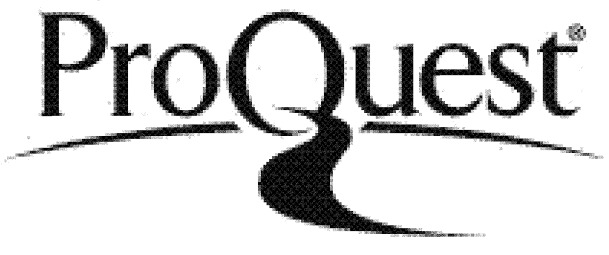
TOXINS AND BLOWFLY POPULATION DYNAMICS

Thesis submitted for the degree of
Doctor of Philosophy
at the University of Leicester

by

Michael Bruce Forrest BSc, MSc (Leicester)
Department of Zoology
University of Leicester

July 1996



ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

CONTENTS

	ACKNOWLEDGEMENTS	vii
	ABSTRACT	viii
1	CHAPTER 1 INTRODUCTION	1
1.1	General introduction and aims	1
1.2	Introduction to the study species	4
1.2.1	The life history of *L. sericata*	4
1.3	The toxins used in this study	5
1.3.1	Cadmium	5
1.3.2	Deltamethrin	7
2	CHAPTER 2 GENERAL METHODS	9
2.1	Maintenance of stock fly populations in the laboratory	9
2.2	Preparation of the standard fly diet	9
2.3	Preparation of the diets containing toxins	10
2.4	Selection of the deltamethrin dose used in the experimental work	10
2.5	Disposal of discarded diet	11
2.6	Experimental environment	11
3	CHAPTER 3 FIELD POPULATION STUDIES	12
3.0	ABSTRACT	13
3.1	INTRODUCTION	13
3.1.1	Introduction and aims	13
3.1.2	Spatial distribution	14
3.1.3	Models of population structure	15
3.1.4	Temporal distribution and dynamics	17
3.2	METHODS	18
3.2.1	Site descriptions	18
3.2.2	Larval trap design and arrangement of traps in the field	18

3.2.3	Adult trap design and arrangement of traps in the field	21
3.2.4	Preparation and handling of the carcasses	21
3.2.5	Incubation pupae and identification of adults	23
3.2.6	Analysis of field data	23
3.2.7	Processing of weather data	26
3.3	RESULTS	27
3.3.1	Weather data	27
3.3.2	General overview of the fly species reared from the baited traps	29
3.3.3	Changes in the fly community of the two transects	30
3.3.4	The community of flies arising from each carcass	33
3.3.5	Comparison of the *Lucilia* species and *Calliphora* species populations as indicated by the two trapping methods	34
3.3.6	Pattern analysis	35
3.4	DISCUSSION	71
3.4.1	Why were there few *Lucilia* Species?	71
3.4.2	Differences between the *Lucilia* species found on the each transect	72
3.4.3	The seasonality of the fly species found	73
3.4.4	The species composition in each individual patch and the local community	74
3.4.5	Aggregations and population structure	75
3.4.6	The question of dispersion and future work	76
3.4.7	Summary	77
4	CHAPTER 4 METABOLIC COSTS OF DETOXIFICATION	78
4.0	ABSTRACT	78
4.1	INTRODUCTION	79
4.1.1	General aims	79

4.1.2	Physiological ecotoxicology	79
4.1.3	Scope For Growth	83
4.1.4	Metabolism and allometric relationships	83
4.1.5	Summary and hypotheses	85
4.2	METHODS	87
4.2.1	Rearing of experimental animals	87
4.2.2	Respirometer operating procedure	87
4.2.3	Processing of respirometry data	89
4.2.4	Analysis of respirometry data	90
4.3	RESULTS	91
4.3.1	General comments about the results	91
4.3.2	The effects of deltamethrin and cadmium upon respiration rate	91
4.4	DISCUSSION	98
4.4.1	The allometric relationship between mass and respiration rate	98
4.4.2	Future respirometry work	99
4.4.3	The implications of the observed respiratory rates for scope for growth	99
5	CHAPTER 5 THE INTERACTION OF POPULATION DENSITY AND TOXINS - THE COSTS TO THE LARVAE AND ADULTS	101
5.0	ABSTRACT	102
5.1	INTRODUCTION	102
5.1.1	Introduction and aims	102
5.1.2	The effect of population density upon larval growth	102
5.1.3	The effect of population density and toxins on the immature stages	103
5.1.4	The consequences of larval stress on the adult stage	104
5.2	METHODS	106
5.2.1	Larval population density experiments	106

5.2.2 Measuring adult longevity and fecundity 107
5.2.3 Analysis of the results 107

5.3 RESULTS 108
5.3.1 Changes in larval mass during early development 108
5.3.2 The effects of increasing larval population density and the presence of toxins in the larval diet upon pupal mass 111
5.3.3 The effects of increasing larval population density and the presence of toxins in the larval diet upon adult mass 113
5.3.4 The effects of increasing larval population density and the presence of toxins in the larval diet upon the egg to adult development period 114
5.3.5 The effects of increasing larval population density and the presence of toxins in the larval diet upon the survival to adult emergence 116
5.3.6 Adult longevity 118
5.3.7 Lifetime female fecundity 119

5.4 DISCUSSION 128
5.4.1 The effects of increasing larval population density and the presence of toxins in the larval diet upon the growth and development of the larvae 128
5.4.2 Longevity and fecundity of the adult flies 130

6 CHAPTER 6 POPULATION DYNAMICS 132

6.0 ABSTRACT 133

6.1 INTRODUCTION 133
6.1.1 Introduction and aims 133
6.1.2 Basic population dynamics 134
6.1.3 Nicholson's blowflies 136
6.1.4 Daniels blowflies 136

6.2 METHODS 138
6.2.1 Life-table analysis 138
6.2.2 Measurement of the density-dependent mortality 139
6.2.3 Autocorrelation analysis 140

6.2.4	Assumptions used in computing the population-dynamics simulation model	141
6.3	RESULTS	142
6.3.1	Life-table analysis	142
6.3.2	Summary of the fecundity values measured in the restricted density experiments carried out in Chapter 5 that are used as parameters in the population model	144
6.3.3	Calculation of the density-dependent mortality during the development period	144
6.3.4	The egg-to-adult developmental period	145
6.3.5	The relationship between larval population density and mean pupal mass	146
6.3.6	The population simulation model	148
6.3.7	The deterministic simulation model of the control population dynamics with estimates of parameters calculated from the experiments	153
6.3.8	The effect of varying the mean pupal mass cut-off	154
6.3.9	The effect of varying mean adult longevity	158
6.3.10	The effect of varying egg production	161
6.3.11	The effect of varying the strength of density-dependence	164
6.3.12	The effect of varying the egg-to-adult developmental period	167
6.3.13	The population dynamics predicted by the stochastic model and comparisons of the control and cadmium populations	170
6.3.14	Comparisons of the models using the mean number of adults present, mean pupal mass, and pupal cohort biomass predicted by the control and cadmium models	173
6.4	DISCUSSION	178
6.4.1	The development time and density-dependent mortality	178
6.4.2	The parameter estimates used in the model	178
6.4.3	The driving forces of the dynamics	180
6.4.4	The performance of the stochastic models	182
7	CHAPTER 7 DISCUSSION	184
7.1	The link between ecotoxicology and population dynamics	184

7.2 Extrapolating between laboratory experiments and natural populations..... 186
7.3 The impact of toxins upon natural populations..... 187
7.3.1 Patchy populations..... 187
7.3.2 Classical metapopulations..... 189
7.4 Conclusion..... 191

APPENDIX 1: The raw species data collected during the field work..... 192

APPENDIX 2: The raw respirometry data used for the comparisons of respirometry rate of *L. sericata* larvae..... 231

APPENDIX 3: The raw respirometry data collected for *C. vicina* during preliminary experiments..... 234

APPENDIX 4: Life-table analysis..... 236

APPENDIX 5: The time series data collected by Susan Daniels (1994)..... 248

REFERENCES..... 252

ACKNOWLEDGEMENTS

There are many people whom I would like to thank for their assistance and support during the course of this study. First my two supervisors Professor R. H. Smith and Dr. F. Clark: Rob for the many hours he has spent with me discussing the statistical analysis of the data and for his helpful comments about the thesis and Frank for his continued help and friendship throughout my undergraduate and postgraduate days at Leicester University.

I would also like to thank the members of the zoology department and my friends Andy, Steph, Alec and Alison who have always been a source of great encouragement and support.

Finally thanks to Vikki for everything, especially for not complaining about the smell of maggot infested carcasses that lingered in our car whilst I was carrying out the field work!

ABSTRACT

This thesis studies the effects of toxins upon larvae of the blowfly *Lucilia sericata.* A field study of fly populations infesting carcasses showed aggregations in space and time of a number of fly species, although *L. sericata* was not common. The presence of cadmium or deltamethrin in the larval diet was shown to have deleterious effects upon the larvae. Development was slowed down and the resultant adults were smaller. When the diet contained cadmium, adults had a lower fecundity than those arising from larvae fed upon the control diet. These effects became more pronounced as larval population density was increased.

Models were constructed that simulated the population dynamics of *L. sericata* under two conditions. In each population, the larval diet was limited to 20 g/day whilst in one the diet was contaminated with 50 mg Cd/kg diet. These models allowed the underlying dynamics and their driving forces to be identified. The control model predicted sustained population cycles with a period of 67 days, approximately twice the generation time calculated from cohort life-tables. The cadmium model predicted that these cycles would be dampened and the mass of individual pupae increased relative to those from the control simulation model. These theoretical results, which apparently contradict the predictions made by scope for growth theory, are consistent with results from a long-term population study and were due to the interaction of cadmium with the effects of population density.

CHAPTER 1 INTRODUCTION

1.1 GENERAL INTRODUCTION AND AIMS

Pollution of the environment is an area of great concern and, over the past few decades, has given rise to the science of ecotoxicology. Ecotoxicology deals with pollutants in the environment and the effects that they have upon living organisms. Under this broad topic of ecotoxicology there are three different levels of study. The first of these levels, which is fundamental to any higher level of study, deals with the effects that toxins have upon the individual, the level of ecophysiology. At higher levels the effects upon populations (the demoecological level) and upon whole ecosystems (the synecological level) may be studied (Ramade (1979)). This thesis examines the sub-lethal effects of toxins from the level of the animals' physiology to the level of the long-term density-dependent population dynamics of *Lucilia sericata* (Meigen), providing links between these two areas of study.

