated by the point analysis method described by Brown (1954), was as follows in August 1972: 23.44% ryegrass (Lolium perenne),

49.90% Poa trivialis, 3.44% paspalum (Paspalum dilatatum), 8.85% white clover (Trifolium repens), 12.08% weeds, and 2.29% bare ground.

The land had not been treated with any insecticide since 1964.

The study site was on a gentle slope facing north-east. From 1969 until mid 1972 the land was grazed by the Genetic Section stud sheep stock, at between 12 and 16 ewe equivalents per hectare.

This was the only site at which a comprehensive population study on all stages of the insect was carried out. From pilot sampling there appeared to be no obvious way of stratifying the area on different levels of soldier fly population density. Thus, sampling for all stages was carried out in a proportionally stratified random way to gain an even coverage of the area (Cochran 1963).

Initially an area of 36.6 x 36.6 m was divided into four strata each 18.3 x 18.3 m. During mid 1970 the sampling area was increased to form a 73.2 x 73.2 m area divided into eight strata each 36.6 x 18.3 m. These strata were located approximately in the centre of the paddock and were well clear of any fences or gateways.

(ii) Whakatane (Bay of Plenty)

This area was situated on Mr. Baird's town milk supply dairy farm, approximately 8 km north of Whakatane, on the Rangitaiki Plains. The soil type was Paroa silt loam, and the whole farm was situated on flat land. Nine hectares of heavily infested soldier fly land was to be surface cultivated in the autumn of 1970 (see Wilcocks and Hewitt 1971). A study site was established to (1) monitor the effect of cultivation on the soldier fly population, (2) assess the rapidity of re-infestation and (3) monitor the population change in the control area. Only the third of the above aims is reported here.

The control area occupied 3010 sq. m., and was divided into four 27.43 x 27.43 m strata situated well clear of gates and fences in the middle of a 9 ha. paddock. The original pasture was at least ten years old, and had the following composition in August 1972: 15% ryegrass (Lolium perenne), 3.33% paspalum (Paspalum dilatatum), 23.33% Poa trivialis, 2.5% prairie grass (Bromus unioloides), 1.39% timothy (Phleum pratense), 40.17% clovers (Trifolium spp.), 11.11% weeds, 4.17% bare ground. The farm was grazed by 180 - 210 cows on an approximate 21 day rotation.

(iii) Karaka (South Auckland district)

A study site was set up during the middle of 1971 on Mr. Pert's farm at Karaka, to monitor adult emergence during the 1971/72 season. The site, 73.15 x 73.15 m divided into eight strata each 18.29 x 36.58 m, was situated well clear of any fence and gate ways, and in a paddock with a northerly aspect. The soil type was the Karaka complex, and the pasture which was at least ten years old had been oversown with ryegrass the previous two autumns. The pasture composition in August 1972 was as follows: 16.25% ryegrass (Lolium perenne), 3.75% paspalum (Paspalum dilatatum), 44.69% Poa trivialis, 16.56% clovers, 13.17% weeds, 6.15% bare ground.

The property was a town milk supply dairy farm, and was grazed by 180 cows on a two to three week rotation.

### 3. Choice of the Sampling Unit

(i) Introduction

Morris (1955) has suggested the following six criteria, modified by Southwood (1966), for choosing the most appropriate sampling unit:

- (1) It must be such that all units of the universe have an equal chance of selection.
- (2) It must have stability (or if not its changes should be easily and continuously measured - as with the number of shoots in a cereal crop).
- (3) The proportion of the insect population using the sample unit as a habitat must remain constant.
- (4) The sampling unit must lend itself to conversion to unit areas.
- (5) The sampling unit must be easily delineated in the field.
- (6) The sampling unit should be of such a size as to provide a reasonable balance between the variance and the cost.

Since the egg, larval and pupal stages of soldier fly occurred in the ground and the adults emerged from it, the assessment of the absolute population of each stage presented no real problem. The sampling unit was a given area of pasture, taken to a certain depth for the subterranean stages. The choice of the sampling device used and the timing of sampling for each stage is given below.

#### (ii) The Larval Stage

The sample was taken with a soil corer similar to that described by O'Connor (1957), but fitted with a hammer. The necessary depth to sample was unknown, and the following work on larval vertical distribution was carried out to determine this.

#### Larval Vertical Distribution

Introduction The larvae are subterranean and usually found in close association with plant roots (Irwin-Smith 1920). She reported that under lawn conditions in New South Wales, Australia, during April, the majority of the larvae were found in the top 10 cm. There appeared to be a greater number of large larvae in the top 5 cm whilst

smaller larvae were found at the 7.5 - 10.0 cm level among the fine grass rootlets. A few medium sized larvae ( 5 - 8 mm long ) were found at the 25 cm level.

Both Marryatt (1944) and Timlin (1969) commented that under pasture conditions in New Zealand, larvae were usually found in the top 5 - 7.5 cm where the plant roots were most numerous. Both reported a tendency for the smaller larvae to predominate at slightly greater depths, and according to Timlin (1969) a few larvae occasionally migrated to a depth of about 20 cm.

Campbell (1968) found that in California under lawn conditions no larvae occurred more than 12.5 cm below the soil surface, and he reported that the majority of the larval population occurred in the top 7.5 cm. This apparently reflected the grass root distribution.

In the sugar cane fields of Queensland, Australia, Moller and Mungomery (1962) and Wilson (1969) reported that larvae could be found feeding on the roots of cane and grasses to depths of between 30 and 50 cm. The vertical larval distribution appeared to depend largely on the degree of moisture present, the larvae tending to go deeper in search of moister conditions.

Field work carried out on the larval vertical distribution To determine the maximum depth of soil samples to assess the larval population effectively under pasture conditions, the following was carried out at the Hamilton and Whakatane sites.

At Hamilton, the larval population was sampled on 16.12.69 and 2.6.70. On the first occasion twelve 7.62 cm diameter cores, 20.3 cm deep were taken in a stratified random manner, six cores from each of the two 18.3 x 36.58 m strata. Each core was divided into three parts representing the vertical levels 0 - 10.16 cm, 10.16 - 15.24 cm

and 15.24 - 20.32 cm, and the larvae were extracted from each using the washing method described by Wilcocks and Oliver (1971). Results are shown in Table 8.

Table 8 Vertical distribution of larvae at the Hamilton site (16.12.69).

<u>Depth in cm</u>	<u>Mean no. of larvae / core</u>	<u>% of total</u>
0.00 - 10.16	26.75	85.6
10.16 - 15.24	3.25	10.4
15.24 - 20.32	1.25	4.0

The above experiment was repeated in a slightly modified form on 2.6.70. Ten 7.62 cm diameter cores, 25.4 cm deep were taken in a stratified random manner, five from each of the two strata. This time, each core was divided into five parts, representing the vertical levels 0 - 5.08 cm, 5.08 - 10.16 cm, 10.16 - 15.24 cm, 15.24 - 20.32 cm, and 20.32 - 25.4 cm. Table 9 shows the results.

Table 9 Vertical distribution of larvae at the Hamilton site (2.6.70)

<u>Depth in cm</u>	<u>Mean no. of larvae / core</u>	<u>% of total</u>
0.00 - 5.08	10.0	74.63
5.08 - 10.16	3.2	23.88
10.16 - 15.24	0.2	1.49
15.24 - 20.32	0.0	0.00
20.32 - 25.40	0.0	0.00

The above experiment was repeated at Whakatane on 4.8.70.

Twenty-four 7.62 cm diameter cores, 25.4 cm deep were taken in a stratified random manner, six per strata. Each core was divided into five parts as at Hamilton on 2.6.70. Table 10 shows the results. All the larvae from samples 1, 6, 7, 16 and 21 were weighed and classified on the log weight scale (Table 11).

Table 10 Vertical distribution of larvae at the Whakatane site (4.8.70).

<u>Depth in cm</u>	<u>Mean no. of larvae / core</u>	<u>% of the total</u>
0.00 - 5.08	49.58	77.43
5.08 - 10.16	11.12	17.37
10.16 - 15.24	2.37	3.70
15.24 - 20.32	0.75	1.17
20.32 - 25.40	0.21	0.33

Table 11 Vertical distribution of the different larval classes at the Whakatane site.

<u>Class</u>	<u>% of each class at the different depths in cm</u>				
	<u>0.00-5.08</u>	<u>5.08-10.16</u>	<u>10.16-15.24</u>	<u>15.24-20.32</u>	<u>20.32-25.40</u>
0	39.02	6.98	0.26	0.0	0.0
1	4.38	2.63	1.55	0.0	0.26
2.3	11.96	1.56	0.78	0.0	0.0
4.5	4.76	2.22	0.74	0.0	0.0
6	5.30	1.59	0.04	0.0	0.0
7.8.9	15.19	0.51	0.0	0.0	0.0

Discussion The above results support the observations of Marryatt (1944), Campbell (1968) and Timlin (1969) showing that the vast majority of the larval population occurs in the top 10.16 cm under pasture conditions. This depth coincided with the region of maximum root concentration in the study areas. A small percentage of larvae were found between 15.24 and 25.40 cm.

There was a higher percentage of larvae between the 10.16 and 20.32 cm level at Hamilton during the summer (14.4% of the larval population) relative to the winter (1.49%). This perhaps could have been due to a difference in soil moisture between the two sampling dates. However, differences in larval age structure and densities probably also affect vertical distribution. All the larval classes occurred at their highest levels in the top 5.08 cm mirroring the vertical distribution of the larvae as a whole. However, beneath the 5.08 cm level, there was a marked tendency for the smaller larvae to predominate.

Based on the above information and in consideration of the degree of sampling precision that was practically obtainable, a 15.24 cm deep core was considered to be satisfactory for assessing the larval population under pasture conditions.

Time of larval sampling The larval population was sampled at monthly intervals throughout the year so that both the larval population and class structure in association with the insectary life history work could be monitored.

### (iii) The Pupal Stage

The pupae occurred just beneath the soil surface. A suitable surface area of pasture to a depth of 1.5 cm was used as the sampling unit. In practice a 4 cm deep core was taken with a stirrup

corer, to allow the surface layer to be lifted without breaking. Before extracting the pupae the extra soil was cut off.

Time of pupal sampling The pupal population was assessed for the two main periods of adult emergence, spring and autumn. Pupal samples were taken immediately after the first adults had been observed in the field. This was possible since the pupal skins of newly emerged adults were still easily recognisable after one to two weeks, and thus an assessment of the total pupal population before emergence began could be made by combining the number of live pupae with the number of pupal skins. Also, the first week of adult emergence was usually low thus the bulk of the pupal population was still developing at the first sampling.

As the adult emergence period lasted over a period of 7 to 8 weeks, and the pupal stage lasted only a month, a second lot of pupal samples was taken approximately four weeks after the first.

#### (iv) The Adult Stage

The number of adults emerging per unit area of land was assessed by trapping them on emergence. The trap used is described by Oliver (1973) and briefly consisted of a conical shaped piece of organdie attached to a PVC flange at its base, and leading into a collecting bottle at the other end. A wire loop was pegged through the PVC flange anchoring the trap and taking up any unevenness in the ground. The diameter of the loop also set the area over which the cage collected. A pyramidal stock cage, fitted over the whole, acted as a support for the emergence cage by means of a thick rubber band suspended from its apex to the collecting bag. Before setting the cage, the grass to be covered was cut to a height of 2 cm to ensure a close fit to the ground, and to make checking of

the ground for adults easier when the cages were cleared.

Time of sampling for the adult stage The emergence cages were set well before the commencement of the spring emergence, and were not removed from the field until after the autumn one. To ensure that emergence had ceased, the cages were not removed until two consecutive weeks of zero emergence had been recorded. During the two main emergence periods, the cages were cleared weekly and relocated fortnightly. During the intervening summer period, the cages were cleared fortnightly and relocated once a month. The reason for the regular repositioning was to prevent an atypical microclimate developing under the cages compared to that of the rest of the paddock.

(v) The Egg Stage

The eggs are laid in clusters either just beneath the soil surface in cracks, or on the soil surface beneath a clover stolon or grass stem. A suitable surface area of pasture to a depth of 1.5 cm was used as the sampling unit, and collected in the same way as for pupal sampling.

Time of sampling for the egg stage These were sampled for approximately fourteen days after the commencement of the week during which total adult emergence was equal to or exceeded  $10/m^2$ . Thereafter eggs were sampled for every two weeks for as long as the weekly emergence was equal to or exceeded the above figure. When weekly adult emergence was below this level, it was not within the available resources to take enough samples to make an estimate of the egg population with any worthwhile degree of precision (see p. 91 & 125).

#### 4. Extraction of the Various Stages

##### (i) The Larval Stage

The method developed by Wilcocks and Oliver (1971) was initially used for extracting soldier fly larvae. The extraction efficiency of the above method was tested for class one larvae and above, and found to be reasonably good. However, no specific test was carried out for the very small larvae in the class 0 group, since firstly they were initially unavailable, and secondly, during the winter of 1970, both at Hamilton and Whakatane sites it appeared that by July (approximately two to three months after the autumn emergence) the whole larval population was being efficiently extracted. Class 0 larvae were being recovered and the population was showing no sign of further increase. However, during the winter of 1971 at Hamilton, the larval population continued to show considerable increases for several months after the autumn emergence had concluded (Fig. 19a). The main reason for this must have been due to the inefficient extraction of the class 0 larvae.

From the Hamilton population data it was estimated that at the end of May 1971 only about 10% of the class 0 larvae were being extracted. Most of the loss was possibly occurring in the rotary sieves due to mechanical damage. Thus, it was considered that the extraction technique could be improved by abandoning the heavy water jetting, occasional shaking of the sieves and the intersieve. The above modified method was tested by washing ten reconstituted (7.6 cm diameter, 15.2 cm deep) samples each seeded with 15 class 0 larvae (approximately two months old). Sixty-one percent of the larvae were recovered, which was a considerable improvement.

The washing process was divided into sections, to assist in determining the degree that each part contributed to the overall loss of this group of larvae. Essentially, the same method as described above, was used i.e. the seeding of reconstituted samples. The following results were obtained:

<u>Section of washing process</u>	<u>% loss of class 0 larvae</u> (2 months old)
1.The action of the rotary sieves in the water bath	19
2.The separation of larvae from the coarse plant material	5
3.The entire flotation process	10
4.The final separation of larvae from the fine plant material	5
Total overall loss	39

The greatest single loss was due to the rotary sieves. To overcome this, a new method of breaking up the soil core was developed. The intact soil core was dispersed by the up and down movements of a bladed plunger in a cylinder of water (90 cm high, 14 cm diameter). When this method was used to replace the rotary sieves, 83% of the seeded larvae were recovered. However, considerable difficulty was experienced in removing the fine mineral particles from the rest of the sample before the floatation process. This was carried out by frequent gentle washings from one half rotary sieve to the other, but was time consuming.

It can be seen that the use of the 'plunger method' to disperse the soil particles caused very little mechanical damage to the small

larvae. However, the elimination of the fine mineral particles before the flotation process was a problem, and work is still in progress on developing the above method further.

(ii) The Pupal Stage

Hand sorting was used to extract pupae from samples. The main reason for adopting this method was that live undamaged female pupae were required to estimate adult female fecundity. The pupal skin was easily damaged, and this ruled out any mechanical extraction method.

Located just beneath the surface, the pupae were easy to find by systematically scratching away the whole surface area of the sample to a depth of 1.5 cm, with a pair of forceps. To check the accuracy of this method, one sample in six was selected at random (ten samples in all) and double checked by another sorter. This indicated an initial percentage recovery of 93%. In addition, spot checks were made at each pupal sorting session, and the recovery rate was always found to be above 90%.

(iii) The Adult Stage

The number caught by each emergence cage was counted. On clearing the cages, the ground and the inside of the cage was carefully checked for live or dead adults and these were added to the collection bag.

(iv) The Egg Stage

Egg clusters were counted by hand sorting the sample under a microscope ( x5 ). It was found to be much easier to count egg clusters by hand sorting than to extract individual eggs using a mechanical method. The mean number of eggs per cluster was

estimated at  $42.03 \pm 7.96$  ( $n = 61$  clusters). As for pupal samples, the surface area was systematically removed to a depth of 1.5 cm using a pair of forceps.

The accuracy of the above method was checked in the same manner as for pupal extraction, and in none of the samples checked were additional clusters found. However, it is probably advisable to assume a possible 10% loss in numbers due to sorter error.

#### 5. Choice of the Sampling Unit Size

The frequency distribution of samples from naturally occurring animal populations usually tends to show overdispersion, and I. rubriceps is no exception. As a general rule, when sampling such a population, it is more precise and informative to take a large number of small samples than a smaller number of large ones (Morris 1960, Cassie 1963b).

A rational choice between two sizes of unit may be made by selecting the unit that gives the smaller variance for a given cost or the smaller cost for a prescribed variance (Cochran 1963). However, in many practical problems there may be imponderable factors. One type of unit may have some special convenience or disadvantage that is difficult to include in the calculation of costs. Also since population density and hence variance is usually fluctuating it is probably not practicable to put too much stress on a precise determination of optimum sample unit size (Southwood 1966). Yates and Finney (1942) found for wireworm sampling that although the 4 and 6 inch diameter corers were equally efficient at low densities, at high densities the comparative efficiency of the six inch sampler fell off. However, even rough costings of different experimental techniques will usually help enormously in making efficient use of

limited resources (Fisher 1947). Thus, the size of the sample unit was chosen based on a combination of Cochran's suggested method and a subjective evaluation of certain cost factors which were difficult to measure.

(i) The Larval Stage

Four different sizes of soil corer, 2.54, 3.81, 6.35 and 7.62 cm diameter, were compared at the Hamilton site, and in addition a 10.16 cm diameter core was evaluated at Whakatane (Table 12).

Table 12 Comparison of different sized larval sampling units re cost and variance.

<u>Volume ratio</u>	<u>Cu' Su' 2</u>	
	<u>Hamilton site</u>	<u>Whakatane site</u>
1 (2.54 cm diameter corer)	167.08	94.24
2.25	152.93	137.34
3.25	71.38	-
6.25	74.21	40.01
9 (7.62 cm diameter corer)	23.82	19.18
12.25	15.20	-
15.25	11.43	-
16 (10.16 cm diameter corer)	-	18.09
25	-	7.94
Population density / m <sup>2</sup>	7833	3243

All cores were taken to a depth of 10.16 cm and in each case the larvae were extracted using the method described by Wilcocks and Oliver (1971). The different size cores were taken in clusters as close together as possible to minimise random effects between them, and twenty such clusters were taken in a random stratified manner.

The variance of each unit was reduced to a common basis ( $S'_u{}^2$ ) by dividing it by the volume ratio of a particular corer. This ratio was based on the volume of the smallest unit equalling 1. The cost of each unit was similarly reduced ( $C'u$ ). A  $\log(X + 1)$  transformation was used for comparing the variances (see p. 89). Then, according to Cochran (1963), the relative net cost for the same precision for each unit would be proportional to  $C'u S'_u{}^2$ , or alternatively the relative net precision of each will be proportional to  $1/C'u S'_u{}^2$ .

To make an estimate for intermediate and higher volumes of soil than were actually taken, the number of larvae in one particular size core were added to the number in another taken in the same cluster. The assumption that the number of larvae present in the combined volume of two cores is equal to the number present in the same volume of soil if taken as one unit is not theoretically correct, but probably acceptable for practical purposes.

The cost per unit was assessed for two phases of the operation (1) the taking of the sample in the field and (2) processing the sample in the laboratory.

(1) Unfortunately not all of the samplers had hammers. This was not considered important with respect to the 2.54 cm corer, but

the 3.81 and the 6.35 cm cores . took considerably longer to take because they were of the stirrup type. Thus, initially only the 2.54, 7.62 and 10.16 corers were arbitrarily assessed for the amount of physical effort involved in taking the soil samples and moving the corer from one sampling position to the next. The above were rated so close to their relative volumes that on reduction to a common unit there was little to choose between them. Thus, this cost per unit volume was assumed to be constant.

(2) The time taken per sample until the final sorting phase was reasonably constant due to the mechanisation of the process. The cost for the sorting phase was taken as proportional to the actual number of larvae that had to be picked out by hand. The 7.62 cm diameter soil corer was chosen for the following reasons; the volume of soil from the 10.16 cm corer caused ~~considerably~~<sup>considerably</sup> more wear and tear to the washing equipment, and also created a larger soil disposal problem. An intermediate size between 7.62 and 10.16 cm was not chosen , since it would have had to be especially made, and this did not seem warranted from the results shown in table 12.