There have been many studies upon the physiological aspects of toxins. Such studies may be highly specific studying the effects of the toxin upon single metabolic processes. These give little information as to how the toxin will affect the population as a whole. A more useful way of studying the effect of toxins has been to measure the effect upon 'Scope For Growth' (Warren and Davies (1967); Calow (1989, 1981); Maltby and Naylor (1990); Anderlini (1992)). The presence of a toxin at a sub-lethal concentration may incur an energetic cost to the organism. An energetic cost may result in energy being diverted away from growth and reproduction to the detoxification processes *i.e.* cause a reduction of the scope for growth. A reduction of the scope for growth may manifest itself in a variety of ways such as a slower growth rate or a reduced reproductive output.

An example of a reduction in scope for growth is provided by the effect of zinc on the freshwater shrimp *Gammarus pulex* (L.). Maltby and Naylor (1990) showed that the presence of zinc reduced the amount of energy absorbed but did not have any effect upon the respiratory loss of energy. The effect on reproduction was to reduce the size of offspring released in the brood produced subsequent to exposure to the zinc. The number of broods aborted also increased. This example illustrates clearly how the scope for growth of *Gammarus* has been reduced in terms of reduced reproductive output. Thus, in the presence of a toxin the reproductive output may be lowered but this still does not show how the population dynamics may be affected. The effects of toxins on the metabolic rate and life-history parameters of *L. sericata* are the subjects of

Chapters 4 and 5.

It is important to know how the toxin may affect a population as this may have consequences for the whole ecosystem in which that population lives. Not only that but populations can no longer be treated as isolated entities, they may now be considered as local populations, being part of a metapopulation (Hanski and Gilpin (1991); Harrison (1991)). Thus a toxin having an effect upon a local population may also have consequences on the larger scale of the metapopulation.

The effect of a toxin upon a population cannot be considered purely in the static sense of a reduced scope for growth of a single cohort. It must be considered in the long-term sense in which the fecundity of the organism in question may contribute towards its abundance but only in conjunction with the other factors that control the population dynamics, particularly density-dependent factors. That populations are regulated by density-dependent factors was studied by Nicholson (1954 a, b).

Nicholson (1954 a, b) studied the population dynamics of laboratory cultures of *Lucilia cuprina* (Wd.). His experiments tested the hypothesis that populations were kept in balance by density-dependent factors. In a series of experiments he investigated the effects of limiting food to either the adult flies or the larvae. His results showed clearly how populations could be regulated by such density-dependence, and also highlighted the importance of a time delay between the cause of a population increase and the response of the population to this increase, in the resultant dynamics of the population. The populations he studied showed regular fluctuations of the adult numbers over a period of about 40 days. His experiments have inspired many biologists to investigate these processes further both biologically and mathematically.

Daniels (1994) repeated Nicholson's work but used *L. sericata*. Her experiments studied the population dynamics in two series of fly populations; in both series the larval diet was limited and in one series in the larval diet was contaminated with cadmium. Under the control conditions Daniels observed the same type of dynamics as Nicholson, though the time scale of the fluctuations differed. When the diet contained cadmium these cycles were destroyed. Not only that but the mean mass of individual pupa and biomass of pupal cohorts of the cadmium populations were higher than in the control populations. These results were contrary to the predictions made by scope for growth theory. Whilst Daniels demonstrated the impact of cadmium upon the population dynamics she did not formalise a link between the dynamics and the sub-lethal effects of cadmium. Providing such links is the subject of Chapter 6 in which studies were made of the processes driving population dynamics in laboratory-

maintained cultures of *L. sericata*. This was achieved through the construction of a simple population simulation model based upon biological parameters. The model illustrates the importance of the different factors involved in driving the dynamics under deterministic and stochastic conditions and can also predict how the population dynamics may vary when the larvae are exposed to a limited food supply contaminated with cadmium.

Within this thesis I shall also consider how toxins may affect natural populations. In order to hypothesise how a toxin may affect a natural population of blowflies it is important to know something of the nature of such populations. An extensive field study of the natural populations and communities of carrion feeding flies was carried out (Chapter 3). The questions being addressed were: first, do carrion feeding flies exist in discrete populations that are stable over time, and second, how does the community structure vary over time? Any population structure observed was considered in the context of current metapopulation theory. Such a basic understanding of the natural population structure is necessary in order to understand how a toxin may affect natural populations.

Carcasses provide organisms such as blow flies with a resource that is patchy in both time and space. Such resource patches are exploited by animals ranging from large scavengers to insects. Insects characteristically use these resource patches for reproduction by laying their eggs, or live young, upon them. The resource patch provides immature stages of the insects with a valuable source of energy that can be used for their growth. The ephemeral nature of such resources, however, prevents local populations from reaching an equilibrium, the resource is usually only sufficient to raise one generation. Upon reaching maturity the young adults must disperse and find another suitable patch on which to reproduce.

The resource patch is therefore very important as the presence of patches, and their quality will ultimately determine the numbers of individuals and species emerging from them which in turn determines the nature of the local insect community. Patch quality may vary with age or size of the patch, or through the patch being contaminated by some toxicant. The size of the patch is important as a small patch would only be able to support a few individuals. As patch size decreases, the level of competition increases. The presence of a toxin in a patch would provide an additional stress. The experiments carried out in Chapters 4 and 5 investigate the effects of the toxins upon cohorts of larvae reared upon individual-limited resource patches contaminated with toxins.

1.2 INTRODUCTION TO THE STUDY SPECIES

L. sericata Meigen is a blowfly belonging to the family Calliphoridae of the Dipteran sub-order Cyclorrhapha. This sub-order also includes the fleshflies (Sarcophagidae) and houseflies (Muscidae). *L. sericata* was the chosen study species as it is easy to breed in the laboratory and has already been studied extensively in the past in both field and laboratory conditions.

One of the reasons that *L. sericata,* and other Calliphoridae species, have been studied is that they are of economic importance due to their adverse effects upon live stock. The larvae of *L. sericata* and *L. cuprina* are responsible for myiasis on sheep (French, Wall, Cripps and Morgan (1994); French, Wall, and Morgan (1995); Dymock and Forgie (1993); Dymock, Peters, Herman, and Forgie (1991); MacLeod (1937); Davies (1934)). The larvae feed upon the flesh of the living animal often causing considerable damage. The annual cost to the Australian sheep industry is high, around $A150 million. In a survey of English and Welsh farmers 80% reported having at least one case of blowfly strike (French, Wall, Cripps and Morgan (1992)). Calliphoridae species have also been implicated in the transmission of diseases to other animals. In South Africa two Calliphoridae species have been shown to be partly responsible for the spread of anthrax, a disease that threatens many game animals and some rare species such as roan antelopes (Braack and De Vos (1990)).

L. sericata also feeds on carrion in addition to living flesh. This species, along with other carrion-feeding flies, play an important role in the break down of organic matter and the recycling of nutrients (Putman (1983)). In their role as carrion feeders the genus *Lucilia,* and other carrion feeding flies, have been studied to identify the mechanisms facilitating the coexistence of species in a patchy environment (Hanski (1987)). Their habit of colonising carcasses has also made them of use in forensic science. The species present and the stage of development can yield information relating to the time, and in some cases the place, of death (Greenberg (1991); Smith (1986)).

1.2.1 The life history of *L. sericata*

The adult flies oviposit upon a carcass, or wound on a sheep, depositing the eggs in natural orifices. The larvae pass through three larval instars before pupating, as do all species of fly belonging to the sub-order Cyclorrhapha. The different instars can be determined by the presence of 1, 2, or 3 slits in the posterior spiracle (Smith (1986)). Upon completing growth the larvae cease feeding and enter a wandering phase during which they leave the carcass and find a suitable site for pupation. The duration of the

wandering phase is variable, in some flies it lasts for over a week and in species that enter a diapause it may last for up to 10 months (Delinger and Zdárek (1994). Third-instar larvae of *L. sericata* enter a diapause stage during which they over winter (Cousin (1932) and Mellanby (1938) cited from Cragg and Cole (1952)). Not all flies lay eggs, those belonging to the family Sarcophagidae are viviparous and deposit first-instar larvae upon the carcass. In both cases the resultant larvae feed upon the carcass and grow.

The duration of the larval and pupal periods is not fixed and is greatly influenced by environmental variables. Temperature is of great importance in determining the duration of egg, larval, and pupal development. Davies and Ratcliffe (1994) showed how low temperatures prolonged each of these stages in *Calliphora vicina*. The wandering phase of *Sarcophaga perigina* can be prolonged as long as the larvae are in a wet environment (Delinger and Zdárek (1994)).

1.3 THE TOXINS USED IN THIS STUDY

The two toxins used during the course of this study were cadmium and deltamethrin. Cadmium was used as there was information relating to the long term population dynamics of *L. sericata* under polluted and control conditions (Daniels (1994)). Deltamethrin was used as it provided a contrasting toxin to cadmium. Cadmium is non-metabolisable whilst deltamethrin can be broken down by enzymatic processes.

1.3.1 Cadmium

Cadmium, a non-essential heavy metal, was first recognised in ores containing zinc carbonate in 1817. Cadmium occurs naturally in soils, the level depending upon the type of parent rock that it originates from. Lund, Betty, Page and Elliot (1981) carried out a survey of soils originating from different rocks in the Santa Monica Mountains in California. Soils originating from shale parent material had the highest concentration of cadmium (7.5 μg/g) whilst soils arising from sandstone and basalt had the lowest concentrations (0.84 μg/g).

In addition to naturally occurring cadmium there are also inputs of cadmium into the environment through its industrial uses. Cadmium has a number of uses such as electroplating, as a pigment in paints and plastics, and as cathode material in nickel-cadmium batteries. Cadmium is also a by-product of zinc and lead mining and smelting. Goyer (1986) cites a figure of 1000 tons being released into the atmosphere in America through the burning of fossil fuels during 1977. Goyer (1986) also cites that respirable

cadmium may occur through the workplace or through inhalation of tobacco smoke. One cigarette contains 1-2 μg cadmium, 10 % of this is inhaled.

This cadmium pollution may eventually find its way into terrestrial or aquatic ecosystems. Much work has been done on the effects of mining upon heavy metal levels in the environment. For example Roberts and Johnson (1978) showed that the levels of lead and zinc around old mine spoil heaps in North Wales were in the region of 5000 μg Pb/g soil and 11000 μg Zn/g soil. These metals were carried away by the wind and deposited downwind of the mine complex. Leaching of metals from spoil heaps can introduce them into the aquatic environment.

Once in the environment cadmium, and other heavy metals, may enter the food chain. Martin and Coughtrey (1975) studied levels of cadmium in a woodland ecosystem close to a lead-zinc smelter at Avonmouth. The soil had cadmium levels of 42 ppm in the topsoil (5 cm below the litter) and 14 ppm in the clay soil (10 cm below the surface). Levels of up to 25 ppm were found in living plant material. At a slightly higher level in the food chain detritivorous invertebrates such as earthworms and the woodlouse (*Oniscus asellus*) showed levels of 122.8 ppm and 171.0 ppm respectively. Carnivores such as the thrush (*Turdus philomelos*) showed greatly elevated levels; a level of 387 ppm was found in the kidney (all values refer to dry weight). Thus cadmium not only enters the food chain, it is accumulated at higher trophic levels. In a later study Martin and Coughtrey (1976) re-analysed their data and made comparisons of cadmium levels in invertebrates with those of lead and zinc. The results of this study showed that cadmium was accumulated more than lead or zinc when compared with levels in the food materials. They suggested that cadmium may have been released from the food source more readily than lead or zinc (Martin, Coughtrey and Young (1976)).

Shore (1995) reviewed the literature for data relating to soil concentrations and the concentrations of cadmium in small mammal species. He showed a strong correlation between these two parameters and also showed a species-to-species difference. The highest concentrations were found in the liver and kidney of the common shrew (*Sorex araneus* L.), these were 578 mg/kg and 253 mg/kg (dry weight) respectively. The lowest levels in the species he studied were in the wood mouse (*Apodemus sylvatica* Hinton) with 18.2 mg/kg and 41.7 mg/kg (dry weight) in the liver and kidney respectively. Similar results were also found by Roberts and Johnson (1978). These different levels may be due to the different feeding habits of these animals. The common shrew is a carnivore and so feeds upon the invertebrates which will already have accumulated cadmium. The wood mouse is a predominantly herbivorous omnivore, the carnivorous habit of the animal being restricted to the summer months.

The accumulation of cadmium in the garden snail (*Helix aspersa*) has also been demonstrated by Laskowski and Hopkin (1996). Blowflies that live in an area contaminated by heavy metals may therefore be exposed to them through their feeding upon contaminated carcasses.

Cadmium is toxic because it displaces copper and zinc ions from their binding sites in metalloproteins. Such displacement of ions may result in the loss of the enzymatic function of some proteins. Reduced activity of the enzymes succinate dehydrogenase and xanthin dehydrogenase in the presence of elevated cadmium levels has been demonstrated by Weismann and Reháková (1994). Reddy and Bhagyalakshmi (1994) showed that cadmium caused major alterations in the oxidative metabolism of the edible crab (*Scylla serrata).*

The toxicity of cadmium has been shown to vary with dietary content. The toxicity of cadmium and lead decreases with increases in the protein content of the diet. Vitamin C has been shown to reduce lead and cadmium absorption from the intestine, deficiencies of calcium and iron may also increase its absorption. The toxicity of cadmium, and other metals such as copper and tin, is also reduced by the presence of metallothionein. Metallothioneins are proteins rich in sulphydryl groups (SH) due to the presence of many cysteine groups within them. It is these SH groups that are responsible for chelating the metal, so making it less toxic (Barnes, Calow, and Olive (1989)). Metallothioneins are found in most organs but are found in the highest concentrations in the kidney. These proteins detoxify cadmium by binding the metal. The cadmium-thionein accumulates without any adverse effects in the kidney unless the dose of cadmium exceeds the detoxifying capacity of the body (Goyer (1986)).

1.3.2 Deltamethrin

Pyrethrum insecticides are naturally occurring chemicals produced by the Dalmation pyrethrum *Chrysanthemum cinerariaefolium* (Visinii). They have been in use as insecticides since before the first century AD. The natural compound has been used as a structural model from which many synthetic pyrethroids have been produced. One of these synthetic pyrethroids is deltamethrin, which was first synthesised in 1974. Deltamethrin is a photo-stable compound with a low solubility in water (0.002 mg/l) and a melting point of 98-101 °C.

Pyrethroids can be divided into two classes on the basis of their effects upon insects. Gammon, Brown and Casida (1981) demonstrated two types of response to pyrethroids in the cockroach *Periplanata americana.* Type 1 pyrethroids induced

repetitive firing of cercal sensory neurones. Type 2 pyrethroids did not affect sensory neurones in this way but caused a burst of activity in cercal motor neurones. Deltamethrin, and other pyrethroids with an alpha cyano group, cause the Type 2 response. The toxic effects of pyrethroids are thought to be through reducing closing of sodium channels, which may alter the concentration gradients of Na^+ and K^+ ions across membranes.

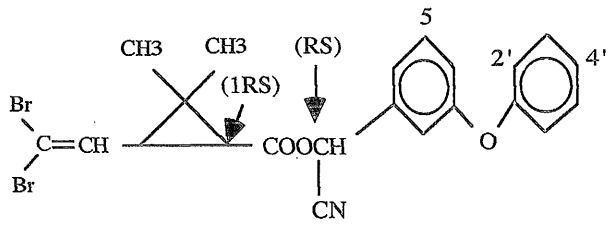


Figure 1.1 The chemical structure of deltamethrin (Aldrige, 1990)

The use of pyrethroids, such as deltamethrin, has been favoured due to their high toxicity to insects whilst being relatively harmless to mammals and birds, and their rapid breakdown in the environment. Rats have been shown to withstand concentrations of up to 50 mg/kg in their food whilst showing no ill effects, and the level for mice was higher at 100 mg/kg. The low toxicity to mammals is because it is rapidly broken down. Ruzo, Unai, and Casida (1978) showed that the pyrethroid was hydroxylated in the 4', as well as in the 2' and 5 and is rapidly excreted in the faeces. When the ester bond is broken, the alcohol moiety produces phenoxy benzoic acid and hydroxy benzoic acid, which are excreted. The cyano group is released in the stomach producing thiocyanate and 2-imino thiazolidine-4-carboxylic acid which are rapidly excreted. Finally the dibromo chrysanthemic acid is excreted.

Deltamethrin does not persist in the environment for very long. Its half life in soils depends upon the soil type, and it may persist for 72 days in an organic soil. Once in the soil deltamethrin is highly immobile due as it is generally insoluble in water and is strongly adsorbed in soil (Mestres and Mestres (1992)). Thus, as an environmental pollutant deltamethrin provides a sharp contrast to cadmium which cannot be broken down in the environment and is highly soluble in water. The persistence of cadmium in the environment is demonstrated by Brallier, Harrison, Henry and Dongsen (1996). They showed that cadmium from sewage sludge applied as a fertiliser was still available for plant uptake 16 years after its application.

1.4 THE MAIN OBJECTIVES OF THE THESIS

The main objectives of this thesis were to achieve the aims of ecotoxicology by studying the effects of a toxin from the level of physiology to the level of long-term population dynamics. The two toxins investigated were selected as they are detoxified by contrasting mechanisms; cadmium by binding to metallothioneins and deltamethrin by enzymatic degradation. The effects of the toxins at the physiological level were the subject of Chapter 4 where the hypothesis that the presence of a toxin in the larval diet may incur an energetic cost to the larvae was investigated. Such an energetic cost may manifest itself as a reduction in the scope for growth of the larvae which in turn may have consequences for the adult flies, this was the major hypothesis investigated in Chapter 5. The main hypothesis investigated in Chapter 6 was that a reduction in the scope for growth may have consequences for the long-term population dynamics. Predictions about the long-term population dynamics were made via construction of a population model. This model was based upon life-history parameters that were studied experimentally in Chapters 5 and 6. The experiments carried out in Chapters 4, 5, and 6 allowed certain speculations to be made as to how a toxin may affect the natural population structure of blowflies observed in the field, the natural population structure was studied in Chapter 3.

CHAPTER 2 GENERAL METHODS

2.1 MAINTENANCE OF STOCK FLY POPULATIONS IN THE LABORATORY

Cultures of *L. sericata* were maintained in perspex aquaria (40 * 28 * 23 cm) that were laid on their side. The openings to the aquaria were closed by a net covering secured by elastic around the edge of the aquaria. Access to the aquaria was made possible by the presence of a draw string in the net. The flies were supplied with 20 g of diet at 2 day intervals, except that on Fridays they were supplied with 30 g to compensate for the weekend. The fly diet was placed in a small plastic tub which was itself placed inside a rectangular tub containing vermiculite. The vermiculite supplied the wandering larvae with a medium in which they could pupate and also removed excess moisture from the larvae, preventing them from climbing out of the rectangular tub. The flies were supplied with dried fly diet, sucrose, water and fresh fly diet. The water and sugar were replaced once a week, the dried diet once every 6 months. All experimental flies were taken from this stock cage. The stock cage of flies, all experimental larvae and adult flies were kept in controlled environment. They were exposed to a constant 12 hours of light and 12 hours of dark routine. The temperature was maintained at a constant 25°C and the humidity at approximately 50%.

2.2 PREPARATION OF THE STANDARD FLY DIET

The fly diet was made according to the recipe of Daniels, Simkiss, and Smith (1991). To make 1kg of the diet the following ingredients were used 20 g agar, 200 ml horse blood, 50 g yeast, 800 ml water. The agar was placed in a 1l conical flask with approximately 700 ml water. The remainder of the water was used to mix with the yeast, making a thin paste, and also to rinse out any remaining blood from the bottles after they had been emptied. The agar/water mix was stirred and then placed in a microwave to heat for 3.5 minutes. After this period of time the flask was checked at thirty second intervals to prevent it from boiling over. Once the agar water mix was heated sufficiently, indicated by the solution becoming transparent, the yeast/water mix was added and thoroughly mixed in followed by the 200 ml of horse blood. The resultant solution was then poured out into a plastic container and allowed to set.