#### (ii) The Pupal Stage

If each large unit in a sample is divided into M small units and data is recorded separately for each of the small units, a comparison can be made of the precision of the large and small units. Such a comparison is based on an <sup>2</sup>analysis of variance between large and small units (Cochran 1963).

Thus, a 20.32 x 20.32 cm turf, cut to a depth of 5.08 cm was divided into four 10.16 x 10.16 cm subunits. Eight of the larger samples were taken in a stratified random manner from each of the sites at Hamilton and Whakatane.

A second site was sampled in the Whakatane area (the Rangitaiki Plains Dairy Company demonstration farm) only for the comparison of pupal and adult sample unit sizes. Comparisons were made amongst 412.9, 206.45 and 103.23 cm<sup>2</sup> units, a log (X+1) transformation being used to compare the variances (see p. 89), which were reduced to a common basis based on setting the surface area of the smallest sample equal to 1.

As all the samples were dealt with in the laboratory on ~~a the~~ <sup>smallest unit</sup> ~~quarter~~ basis, the cost of handsorting was assumed constant per unit area. The cost of taking the samples in the field was not measured. It was assumed to be constant on a common unit basis. This was not wholly correct but it did make some allowance for the negative mental attitude associated with handling a larger sample in the laboratory.

As can be seen in table 13, the smallest unit was the most efficient sampling size, and was chosen. An even smaller unit was not considered, to minimise the number of zero counts.

Table 13 Comparison of different sized pupal sampling units re cost and variance.

Area of sampling unit in cm <sup>2</sup>	Cu'Su' <sup>2</sup>		
	Hamilton	Whakatane 1	Whakatane 2
412.9	16.05	12.00	23.36
206.45	13.73	9.13	16.98
103.23	8.83	6.67	13.97
Population density / m <sup>2</sup>	206	763	288

(iii) The Adult Stage

Four different sized emergence cages were compared, 17.78, 35.56, 53.34 and 71.12 cm diameter. The cages were set in clusters of the four different sizes, the clusters being arranged in a stratified random manner. The complete catch of the autumn of 1970 was analysed using a log X transformation (see p. 89). The variances and costs were both reduced to a common basis, based on setting the surface area of the smallest cage equal to 1. The major cost taken into account was that of counting the number of adults caught, and this was taken as being proportional to the number. The results are shown in table 14.

Table 14 Comparison of different sized adult sampling units re cost and variance.

<u>Sample unit size</u> diameter in cm	<u>Cu'Su'<sup>2</sup></u>		
	Hamilton	Whakatane 1	Whakatane 2
17.78	50.50	50.45	44.1
35.56	3.99	7.12	8.3
53.34	1.36	3.81	2.51
71.12	1.10	0.33	1.06
Population density / m <sup>2</sup>	116	149	84

Considering the results, there was little to choose between the 53.34 and 71.12 cm diameter cages, except at Whakatane site 1 where the larger cage proved markedly more effective. The largeness of the difference in this case was rather more than would have been expected, and was probably due to the fact that the total

number of adults caught by the 71.12 cm cage<sup>w</sup> as lower than the number caught by the 53.34 cm one. This result was not expected and considered to be a chance happening of the sampling procedure. The 53.34 cm cage was chosen as the sampling unit, as consideration had to be given, not only to their building cost, but also to stock cages to protect them.

(iv) The Egg Stage

Two sized sampling units were compared at Hamilton, a 7.62 cm and a 13.57 cm diameter sampler (Table 15). Twenty-four pairs of units were taken in a stratified manner. A log (X + 1) transformation was used on the raw data (see p. 89) and the variance and cost were reduced to a common basis.

Table 15 Comparison of different sized egg sampling units re cost and variance.

<u>Sample unit size</u>	<u>Cu'Su'<sup>2</sup></u>	
diameter in cm	2.4.71	19.4.71
7.62	0.84	35.83
13.97	0.50	21.77
Population density		
Egg clusters / m <sup>2</sup>	19.73	213.17

The cost per sample was estimated by the time taken to sort through the unit. There was a psychological effect in that it was very boring to sort through the larger samples. This was not reflected in the time taken to sort the samples, but in the time taken between samples which was not measured. Thus, it was decided to use the smaller unit.

## 6. Method of Analysis Adopted

There is at present some lack of agreement on the best method of analysing life table data. Those methods which depend solely on regressional or multiregressional techniques (Morris 1963, Watt 1963 and Mott 1966) have been criticised by Hassal and Huffaker (1969), Varley and Gradwell (1970) and Luck (1971) for their inability to explain changes in either population density or average levels from year to year in biologically meaningful terms. Population models developed in such a way are only able to predict population change on an empirical basis. Watt (1962) concluded that 'the main advantage of multiple regression analysis is that its procedures are mathematically straightforward rather than that the fitted equations bear close correspondence to events in biological reality'.

However, the methods of analysis developed by Varley and Gradwell (1960, 1963a, 1963b, 1965, 1968)<sup>are</sup> claim<sup>ed</sup> to build a population model which not only predicts population change, but also explains the biological mechanisms involved. Also this method is simpler in the initial stages, and was thus adopted.

Initially Varley and Gradwell's method comprises a visual comparison of graphs showing the change in the log survivals for the different age intervals and that for the generation, each plotted against time. Such an analysis should not only identify the key factor, but also show which survival values are so small or constant, that, at least in the initial stages of model building, they can be considered as constant (Varley and Gradwell 1970).

## 7. Transformation

The majority of statistical procedures assume a normal, or an approximation to a normal distribution, with the variance being independent of the mean and its components being additive (Southwood 1966). However, for most biological populations the frequency distribution is usually positively skewed, with the variance appearing to be approximately proportional to the mean's magnitude (Finney 1941). Beall (1942), Cochran (1963) and Snedecor and Cochran (1968) have discussed the importance of stabilizing the variance to allow the data to be analysed without the risk of errors. This can be done by transforming the raw data to a new scale which makes the variance independent of the mean (Morris 1955). Concerning the choice of the correct transformation, Southwood (1966) has pointed out that although there are precise transformations for particular distributions, in practice where sampling and extraction errors are fairly large, it is usually found adequate to transform the data from slightly over-dispersed data using square roots, and that from distinctly aggregated populations by using logarithms. Cassie (1968) in discussing the fitting of mathematical models to overdispersed plankton populations, commented that the log-normal did as well as any, at least when the mean was large. In view of the above, a logarithmic transformation was tried, and its effect on stabilizing the variance assessed by graphing the transformed mean against the transformed variance (Figs. 16 & 17). Originally each stage was plotted separately, but since they tended to show identical relationships, they were combined. Relative independence <sup>of</sup> ~~from~~ the mean from the variance was obtained, and the transformation adopted.

In adopting the above transformation, one was faced with the decision of how to present the mean in the final results. Morris

FIGURE 16

Relationship between the variance and mean of the raw data  
from sampled populations of I. rubriceps.

FIG. 16

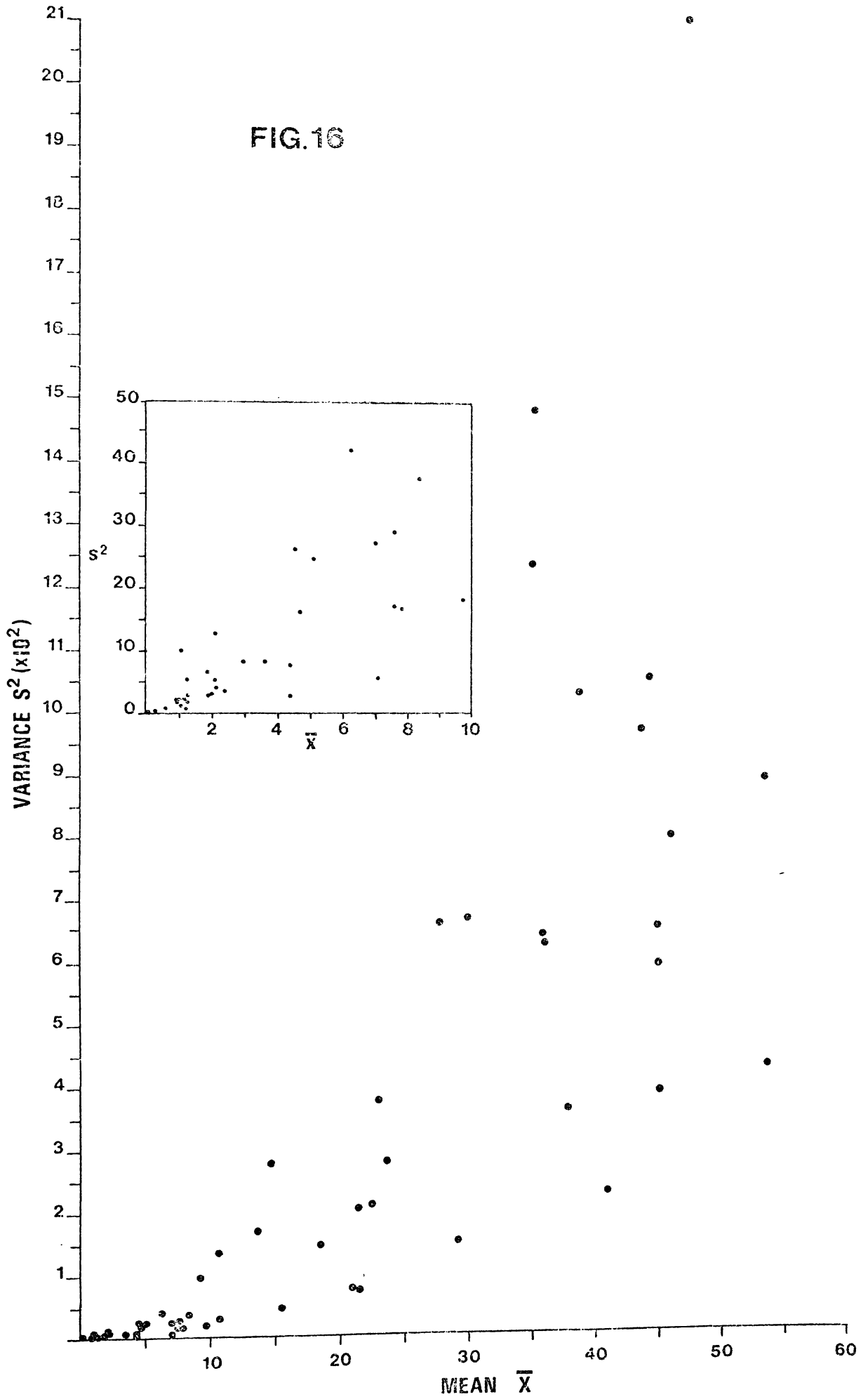
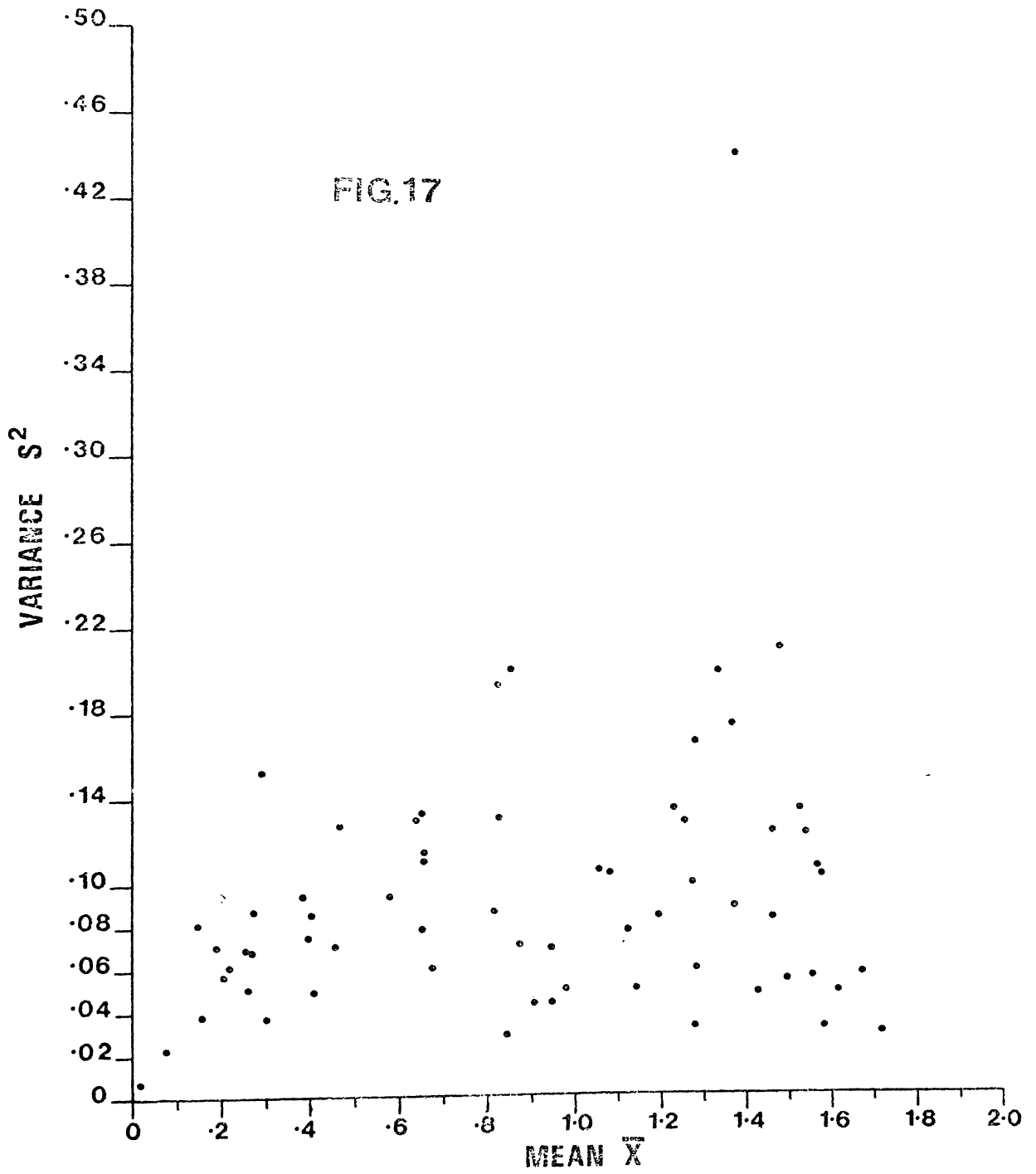


FIGURE 17

Relationship between the variance and mean of  $\log (X + 1)$   
transformed data from sampled populations of I. rubriceps.  
The same data was used for Figs. 16 and 17.



(1955), Le Roux and Reimer (1959), Harcourt (1961), van Emden, Jepsen and Southwood (1961) and Lyons (1964) have all commented that there is much to commend the use of the arithmetic mean in population studies. Concerning life table analysis, the two major problems of using a transformed mean, are where means based on different transformations need to be compared, and where the transformed mean's biased relationship to the arithmetic mean changes depending upon the degree of over-dispersion of the population.

In the present case the first problem did not arise, and the log transformation appeared to be suitable for all stages in the life cycle. However, the second difficulty could exist.

It is the inter-relationships between the survival values of the different stages, and their individual relationship with the survival of the whole generation, that any analysis carried out on the data is designed to show. Thus, a changing bias from stage to stage between the geometric and arithmetic mean, assuming it occurs in the same order and at the same level, should not alter the end result whether the analysis uses the arithmetic or geometric mean. The order change of the bias from stage to stage probably remains the same, however, the degree of the bias will change depending on changes in the degree of overdispersion of the various stages from year to year. Whether this should have very much effect on the end result is questionable, particularly when it is usually only one stage's survival which is largely responsible for the changes in survival of the whole population (Watt 1963). In fact, one might argue that any differences between arithmetic mean or geometric mean based survival value inter-relationships, were due to the latter measuring an extra component, the change in over-dispersion of the population

from stage to stage, or from one population level to the next. Thus, an analysis based on geometric means would not only assess the action of various mortality factors on the different stages, but would also assess the interaction of these factors with the distribution of the stage's population. This might produce a more biologically meaningful result.

It was decided to compare the use of the arithmetic mean and the geometric mean on the final result of any analyses carried out, to see if there were any major differences between the two.

#### 8. Sampling Precision

Morris (1955, 1960) has commented that the level of precision required for most entomological intensive sampling work is not yet known, since no detailed field projects on population dynamics have yet been satisfactorily completely analysed. Thus, the level selected is usually rather an arbitrary one, and Morris (1955) adopted an error of 10% of the mean, on the basis that this would be at about the same level as the accuracy of the relevant extraction method. Harcourt (1961, 1962), Le Roux and Reimer (1959) and others have accepted the above level of precision as a reasonable standard

In computing the number of samples (N) for a given level of precision, Morris (1955) used the following formula:

$$N = s^2 / (10\% \bar{x})^2$$

Thus,  $\pm 10\%$  of the mean corresponds to the approximate 70% confidence limits. The 95% confidence limits are the more usual

ones encountered in statistical analyses, and for approximately the same number of samples, the confidence limits would be  $\pm 20\%$  of the mean (Morris 1955). It was considered to be better to adopt the 95% confidence limits as this would give a truer picture of sampling precision. In setting a precision level for soldier fly sampling, 95% confidence limits of  $\pm 20\%$  of the mean were aimed for.

However, in certain instances, as with egg sampling, manual resources put certain restrictions on the number of samples that could be taken.

Most workers to date have used the arithmetic mean for analysing their data (Morris 1955, Le Roux & Reimer 1959, Harcourt 1961, 1962, 1964, 1969, Cheng & Le Roux 1966, Campbell 1967). Where their distributions have departed from normality to the extent that a transformation was needed to stabilize the variance, they have been faced with the problem of wishing to use means based on the raw data while using variance components based on the transformed data. Morris (1955) has proposed a method for setting the degree of precision required in terms of the untransformed mean, but using the log transformed variance. However, in the case of soldier fly the degree of precision was initially based on the transformed data. This was done because a transformation was required to stabilise the variance and it was considered that the ratio between geometric means would be as good an estimate of the survival of a particular stage as any other. In the case of the arithmetic mean being adopted in the end, the 95% confidence limits in terms of the original variable, following a log transformation can be obtained from the transformed data, assuming  $N$  is large, from the formula below (Dr. J. Darwin, Applied Maths. Div., D.S.I.R.

Wellington. 1969 pers. comm.).

$$\text{antilog} \left( \bar{x} + 1.15s^2 \pm 2 \sqrt{s^2/n + 2.65 s^4/n-1} \right)$$

## A Method for Estimating the Fecundity of Natural Populations

### 1. Introduction

of I. rubriceps

Regression sampling is a useful ecological tool when certain variables in the field are laborious to estimate directly, but may nevertheless be correlated with other variables which are more easily estimated (Cassie 1968). In soldier fly, the eggs are mature on emergence, and thus, the total potential fecundity can be assessed by examining the ovaries. However, it was considerably easier to weigh the female pupae than to count the number of eggs contained in the ovaries of newly emerged adults. Since in a wide range of insects it has been found that fecundity is proportional to pupal and adult weight and/or size (Richards and Waloff 1954, Miller 1957, Waloff and Richards 1958, Miller 1963, Embree 1965, and Carne 1969), a relationship was sought between pupal weight ( $X$ ) and fecundity ( $Y$ ), to enable the assessment of the mean fecundity of the female population based on an estimate of mean female pupal weight. Female pupal weights will vary, and any estimated value of the mean pupal weight will have an error term connected with it. Because other sampling errors were in the range of 10 - 20% of their respective means, it was attempted to minimise the sampling error of the female pupal weight to under 5% and regard this as negligible.

## 2. Methods and Materials

Pupae were collected in the field during the 1970 and 1971 seasons. It was initially assumed that the relationship between female pupal weight and fecundity was the same for geographically isolated populations. Thus, the results from pupae collected from Whakatane and Hamilton were pooled.

All undamaged pupae were cleaned and weighed.

A distinction between male and female pupae could be made on weight, but there was a considerable region of overlap. To prevent discrimination against small female pupae, both male and female were reared, the adult males being discarded on emergence. Pupae were kept individually on moist filter paper in petri dishes under insectary conditions closely corresponding to field conditions for that particular time of the year. After emergence, female adults were pinned through the thorax in a waxed dish. Two small pieces of damp filter paper were placed above and below the abdomen to extend behind it. This provided the moist tactile conditions which seemed suitable to promote egg laying. Females were left as above for 24-48 hours, the filter paper being kept moist throughout.