2.3 PREPARATION OF THE DIETS CONTAINING TOXINS

For flies that were reared on a cadmium diet the diet was made in the same way as

above but with the inclusion of cadmium acetate at a concentration of 50 mg/l diet. The cadmium was dissolved in approximately 30 ml of water and was added to the diet after the blood had been mixed in. Gloves, laboratory coat, and face mask were worn at all times that raw cadmium acetate was being handled. Gloves were always worn whilst handling the diet.

The mixing of the diet containing deltamethrin was very similar to that of the cadmium diet except that the deltamethrin had to be dissolved in a solution of 1 part acetone and 2 parts petroleum ether. The diet was made up as needed rather than using a stock solution. 0.2 mg of deltamethrin was dissolved in 0.4 ml of the acetone/ether solution. This was mixed with approximately 5 ml water and added to the diet after the blood had been added and the diet had cooled to approximately 40°C before addition. This was done to prevent the instant evaporation of the highly volatile solvent mix. The same safety precautions were followed as for the cadmium diet. Both diets were stored in separate labelled containers and kept in a refrigerator at approximately 5 °C.

2.4 SELECTION OF THE DELTAMETHRIN DOSE USED IN THE EXPERIMENTAL WORK

The dose of deltamethrin used in the experiments was selected by carrying out a dose response experiment. A range of deltamethrin doses (0.4, 0.35, 0.3, 0.25, 0.2, and 0 mg/kg) was used in the larval diet and the number of adult flies obtained was recorded. The deltamethrin dose required to give a 50% mortality was 0.2 mg/kg. An additional control set of larvae were fed on a diet which contained only 2 ml of the acetone/ether mix, this solvent mix was required to dissolve the deltamethrin. No effect upon mortality was observed and so the 0.4 ml of solvent actually used in the experiments can be considered to be inconsequential.

The cadmium dose of 50 mg/kg diet was selected in order to facilitate comparisons between the model of population dynamics and life-history parameters measured in this thesis with the long term population dynamic observed by Daniels (1994).

2.5 DISPOSAL OF DISCARDED DIET

All plastic containers that had been used for rearing larvae on either diet were sent for incineration through the clinical waste disposal system. All discarded adult flies, pupae, dead larvae and unused diet were dealt with in this manner.

CHAPTER 3 FIELD POPULATION STUDIES

SECTION INDEX

		Page
3.0	ABSTRACT	13
3.1	INTRODUCTION	13
3.1.1	Introduction and aims	13
3.1.2	Spatial distribution	14
3.1.3	Models of population structure	15
3.1.4	Temporal distribution and dynamics	17
3.2	METHODS	18
3.2.1	Site descriptions	18
3.2.2	Larval trap design and arrangement of traps in the field	18
3.2.3	Adult trap design and arrangement of traps in the field	21
3.2.4	Preparation and handling of the carcasses	21
3.2.5	Incubation pupae and identification of adults	23
3.2.6	Analysis of field data	23
3.2.7	Processing of weather data	26
3.3	RESULTS	27
3.3.1	Weather data	27
3.3.2	General overview of the fly species reared from the baited traps	29
3.3.3	Changes in the fly community of the two transects	30
3.3.4	The community of flies arising from each carcass	33
3.3.5	Comparison of the *Lucilia* species and *Calliphora* species populations as indicated by the two trapping methods	34
3.3.6	Pattern analysis	35
3.4	DISCUSSION	71
3.4.1	Why were there few *Lucilia* Species?	71
3.4.2	Differences between the *Lucilia* species found on the each transect	72

3.4.3 The seasonality of the fly species found..... 73
3.4.4 The species composition in each individual patch and the local community..... 74
3.4.5 Aggregations and population structure..... 75
3.4.6 The question of dispersion and future work..... 76
3.4.7 Summary..... 77

3.0 ABSTRACT

Populations of carrion feeding flies were studied on agricultural land in Leicestershire. The common species found (*C. vicina* and *M. prolapsa*) both showed aggregated distributions. These aggregations did not appear to represent stable, discrete populations *i.e.* they were not stable over time. Analysis of the spatial distribution of these two species within any given sampling period did not show any significant association between them, either positive or negative, the two species were independently distributed. The temporal distribution of these species showed that they were clearly separated over time, C. *vicina* being most abundant in the cooler times of the year. The ecological significance of the spatial and temporal distribution is discussed with reference to existing spatial population models and theories of species coexistence in patchy environments. The study species *L. sericata* was not found in sufficient numbers to warrant continuation of this work beyond the present study.

3.1 INTRODUCTION

3.1.1 Introduction and aims

A primary consideration of insects relying upon patchy resources is that of the spatial structure of the population. Do discrete populations exist in the field and if so over what spatial scale do they exist? Are they stable over time? A number of workers have studied field populations of carrion feeding flies (French, Wall, Cripps and Morgan (1994); Dymock and Forgie (1993); Braack and Retief (1986); Isiche (1990); Wall, Green, French and Morgan (1992)). In all these studies the populations of flies were found to have distinct habitat preferences. Braack and Retief (1986) studied the habitat preferences of two Calliphoridae species *Chrysomya albiceps* (Weidemann) and *Chrysomya marginalis* (Weidemann). Both of these species were trapped more numerously in forested areas than in open scrub, and both avoided arid areas. The activities of man may also encourage certain species of fly. French, Wall, Cripps and

Morgan (1994) and Wall, Green, French, and Morgan (1992) showed that the presence of sheep led to higher numbers of the blowfly *Lucilia sericata* (Meigen).

On the basis of such results one may expect to find different communities of flies in different habitats. A logical succession from these findings is to consider the nature of the organisation of such communities within a given habitat. During this study I looked at populations and communities of flies found in areas of uniform habitat, hedgerows. This was achieved by using traps, baited with a day old chick, laid along two transects. The organisation of these populations and communities will be considered at two different levels *i.e.* spatial and temporal. Three main questions were asked.

1) What is the population structure of *L. sericata* in the field?

2) Can temporally stable aggregations of *L. sericata* be identified in the field?

3) How do toxins affect the population structure of *L. sericata* in the field?

3.1.2 Spatial distribution

The spatial distribution of the populations can be considered at two levels, the individual resource patch - in this case a day old chick carcass - and at the level of the whole transect. Each carcass could potentially give rise to a number of different species of fly, but it is unlikely that each carcass would give rise to all the species represented in that particular habitat. Working with snail carcasses, Beaver (1977) showed that the species composition changed considerably between individual carcasses. For one of his samples Beaver records a total of eleven species although there was a mean of only 4.07 species per snail. Kuusela and Hanski (1982) found similar results, recording a total of ten species with a mean number of 2.78 species per carcass.

The effect of carcass type upon species composition has also been considered. Kuusela and Hanski (1982) failed to show any significant differences in the fly communities arising from a range of carrion types, within the size range they used. Kneidel (1984a) suggested that some species of fly are more specialised for breeding in certain carrion types whilst others are generalists and use a wide range of organic sources. Dymock and Forgie (1993) showed that *L. sericata* was collected more often than some other Calliphoridae species from small bird carcasses. The size of the carcass must affect the number of species arising from it. Kneidel (1984a) showed that small mammal carcasses, which decomposed in less than one week, gave rise to one dominant species; *C. vicina* in spring and autumn, and *Phaenicia caeruleiviridis* in the summer.

On any one carcass a succession of fly species can be seen that colonise the carcass at different stages of decay. Studies of the faunal succession on human corpses have allowed 8 waves of arthropods to be identified (Smith (1986)). Isiche (1990) studied the flies feeding upon mice carcasses of different ages in two habitats. His work revealed a preference of *Calliphora vicina* (Robineau-Desvoidy) for carcasses exposed under shaded conditions. *L. sericata,* however, showed a preference for carcass that were exposed to sunlight. These results are also supported by the work of Smith (1986). When the age of the carcass was considered, both of the above species preferred fresh carcass whereas the Sarcophagidae *Parasarcophaga caerulences* (Zetterstedt) preferred carcasses that were 4 - 6 days old. Thus, a small carcass that is eaten quickly by early colonisers would not be available to support late colonisers.

The community of flies arising from a carcass is therefore variable and subject to a number of factors. First, season will affect which species are available to colonise a carcass. Second, those species present at that time must find the carcass before it is removed by larger vertebrate scavengers or before the carcass becomes unsuitable for colonisation, through desiccation for example. Once the carcass has been colonised the different species may be exposed to predation or parasitism. In addition to this, within each individual carcass there is intense competition both inter- and intraspecific. Thus, the community composition at this patch level can be highly variable.

Bearing in mind that there are several factors affecting the community at the patch level one may expect that the occurrence of any one species in any patch to be variable. On the other hand the different species may show patterns in their distribution. Beaver (1977) analysed the population data collected from a series of dead snails. He made a total of 7 collections and analysed their dispersion. The results of his analysis were variable, some of his data sets showing that the distribution was significantly more regular than random in some cases. The spatial distribution of the different fly species, in this study, will be analysed using Greig-Smith's (1964) method of pattern analysis. This technique has been applied mainly to plant communities and has shown different scales of heterogeneity. If such analysis is applied to data from a transect it will reveal either the random nature of the dispersal of a species or an aggregated distribution, the question of interpretation then arises. In the following section different models of population structure are considered.

3.1.3 Models of population structure

In recent years it has become more frequent to consider populations not as isolated entities but as a number of connected populations, collectively known as a

metapopulation. A population may be defined as an ensemble of interacting individuals of the same species each with a finite lifetime; metapopulations are ensembles of interacting populations each with a finite lifetime (Hanski & Gilpin (1991)). Harrison (1991) has proposed four different types of metapopulation, described below.

i) Classical metapopulations are those that consist of a number of discrete local populations, which are subject to local extinction; but the regional population persisting through colonisation and re-colonisation of the local patches.

ii) Mainland-island and source-sink metapopulations. In the mainland-island model there are a number of local populations arising from patches of various sizes. The smaller patches may support populations but are subject to extinction. The presence of a large "mainland" patch ensures a fresh supply of colonists for smaller patches. Consequently on a regional scale the population remains fairly stable with local extinctions being of little consequence to the regional population dynamics.