The reason for the above method was to get the female to lay as many eggs as possible, since laid eggs were considerably easier to count than those still in the ovaries. Usually under these stress conditions once laying started it continued until either the female died or had laid her full complement.

The eggs laid were carefully removed and placed in a petri dish that had been lightly coated with vaseline. This facilitated

their counting under a microscope. Any eggs remaining in the ovaries were also counted. Occasionally the ovaries were gelatinous masses and the eggs were uncountable. Such specimens were discarded. The results are shown in Fig. 18.

### 3. Discussion

There was a good agreement between adult fecundity and female pupal weight, 71% of the variation in fecundity being associated with its lineal regression on pupal weight. Part of the remaining 29% was probably associated with variation in egg size. This was not actually measured, but it was noticed that the eggs of less fecund females were usually larger than those of more fecund females from pupae weighing about the same.

The two major factors which could affect variations in fecundity are nutrition during the larval stage and the genetic makeup of the individual. From the life history work carried out in the insectary, where a wide range of larval weights were obtained from larvae reared under very similar conditions, the latter factor may be the most important; at least as far as individual variation is concerned, with the former possibly influencing changes in overall population fecundity.

The less fecund females may be able to fly further because of a differential reduction in body weight affecting the ovaries rather than the wing muscles. The above has been reported for the spruce budworm Choristoneura fumiferana (Miller 1963). Thus, reduced fecundity due to a nutritional stress or to genetic factors could lead to an increase in the dispersal power of the female adult, with obvious survival value. In this context, it can be seen that a constant variation in the fecundity of the population

FIGURE 18

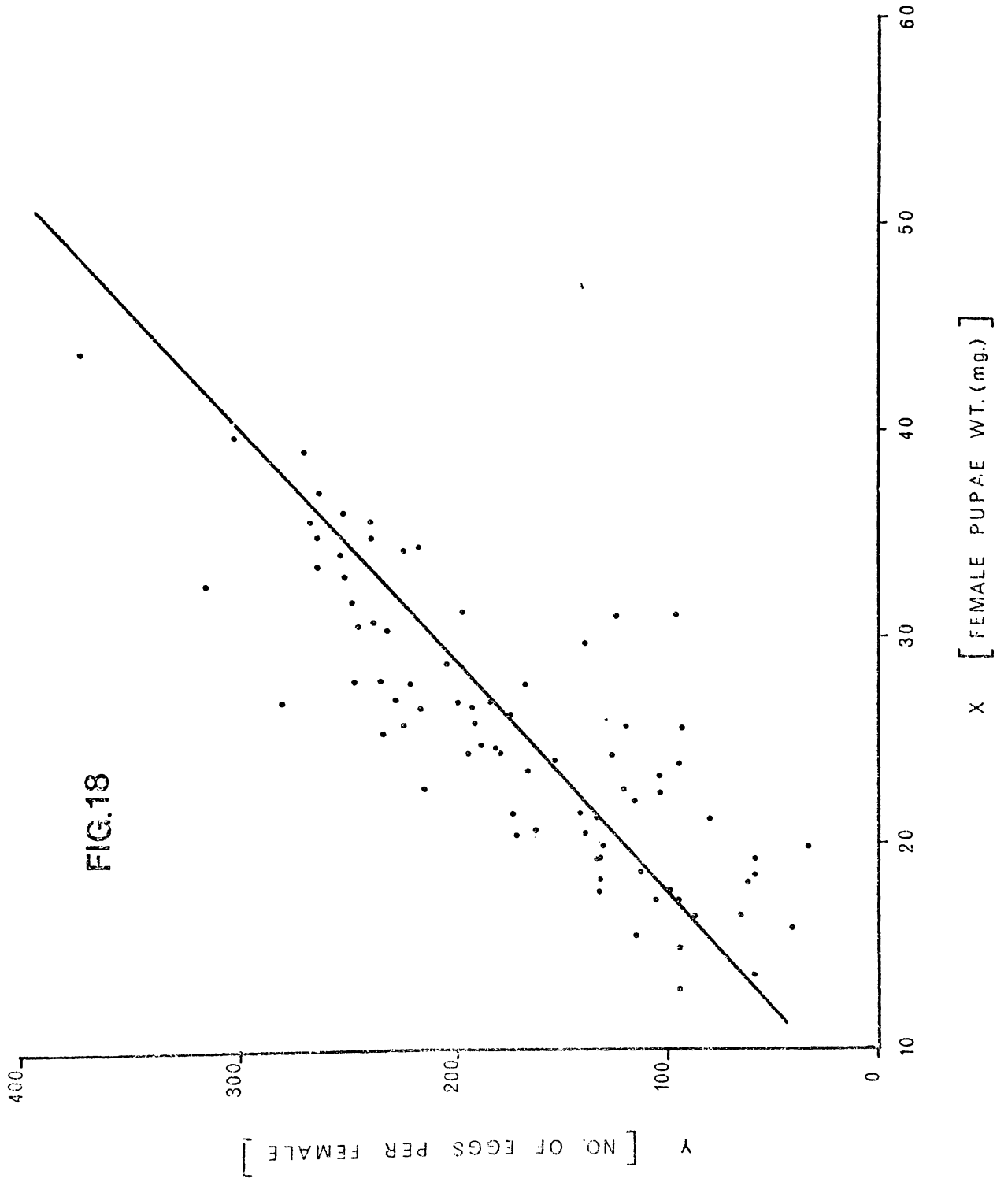
The relationship between fecundity (Y) and female pupal weight (X).

The regression equation was  $Y = -58.2420 + 9.0355X$

$b = 9.0355$  \*\*\*

$r^2 = 0.7144$

FIG.18



maintained by genetic control, would give the population as a whole, a high degree of opportunism, both to exploit its present environment and ones further afield.

## Analysis of Results

### Hamilton site

#### 1. Introduction

An intensive population study of I. rubriceps was carried out at the Hamilton site, and the results are presented in Figs. 19 - 22, Appendices 2 - 6, and Table 16).

To simplify the interpretation of the population data; only the two main periods of emergence per season were considered and it was also assumed that the majority of individuals had a life cycle of approximately 24 months.

#### 2. Method of Population Analysis

An analysis of the collected data based on generation survival was not possible at this stage because of the difficulties in correctly age grouping the larval population. It was not possible to separate those larvae associated with the spring emergence from those associated with the autumn emergence of the same season. Considering the two year life cycle, a possibility was to analyse the data on a season basis and to treat the alternate seasonal populations as separate entities. However, in view of the limited amount of data available the analysis was put on a year to year basis. Thus, generation survival was replaced by the survival of the whole larval population from the September period of one year to the same time the following one. The above was termed

## FIGURE 19

The increases in the larval population which occurred during the early winter of 1970 and throughout the winter of 1971 (Fig. 19a) were due to the young larval population which hatched during the respective autumn emergences being progressively extracted by the washing process. Similarly, the peak which occurred during March 1971 probably owed its origin to the previous spring emergence period. In the case of Fig. 19b, the same applies, together with a change in the degree of overdispersion of the population. Reductions in larval numbers during the spring and autumn emergence periods were to be expected due to larvae entering the pupal stage. The number of live larvae were plotted separately from the dead ones. In subsequent analyses, the live larval (and pupal) populations were treated as the total population. This was done to avoid estimating the same dead larval (and pupal) population more than once, since it took over three months for the dead individuals to decompose to an unrecognisable state under field conditions. Also, the vast majority of the recovered dead larvae were over one year of age, and were thus not representative of the whole dead larval population.

### FIGURE 19a

The changes of the larval population with time at the Hamilton site. Results are based on raw data.

FIG.19a

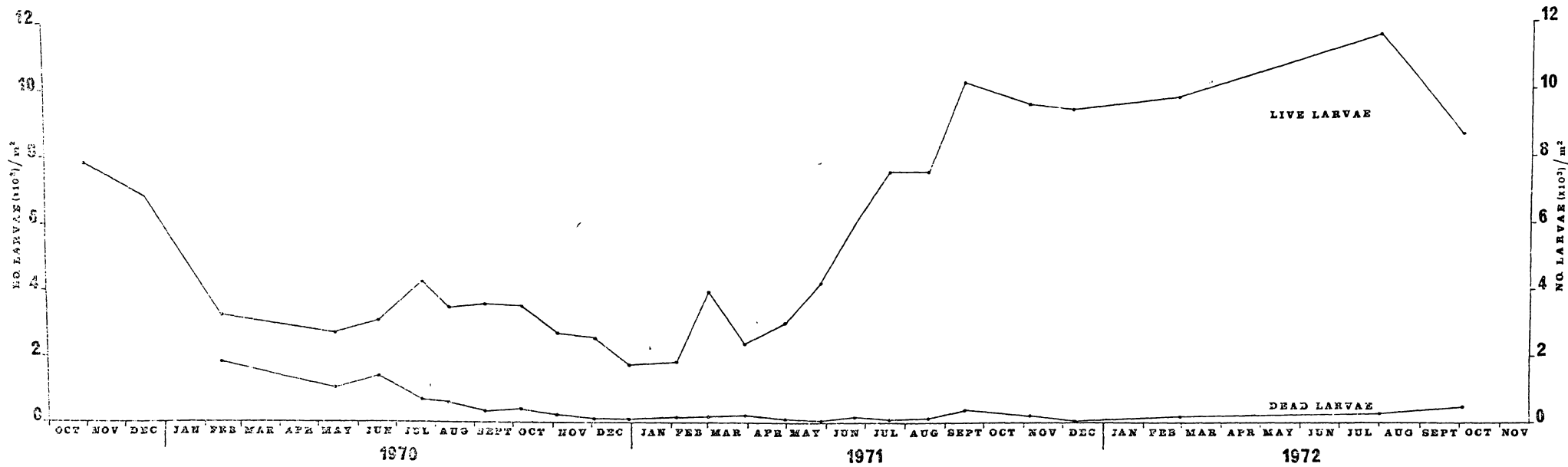


FIGURE 19b

The change of the larval population with time at the Hamilton site. Results based on  $\log (X + 1)$  transformed data.

FIG.19b

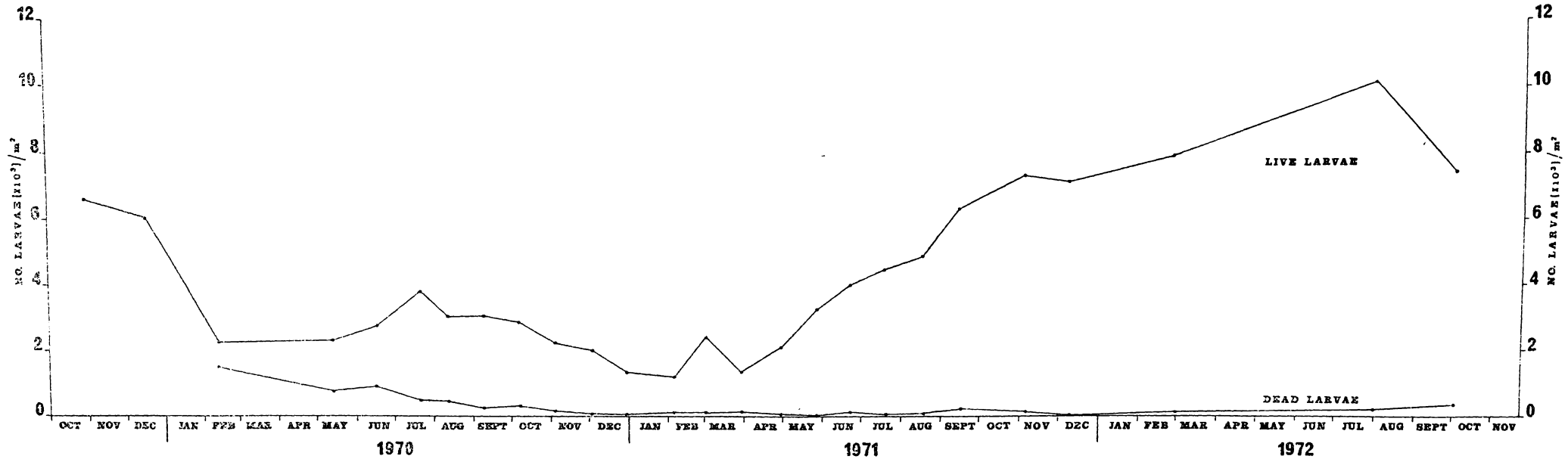


Table 16 The number of 0+ and 1+ larvae / m<sup>2</sup> (as classified during the early spring of each year) at the Hamilton site.

A.M. = nos. based on the arithmetic sample mean.

G.M. = nos. based on the geometric sample mean.

<u>Larvae</u>	<u>8.9.70</u>		<u>16.9.71</u>		<u>2.10.72</u>	
	<u>A.M.</u>	<u>G.M.</u>	<u>A.M.</u>	<u>G.M.</u>	<u>A.M.</u>	<u>G.M.</u>
0+	485	414	6201	3839	2995	2626
1+	3116	2661	4108	2544	5706	5003

Considering the A.M. data, the majority of the 1+ larvae on 16.9.71 must have been 0+ larvae on 8.9.70, Thus, the 0+ larvae were grossly underestimated during the winter of 1970. The main contributing factor here was probably chance. Although small larvae were being picked up by the washing process (albeit not very efficiently), the subsample chosen for weighing did not contain very many of them. Unfortunately this was not detected until the data was first analysed in December 1970. Henceforth, the size of the subsample was increased and a check was made to ensure that it was as representative as possible of the whole sample.

FIGURE 20

Estimated number of pupae associated with each of the main emergence periods at the Hamilton site. The outlined histogram represents results based on the raw data, while the solid one results based on a  $\log (X + 1)$  transformation.

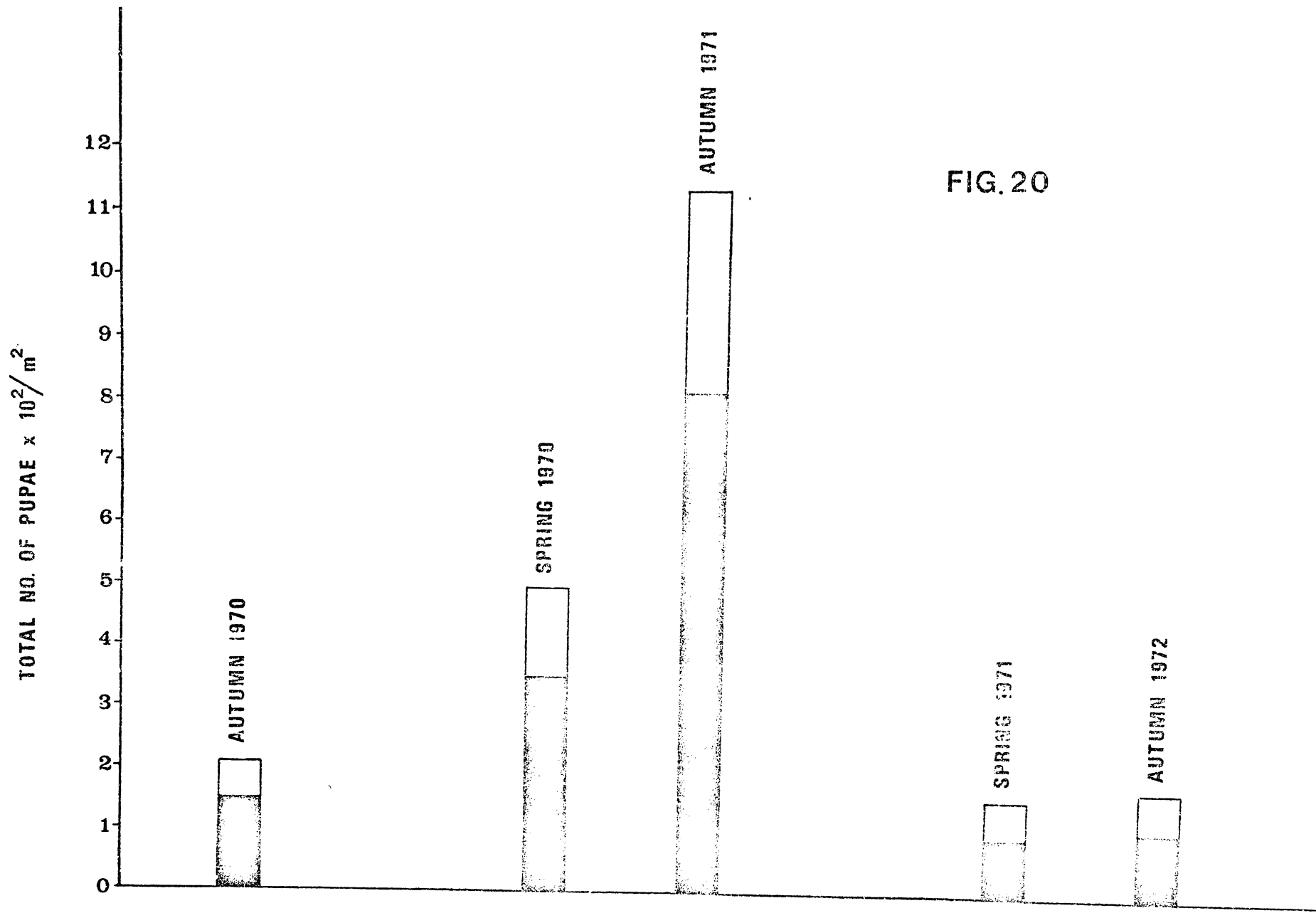


FIG. 20

FIGURE 21

Estimated number of adults which emerged during each of the main emergence periods at the Hamilton site. The outlined histogram represents results based on the raw data, while the solid one, results based on a log (X+1) transformation. The commencement and conclusion of each of the main emergence periods are shown below, together with the overall sex ratio for the relevant period. The significance given is the significance of the difference from a 50:50 ratio based on a chi-square test.

<u>Emergence period</u>		<u>Male : Female</u>	<u>Signifi-</u> <u>icance</u>
Autumn 1970	23. 3.70 - 5. 5.70	67.77 : 36.23	***
Spring 1970	6.11.70 - 8. 1.71	48.25 : 51.75	-
Autumn 1971	12. 3.71 - 30.4. 71	33.26 : 66.75	***
Spring 1971	12.11.71 - 31.12.71	54.20 : 45.80	*
Autumn 1972	24. 3.72 - 5. 5.72	61.25 : 38.75	***

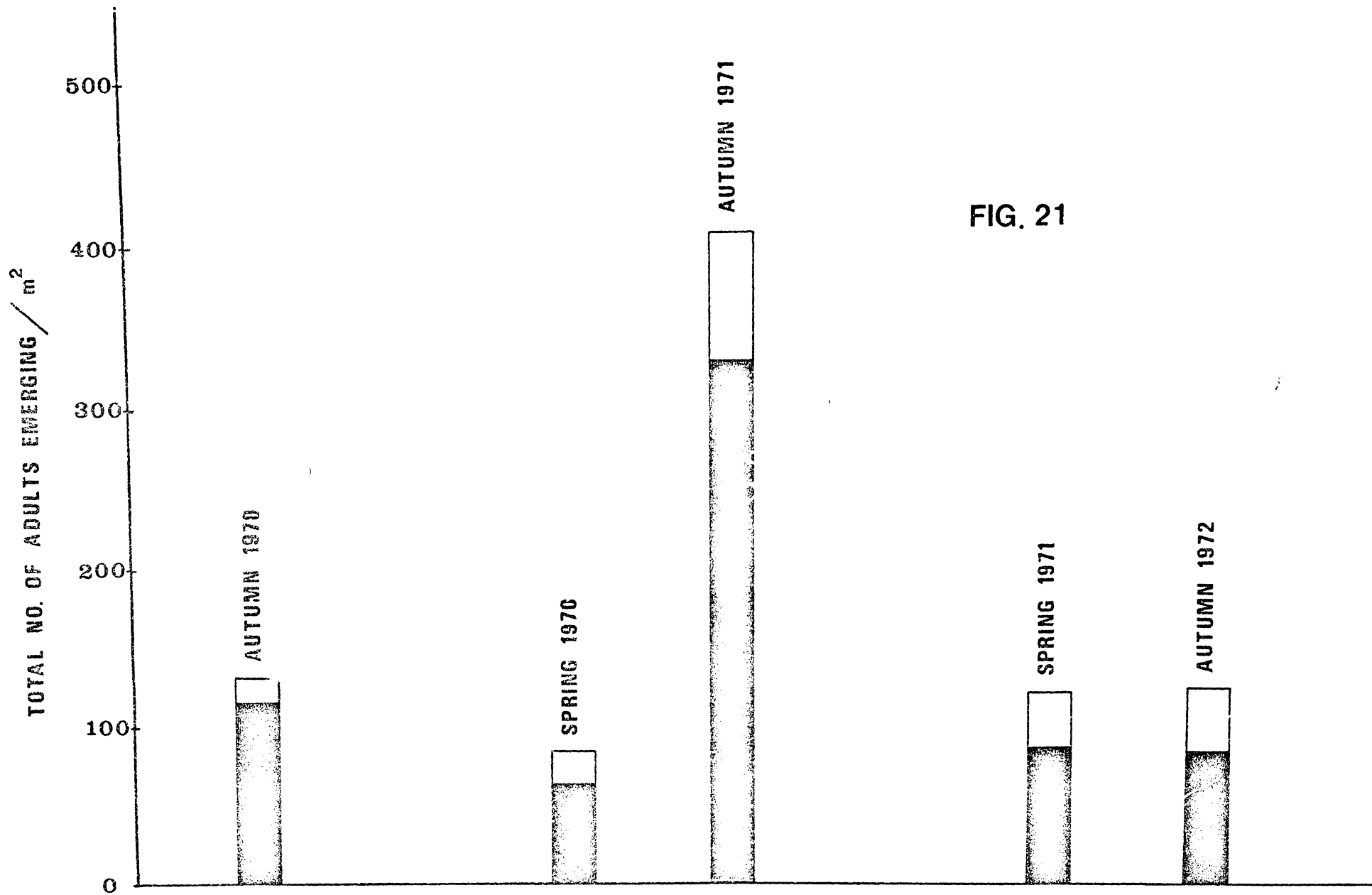


FIG. 21

FIGURE 22

Estimated number of eggs laid during each of the main emergence periods at the Hamilton site. The outlined histogram represents results based on the raw data, while the solid one, results based on a  $\log (X+1)$  transformation.