The source-sink model is similar to the mainland island model in that there is again a "mainland" patch and smaller local patches but in this case the local patches are of lower quality and are unsuitable for reproduction.

iii) Non-equilibrium metapopulations. In this model local extinctions are not compensated for by re-colonisation but occur as part of a regional decline.

iv) Patchy populations. A feature of the three previous models has been the presence of distinct local populations, which may exist at equilibrium, with limited movement between them. In this fourth category dispersal between patches is high so that local extinctions become greatly reduced and local populations become blurred. Patchy populations are characteristic of species occupying ephemeral habitats.

Another model used to describe such populations of animals that depend upon ephemeral resources has been proposed by Doube (1986). Doube proposes five levels of spatial organisation. Level 1 (the patch community) deals with the community of animals found within a single patch, a patch being a single carcass for example. Level 2 (the local community) deals with the community of animals arising from a number of patches occurring in an area of uniform habitat in which immigration from adjacent communities are minimal. Level 3 (the regional species pool) refers to the combination of a series of local communities. The final two levels deal with the species pool within and between continents and so were beyond the scope of this study.

3.1.4 Temporal distribution and dynamics

The populations studied here will be considered in two ways. First they will be studied for seasonal stability *i.e.* are they just transient structures or permanent features? Wall, Green, French, and Morgan (1992) found aggregations of blowflies in the field but these were not persistent in particular areas over time. A second consideration is that of seasonality of the different species. Over the course of my sampling program I expected to observe seasonal changes in the community composition, the changes in composition reflecting the ecology of the individual species.

3.2 METHODS AND SITE DESCRIPTIONS

3.2.1 Site descriptions

All field work was carried out between May and December of 1994, on the land of Brooksby Agricultural College, Leicestershire, Grid reference SK671161, (Figure 3.1). The samples were collected from two transects that lay along hedgerows. The two transects were selected for their different aspects as this may affect the species composition on each transect. Transect 1 faced south-west and recieved much sunlight whilst transect 2 faced north-west and was in constant shade.

Traps 1-24 on transect 1 were in a field that had been left fallow for the year. The field had a fertiliser applied at least once and was ploughed during August. Traps 25-28 were along the edge of a small spinney; they were slightly out of line with the other traps in order for them to have the same aspect. Traps 29-43 ran along the edge of a field containing a crop of forage maize. Traps 44-64 were placed on the edge of a field containing a crop of wheat, which was harvested during the last two weeks of August. All of the traps, except those along the spinney, were bordered on the north east side by a narrow shelter belt that contained some mature trees and a lower shrub layer containing hawthorn (*Crataegus monogyna*), young conifers, and ash trees (*Fraxinus excelsior*). There was a dense ground flora predominantly of grass (Graminae spp.) but with abundant nettles (*Urticadioica*) and thistles (*Cirsium spp.*).

Traps 1-4 on transect 2 were placed along a hedgerow in a small grass pasture which was ungrazed. Traps 5-18 were also in grass pastures, these pastures were grazed by sheep. Traps 19-29 were in a field that had been left fallow; the field was grazed by sheep but not until August. Traps 30-43 were in a field that had been left fallow but was ploughed in August. Traps 44-52 were in a small pasture that was grazed by horses. Traps 53-68 were in a fallow field that was ploughed during June. All of the traps were bordered on the South side by a hedgerow dominated by hawthorn; the main road lay along this hedgerow.

3.2.2 Larval trap design and arrangement of traps in the field

Each trap consisted of a glass jar and a plastic lid. Each lid had three holes (11 mm diameter) drilled in it to allow access for the flies. Each trap contained a single, dead, day old chick which was inside a small plastic container placed inside the trap (Figure 3.2 a). Each trap was tied by a length of cord to a nearby tree or fence post, to prevent the removal of the traps by large animals. The traps were placed in a shallow hole to

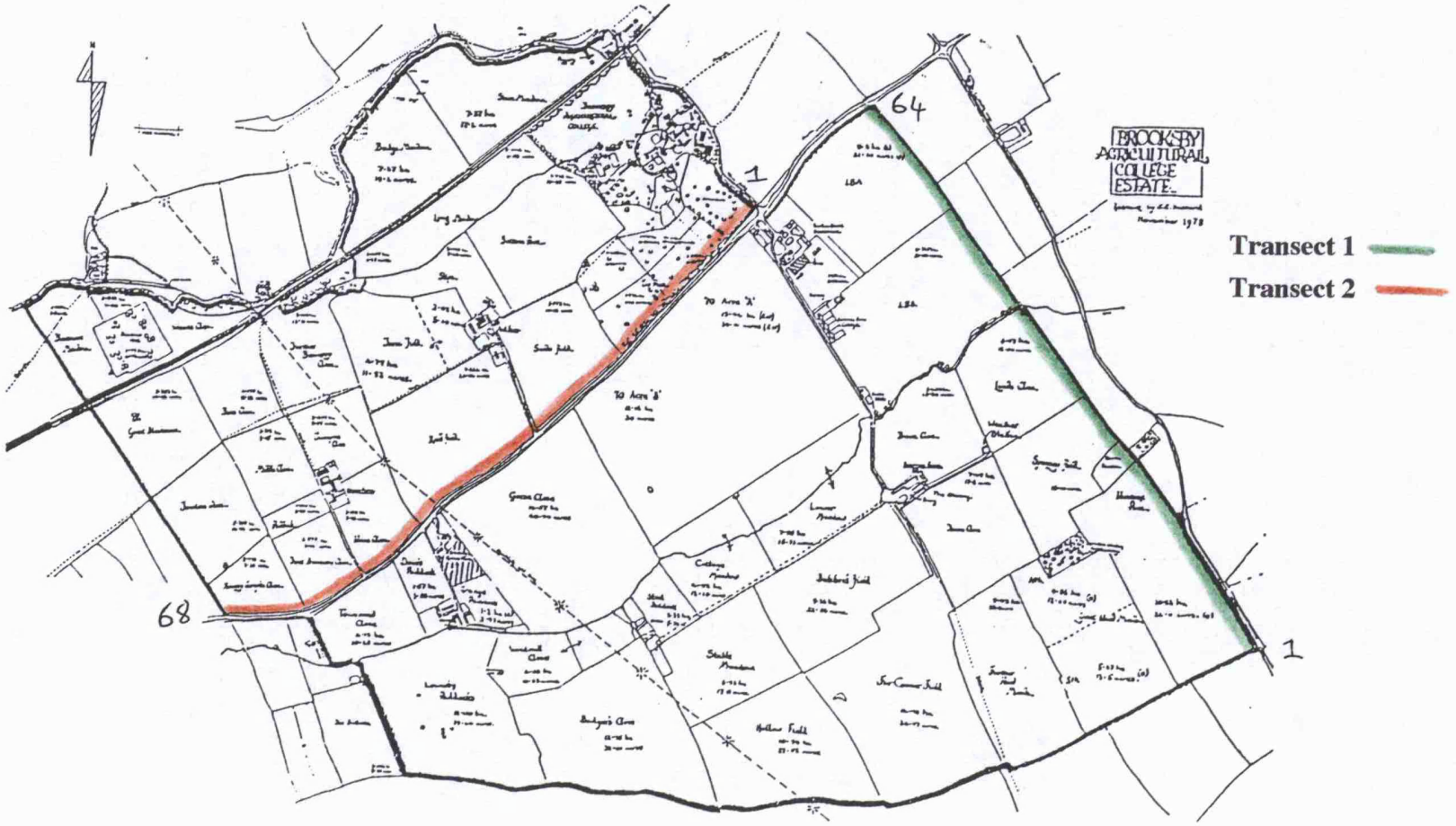


Figure 3.1) The position of the transects at Brooksby.

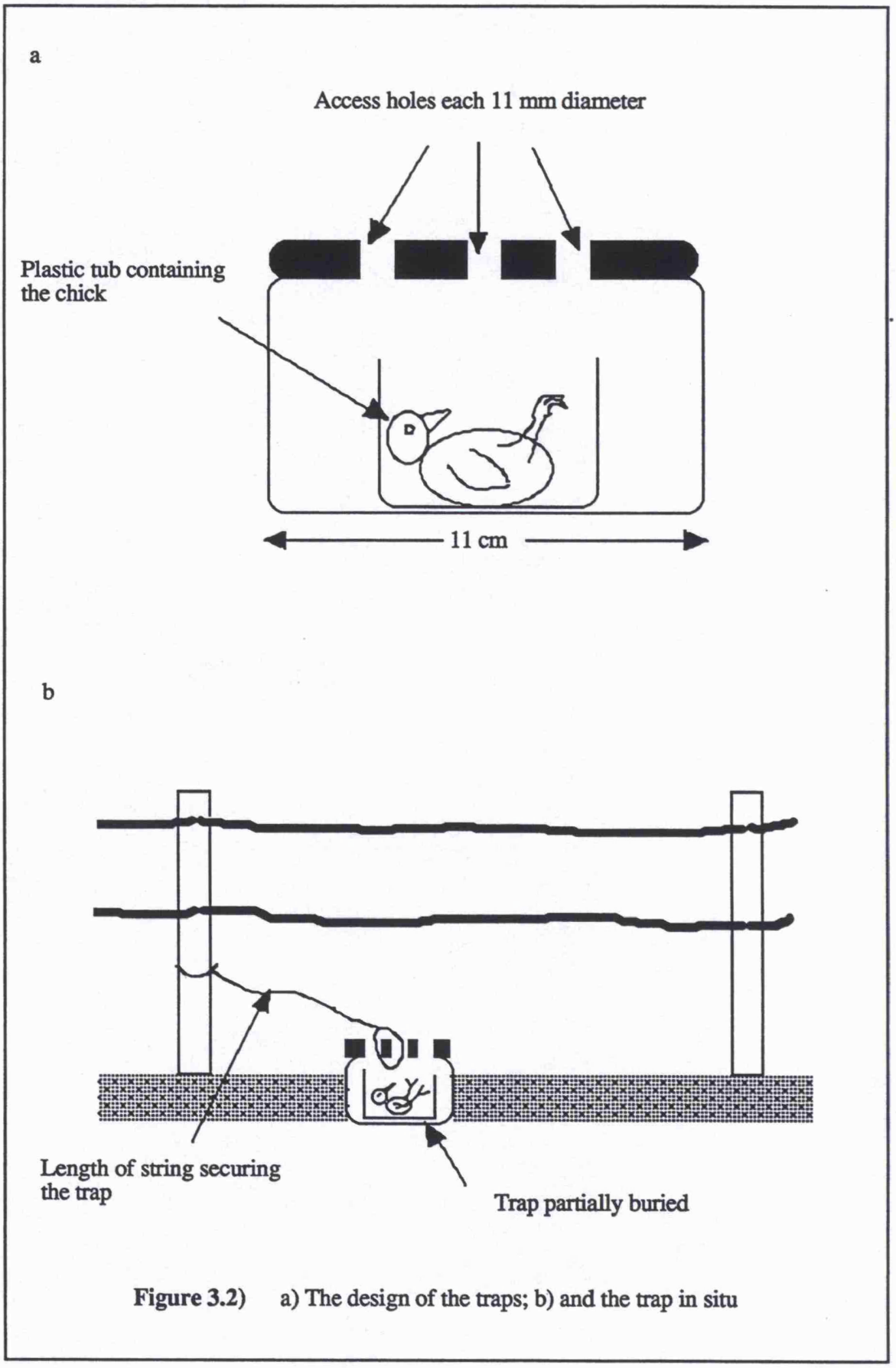


Figure 3.2) a) The design of the traps; b) and the trap in situ

keep them upright (Figure 3.2 b). To set the traps a chick was placed inside the trap whilst still inside a plastic container.