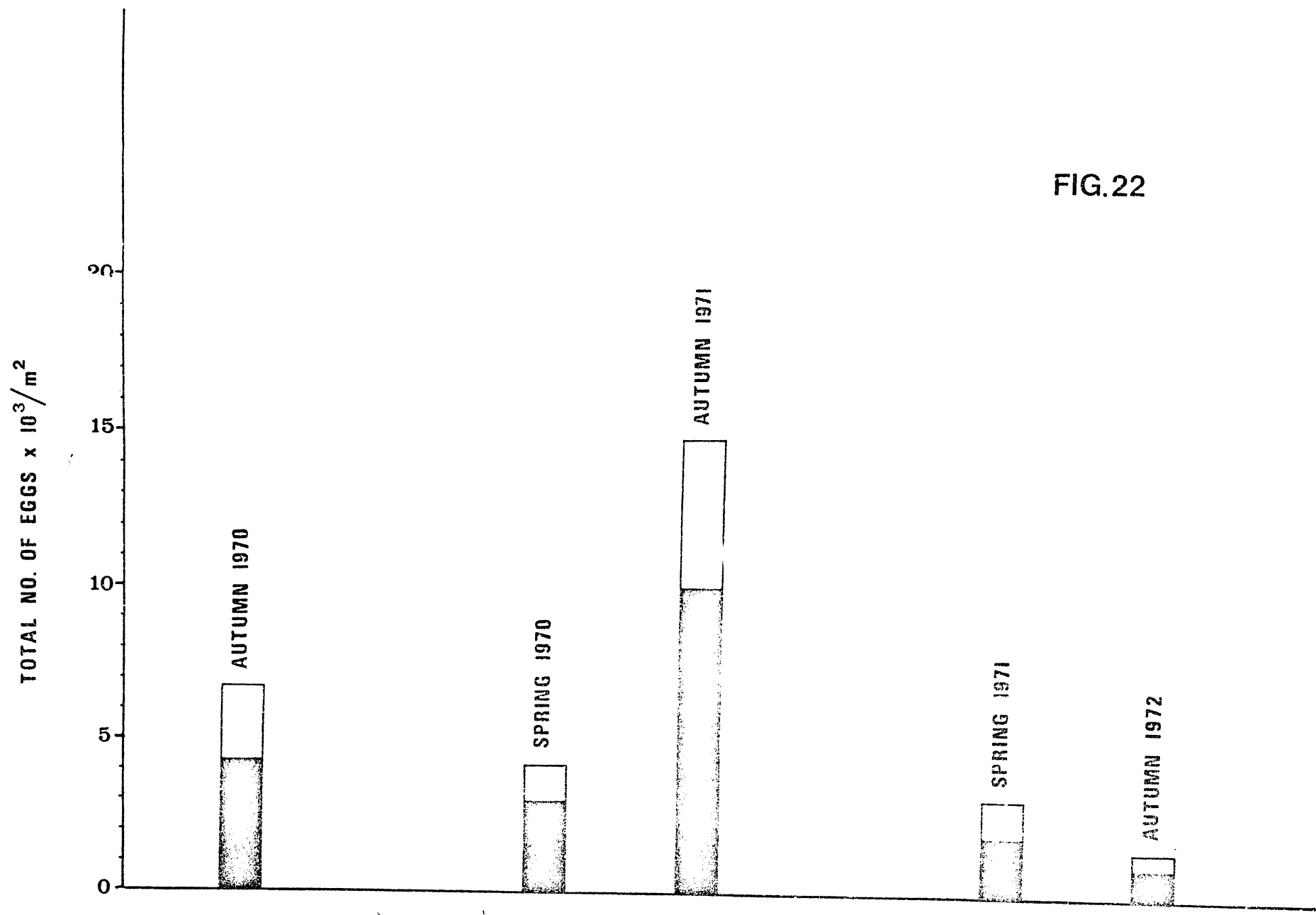


FIG.22

the population trend for the insect and all other survival values were related to it. September was chosen for two reasons. At this time even the larval extraction method initially adopted appeared to be reasonably efficient. Also, it had been shown that this was the best time of the year to classify the larval population on an age basis.

The following are the survival values that were analysed (Table 17).

(1) Yearly population trend. The survival of the whole larval population from approximately the September period of one year to that of the next.

Because of the initial difficulty in assessing the larval age structure, two other survival values based on the movements of the whole larval population were estimated. These were as follows:

(2) The survival of the whole larval population from September to February.

(3) The survival of the whole larval population from February to September.

February was chosen as representing a time intermediate between the two main emergence periods per season, when the majority of the population would be in the larval stage. However, at that time probably not all of the larvae from the previous spring emergence were being extracted, and a few larvae would already have entered into the pupal stage for the beginning of the coming autumn emergence. Thus, the above two estimates were probably biased, the first one beneath its proper value and the second one above. However, assuming that these biases remained reasonably constant, the above (one encompassing the spring emergence period

and the other the autumn one) were initially useful in interpreting changes in the larval population which occurred during the year.

Following the adoption of the larval classification scheme, the following were calculated.

(4) The survival of the 0+ larval population during the subsequent year. This equalled the number of 1+ larvae<sup>present</sup> during September in year  $N + 1$  divided by the number of 0+ larvae in year  $N$ .

(5) The survival of the 1+ larval population during the immediately following season. This equalled the total number of pupae associated with a season's emergences divided by the number of 1+ larvae present during the prior September period.

It was not always possible to estimate by sampling, the complete pupal population associated with a given emergence period. Thus, pupal survival for a particular emergence period was assumed to be constant and the total number of pupae were estimated by dividing the total number of adults which emerged by the estimated pupal survival.

(6) The survival of the egg and 0+ larval population from a season's two emergence periods up to the following September. This equalled the number of 0+ larvae present during September divided by the total number of eggs laid during the previous season.

Since egg sampling usually only covered the peak of the emergence period, the number of eggs laid during the whole period was calculated by multiplying the total number of females which emerged by the mean fecundity per female by the estimated survival of the adult population. The spring and autumn estimates were added together to give the estimated number of eggs laid per season.

The above assumed that adult survival was constant throughout any one emergence period. The assumptions that both pupal and adult survivals were constant for a given period were probably not entirely valid. However, since these values were assessed for the peak periods of any given emergence, the above assumptions were considered reasonable for all practical purposes.

The following values were estimated for both the spring and autumn emergence periods separately.

(7) Pupal survival. This equalled the number of adults which emerged over a certain period divided by the estimated number of pupae which would have emerged as adults during the above period.

(8) Sex ratio. A 50 : 50 sex ratio was assumed and the sex ratio was treated as a survival value (Morris and Miller 1954). The actual number of females which emerged during an emergence period was doubled to give a corrected 50 : 50 sex ratio estimate of the total adult population. This corrected estimate was divided by the total adult population which emerged, to give the survival value.

(9) Fecundity. The mean number of eggs per female was estimated at 172 and this was arbitrarily defined as a female normal complement (Morris and Miller 1954). For each emergence period the actual mean fecundity of the female population was estimated. Then the number of normal females required to lay the same number of eggs as the actual females present was calculated. This figure was multiplied by two (to balance the calculation for the male component of the population) then divided by the corrected sex ratio estimate of the total adult population to give the survival value.

(10) General adult survival was assessed by dividing the estimated number of eggs laid in the field over a given time by the total possible number of eggs which could have been laid if each female present had laid her full complement.

In carrying out the actual analysis, the survival values were converted to logarithms (to the base ten) and expressed in their minus form as  $k$  values (Varley and Gradwell 1970).

## 2. $k$ Value Analysis

The above analysis was carried out based on both the raw and transformed data. The former has been the form adopted by the majority of workers in this field (Morris 1955, Harcourt 1961, 1962, 1964 & 1969, Le Roux & Reimer 1959, Embree 1965, Campbell 1967, Cheng & Le Roux 1966, Varley & Gradwell 1970, Foltz et al. 1972). After their presentation, any differences between the two are discussed.

It must be stressed at this point, that the amount of data available was small. Thus, although this initial analysis of results is useful in gaining some ideas of how the population dynamics of the insect function, any conclusions must be regarded as tentative.

### (i) Analysis of $k$ values based on the raw data

It can be seen by inspection of Fig. 23 that  $k_2$  followed the general trend of  $K$  better than any other value.  $k_1$  and  $k_{10}$  also have the same basic pattern. On the other hand,  $k_6$  appeared to have the opposite type.  $k_{12}$  had a different shape altogether to  $K$ , and the other  $k$  values showed, at least in part, trends either resembling  $K$ , i.e.  $k_3$ ,  $k_7$ ,  $k_8$ ,  $k_9$ , and  $k_{11}$ , or resembling  $k_6$ , i.e.  $k_4$  and  $k_5$ .

FIGURE 23

The interrelationships of the individual  $k$  values with each other and with the population trend  $K$ . The solid line represents those values based on the raw data, while the dotted line those values based on the  $\log (\lambda+1)$  transformed data.

FIG. 23

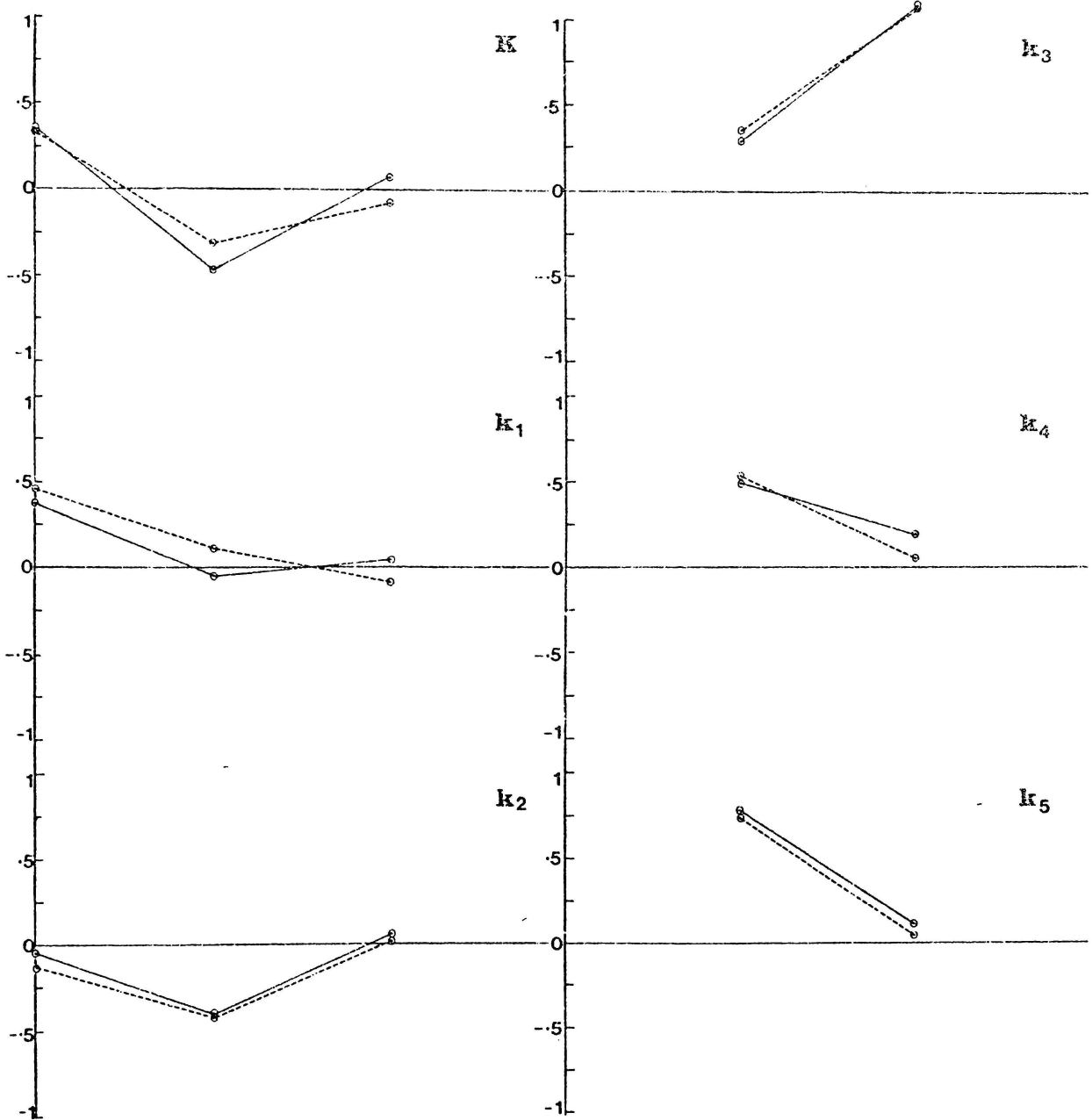


FIG.23 (cont.)

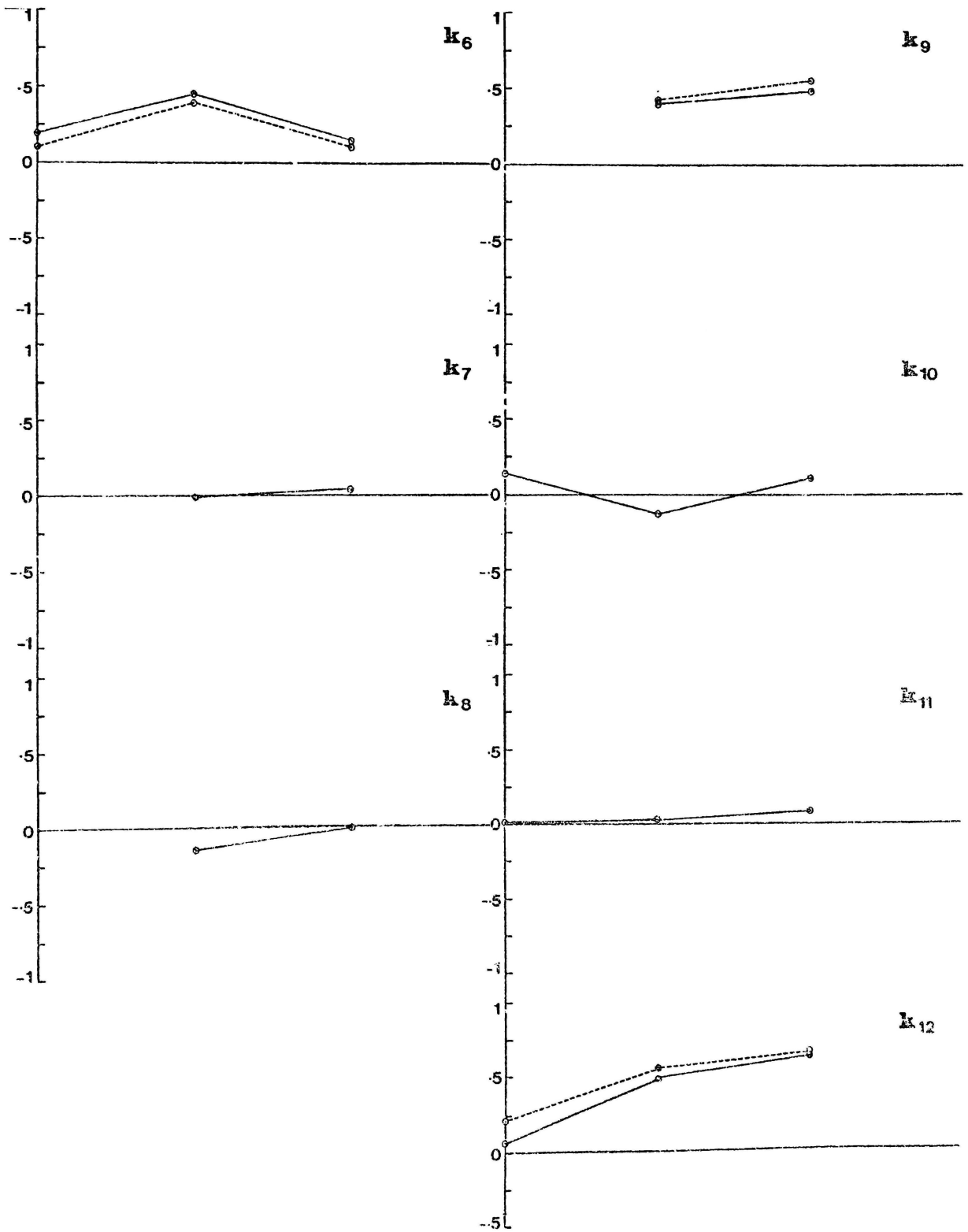


Table 17 The survival values (s) and k values of the various stages at the Hamilton site. pop = population.

	<u>Raw data</u>		<u>Transformed data</u>	
	<u>s</u>	<u>k</u>	<u>s</u>	<u>k</u>
1. Population trend (K)				
13.10.69 - 8. 9.70	0.4595	0.3378	0.4718	0.3263
8. 9.70 - 16. 9.71	2.8628	-0.4567	2.0758	-0.3173
16. 9.71 - 2.10.72	0.8441	0.0736	1.1954	-0.0774
2. Larval pop Sept. - Feb. ( $k_1$ )				
13.10.69 - 12. 2.70	0.4182	0.3786	0.3538	0.4512
8. 9.70 - 1. 3.71	1.1169	-0.0479	0.7906	0.1021
16. 9.71 - 28. 2.72	0.9551	0.0200	1.2414	-0.0937
3. Larval pop. Feb. - Sept. ( $k_2$ )				
12. 2.70 - 8. 9.70	1.0989	-0.0407	1.3335	-0.1252
1. 3.71 - 16. 9.71	2.5632	-0.4087	2.6257	-0.4193
28. 2.72 - 2.10.72	0.8838	0.0536	0.9629	0.0164
4. 0+ larval pop during the subsequent year.				
16. 9.71 - 2.10.72	0.9202	0.0361	1.3061	-0.1149
5. 1+ larval pop during the following season ( $k_3$ )				
1970 - 71	0.5241	0.2806	0.4375	0.3590
1971 - 72	0.0806	1.0937	0.0808	1.0926
6. A seasons eggs & 0+ larval pop up to Sept. ( $k_4$ ).				
1970 - 71	0.3267	0.4859	0.2972	0.5269
1971 - 72	0.6372	0.1958	0.8739	0.0586
7. Spring pupal stage ( $k_5$ )				
1970 <sup>1</sup>	0.1701	0.7694	0.1821	0.7397
1971 <sup>2</sup>	0.7688	0.1141	0.9098	0.0410

Table 17 continued

Date	Raw data		Transformed data			
	<u>s</u>	<u>k</u>	<u>s</u>	<u>k</u>		
8. Autumn pupal stage ( $k_6$ )						
1970 <sup>3</sup>	0.6317	0.1995	0.7738	0.1114		
1971 <sup>4</sup>	0.3602	0.4435	0.4045	0.3931		
1972 <sup>5</sup>	0.7089	0.1494	0.7720	0.1124		
9. Spring adult stage						
i. sex ratio ( $k_7$ )						
1970	1.0350	-0.0149	} the same			
1971	0.9160	0.0381				
ii fecundity ( $k_8$ )						
1970	1.4186	-0.1516				
1971	1.0345	-0.0145				
iii general ( $k_9$ )						
1970 <sup>6</sup>	0.3916	0.4071	0.3703	0.4315		
1971 <sup>7</sup>	0.3173	0.4985	0.2758	0.5594		
10. Autumn adult stage						
i. sex ratio ( $k_{10}$ )						
1970	0.7246	0.1399	} the same			
1971	1.3348	-0.1252				
1972	0.7750	0.1107				
ii. fecundity ( $k_{11}$ )						
1970	0.9715	0.0126				
1971	0.9515	0.0216				
1972	0.8207	0.0858				
iii general ( $k_{12}$ )						
1970 <sup>8</sup>	0.8440	0.0737	0.6090	0.2154		
1971 <sup>9</sup>	0.3308	0.4805	0.2762	0.5588		
1972 <sup>10</sup>	0.2327	0.6332	0.2238	0.6502		

Table 17 continued

Pupal survival was based on the number of adults emerging between the two specified dates divided by the number of pupae assessed on the specified date(s).

1. adults: 13.11.70 - 18.12.70  
pupae: 12.11.70
2. adults: 22.10.71 - 23.12.71  
pupae: 26.10.71 & 22.11.71
3. adults: 2. 4.70 - end of season  
pupae: 6. 4.70
4. adults: 12. 3.71 - end of season  
pupae: 22.3.71 & 19. 4.71
5. adults: 10. 3.72 - 12. 5.72  
pupae: 13. 3.72 & 8. 4.72

General adult survival was based on the total number of eggs assessed on the specified date(s) divided by the product of the mean population fecundity and the number of females emerging between the two specified dates.

6. eggs: 13.11.70, 14.12.70 & 22.12.70  
adults: 13.11.70 - 24.12.70
7. eggs: 3.12.71  
adults: 19.11.71 - 3.12.71
8. eggs: 16. 4.70  
adults: 8. 4.70 - 16. 4.70
9. eggs: 2. 4.71 & 19. 4.71  
adults: 19.3..71 - 23. 4.71
10. eggs: 17. 4.72 & 1. 5.72  
adults: 7. 4.72 - 5. 5.72

The  $k_1$  and  $k_2$  factors were of particular interest, since they incorporated the functioning of the individual  $k$  values operating through the spring and autumn emergences respectively.

$k_1$ , although contributing to the initial decrease in  $K$ , afterwards tended to remain reasonably constant.  $k_7$ ,  $k_8$  and  $k_9$  all showed the same trend between the 1970/71 and 1971/72 seasons, however,  $k_5$  decreased considerably. The reduction in  $k_5$  could have been important in reducing the increase shown in the  $k_1$  value (see later). The other factors contributing to the  $k_1$  value were the survival of the 1+ larvae which would pupate during the spring, the survival of the larval population present in September that would still be in the larval stage during February and the survival of the eggs and 0+ larval population originating from the spring emergence. This larval component will be discussed later in conjunction with the similar component of  $k_2$ .

The various factors contributing to  $k_2$  were the survival of the 1+ larval population which were going to pupate during autumn, the survival of the larval population present in February that would still be in the larval stage during September, the survival of the eggs and 0+ larval population originating from the autumn emergence and the various  $k$  factors concerned with the pupal and adult stages of the autumn emergence. Considering the latter initially, it can be seen that  $k_6$  had a pattern that tended to compensate for changes in  $k_2$ .  $k_{10}$  had a similar pattern to  $k_2$ ; whilst  $k_{12}$  had a distinctly different one.  $k_{11}$  appeared to remain reasonably stable. Unfortunately, the larval components on  $k_1$  and  $k_2$  could not be separated. There was not enough information on the survival of the 0+ larval population in the

September of year N through to the same time period in year N + 1, to make any comment on its contribution to K. Although it was of interest to note that during the 1971/72 season the survival of this larval group was very high. There was only sufficient data to obtain two estimates of  $k_3$  and  $k_4$ , however, it can be seen that  $k_3$  followed the same trend as K, whereas  $k_4$  tended to compensate for it. From the above, it would appear that the two key factors responsible for the trend of K, were  $k_3$  and to a lesser extent  $k_{10}$ .

(ii) Analysis of k values based on transformed data

As can be seen from Fig. 23, the analysis based on the transformed data differed only slightly from that based on the raw data. Except for  $k_1$ , all the various k values had the same basic pattern, although the magnitude was different in a number of cases. In  $k_1$  there was an interesting difference, since it continued to decrease over the sampled period. This effect gave slightly more emphasis to the apparently compensating effect that  $k_1$  had on the value of  $k_2$  in affecting K. To some extent this increased compensation could also be seen in  $k_4$ . The above gave more emphasis to  $k_3$  being the key factor, which was modified in its effect by  $k_4$ ,  $k_5$  and  $k_6$ .

(iii) Comparison of analyses based on raw and transformed data

Snedecor and Cochran (1968) argue that the median (as a measure of the central tendency) of a skewed distribution generally "seems to represent people's concept of an average better than the mean". Similarly, when considering the average interaction between the environment and an insect population, the present author suggests that the changes of the central tendency of the distribution probably gives a better ecological interpretat-

ion of what is happening at a particular point in time and space rather than changes of the arithmetic mean. For the above not only estimates the effect of the environment on the population as far as numerical changes are concerned, but also allows for the change in the distribution of the animal in response to its environment to be taken into account.

For many naturally occurring populations a log transformation is suitable for normalising the distribution. In this case the geometric mean is generally the best measure of the central tendency of the distribution (Morris 1955). Also, the normalising effect on the original skewed distribution, permits the use of most of the parametric statistical analyses. In addition, the log transformation has the following advantage. In investigating the comparisons between population levels, one is usually interested in some environmental factor causing the difference. This factor probably has an exponential effect on the population numbers, since changes in animal populations usually occur on a geometric scale (Beaver 1966). Thus, the log number of beasts is an estimate of the environmental property measured on a linear scale (Cassie, 1970 pers. comm.).

The apparent difference between the two forms of analysis (based on raw data and based on transformed data) outlined previously, was due to the changing arithmetic mean : geometric mean ratio, as the degree of over-dispersion of the population changed (Table 18). During the autumn and winter of 1971 the larval population was considerably more overdispersed, probably due to the dominance of the O+ larval population, than at any other time. Thus, compared with the raw data based survival values, those

based on the transformed data measured an additional component, the change in the degree of overdispersion of the population.

For reasons outlined above, it was considered that the analysis based on the transformed data probably led to a better ecological interpretation. Perhaps with the development of more sophisticated non-parametric techniques, the use of the median might be another method worth considering in analysing over dispersed populations.

#### 4. Discussion

There was obviously not enough data to prepare a mathematical model of the population dynamics of the insect, however, a tentative qualitative descriptive one based on the data to hand would be helpful in summarizing the present knowledge (in the following discussion Fig. 23 should be consulted with reference to the changes of the individual  $k$  values).

The larval population dropped considerably during the summer period of 1969/70, and remained at a generally low level during the following winter (Fig. 19b). Owing to reasonably successful spring and autumn emergences during the 1970/71 season (Figs. 21 & 22), the population recovered to remain at a generally high level through to the end of the 1972 winter.

It would appear that  $k_3$  could be one of the key factors determining changes in  $K$ . A major contributing factor to the drop in larval numbers during the 1969/70 summer was undoubtedly the drought (Table 19). Large numbers of 1+ dead larvae were recovered from the sampling during the late summer and autumn months of 1970. From this, it could be assumed that the survival value for the 1+ larval population during the 1969/70 season was

Table 18 The change in the geometric/arithmetical mean ratio (expressed as a percentage) for the larval population at the Hamilton site.

<u>Spring</u>	<u>Ratio as %</u>	<u>Summer</u>	<u>Ratio as %</u>
30.10.69	83.17	12.2.70	70.37
8. 9.70	85.35	1. 3.71	60.44
16. 9.71	61.92	28. 2.72	80.48
2.10.72	87.68		

Table 19 Rainfall recorded at the Hamilton site for the months preceding autumn and spring emergences respectively.

<u>Preceding autumn</u>	<u>mm rain</u>	<u>Preceding spring</u>	<u>mm rain</u>
1.1.70 - 1.3.70	55.7	1.9.70 - 1.11.70	314.9
1.1.71 - 1.3.71	195.7	1.9.71 - 1.11.71	351.5
1.1.72 - 1.3.72	55.8		

was probably low, and mainly affected the autumn emergence.

Considering possible factors responsible for variations in  $k_3$  from the incomplete data collected, it would appear as though soil moisture and temperature conditions during the months of January and February could be important. It can be seen that the months preceding the autumn emergence were much drier during the 1969/70 and 1971/72 seasons than during the 1970/71 season (Table 19). During the 1970 and 1972 summers the surface soil conditions were observed to be very dry, and it was assumed that the soil temperatures would have been correspondingly higher than during the

summer of 1971. Unfortunately, soil temperature recordings were not commenced until March 1971, however, during February of 1972 the temperatures at the 1.5 cm level exceeded 30 °C for between 4 and 5 hours on several consecutive days, and on two occasions the temperature exceeded 40 °C at this depth (Fig. 6). The above, together with the fact that larvae kept at 30 °C for four days under optimal moisture conditions (N = 400 larvae) suffered 93% mortality indicate that the large number of dead 1+ larvae that were recovered during the summer and autumn of 1970 probably died of a combination of heat and lack of moisture. Possibly heat was the more important, since on dissection, the internal contents of the majority of the larvae had been attacked by bacteria, and had undergone a considerable degree of liquification. Why more dead larvae were not recovered on 28.2.72 as compared with during 1970 was probably because the hottest part of the January-February 1972 period did not occur until the second week in February. Thus, many of the larvae affected were probably still of the usual colour and body shape and not taken for dead (sampled larvae were not given a live test, but classified live or dead on general appearance. See life history section). The drought conditions started much earlier in the 1969/70 season, and thus by the February period dead larvae were apparent.

The soil moisture and temperature conditions during the months preceding the spring emergence were not thought to have much detrimental effect on larval survival (Fig. 6. Table 19). Thus, the main component of  $k_3$  can probably be associated with those larvae due to pupate during the autumn emergence.

The mid to late summer drought conditions could have a

differential effect on the different age groups of the larval population. Both from the data based on the number of pupae present during the subsequent 1970/71 season after the 1969/70 drought (Fig. 20), and also the decrease in the  $k_4$  value during the 1971/72 season, it would appear that although all stages are probably affected to some degree, those larvae which are going to enter into the pupal stage during the coming autumn are the worst hit. Since larvae go into the pupal stage in approximately the top 1.5 - 2.0 cm of soil, it is very possible that the penultimate larvae are also as close to the surface during the month or so before they enter into the pupal stage. The above differential in survival value amongst the larval population could perhaps reflect the slightly different positions taken up by different larval groups in the soil profile. Thus, although it would appear from the depth work that the majority of the larval population occur in the top 5.08 cm, larvae in their penultimate instar were probably on the whole closer to the surface than the other age groups; and possibly distances of only 1-2 cm could make the difference between survival or death. Supporting the above contention is the very high survival of the 0+ larval population during 1971/72 compared with the survival of the 1+ larval population during the spring and summer months of the 1971/72 season (Table 17).

From the changes of the different larval classes during the winter of 1971 (Fig. 14), it can be seen that both the spring emergence of 1970, as well as the autumn emergence of 1971, contributed to the larval population recovery. In this particular case the autumn contribution was the most important, however, this is

not always so, for in the following season (1971/72) the spring contributed almost twice as many new larvae to the population as did the autumn one (assuming the same rate of survival for the egg population)(Fig. 22). Thus, although the larval numbers remained relatively stable during 1972, the age distribution of the larvae altered considerably. As can be seen by inspecting Figs. 14 & 22 (also life history section), the bulk of the 0+ population at september 1972 was contributed by the previous spring emergence rather than the autumn one, thus, the high numbers of class 2.3 larvae to class 0 and 1 larvae compared to the same period of 1971.

From the above (also Figs. 20-22), it can be seen that the autumn emergence need not always be the most important. This would be expected to be the case in the 197<sup>3</sup>/~~3~~<sup>4</sup>/~~5~~ season at the Hamilton site.

The above information tends to support the idea of the modification and compensation of the action of  $k_3$  by those factors which contribute to  $k_1$  (Fig. 23 and p. 105 ). The major components of  $k_3$  were probably mainly associated with the autumn emergence period. Thus, the continuing decrease in the  $k_1$  value reflected the spring emergence of 1971 being almost as successful in number of eggs laid per square meter as the one of 1970.

The  $k$  factors associated with pupal survival appeared to act in a compensating fashion to the population trend. The reduction in  $k_5$  made a major difference to the number of adults present during the spring of 1971, and it was probably the larvae from this spring emergence that were the major influence in maintaining the larval population numbers during 1972. The pattern of  $k_6$  would also appear to compensate for the actions of  $k_3$ .

Both  $k_5$  and  $k_6$  considered separately showed some trends of a density dependent relationship, although of course, not enough data was available to be certain. It was not at all clear what the actual factors operating on the pupal population were. Since any signs of disease from the pupal sampled population were slight and no parasites were found, possible predation was the main mortality factor. Osborn (1972 pers. comm.) has reported the discovery of a pupal parasite Neurogalesus sp., in Australia, however its importance there is still unclear. Bird predation could have been the most important, for large flocks of starlings (Sturnus vulgaris) and mynahs (Acridotheres tristis) were observed during the autumn of 1971 particularly, working over the paddock in a systematic manner pecking at the ground. Since soldier fly were the only insect present in large enough numbers to warrant such behaviour, it was assumed that these were being eaten. Both larvae and pupae were probably effected, but pupae mainly, considering that on the whole they would have been bigger and closer to the surface. From pit traps set during the summer and autumn of 1972, carabid and staphylinid larvae were collected and these were probably also preying on the larval and pupal stages.

No specific predator was found for any stage. Eggs and small larvae were probably attacked by the centipede Lamyctes emarginatus, the larval and pupal population by the predators already mentioned above in association with pupal survival, and the adults by field spiders and birds (Table 20). Also, after the drought of 1970, many larvae were found attacked by bacteria and fungi, but these were not thought to be the primary cause of death (Dr. Ostwick, N.R.A.C. Fellow 1970 pers. comm.) but secondary

to heat exposure or moisture stress. However, right through the year a small proportion of dead larvae were removed from every sampling, and the majority of these showed signs of a bacterial infection. No larval parasites were found.

Pupae reared for fecundity estimation work, occasionally suffered a high degree of fungal attack which led to their death. The attacks usually started around the emergence splits in the head and thoracic region. These splits could have been partially opened in the washing and cleaning of the pupae necessary before weighing. A similar condition could occur in the field, if, either due to mechanical injury or premature splitting, the pupal skin was opened before the adult was ready to emerge, then non-pathogenic bacteria or fungi could gain a hold. This could lead to the death of the individual. During the larval life cycle, bacteria could probably gain entry in the same way due to faulty ecdysis.

There were three survival values associated with the adult stage, sex ratio, fecundity and one assessing all other factors. The spring sex ratio remained reasonably stable, however, the  $k$  values associated with the autumn sex ratio showed the same basic pattern as the population trend. Thus, it would appear that the sex ratio favouring the females was a conducive factor to population increase. However, this factor could only operate within certain limits, since if there was a greatly unbalanced sex ratio in favour of the females, probably not all of them would be mated. This would lead to a relatively low survival value for the adult population. At this stage it is difficult to comment on any possible factor that might have influenced the sex ratio.

Table 20 The number of soldier fly found in the guts of birds shot on No. 2 Dairy, Ruakura Agricultural Research Centre, during the autumn of 1973. F = female, M = male.

	<u>Adults</u>	<u>Pupae</u>	<u>Larvae</u>
1. Starling	1 F	2	-
2. "	1 F	-	-
3. "	-	-	-
4. Mynah	15 F	-	-
5. "	1 F, 2 M	1	1
6. "	30 F, 30 M	-	-
7. "	1 F	-	-

The k values associated with adult fecundity showed a slight increasing trend. Both spring and autumn fecundities, if considered separately, showed decreases associated with increases in the larval population measured just prior to the pupal period. (Table 21). Also the fecundity of the spring adult population

Table 21 Relationship between mean fecundity and level of larval population just prior to the commencement of the pupal period.

	<u>Mean fecundity</u>	<u>Larval population (prior to emergence).</u>
Autumn 1970	167	2,300 / m <sup>2</sup>
" 1971	163	2,400 / m <sup>2</sup>
" 1972	141	8,000 / m <sup>2</sup>
Spring 1970	244	2,900 / m <sup>2</sup>
" 1971	177	6,400 / m <sup>2</sup>

appeared to be consistently higher than that of the autumn one. Possibly both of the above trends were due, to some extent, to the quantity and/or quality of the available food. The possible relationship of the first is rather obvious. The difference between the level of the spring and autumn fecundities may be due to the differences in the seasonal growth pattern of the pasture. The spring flush of growth would seem to provide a more abundant supply of food for the last instar larvae going to pupate during the coming spring emergence than would the mid summer growth for the similar stage about to pupate during the autumn. Another explanation for the above is that the difference is due to genetic factors. However, it would appear that the effect of fecundity on the population trend is small.

Variations in the fecundity of the female, could influence the mean number of eggs laid per cluster. However, this was not investigated, and the number of eggs per cluster was assumed to remain reasonably constant throughout the length of the reported study.

The adult mortality factors  $k_9$  and  $k_{12}$  assessed all forms of mortality, including migration. Considering that the study area was surrounded by soldier fly infested pasture, migration into and out of the area was assumed to be equal, and no estimate was made of it. The increase in  $k_9$  might have been due to the increase in adult density during the 1971 spring compared with the previous one, however, there is very little supporting evidence to comment further.

Initially the increase in  $k_{12}$  between 1970 and 1971 could have been as a compensating reaction to the very big increase in

adult population (Fig. 21). The adults, being slow and weak fliers, and having long rest periods on the pasture, would be easy prey for a wide range of predators, from birds to salticid spiders. However, the continual rise by 1972 must have been due to some other factor. Weather conditions which affected flight activity could also act as a mortality factor by preventing mating. Generally, the males flew in search of females to mate, and flight activity occurred at its peak on warm, bright, still days. The presence of light winds (1-2 m/sec. and above) stopped all flight activity completely. From observations, considerably more windy days occurred during the flight period of 1972 than 1971 and on the whole weather conditions were not so conducive to maximum flight activity.

It is difficult at this stage to say how important the  $k_9$  and  $k_{12}$  values concerned with the adult stage were in contributing to changes in the population trend. From the data available, no clear cut relationship was apparent.

In summary, it would appear that  $k_3$  is the major key factor, with  $k_{10}$  probably also exerting some influence.  $k_4$ ,  $k_5$  and  $k_6$  seem to partially compensate for the effect of  $k_3$  on the population trend.

### Whakatane site

#### 1. Introduction

The major reason for setting up this site was to evaluate the autumn surface cultivation method for controlling larval numbers (Wilcocks and Hewitt 1971) and to investigate the speed of re-infestation. It was envisaged that life tables would be set up for both the control and the experimental areas, however, since

labour resources were limited, the above had to be abandoned. A limited amount of data was collected from the control area and is presented and discussed below.

## 2. Results and Discussion (Appendices 7-11)

Although there was a relatively large adult emergence during the autumn of 1970 (Table 22), the actual number of eggs laid considerably exceeded the expected number. Estimated adult survival was 1.79 (Table 23). This indicated that during the emergence period there must have been an overall migration of adult females into the control area. The probable reason for this was that during the main part of the emergence period the grassed control area was situated in the middle of 9 ha of bare soil under intensive surface cultivation. Thus, females emerging from the area under cultivation showed a distinct preference for laying their eggs under pasture conditions.