The traps were arranged along two transects, each laid along a boundary of the college's land. On both transects the traps were spaced at 25 m intervals, measured by pacing the distance between each trap. The first transect had 64 whilst the second transect had 68 traps. The carcasses were left out in the traps for two weeks before being recovered. When they were recovered a perforated lid was placed on the container, which allowed any larvae to breath. After their return to the laboratory the carcasses were incubated in a fume cupboard at ambient laboratory temperature, until they were disposed of. In total there were 16 sampling sessions.

3.2.3 Adult trap design and arrangement of traps in the field

In order to assess the adult population of flies and the degree of bias of the larval traps, attractive target traps were used (Figure 3.3). These traps were built according to the design of Wall, Green, French and Morgan (1992). The targets measured 46 cm * 46 cm and were covered on both faces by yellow polythene sheets. The sheets were coated with standard grade Oecotak®, a non setting adhesive. At the base of the target a halved drinks can was attached and a small plastic tub placed inside it. The plastic tub contained ox liver and 10% sodium sulphide solution. The opening to the plastic tub was covered by nylon netting which was held in place by an elastic band. The target was attached to the end of a 50 cm aluminium pole. The pole was driven 30 cm into the ground leaving the target 20 cm above the ground.

A total of sixteen traps were built, eight traps being used on each transect. The traps were placed at 200 m intervals and were arranged so that the target faced the centre of the field. The traps were visited after 72 hours and any adult flies were removed and placed in white spirit which removed the Oecotak®. Upon returning to the laboratory the flies were transferred from the white spirit into 70% ethanol. This procedure was carried out once during each larval sampling period from September to December. The sampling of the adult population was initiated by the poor catch of *Lucilia* species in the larval traps.

3.2.4 Preparation and handling of the carcasses

Carcasses were prepared prior to each trapping session. This involved the carcasses being placed in a small plastic tub and their abdomen being slit open to increase the attractiveness of the carcasses to the flies. The tub containing the chick was then closed

and the lid labelled with the trap and transect number. This preparation was carried out on the day before the traps were set. The prepared carcasses were stored in a cold room at 5°C until they were taken out to the field.

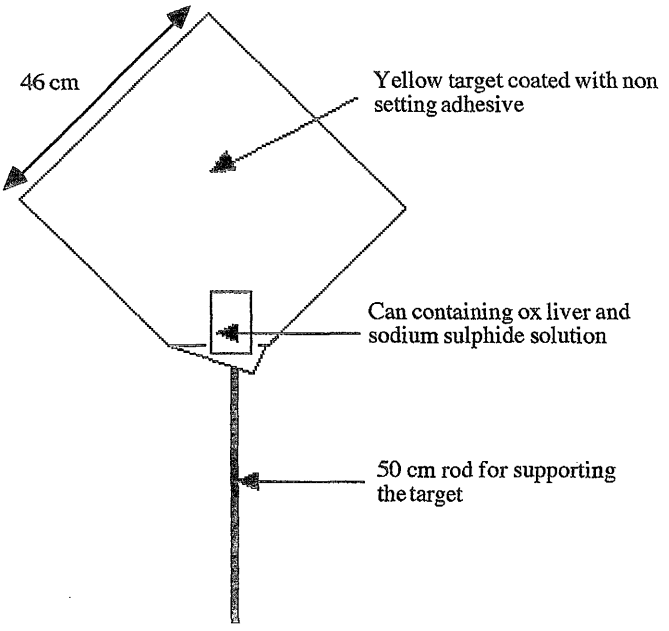


Figure 3.3) The attractive target traps

In the days following their retrieval from the field the carcasses were examined every day. Any carcasses that were found with maggots were transferred, in their plastic tubs to a larger plastic "incubation" container which had sawdust in the bottom, to act as a pupation medium (Figure 3.4). The incubation containers were still kept in a fume cupboard at this time. When the maggots had eaten sufficient they left the chick and crawled into the sawdust to pupate, the carcass could then be removed from the incubation container and disposed of.

The discarded carcasses were placed inside a plastic bag which was sealed, labelled and placed in the deep freeze until it was disposed of in the biological waste bins. Those carcasses that were not infested with maggots were kept for four days, to allow for any

eggs to hatch, after which time if no maggots were observed they too were discarded in the manner described above. Whenever the carcasses were handled protective clothing was worn *i.e.* face mask, gloves, and lab. coat. All handling of the carcasses was carried out in a fume cupboard.

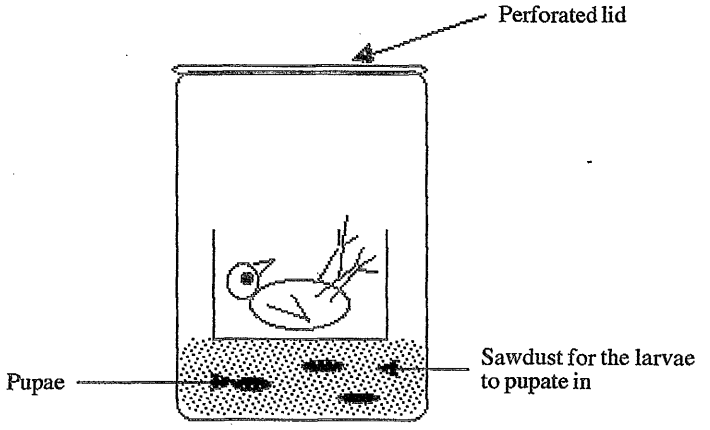


Figure 3.4) A larval incubation container

3.2.5 Incubation of pupae and identification of adults

When the carcasses had been removed the incubation containers were transferred to a constant temperature room that was maintained at 25 °C. The incubation containers were stored for at least four weeks to allow any adult flies to emerge. Any adults that did emerge were identified to species level and counted. Identification was achieved using a number of keys (Rognes (1991); Smith (1986, 1989); Oldroyd (1970); Erzinclioglu (1985); D'Assis Fonseca (1968); Chinery (1993); Pont (1979); Disney (1983); Van Emden (1954)). Only the number of adults was recorded as this represents the next generation of flies.

3.2.6 Analysis of field data

i) Sørensons coefficient of similarity

The similarity between the two transects in terms of their species composition was calculated using Sørensons coefficient of similarity. This was used to compare the

overall similarity of the species composition of the two transects and was calculated using the species records from the whole of the sampling season. The formula used is shown below.

$$C_S = 2J / (a + b)$$

Where:- J = the number of species in common to both transects
a = the number of species on transect 1
b = the number of species on transect 2

ii) Species associations

For each sampling session the species arising from each individual carcass were recorded. In order to test the null hypothesis that there were no associations between different species, the two tailed probability was calculated using Fishers Exact Test. For each species pair a 2*2 contingency table was produced in which was recorded the number of traps with both species, one species only, or in which neither species was found. The data from the two transects were combined for this analysis. The analyses were carried out using the GENSTAT® statistical package.

iii) Pattern analysis

The numbers of each species reared from each carcass were recorded as described in section 3.2.5. This gave a linear frequency of the species and number of individuals reared from each trap. The data for the most abundant species only were analysed. The data were analysed using the Greig-Smith (1964) method of pattern analysis, which is a nested analysis of variance. In this analysis the data for the transect were then divided into a number of blocks of decreasing size (2*32 traps, 4*16 traps, 8*8 traps, 16*4 traps). The structure of this analysis is shown below and illustrated in Figure 3.5.

Source of variance	Degrees of freedom
Between blocks of 32 traps	1
Between blocks of 16 traps within blocks of 32	2
Between blocks of 8 traps within blocks of 16	4
Between blocks of 4 traps within blocks of 8	8
Between blocks of 2 traps within blocks of 4	16
Between individual traps (error)	32
Total	63

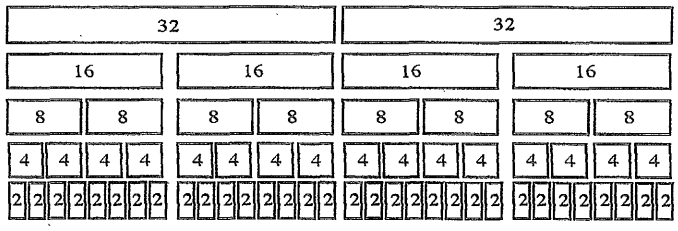


Figure 3.5) The basic design of the nested analysis of variance showing how the data for each transect was divided up for the analysis

For each level of the analysis the mean square (variance between blocks) was recorded, calculated using a balanced analysis of variance model in Minitab®. The mean square values could then be plotted against the block size. If the flies were distributed evenly along the transect the resultant graph would give a straight flat line. If, however, aggregations were present then this would be indicated by the presence of peaks on the graph. The peaks correspond to the block size over which the aggregations are present. The result is essentially descriptive; probability levels are unreliable and will therefore not be used here.