Because of the above, the O+ larval population was very high during the early winter of 1970 (Fig. 15). However, during the months following the end of July, there was a dramatic drop in larval numbers (Fig. 24). Although all age groups were affected to some degree, the class O larvae suffered more than any other group (Fig. 15). In general, the O+ larval population was drastically reduced, and the effects of this can be seen in the size of the adult autumn emergence in 1972, compared with the size of the previous two (Table 22). The major reason for this drop in larval population was probably that at the beginning of August 1970 the land was waterlogged for several days, surface water being present for three to four days.

Throughout the rest of the winter, spring and early summer,

FIGURE 24

The changes of the larval population with time at the  
Whakatane site. Results based on a  $\log (X+1)$  transformation.

FIG. 24

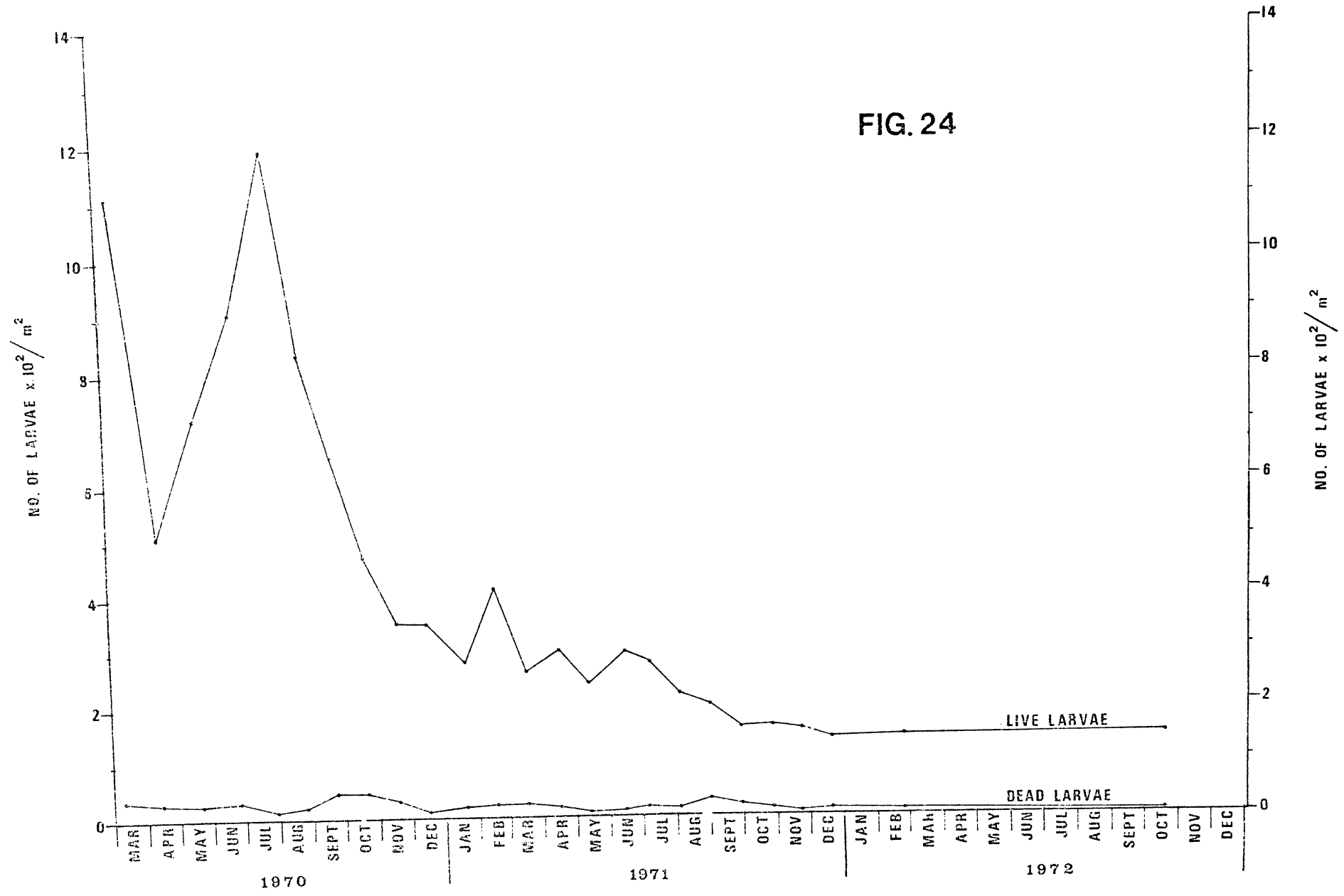


Table 22 Estimated number of adults which emerged / m<sup>2</sup> during the main emergence periods at the Whakatane site, based on raw and transformed data.

<u>Emergence period</u>	<u>Raw data</u>	<u>Log (X+1) transformed data</u>
Autumn 1970 6.3.70 - end of season	206	149
Spring 1970 10.11.70 - 29.12.70	13	9
Autumn 1971 2.3.71 - end of season	301	225
Spring 1971 10.11.71 - 28.12.71	35	21
Autumn 1972 13.3.72 - end of season	28	18

Table 23 Estimated adult survival at the Whakatane site. Adult survival values were based on the raw data, so as to aid in the interpretation of possible migratory movements of the adults.

<u>Emergence period</u>	<u>Survival value</u>
Autumn 1970 ( Eggs assessed 8.4.70 Female adults 2.3.70 - 8.4.70 )	1.79
Autumn 1971 ( Eggs assessed 25.3.71 & 8.4.71 Female adults 9.3.71 - 6.4.71 )	0.13

the larval population continued to fall. The spring adult emergence was a small one compared with that which occurred at Hamilton (Table 22 & Fig. 21). However, the larval population showed a small peak during February 1971 which must have been due to larvae from this emergence. The adult emergence during the autumn of 1971 was a large one and reflected the relatively successful survival of the 1+ larval group through the preceding winter. However the survival of the adult population was extremely low, 0.13 (Table 23). This probably reflected the reversal of the overall migration into the control area which took place the year before. Now with the surrounding population considerably reduced by the previous year's control technique, there would have been an overall migration out of the control area into the surrounding pasture. Probably due mainly to the above, the larval population continued to fall overall during the rest of 1971 (Fig. 24), and became again dominated by the 1+ population (Fig. 15).

The spring adult emergence of 1971 was considerably larger than that of the previous year, and in fact larger than the one of the following autumn (Table 22). This was most probably due to the differential survival of the different larval age groups during the winter of 1970.

During the 1971/72 season adult migration into and out of the control area probably tended to balance out, and the continuing fall in the larval population which had been taking place during the last 18 months was checked. In fact during 1972 the larval population showed some signs of increasing. The larval population in the immediately adjacent area had been slowly increasing since the

1969/70 season, and towards the end of 1972, this and the control population were slowly reaching an equilibrium level.

Pupal survival did not seem to be related to density (Table 24), however, female fecundity did show a trend towards increasing as the larval population decreased (Table 25). Also, as at the Hamilton site, the mean fecundity of the spring emergence appeared to be higher than that of the autumn one of the same season (Table 25).

#### Comparison of the Results from the Two Sites

Of main interest was the drastic effect flooding had on the Whakatane larval population compared with drought on the Hamilton one. The larval population showed a considerable amount of differential age survival at both sites. The drought conditions during the summer mainly affected the 1+ larval population; whereas the winter flooding mainly the 0+ population. Here was the first indication of how the key factor could well vary from one environment to another, and thus the inherent dangers of only developing a predictive model for one district, or in fact one soil type or aspect (Morris 1971).

At the Whakatane site, pupal survival seemed to be completely independent of density, whereas at the Hamilton site there was some indication of a density dependent relationship. This was of particular interest since flocks of mynahs and starlings were often observed at the Hamilton site during the pupal period, but not at the Whakatane site. Further work concerning the effect of bird predation might be of considerable interest. However, the level of pupal survival at Hamilton was consistently higher than at

**Table 24** Estimated pupal survival (P.S.) at the Whakatane site. The estimated pupal population (P.P.) associated with an emergence period is shown. Results are based on raw, and log (X +1) transformed data.

<u>Emergence Period</u>	<u>Raw data</u>		<u>Transformed data</u>	
	<u>P.S.</u>	<u>P.P.</u>	<u>P.S.</u>	<u>P.P.</u>
Autumn 1970 adults 2.4.70 - end of season pupae assessed 31.3.70	0.15	1375	0.13	1147
Spring 1970 adults 10.11.70 - 8.12.70 pupae assessed 10.11.70	0.14	93	0.15	60
Autumn 1971 adults 9.3.71 - 11.5.71 pupae assessed 16.3 & 15.4.71	0.29	1038	0.26	865
Spring 1971 not assessed	-	-	-	-
Autumn 1972 adults 7.3.72 - end of season pupae assessed 6.3 & 4.4.72	0.14	196	0.13	135

**Table 25** Relationship between mean adult fecundity and the level of the larval population just prior to the commencement of the pupal period.

<u>Period</u>	<u>Mean fecundity / female</u>	<u>Larval population</u> <u>∠<sub>m</sub></u>
Autumn 1970	127	11,118
Spring 1970	186	6,487
Autumn 1971	176	4,106
Spring 1971	-	-
Autumn 1972	184	1,430

Whakatane, due to some unknown factor.

When the data relating autumn adult fecundity to the larval population just prior to the commencement of the pupal period was pooled from both sites, a significant correlation was established between the two (Fig. 25). Over 86% of the variation in fecundity was due to its linear regression on the larval population.

The probable effect of the higher larval numbers was to cause a food shortage for the last instar larvae. Thus, the above regression would seem to indicate that the availability of food during the last months of the larval period has a considerable influence on the fecundity of the female adult. This also appears to substantiate the previously suggested explanation for the spring adult population having a higher average fecundity than the autumn one (see p. 116).

FIGURE 25

The relationship between mean autumn adult fecundity (Y) and the larval population measured just prior to the commencement of the pupal period (X).

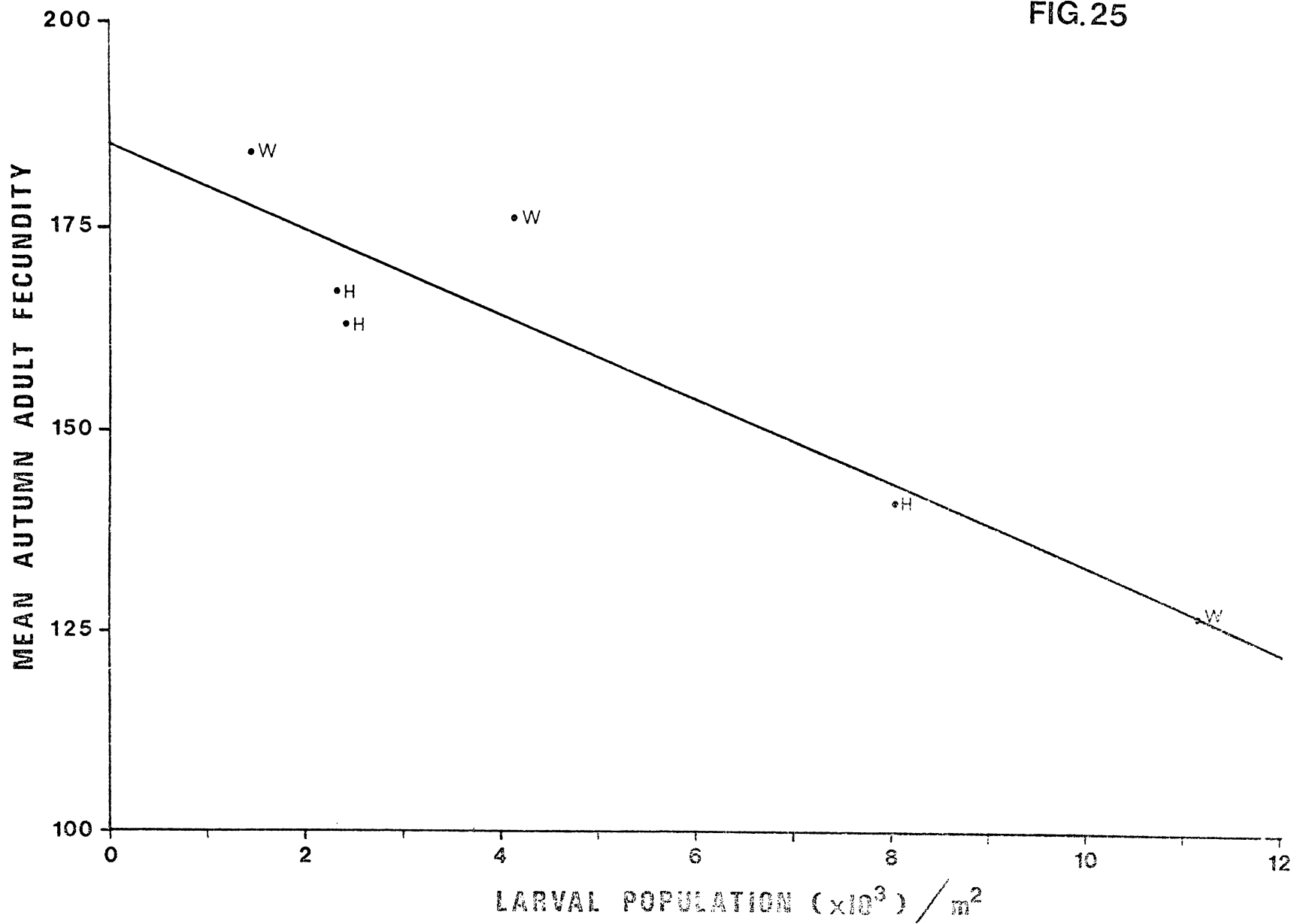
Data from the Hamilton (H) and Whakatane (w) sites was pooled.

The regression equation was  $Y = 185.1 - 0.0052 X$

$b = **$

$r^2 = 0.8603$

FIG.25



FEASIBILITY OF A POPULATION TABLE FOR I. RUBRICEPS

From Table 17 it can be seen that it is theoretically feasible to develop a population table for soldier fly under pasture conditions.

The pupal, adult and egg populations can be assessed for the two main flight periods, and adult fecundity can be estimated from female pupal weight. The adult population is probably the simplest to sample for. Once the emergence cages have been set, they only need clearing once a week and randomly relocating once a fortnight. The periods of adult emergence can be used to set the time for sampling the pupal and egg stages.

The larval population needs to be sampled in the September period, and chronologically classified at this time.

In certain cases the practicality of taking sufficient samples to meet the 95% confidence limits of  $\pm 20\%$  of the mean would need to be carefully considered. The population level, the number of different sites being monitored, and the availability of manpower would be the main factors influencing the possible number of samples taken. For example, at the Hamilton site, the number of egg samples needed to fulfil the above statistical requirements would be extremely high, especially when it is realised they need to be taken every two weeks during the peak emergence period. Thus, it might be found easier to combine adult survival with egg and young larval survival. If the larval extraction method can be improved to extract one month old larvae, the above survival value would still retain a considerable amount

of its time specificity. Since Morris (1963) and Embree (1965) found that sampling errors were not responsible for most of the unexplained variance in their predictive models, much wider 95% confidence limits ( $\pm 50 - 60\%$  of the mean) could probably be tolerated.

Thus, although the sampling scheme for developing population tables (Table 17) is theoretically feasible, certain modifications, both as to confidence limits set and actual survival values measured would probably have to be made according to the prevailing practical conditions. Table 26 is given as a guide to the time taken for processing a given number of samples for the various stages. However, having ascertained the feasibility of establishing population tables, whether it is the best course to follow as far as developing control methods should be considered.

Table 26 The approximate time taken for one man to collect and process one sample for each of the various stages.

<u>Stage</u>	<u>Operation</u>	<u>Time taken in mins.</u>
Adults	1. Assembling necessary gear before leaving for the field	1
	2. Changing collection bag	6 - 12 <sup>1</sup>
	3. Changing collection bag and relocating cage	9 - 18 <sup>1</sup>
	4. Counting and recording in lab.	0.5 - 3
Eggs/Pupae	1. Assembling the necessary gear before leaving for the field	1
	2. Taking sample in field	2 - 4 <sup>1</sup>
	3. Sorting and recording in lab.	10 - 15
Larvae	1. Assembling necessary gear before leaving for the field	1
	2. Taking sample in the field	3 - 6 <sup>1</sup>
	3. Washing process	16
	4. Sorting and recording	3 - 20+ <sup>2</sup>

<sup>1</sup> The range shown indicates the effect of prevailing weather conditions in the field. An additional factor in the case of the adult stage, was the number which were in the body of the trap, but not in the collection bag.

<sup>2</sup> This rather wide range indicates both the variability in number of larvae per sample and the amount of fine plant material which had to be sorted through.

THE USEFULNESS OF THE 'LIFETABLE APPROACH' FOR  
DEVELOPING CONTROL MEASURES FOR INSECT PESTS

The usefulness of any research method in tackling an insect pest problem must be judged on its ability to develop a control management programme. That the actual control methods of such a programme are best developed by initiating work orientated to developing descriptive mathematical models of the pest situation is considered questionable by the present author.

The philosophy of the above approach is to model both the key and other variables so that ultimately various environmental manipulations can be simulated on a computer, and their effect on the pest population estimated (Holling 1963, Watt 1964, 1966, 1970, Chant 1966, Pottinger 1967, and Varley 1970). Thus, the form of pest management is chosen by computer simulation. The limiting factor to obtaining this goal is that man would need to develop biological knowledge to an all-embracing level of integration (Clark et al. 1967). However, at a lower level of expectancy, many authors (Morris 1963, Chant 1964, 1966, Campbell 1967, Harcourt & Le Roux 1967, Pottinger 1967, and Clark 1970) consider that from the analysis of a series of life tables, a better understanding should be gained of the important regulatory mechanisms and associated environmental factors involved in determining a particular pest's population dynamics. Several authors (Morris 1963, Chant 1966, and Pottinger 1967 to name a few) have also expressed the hope that from an understanding of the mortality factors already operating in the agro-ecosystem, the most effective factors will be able to be manipulated so as

to reduce and maintain the pest population at a permanently low level.

The above hope is based on some rather tenuous assumptions, and does not take into account the cause of the pest situation. Pest outbreaks are usually man-made situations resulting from an over-simplification of the environment (Solomon 1964, Chant 1964, and Cole 1966), and the majority of agro-ecosystems are pest situations just waiting to develop. It would seem to be a biological law that simple systems, if created from more complicated ones, will always tend to become more complex (Margalef 1963). Invasion by a pest is one of the first stages in this process. Thus, the major factors which maintain most insects as pests are those directly resulting from man's action to maintain mono or very simplified cultural systems. The factors that are operating in regulating the insects' numbers under such a system must be inefficient from man's point of view by the very fact that the insect is a pest. That these inefficient factors, once they have been isolated, can be manipulated into efficient ones is by no means certain. Whether they can be manipulated at all is open to considerable doubt, for if the key factor turns out to be some aspect of weather conditions, we are often no closer to developing a control method than before.

In considering developing control methods, it should be remembered that man will have to interfere again with the agro-ecosystem to control the pest situation. That this interference should be made in such a way as to augment any existing control factors is not necessarily valid, although if it can be done so much the better; since man may more effectively be able to control

the pest by the introduction of a technique which does not take existing controlling factors into account. As Chant (1964) commented, rather than think in the usual way of restoring natural balance, one must think in terms of creating something entirely new that will be an effective substitute for what has been lost. To accomplish this, the mathematical modelling of the pest situation as it were in situ, is of very little practical help. Morris (1963) commented after 18 years of work developing and analysing life tables of the spruce budworm, that nothing new was able to be added to the cultural control practices initially recommended in 1912. Even Watt (1970) conceded that probably the greatest value of system modelling was in pointing out to the modeller connections between different parts of the system which might otherwise not have occurred to him.

It is suggested that a more practical method for developing control measures is an ecologically based experimental approach. In fact, this is basically the method by which, to date, all successful integrated control measures have been developed. In brief, the agro-ecosystem in which the insect occurs should be studied with the view of seeing how it can be modified to exploit some vulnerable aspect in the pest's life cycle, yet still retain those qualities for which it was first designed. An intensive and systematic study of the insect's life history needs to be carried out, with the object of identifying and describing the relevant elements of the pest situation (Clark 1970). This information is vital to developing any control method. Yet, how one proceeds after the analysis of this initial information will depend so much on the particular insect pest and the agro-eco-

system in which it occurs (Southwood & Way 1970). There are three main possibilities. First, some aspect of the agro-ecosystem may be able to be changed physically in some way either in space or time to minimise the effect of the pest. Secondly, some element may be added to the system, such as a biological control agent or an insecticide. Thirdly, the original function for which the agro-ecosystem was designed should be reassessed and possibly altered.

Although the experimental, quasi intuitive development of control methods has received some hard knocks from various authors (Chant 1966, Clark et al. 1967, Pottinger 1967, Mott 1969, Clark 1970, and Watt 1970) in recent times, it is contended that this approach, if carried out along rational guidelines, is a sound method for developing control methods. In developing an integrated control programme, past experiences in research, close observations, research in other areas and imagination are important in suggesting leads for detailed study (Rabb 1970). Indeed it is something of an art as well as a science (Huffaker 1970). The development of a control method along these lines should not in any way be confused with an ad hoc method. From the initial study of both the attributes of the agro-ecosystem and the insect, several leads should present themselves. The ecological processes involved in a promising line of control, should then be carefully studied, both in the laboratory and under field conditions, so that the method of action of the control method is fully understood.

It must be remembered that man has to maintain a constant input to maintain his agro-ecosystem. This will also apply to pest control. In most pest control programmes there is usually

a compromise between increasing the complexity of the system to control the pest, and maintaining the system simple so that the agro-ecosystem can serve its original function. Because of this compromise situation, it is Utopian to expect any pest control programme to operate without some sort of constant input. For example, in an integrated control programme the situation must be monitored to decide if, and when, any control action needs to be taken. However, in all agro-ecosystems, if they are to be maintained for their original purpose, a palliative form of control is probably all that can be hoped for.

Thus, in summary it is maintained that the usefulness of the life table approach for developing control measures is highly questionable. This is not to be taken as a criticism of life tables as such, or their use in studying and modelling natural populations. However, in the artificial environment of man's agro-ecosystems their practical use is limited by their basically passive observational role. They describe the situation without helping to understand the ecological processes involved (Holling 1963). In a practical situation like insect control, it is more important to understand the functioning of the important, possibly modifiable, ecological processes, and this must depend upon an essentially experimental approach.

The main use of the life table approach is probably for the development of empirically based projection models. Using the above, together with information relating numbers of insects to damage caused, the decision can be made of whether or not any appropriate control action needs to be taken. For example, Le Roux et al. (1965) found that for Spilonota ocellana in Quebec apple

orchards, that insecticides could be left out of spray programmes during the summer if previous winter frosts had exceeded minus 21 °F. (-30 °C).

## CONCLUDING REMARKS

This study has accomplished its main aim of determining the feasibility of establishing a population table (Table 17) for the Australian soldier fly Inopus rubriceps. Assuming a two year life cycle for the majority of individuals and disregarding the low emergence which occurs between the two main periods, a yearly population table was developed, relating the survival of the various stages in the life history with that of the larval population as a whole, from the September period of one year to that of the next. The above system of analysis was adopted to gain as much information as possible from the available data. However, when more results are collected, it could well be found that an analysis based on alternate seasons is more useful in interpreting population changes. Also, it is possible that the spring and autumn emergences for a given season could be pooled without influencing the results over much. However, it would appear impossible at the moment to analyse the data on a generation basis because of the difficulties in ageing the larval population.

The main value of developing population tables is that they enable the development of predictive population models, which together with information relating damage to levels of larval population, would assist in making decisions on use of appropriate control methods. The writer has argued that the building of mathematical models to describe the pest situation 'in situ' is probably not the best method for developing control methods. In most practical situations, such as pest control, there has tended to develop a conflict between those who seek complete understanding

before taking action, and those who take action in a purely intuitive ad hoc way (Tribus 1970). The writer suggests that a compromise be based on an ecologically rational experimental approach, orientated to considering the possibilities of altering the agro-ecosystem in such a way as to exploit some weak link or links in the life system of the pest. In certain cases, the original function of the agro-ecosystem may need to be revised, whilst in others, because of the extremely simple ecosystem which must be maintained for man's original purpose, a palliative form of control will be all that can be expected. In fact, because of the unstable ecological nature of most agro-ecosystems, practically all forms of insect control will be palliative, but will probably vary as to the amount of input required, depending upon how complex man can allow his agro-ecosystem to become while still retaining its original function. The basic purpose of pest management programmes is to reach a compromise between input of control measures and output in production, that is satisfactory both in monetary terms and with reference to currently held social values.

With the considerable amount of work currently under way by Mr. Dixon of the Ruakura Agricultural Research Centre, Hamilton, on improving recommended methods of control (Wilcocks & Hewitt 1971, Wilcocks 1971), and developing new methods, the position is being reached where it can be argued that it is just as important to know when to take control action, as to know what action to take. Thus, the development of suitable predictive models for soldier fly populations is of considerable importance.

## SUMMARY

1. The main aim of this work was to test the feasibility of utilizing life tables, or a similar approach, in the development of a pest management programme for the Australian soldier fly Inopus rubriceps. It was found possible to develop a population table on assuming a two year life cycle for the majority of individuals, and discounting the low adult emergences which occurred between the two main emergence periods per season. The population trend was taken as the survival of the whole larval population from the September period of one year to that of the next, all other survival values being related to this. The two emergence periods per season were treated separately; the following being the survival values assessed:

- (i) The yearly population trend.
- (ii) The survival of the whole larval population from September to February.
- (iii) The survival of the whole larval population from February to September.
- (iv) The survival of the 0+ larval population during the subsequent year.
- (v) The survival of the 1+ larval population during the immediately following season.
- (vi) The survival of the eggs and 0+ larval population from a seasons two emergence periods up to the following September.
- (vii) Pupal survival for both the spring and autumn emergence periods.

(viii) Adult sex ratio for both the spring and autumn emergence periods.

(ix) Adult fecundity for both spring and autumn emergence periods.

(x) Adult survival for both spring and autumn emergence periods.

2. The value of life or population tables as a means of developing control measures is discussed, and the approach is considered to be of questionable merit. It is suggested that control methods are probably more likely to be developed by studying in an ecologically rational experimental way, methods of altering the agro-ecosystem to exploit weak links in the biology or ecology of the pest. In certain cases, changing the original purpose of the agro-ecosystem should be considered. The major usefulness of life or population tables is thought to be in the development of predictive models, which together with information relating damage caused to various levels of larval population would allow decisions on control necessity to be made.

3. A considerable amount of information was collected in the process of the above work, and this is summarized below:

(i) The method of causing damage, plants attacked, symptoms shown by attacked plants, and the pest status of the Australian soldier fly under three different agro-ecosystems is discussed. Pot work confirming the capacity for damage to rye grass (Lolium perenne (Ariki)) by soldier fly is presented.

(ii) The adult stage.

The length of adult life, mating and oviposition behaviour were investigated. The emergence pattern is described

at three sites, and at each it was found that there were two main emergence periods per season, one during the months of November - December and the other during March - April. The sex ratio of emergents and the pattern of emergence within each emergence period are discussed and a possible explanation is put forward for the geographic variation in emergence pattern per season.

(iii) The egg stage

Eggs were found to be laid in clusters ( $42.03 \pm 7.96$  / cluster.  $n = 61$ ) in the top 1.5 cm of the soil.

The effect of temperature on time of development was investigated and it was found that under pasture conditions eggs usually took approximately two weeks to hatch.

(iv) The larval stage

Larvae were reared individually on maize plants in a screen house. The majority of larvae appear to have a life cycle of between 24 and 28 months, the former probably being most common. Possibly up to 10% of the population (based on the survival of reared individuals) come through from eggs to adults in 12 months, while a few take up to 36 months.

A wide range of growth rates was recorded, both in time of increase, and actual weight gain, even from larvae which hatched within hours of each other. The majority of large increases in live weight tended to occur during the spring, summer and autumn months, with a marked tendency for weight to be static or gained only slowly during the winter months.

A larval classification, based on weight was developed, and from both insectary and field studies it was found that the larval population could be divided into two groups, one over one year of

age (1+), and another under one year of age (0+), as measured in the September period of each year.

The vertical distribution of larvae under pasture conditions was investigated, and the majority of larvae were found to occur in the top 10 cm. This depth coincides with the region of maximum root concentration in the study areas. A very small percentage of larvae were found between 15 and 26 cm.

(v) The pupal stage

Pupae were found in the top 1.5 cm of soil and this stage occupied approximately a month.

(vi) The rationale behind the choice of the type and size of the sampling unit for each stage is discussed, as is the timing of sampling.

(vii) Methods of extraction for each stage were developed. In the case of the larval stage various improvements are still under study to increase the efficiency of extracting class 0 larvae as soon after hatching as possible.

(viii) Methods of analysing life table data are discussed briefly and Varley and Gradwell's graphical method was adopted. Use of the raw data or log transformed data is discussed. Both were tried and it is argued that the use of transformed data probably gives a more ecologically realistic interpretation of the data.

(ix) The actual precision required for sampling is discussed and it is considered that  $\pm 20\%$  of the mean (95% limits) would agree reasonably well with the level of precision chosen by other authors. Since Morris (1963) and Embree (1965) found that sampling errors were not responsible for most of the unexplained variance

in their developed predictive models, much wider 95% confidence limits ( $\pm$  50 - 60% of the mean) could probably be tolerated.

(x) A relationship between adult fecundity and female pupal weight was established, which allowed the populations mean fecundity to be estimated by regression sampling.

(xi) The following were the main points emerging from analysis of the population data from the two study sites:

- a. At the Hamilton site the key factor appeared to be survival of the 1+ larval population. Soil temperature during mid and late summer is thought to be the major mortality agent. At Whakatane, the key factor could well be the survival of the 0+ larval population during the winter period. Flooding here was considered to be the main mortality agent. In both cases, a considerable amount of differential survival based on age was observed in the larval population. At the Hamilton site, this could have been due to the vertical distribution taken up by the different aged larvae in the soil, whilst at Whakatane it may have been a function of size, smaller larvae being more susceptible to drowning than larger ones.
- b. A female biased sex ratio during the autumn emergence appeared to favor a population increase at the Hamilton site.
- c. At the Hamilton site, pupal survival tended to compensate for the actions of the key factor, and also showed a tendency to be density dependent. At the Whakatane site, however, pupal survival appeared to be completely independent of density. It was thought that bird predation of pupae could have been an important mortality factor at the Hamilton site, but not at Whakatane.

d. From the high adult survival during the 1970 autumn at the Whakatane site, it would appear that adults prefer to lay their eggs under pasture conditions rather than in bare soil.

e. No parasites were found for any stage. Bacterial and fungal attacks are recorded for the larval and pupal stages, but it is thought that these were possibly secondary infections.

Staphylinids, carabids, centipedes, spiders and birds were considered to be active predators on the different stages, but all were considered to be non-specific.

f. The fecundity of adults from the spring emergence was consistently higher than from the autumn one. Also, there was a significant relationship between the fecundity of the autumn adult population and the density of the larval population prior to the commencement of the pupal period. It is suggested that the availability of food during the last months of the larval period plays an important role in both of the above.

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APPENDIX 1 The proportion (p) and the 95% confidence limits (cl) of the different larval classes at the two study sites. n = number of larvae weighed.

HAMILTON SITE		Larval class						
<u>Date</u>		<u>0</u>	<u>1</u>	<u>2 &amp; 3</u>	<u>4 &amp; 5</u>	<u>6</u>	<u>7,8 &amp; 9</u>	<u>n</u>
16. 6.70	p	.0041	.0222	.1819	.1496	.0872	.5596	242
	cl	$\pm$ .0082	.0189	.0496	.0459	.0363	.0638	
20. 7.70	p	.0096	.0325	.1428	.1308	.1910	.4932	104
	cl	.0191	.0348	.0686	.0661	.0771	.0980	
11. 8.70	p	.0000	.0089	.0536	.1057	.2351	.5967	112
	cl	.0000	.0177	.0425	.0581	.0801	.0927	
8. 9.70	p	.0096	.0403	.0847	.0673	.1528	.6452	104
	cl	.0191	.0386	.0546	.0492	.0706	.0938	
6.10.70	p	.0000	.0102	.0840	.0659	.1616	.6783	98
	cl	.0000	.0203	.0560	.0501	.0744	.0944	
3.11.70	p	.0545	.0091	.0000	.0455	.1519	.7389	110
	cl	.0433	.0181	.0000	.0397	.0684	.0838	
2.12.70	p	.0000	.3610	.1229	.0504	.0561	.4097	93
	cl	.0000	.0996	.0681	.0454	.0477	.1020	
29.12,70	p	.0000	.1805	.1781	.0124	.0894	.5396	62
	cl	.0000	.0977	.0972	.0281	.0725	.1266	

APPENDIX 1 continued

<u>DATE</u>		<u>0</u>	<u>1</u>	<u>Larval class</u> <u>2.3</u>	<u>4.5</u>	<u>6</u>	<u>7.8.9</u>	<u>n</u>
4. 2.71	p	.0132	.1627	.3172	.0488	.0594	.3587	151
	cl	± .0185	.0601	.0757	.0350	.0385	.0781	
1. 3.71	p	.0280	.1635	.0393	.2006	.1298	.4388	143
	cl	.0276	.0618	.0325	.0670	.0562	.0830	
29. 3.71	p	.0254	.3422	.1589	.1510	.1389	.1827	118
	cl	.0290	.0874	.0673	.0659	.0637	.0711	
29. 4.71	p	.0378	.3328	.2770	.0268	.1114	.2142	132
	cl	.0332	.0820	.0779	.0281	.0548	.0714	
27. 5.71	p	.1504	.3085	.2545	.0558	.1092	.1215	226
	cl	.0475	.0614	.0580	.0305	.0415	.0435	
22. 6.71	p	.1270	.3038	.2652	.0538	.1061	.1441	307
	cl	.0380	.0525	.0504	.0258	.0352	.0401	
19. 7.72	p	.3278	.1989	.1958	.0885	.0561	.1333	238
	cl	.0609	.0517	.0515	.0368	.0298	.0440	
18. 8.71	p	.2081	.1809	.2223	.0904	.1055	.1929	245
	cl	.0519	.0492	.0531	.0367	.0392	.0504	
16. 9.71	p	.1573	.2337	.2105	.0976	.1099	.1910	248
	cl	.0463	.0537	.0518	.0377	.0397	.0499	
14. 10.71	p	.2484	.4483	.1377	.0475	.0300	.0899	322
	cl	.0482	.0554	.0384	.0237	.0190	.0319	

APPENDIX 1 continued

Larval class

<u>Date</u>		<u>0</u>	<u>1</u>	<u>2.3</u>	<u>4.5</u>	<u>6</u>	<u>7.8.9</u>	<u>n</u>
5.11.71	p	.1373	.4358	.1594	.0826	.0693	.0975	415
	cl	± .0388	.0489	.0359	.0271	.0249	.0291	
9.12.71	p	.0000	.4612	.2643	.0705	.0691	.1350	369
	cl	.0000	.0519	.0459	.0267	.0264	.0356	
28. 2.72	p	.0078	.3330	.4041	.1280	.0643	.0629	385
	cl	.0089	.0480	.0500	.0341	.0250	.0247	
31. 7.72	p	.1454	.1222	.3478	.1546	.1350	.0985	736
	cl	.0260	.0242	.0351	.0267	.0252	.0220	
2.10.72	p	.0410	.1078	.1954	.1555	.2358	.2644	292
	cl	.0232	.0363	.0464	.0424	.0497	.0516	

WHAKATANE SITE

25. 6.70	p	.2144	.1402	.1861	.1125	.1195	.2272	453
	cl	.0386	.0326	.0366	.0297	.0305	.0394	
28. 7.70	p	.5592	.0541	.1781	.0950	.1049	.2434	532
	cl	.0430	.0192	.0332	.0255	.0265	.0372	
25. 8.70	p	.3713	.0624	.1915	.0701	.0834	.2213	385
	cl	.0492	.0247	.0401	.0260	.0282	.0423	
22. 9.70	p	.1622	.1090	.1543	.0926	.1611	.3209	222
	cl	.0495	.0418	.0485	.0389	.0494	.0627	

APPENDIX 1 continued

<u>Date</u>		<u>Larval class</u>						<u>n</u>
		<u>0</u>	<u>1</u>	<u>2.3</u>	<u>4.5</u>	<u>6</u>	<u>7.8.9</u>	
22.10.70	p	.0000	.0575	.2570	.1447	.1690	.3716	125
	cl	<sup>±</sup> .0000	.0417	.0782	.0629	.0671	.0864	
18.11.70	p	.0000	.1039	.2355	.1371	.1284	.3952	148
	cl	.0000	.0502	.0697	.0565	.0550	.0804	
16.12.70	p	.0000	.1198	.1760	.1413	.1437	.4191	135
	cl	.0000	.0559	.0655	.0600	.0604	.0849	
20. 1.71	p	.0000	.0894	.1111	.1125	.1482	.5389	204
	cl	.0000	.0399	.0440	.0442	.0498	.0698	
16. 2.71	p	.0000	.0719	.1608	.0707	.2006	.4961	234
	cl	.0000	.0338	.0480	.0335	.0523	.0654	
16. 3.71	p	.0000	.1550	.2330	.1567	.1400	.3153	162
	cl	.0000	.0569	.0664	.0571	.0545	.0730	
15. 4.71	p	.0264	.1399	.2605	.1481	.1503	.2748	183
	cl	.0237	.0513	.0649	.0525	.0528	.0660	
13. 5.71	p	.0954	.0395	.2207	.1827	.2121	.2496	149
	cl	.0481	.0319	.0679	.0633	.0670	.0707	
11. 6.71	p	.0458	.1527	.1427	.1120	.1663	.3806	132
	cl	.0364	.0626	.0609	.0549	.0648	.0845	
6. 7.71	p	.0517	.0119	.1614	.1418	.2025	.4210	116
	cl	.0411	.0201	.0683	.0648	.0746	.0917	

APPENDIX 1 continued

<u>Date</u>		<u>0</u>	<u>1</u>	<u>2.3</u>	<u>4.5</u>	<u>6</u>	<u>7.8.9</u>	<u>n</u>
3. 8.71	p	.1074	.0760	.1720	.0704	.2149	.3593	121
	cl	‡ .0563	.0482	.0686	.0465	.0747	.0872	
31. 8.71	p	.0526	.0998	.1917	.0888	.1417	.4251	115
	cl	.0416	.0559	.0734	.0531	.0651	.0922	
28. 9.71	p	.0000	.0145	.1441	.1323	.1137	.5956	82
	cl	.0000	.0264	.0776	.0748	.0701	.1084	
27.10.71	p	.0377	.0754	.1132	.1132	.0617	.5987	53
	cl	.0523	.0725	.0870	.0870	.0661	.1347	
22.11.71	p	.0273	.1290	.1087	.0827	.0903	.5620	124
	cl	.0293	.0602	.0559	.0495	.0515	.0891	
20.12.71	p	.0000	.0722	.0908	.0928	.1030	.6412	58
	cl	.0000	.0680	.0754	.0762	.0798	.1260	

APPENDIX 2 Results of larval sampling at the Hamilton site.

sample unit = 7.62 cm diam. core. n = number of samples taken.

$$k = \frac{\bar{x}^2}{s^2 - \bar{x}}$$

L.S.M. = log sample mean.