If the aggregations observed are real and not an artefact of the analysis they should still be indicated if the analysis is repeated further along the transect (a "frame shift"). On Transect 1 there were only 64 traps so no frame shift was carried out. On Transect 2 there were 68 traps. This allowed the analysis to be carried out on the data collected from traps one to 64 and then with two frame shifts from traps three to 66 and from trap five to 68. If aggregations were observed in each frame shift of the analysis then the aggregation could be considered real.

iv) Temporal stability of aggregations

In order to test for temporal stability of any aggregations a 2 * 2 contingency table was used (Figure 3.6). Each transect was treated separately. The null hypothesis, that trap occupancy in one session is independent of occupancy in another session, was tested using Fishers Exact Test. Significant associations between the traps occupied during consecutive sampling sessions may indicate the presence of temporally stable aggregations.

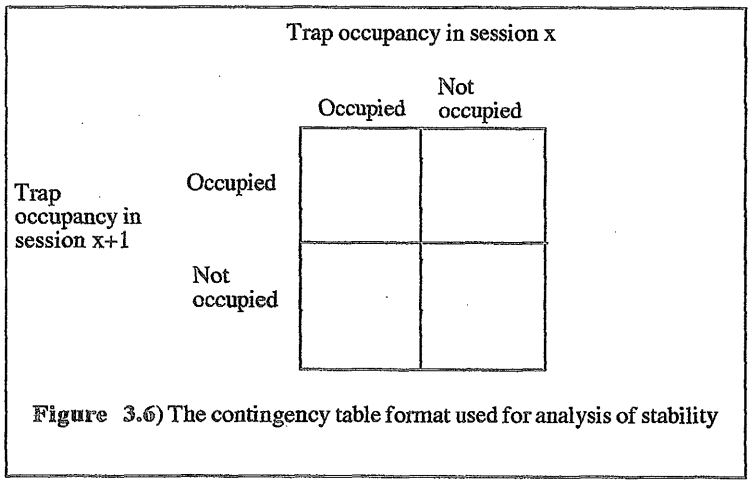


Figure 3.6) The contingency table format used for analysis of stability

3.2.7 Processing of the weather data

The weather data presented in the results section were produced from the raw weather data supplied by Mr. D. A. Mutton of the Cosby weather station. These data took the form of daily records. From the data the mean maximum and minimum temperatures, amount of rain, and hours of sunlight could be calculated for each sampling period.

3.3 RESULTS

3.3.1 Weather data

As the samples were collected over a period of 8 months the weather varied greatly (Table 3.1). Sampling began in May (1994) before the temperatures rose to their summer maximum values. The temperature was highest during July when the mid temperature was 18.6°C (this was calculated as the mean of the mean maximum and mean minimum temperatures). After July the mid temperature fell steadily until December when the mid temperature was 5.7°C.

Table 3.1 Mean maximum and minimum temperatures, mean daily rainfall, and mean daily hours of sunlight during each sampling period.

Sample No.	Sample period	Maximum Temp. (°C)	Minimum Temp. (°C)	Daily rainfall (mm)	Daily hours of sunlight (hrs)
1	12/5-26/5	13.0	7.8	3.8	1.9
2	26/5-9/6	16.7	7.1	0.4	6.4
3	9/6-19/6	19.1	8.6	0.1	8.6
4	19/6-4/7	22.1	12.2	0.8	7.2
5	4/7-21/7	23.8	12.3	0.5	8.6
6	21/7-4/8	24.3	14.2	3.5	4.8
7	4/8-18/8	20.1	11.7	1.5	5.7
8	18/8-1/9	19.8	11.2	1.3	5.5
9	1/9-15/9	16.9	8.8	4.8	4.7
10	15/9-1/10	14.6	9.4	2.3	1.8
11	1/10-13/10	13.4	5.8	0.9	4.2
12	13/10-27/10	12.9	6.7	0.8	2.7
13	27/10-10/11	12.2	6.2	4.7	2.3
14	10/11-25/11	12.6	8.1	1.2	1.5
15	25/11-8/12	9.9	4.5	2.4	1.4
16	8/12-22/12	8.8	3.5	1.6	2.4

The high temperatures and bright sunny days in the period of June to August coincided with a long dry spell during which only 115.7 mm of rain fell (over a total of 92 days).

This was followed by the wettest month of the year (September) with 104.1 mm of rain. The hours of sunlight were highest during June and July after which they fell reaching a minimum in November when there was only 47.28 hours in total. (Figures 3.7a-c).

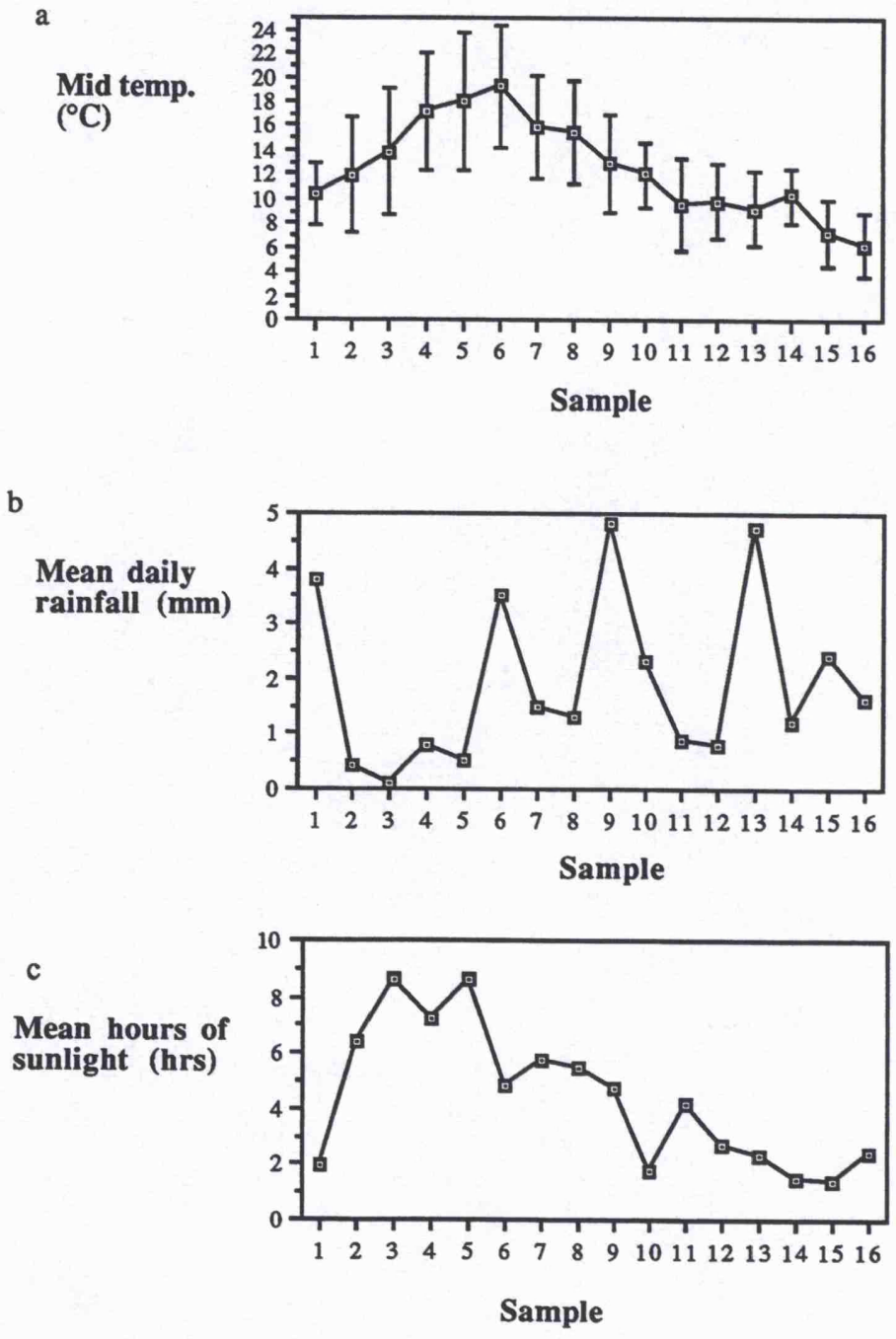


Figure 3.7a-c) Changes in a) the mid temperature, the error bars indicate the mean maximum and minimum temperatures; b) the mean daily rainfall; and c) the mean daily hours of sunlight.

3.3.2 General overview of the fly species reared from the baited traps

The fly community as indicated by the adult flies reared from the chicks was dominated by two species *Calliphora vicina* and *Muscina prolapsa*, which comprised 65.0% and 25.8% respectively of the total number of individual flies reared from both transects during the sampling period (Table 3.2). The remaining 9.2% of the individuals were represented by 12 species. One species *Cynomya mortuorum* was only found on one occasion on Transect 2, this is a scarce species in central and southern England. Seven individuals of another species *Sarcophaga carnaria* were found only on Transect 1. With these exceptions the species composition of both transects was the same. Calculation of Sørensons coefficient of similarity gave a value of 92.3%. The three species of *Lucilia* caught represented only 0.5% of the total number of individuals.

Table 3.2 The total number of adult flies of each species reared from the chick carcasses over the course of the 16 sampling sessions.

Species	Transect 1	Transect 2	% of total
Calliphora vicina (Robineau-Desvoidy)	21464	19776	65.0
Muscina prolapsa (Harris)	11021	5330	25.8
Muscina assimilis (Fallén)	150	656	1.3
Nemapoda nitudula (Fallén)	1870	1307	5.0
Fannia sp (Desvoidy)	23	126	0.2
F. coracina (Loew)	638	286	1.5
F. scalaris (Fabricus)	39	18	0.1
F. manicata (Meigen)	8	26	0.1
Lucilia sericata (Meigen)	15	53	0.1
L. illustris (Meigen)	92	106	0.3
L. caesar (Linnaeus)	36	46	0.1
Ophyra leucostoma (Weidemann)	11	158	0.3
Spinophora bergenstammi (Malloch)	87	59	0.2
Sarcophaga carnaria (Linnaeus)	7	0	0.0
Cynomya mortuorum (Linnaeus)	0	16	0.0
Total	35461	27963	100.0%
Grand total	63424		

3.3.3 Changes in the fly community of the two transects

There were common trends in the population fluctuations of both transects (Figure 3.8 a-b). *C. vicina* was the only species found during the first sampling session on both transects. The number on Transect 1 fell rapidly after this first session and *C. vicina* was replaced by *M. prolapsa* as the dominant species until the ninth session when *C. vicina* numbers rose making it the dominant species once again. The number of *C. vicina* reached a peak at the fourteenth session when nearly 8000 individuals were reared from this transect. The situation on transect 2 was very similar except that *C. vicina* remained the dominant species for the first three sampling sessions. Again it was replaced with *M. prolapsa* as the dominant species until the ninth sampling session. On both transects the resurgence of *C. vicina* showed a brief slump during the thirteenth sampling session. During this autumnal resurgence *C. vicina* was virtually the only species found. Between sessions 10 and 16 only a few individuals of *F. scalaris* and *L. caesar* were found (Table 3.3).