L.C.L. = log 95% confidence limits

R.D. = numbers / m<sup>2</sup> based on the raw data

T.D. = numbers / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>n</u>	<u>k</u>	<u>log (X+1) tranformation</u>		<u>R.D.</u>	<u>T.D.</u>
			<u>L.S.M.</u>	<u>L.C.M.</u>		
30.10.69	20	2.10	1.4876	± 0.1047	7836	6517
16.12.69	12	7.42	1.4585	0.1039	6850	6081
12. 2.70	40	0.83	1.0614	0.1166	3277	2306
13. 5.70	80	3.24	1.0677	0.0548	2702	2343
16. 6.70	40	8.60	1.1374	0.0645	3091	2788
20. 7.70	40	5.95	1.2679	0.0686	4318	3843
11. 8.70	40	4.59	1.1745	0.0724	3503	3058
8. 9.70	40	2.86	1.1769	0.0740	3601	3075
6.10.70	40	12.73	1.1523	0.0572	3135	2896
3.11.70	40	3.25	1.0570	0.0828	2729	2280
2.12.70	39	3.62	1.0098	0.0990	2591	2023
29.12.70	40	2.11	0.8656	0.0899	1760	1390
4. 2.71	40	1.07	0.8178	0.1231	1863	1221
1. 3.71	40	0.52	1.0825	0.1229	4022	2431
29.3 .71	40	0.70	0.8590	0.1401	2422	1366
29. 4.71	40	1.58	1.0274	0.1246	3036	2115
27. 5.71	40	2.66	1.1999	0.1109	4274	3253
22. 6.71	40	1.19	1.2875	0.1293	6039	4029
19. 7.71	40	0.84	1.3334	0.1422	7657	4509
18. 8.71	40	1.01	1.3688	0.1319	7650	4904
16. 9.71	40	1.06	1.4789	0.1449	10309	6583
5.11.71	40	1.91	1.5389	0.1105	9667	7361
9.12.71	40	2.00	1.5117	0.1160	9520	7170
28. 2.72	64	3.28	1.5700	0.0817	9846	7924
31. 7.72	64	3.35	1.6733	0.0601	11690	10125
2.10.72	40	4.91	1.5541	0.0753	8702	7630

APPENDIX 3 Results of pupal sampling at the Hamilton site.

s.u. = sample unit size. n = number of samples taken.

L.S.M. = log sample mean. L.C.L. = log 95% confidence limits.

R.D. = numbers of pupae / m<sup>2</sup> based on the raw data.

T.D. = numbers of pupae / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>s.u.</u>	<u>n</u>	<u>log(X+1) transformation</u>		<u>R.D.</u>	<u>T.D.</u>
			<u>L.S.M.</u>	<u>L.C.L.</u>		
6. 4.70	10.16 cm sq	32	0.4043	± 0.1058	206	149
12.11.70	11.43 cm diam core	40	0.6502	0.1018	460	336
23. 3.70	"	24	0.9443	0.1562	1055	759
19. 4.71	"	40	0.1951	0.0748	83	55
26.10.71	"	64	0.0470	0.0282	16	11
22.11.71	"	64	0.2672	0.0720	137	83
13. 3.72	"	64	0.1298	0.0564	57	34
8. 4.72	"	64	0.2485	0.0662	116	75

APPENDIX 4 Estimated mean female fecundity for the main emergence periods at the Hamilton site.

m.w. = mean female weight. C.L. = 95% confidence limits.

n = no. of female pupae weighed. M.N.E. = mean no. of eggs / female.

	<u>m.w.(mg)</u>	<u>C.L.( mg)</u>	<u>n</u>	<u>M.N.E.</u>
Autumn 1970	24.94	± 3.26	15	167.1
Spring 1970	23.46	3.71	21	244.1
Autumn 1971	24.56	1.47	61	163.7
Spring 1971	26.61	2.61	13	178.0
Autumn 1972	22.07	3.41	20	141.2

APPENDIX 5 Results of adult sampling at the Hamilton site.

Sample unit size = 53.31 cm diameter cage.

n = number of samples taken.

L.S.M = log sample mean.

L.C.L. = log 95% confidence limits

R.D. = number of adults / m<sup>2</sup> based on the raw data.

T.D. = number of adults / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>n</u>	<u>log(X+1)transformation</u>		<u>R.D.</u>	<u>T.D.</u>
		<u>L.S.M.</u>	<u>L.C.L.</u>		
24.12 - 2.3.70	9	0	± 0	0	0
2.3 - 9.3.70	9	0	0	0	0
9.3 - 16.3.70	9	0	0	0	0
16.3 - 23.3.70	9	0	0	0	0
23.3 - 2.4.70	9	0.0530	-	0.99	0.58
2.4 - 10.4.70	9	0	0	0	0
10.4 - 16.4.70	9	1.1143	0.1340	59.60	53.73
16.4 - 22.4.70	9	1.0510	0.1296	48.67	45.85
22.4 - 29.4.70	9	0.6185	0.2200	19.37	14.11
29.4 - 5.5.70	9	0.1338	0.1456	2.48	1.61
6.11 - 13.11.70	32	0.1111	0.0748	2.24	1.30
13.11 - 20.11.70	32	0.5498	0.1000	14.81	11.39
20.11 - 27.11.70	32	0.4315	0.978	10.16	7.61
27.11 - 4.12.70	32	0.5772	0.1058	16.76	12.42
4.12 - 11.12.70	32	0.1106	0.0800	1.82	1.30
11.12 - 18.12.70	32	0.8497	0.1130	34.78	27.16
18.12 - 24.12.70	32	0.0808	0.0528	1.26	0.91
24.12 - 1.1.71	32	0.0188	-	0.28	0.20
1.1 - 8.1.71	32	0.1255	0.0692	2.24	1.50
8.1 - 22.1.71	32	0	0	0	0
22.1 - 5.2.71	32	0.0376	0.0346	0.56	0.40
5.2 - 19.2.71	32	0	0	0	0
19.2 - 5.3.71	32	0.0094	-	0.14	0.10
5.3 - 12.3.71	32	0	0	0	0
12.3 - 19.3.71	32	0.2226	0.0824	4.20	2.99

APPENDIX 5 continued

<u>Date</u>	<u>n</u>	<u>log(<math>\lambda+1</math>)transformation</u>		<u>R.D.</u>	<u>T.D.</u>
		<u>L.S.M.</u>	<u>L.C.L.</u>		
19. 3 - 26. 3.71	32	0.9411	<sup>±</sup> 0.1058	43.86	34.58
26. 3 - 2. 4.71	32	0.7242	0.1166	25.84	19.22
2. 4 - 8. 4.71	32	1.7448	0.1264	299.49	243.98
8. 4 - 16. 4.71	32	0.8020	0.1000	30.03	23.88
16. 4 - 23. 4.71	32	0.1576	0.0632	2.52	1.95
23. 4 - 30. 4.71	32	0.2007	0.0848	3.92	2.63
30. 4 - 7. 5.71	32	0	0	0	0
7. 5 - 14. 5.71	32	0	0	0	0
14. 5 - 21. 5.71	32	0	0	0	0
15.10 - 22.10.71	32	0	0	0	0
22.10 - 29.10.71	32	0	0	0	0
29.10 - 5.11.71	32	0	0	0	0
5.11 - 12.11.71	32	0.0564	0.0421	0.84	0.64
12.11 - 19.11.71	32	0.3451	0.1097	8.52	5.43
19.11 - 26.11.71	32	0.8513	0.1257	39.25	27.27
26.11 - 3.12.71	32	0.8119	0.1094	32.27	24.52
3.12 - 10.12.71	32	0.5623	0.1068	15.65	11.85
10.12 - 17.12.71	32	0.5449	0.0907	13.83	11.20
17.12 - 23.12.71	32	0.3080	0.1082	7.26	4.61
23.12 - 31.12.71	32	0.2187	0.0902	4.61	2.93
31.12 - 21. 1.72	32	0.0188	0.0262	0.28	0.20
21. 1 - 4. 2.71	32	0.0470	0.0392	0.70	0.51
4. 2 - 18. 2.72	32	0.0188	0.0262	0.28	0.20
18. 2 - 25. 2.72	32	0.0094	0.0188	0.14	0.10
25. 2 - 3. 3.72	32	0.0282	0.0315	0.42	0.30
3. 3 - 10. 3.72	32	0	0	0	0
10. 3 - 17. 3.72	32	0	0	0	0
17. 3 - 24. 3.72	32	0	0	0	0
24. 3 - 30. 3.72	32	0.1879	0.0945	4.19	2.42
30. 3 - 7. 4.72	32	0.8011	0.3811	37.72	23.80
7. 4 - 14. 4.72	32	1.0843	0.1184	68.24	49.80
14. 4 - 21. 4.72	32	0.1831	0.0838	3.22	2.34

APPENDIX 5 continued

<u>Date</u>	<u>n</u>	<u>log(X + 1)transformation</u>		<u>R.D.</u>	<u>T.D.</u>
		<u>L.S.M.</u>	<u>L.C.L.</u>		
21. 4 - 28. 4.72	32	0.3329	<sup>±</sup> 0.1178	7.82	5.15
28. 4 - 5. 5.72	32	0.0580	0.0493	1.45	0.64
5. 5 - 12. 5.72	32	0	0	0	0
12. 5 - 20. 5.72	32	0.0104	0.0208	0.77	0.11
20. 5 - 25. 5.72	32	0	0	0	0

APPENDIX 6 Results of sampling egg clusters at the Hamilton site.

s.u. = sample unit size. n = number of samples taken.

L.S.M. = log sample mean. L.C.L. = log 95% confidence limits.

R.D. = the number / m<sup>2</sup> based on the raw data.

T.D. = the number / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>s.u.</u> core diam in cm.	<u>n</u>	<u>log (X+1) transformation</u>		<u>R.D.</u>	<u>T.D.</u>
			<u>L.S.M.</u>	<u>L.C.L.</u>		
16. 4.70	7.62	32	0.0768	± 0.0538	61.66	42.30
30.11.70	"	40	0.0527	0.0366	38.36	28.28
14.11.70	"	40	0.0075	0.0152	5.48	3.73
22.12.70	"	40	0.0646	0.0400	49.32	35.29
2. 4.71	"	24	0.0376	0.0356	27.40	19.73
19. 4.71	"	24	0.2951	0.1188	319.65	213.71
3.12.71	"	64	0.0485	0.0346	41.10	25.86
17. 4.72	11.43	64	0.0357	0.0260	12.18	8.38
1. 5.72	"	64	0.0263	0.0231	9.14	6.14

mean no. of eggs / cluster = 42.03 ± 7.96 (n = 61).

APPENDIX 7 Results of larval sampling at the Whakatane site.

Sample unit size = 7.62 cm diameter core.

n = number of samples taken. L.S.M. = log sample mean.

L.C.L. = log 95% confidence limits.

R.D. = the number of larvae / m<sup>2</sup> based on the raw data.

T.D. = the number of larvae / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>n</u>	<u>log(X+1) transformation</u>		<u>R.D.</u>	<u>T.D.</u>
		<u>L.S.M.</u>	<u>L.C.L.</u>		
10. 3.70	40	1.7129	<sup>±</sup> 0.0528	11962	11118
14. 4.70	24	1.3847	0.0966	5792	5092
20. 5.70	56	1.5275	0.0711	8217	7178
25. 6.70	40	1.6264	0.1164	11830	9071
29. 7.70	40	1.7421	0.0674	13203	11906
25. 8.70	40	1.5901	0.0827	9657	8325
22. 9.70	40	1.4848	0.0814	7596	6487
20.10.70	40	1.3510	0.0895	5682	4708
18.11.70	40	1.2288	0.1034	4886	3498
16.12.70	40	1.2256	0.0872	4073	3472
20. 1.71	40	1.1379	0.1416	4172	2798
16. 2.71	40	1.2945	0.0888	4908	4106
16. 3.71	40	1.1085	0.1169	3601	2598
15. 4.71	40	1.1543	0.0889	3535	2914
13. 5.71	40	1.0752	0.1091	3195	2394
11. 6.71	40	1.1587	0.0857	3568	2939
6. 7.71	40	1.1384	0.1022	3622	2795
3. 8.71	40	1.0416	0.1099	2861	2194
31. 8.71	40	1.0060	0.0983	2591	2003
28. 9.71	40	0.9131	0.1175	2283	1587
27.10.71	40	0.9246	0.1232	2371	1624
22.11.71	40	0.9095	0.1079	2069	1560
20.12.71	40	0.8659	0.1022	1849	1390
24. 2.72	40	0.8764	0.1126	2010	1430
19.10.72	32	0.8791	0.1489	2322	1440

APPENDIX 8 Results of pupal sampling at the whakatane site.

s.u. = sample unit size. n = number of samples taken.

L.S.M. = log sample mean. L.C.L. = the log 95% confidence limits.

R.D. = the number / m<sup>2</sup> based on the raw data.

T.D. = the number / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>s.u.</u>	<u>n</u>	<u>log(X+1) transformation</u>		<u>R.D.</u>	<u>T.D.</u>
			<u>L.S.M.</u>	<u>L.C.L.</u>		
31. 3.70	10.16cm sq.	32	0.9259	± 0.0783	763	720
10.11.70	11.43 cm core diam.	40	0.1709	0.0740	73	47
16. 3.71	"	64	0.9661	0.0626	953	803
15. 4.71	"	40	0.1679	0.0753	78	46
28.10.70	"	64	0.0000	-	0	0
22.11.71	"	64	0.0047	-	2	1
6. 3.72	"	64	0.1148	0.0468	44	29
4. 4.72	"	64	0.3201	0.0697	152	106

APPENDIX 9 Estimated female fecundity for the main emergence periods at the Whakatane site.

m.w. = mean female weight. C.L. = 95% confidence limits.

n - the no. of female pupae weightd. M.N.E. - mean no. eggs/  
female.

	<u>M.W. (mg)</u>	<u>C.L. (mg)</u>	<u>n</u>	<u>M.N.E.</u>
Autumn 1970	20.5206	± 2.1200	34	127.17
Spring 1970	27.0826	± 5.2154	16	186.46
Autumn 1971	25.8894	± 1.0190	184	175.68
Spring 1971	-	-	-	-
Autumn 1972	26.8750	± 3.6654	16	184.59

APPENDIX 10 Results of adult sampling at the Whakatane site.

Sample unit size = 53.31 cm diameter cage.

n = number of samples taken.

L.S.M. = log sample mean

L.C.L. = log 95% confidence limits.

R.D. = number of adults / m<sup>2</sup> based on the raw data.

T.D. = number of adults / m<sup>2</sup> based on transformed data.

<u>Date</u>	<u>n</u>	<u>log(X+1)transformation</u>		<u>R.D.</u>	<u>T.D.</u>
		<u>L.S.M.</u>	<u>L.C.L.</u>		
18. 2 - 6. 3.70	8	0.0973	± 0.1315	3.44	1.12
6. 3 - 13. 3.70	8	0.1349	0.1371	4.52	1.63
13. 3 - 19. 3.70	8	0.0376	0.0752	1.08	0.40
19. 3 - 2. 4.70	8	1.1320	0.3290	87.80	56.12
2. 4 - 13. 4.70	8	1.2953	0.2241	104.48	83.71
13. 4 - 22. 4.70	8	0.4203	0.1490	8.39	7.24
22. 4 - 28. 4.70	8	0.0000	-	0.000	0.00
28. 4 - 5. 5.70	8	0.0000	-	0.00	0.00
3.11 - 10.11.70	32	0.0000	-	0.00	0.00
10.11 - 17.11.70	32	0.0431	0.0442	0.54	0.46
17.11 - 24.11.70	32	0.0376	0.0357	0.65	0.40
24.11 - 1.12.70	32	0.3185	0.1129	7.32	4.84
1.12 - 8.12.70	32	0.1184	0.0622	1.94	1.40
8.12 - 15.12.70	32	0.1081	0.0669	1.94	1.26
15.12 - 22.12.70	32	0.0376	0.0357	0.54	0.40
22.12 - 29.12.70	32	0.0188	0.0262	0.32	0.20
29.12 - 5. 1.71	32	0.0000	0.0000	0.00	0.00
5. 1 - 19. 1.71	32	0.0753	0.0468	1.08	0.85
19. 1 - 2. 2.71	32	0.3309	0.0921	6.99	5.11
2. 2 - 9. 2.71	32	0.0094	0.0188	0.11	0.10
9. 2 - 16. 2.71	32	0.0094	0.0188	0.11	0.10
16. 2 - 23. 2.71	32	0.0000	0.0000	0.00	0.00
23. 2 - 2. 3.71	32	0.5250	0.0450	0.86	0.57
2. 3 - 9. 3.71	32	0.0996	0.0541	1.51	1.15
9. 3 - 16. 3.71	32	0.6291	0.1656	18.40	14.56
16. 3 - 23. 3.71	32	1.2841	0.1521	114.06	81.52

APPENDIX 10 continued

<u>Date</u>	<u>n</u>	<u>log(X+1)transformation</u>		<u>R.D.</u>	<u>T.D.</u>
		<u>L.S.M.</u>	<u>L.C.L.</u>		
23. 3 - 30. 3.71	32	1.2452	± 0.0862	86.08	74.19
30. 3 - 6. 4.71	32	0.9971	0.1511	61.12	39.95
6. 4 - 13. 4.71	32	0.5474	0.1163	16.57	11.30
13. 3 - 20. 4.71	32	0.1451	0.0687	2.58	1.78
20. 4 - 27. 4.71	32	0.0094	0.0188	0.11	0.10
27. 4 - 11. 5.71	32	0.0337	0.0387	0.54	0.36
11. 5 - 25. 5.71	32	0.0000	0.0000	0.00	0.00
15.10 - 26.10.71	32	0.0000	0.0000	0.00	0.00
26.10 - 3.11.71	32	0.0000	0.0000	0.00	0.00
3.11 - 10.11.71	32	0.0000	0.0000	0.00	0.00
10.11 - 17.11.71	32	0.0376	0.0357	0.58	0.40
17.11 - 23.11.71	32	0.1089	0.0551	1.68	1.29
23.11 - 30.11.71	32	0.0337	0.0387	0.58	0.36
1.12 - 7.12.71	32	0.0337	0.0387	0.58	0.36
7.12 - 14.12.71	32	0.3298	0.0904	6.84	5.09
14.12 - 21.12.71	32	0.4249	0.1419	13.83	7.43
21.12 - 28.12.71	32	0.3586	0.1371	10.90	5.74
28.12 - 4. 1.72	32	0.0000	0.0000	0.00	0.00
4. 1 - 18. 1.72	32	0.0808	0.0513	1.26	0.92
18. 1 - 25. 1.72	32	0.1676	0.0808	3.21	2.11
25. 1 - 1. 2.72	32	0.0431	0.0421	0.70	0.47
1. 2 - 15. 2.72	32	0.0808	0.0513	1.26	0.92
15. 2 - 28. 2.72	32	0.0282	0.0314	0.42	0.30
28. 2 - 7. 3.72	32	0.0000	0.0000	0.00	0.00
7. 3 - 13. 3.72	32	0.0000	0.0000	0.00	0.00
13.3 - 20. 3.72	32	0.0337	0.0387	0.56	0.36
20. 3 - 27. 3.72	32	0.0431	0.0500	0.84	0.47
27. 3 - 4. 4.72	32	0.3211	0.1209	8.66	4.89
4. 4 - 11. 4.72	32	0.4753	0.1157	12.85	8.89
11. 4 - 18. 4.72	32	0.1551	0.0738	2.93	1.92
18. 4 - 24. 4.72	32	0.0470	0.0392	0.70	0.51
24. 4 - 2. 5.72	32	0.0470	0.0392	0.84	0.51
2. 5 - 14. 5.72	32	0.188	0.0262	0.28	0.20

APPENDIX 11 Results of egg sampling at the Whakatane site.

s.u. = sample unit size (core diameter in cm).

n = no. of samples taken.

L.S.M. = log sample mean.

L.C.L. = log 95% confidence limits.

R.D. = nos. of egg clusters / m<sup>2</sup> based on the raw data.

T.D. = nos. of egg clusters / m<sup>2</sup> based on the transformed data.

<u>Date</u>	<u>s.u.</u>	<u>n</u>	<u>log(X+1) transformation</u>		<u>R.D.</u>	<u>T.D.</u>
			<u>L.S.M.</u>	<u>L.C.L.</u>		
8. 4.70	7.62	40	0.2688	±0.0832	269	187.85
1.12.70	11.43	40	-	-	0	0
11.12.70	"	40	-	-	0	0
25. 3.71	"	64	0.0874	0.0416	33.35	22.70
8. 4.71	"	64	0.1250	0.0522	51.75	32.54

## ACKNOWLEDGEMENTS

The author is appreciative of study leave granted by the Ministry of Agriculture and Fisheries, and would like to sincerely thank:

Professors J.G. Pendergrast and R.M. Cassie for their helpful criticism of the work

Mr. Bruce Given for his encouragement and making the composite photograph of the life history of I. rubriceps

Mr. Hugh Oliver for his technical help and advice with all facets of the practical work

Messrs. John Meekings and Gary Burton for their assistance in sampling the various stages and processing some of the collected data

The Directors of the South Auckland Dairy Association and the East Coast Dairy Association for their financial assistance

Mr. Roy Hewitt for his agricultural advice and general assistance with work carried out in the Whakatane district

Messrs. R. Baird and G. Pert for the use of their land as study sites, and

my wife Irene for her encouragement and assistance

The articles listed below were reprinted and tucked into the back of the Wilcocks thesis.

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