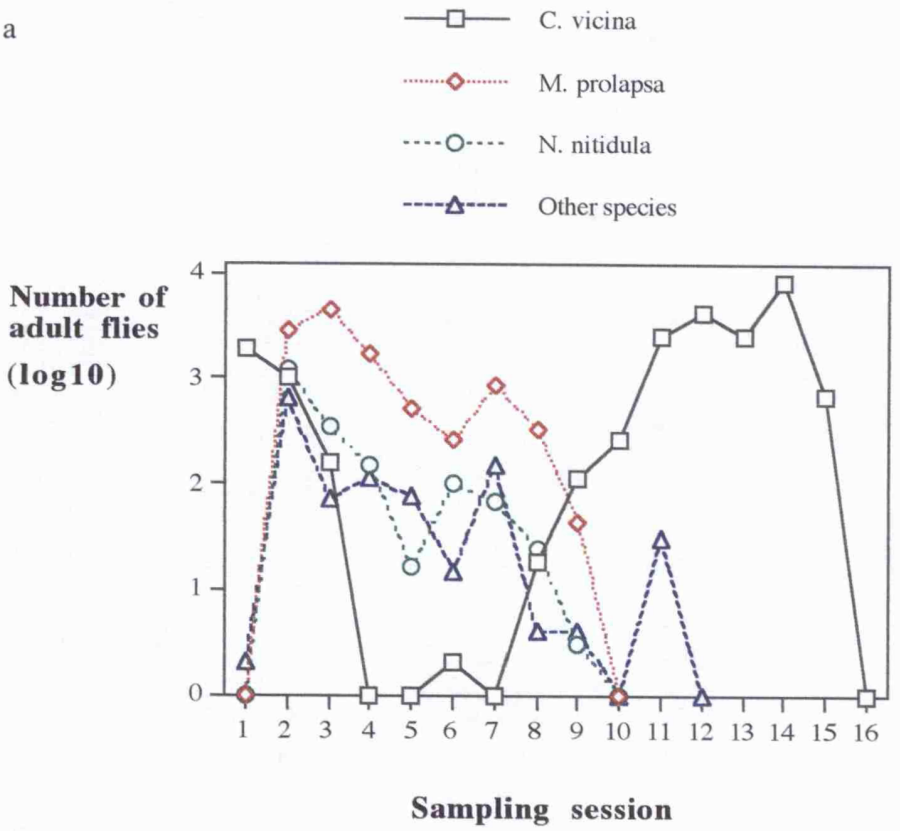
On both transects there was a massive reduction in the number of flies reared between the fourth and tenth sampling sessions. This massive reduction in the number of flies can be seen to coincide with the heat wave that occurred during the summer. It is difficult to say whether this slump was entirely due to the environment or only partly, with the slump representing the seasonal decline of the different species.

If the population fluctuations are considered along with the rainfall data trends can also be seen. *M. prolapsa* populations fell between sampling periods 4-6 after which a small peak occurred on both transects during session 7. The rainfall data in Figure 3.5b shows that this population peak followed a peak in the rainfall during session 6. The next peak in the rainfall occurred during session 9 and on both transects a peak was observed in the *C. vicina* populations during session 12. The amount of rainfall decreased after this period until it reached another peak in session 13. At this time the *C. vicina* populations on both transects were falling. However, following the peak in rainfall the *C. vicina* populations started to grow again and another peak was observed during session fourteen. These results suggest a delayed response by the fly populations to environmental variables, especially the amount of rainfall.

Table 3.3 The number of adult flies of each species reared from the chick carcasses from each transect during the sampling period

		Sample numbers and sample period															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Species	Transect	12/5-26/5	26/5-9/6	9/6-19/6	19/6-4/7	4/7-21/7	21/7-4/8	4/8-18/8	18/8-1/9	1/9-15/9	15/9-1/10	1/10-13/10	13/10-27/10	27/10-10/11	10/11-25/11	25/11-8/12	8/12-22/12
C. vicina	T1	1918	1009	161	0	0	1	0	17	113	268	2527	4202	2451	8110	687	0
	T2	2152	2672	2022	39	6	0	37	10	90	395	2118	3907	1864	4362	102	0
M. prolapsa	T1	0	2854	4527	1645	514	255	848	335	43	0	0	0	0	0	0	0
	T2	0	244	1904	967	1399	96	607	113	0	0	0	0	0	0	0	0
M. assimilis	T1	0	24	32	9	39	12	31	3	0	0	0	0	0	0	0	0
	T2	0	0	386	113	103	5	49	0	0	0	0	0	0	0	0	0
N. nitidula	T1	0	1175	344	146	15	99	65	24	2	0	0	0	0	0	0	0
	T2	0	165	298	259	277	273	32	3	0	0	0	0	0	0	0	0
F.coracina	T1	0	621	16	0	0	0	1	0	0	0	0	0	0	0	0	0
	T2	0	46	159	8	47	16	9	0	1	0	0	0	0	0	0	0
F. manicata	T1	0	0	0	5	3	0	0	0	0	0	0	0	0	0	0	0
	T2	0	0	2	5	4	14	1	0	0	0	0	0	0	0	0	0
F. scalaris	T1	0	0	9	0	0	0	28	0	2	0	0	0	0	0	0	0
	T2	0	0	2	4	0	6	1	2	0	3	0	0	0	0	0	0
F. sp.	T1	0	0	8	11	0	0	3	0	1	0	0	0	0	0	0	0
	T2	0	0	8	34	41	39	0	2	2	0	0	0	0	0	0	0
L.caesar	T1	0	0	0	0	0	0	6	0	0	0	30	0	0	0	0	0
	T2	0	3	0	0	0	43	0	0	0	0	0	0	0	0	0	0
L. illustris	T1	0	0	0	0	16	0	76	0	0	0	0	0	0	0	0	0
	T2	0	41	36	0	0	29	0	0	0	0	0	0	0	0	0	0
L.sericata	T1	1	0	0	5	0	0	9	0	0	0	0	0	0	0	0	0
	T2	31	20	0	0	0	2	0	0	0	0	0	0	0	0	0	0
S.carnaria	T1	0	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0
	T2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. bergenstammi	T1	0	0	6	81	0	0	0	0	0	0	0	0	0	0	0	0
	T2	0	0	1	56	0	0	0	0	2	0	0	0	0	0	0	0
O. leucostoma	T1	0	0	0	0	9	2	0	0	0	0	0	0	0	0	0	0
	T2	0	0	0	14	20	124	0	0	0	0	0	0	0	0	0	0
C. mortuorum	T1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	T2	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0

a



b

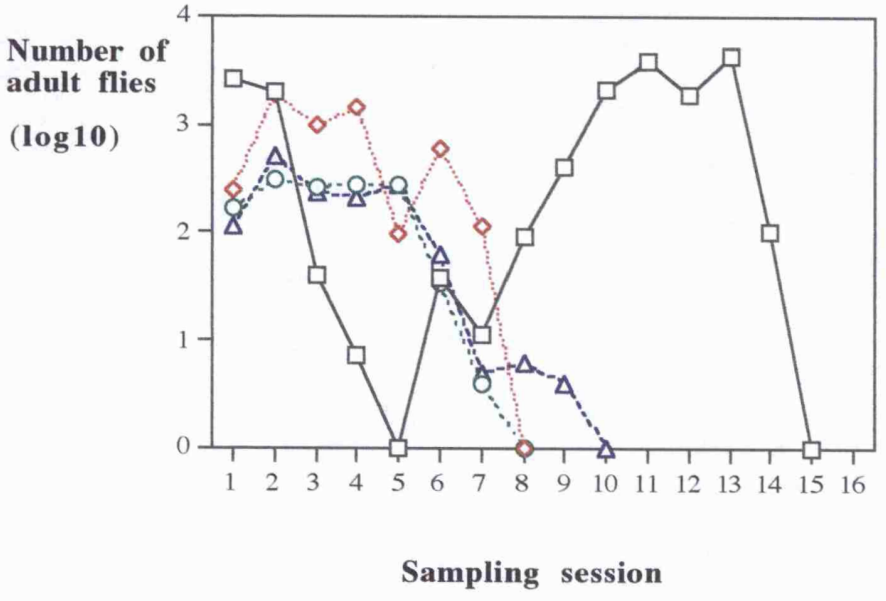


Figure 3.8 a-b) The changes in abundance of the fly species as indicated by the adult flies reared from the chick carcasses from the two transects; a) Transect 1 and b) Transect 2.

3.3.4 The community of flies arising from each carcass

The results so far have given an overview of the local blowfly community and have suggested how the weather may play a role in affecting the populations. In this section the communities of flies arising from each individual carcass will be considered. Before considering the patch community the patch occupancy will be considered. The data in Table 3.4 show that on no occasions were all the traps infested with maggots and that the mean number of species reared from each carcass was always lower than the number of species in the local community (see Appendix 1 for the raw data). There was a strong correlation between trap occupancy on the two transects (r^2=0.64, P=<0.5), which may reflect effects of common environmental factors upon the communities.

Table 3.4 The percentage of traps giving rise to adult flies and the mean number of species found on each occupied carcass from Transect one (T1) and Transect two (T2).

Session	% of traps yielding flies on T1	Mean number of species per trap on T1	Total number species	% of traps yielding flies on T2	Mean number of species per trap on T2	Total number species
1	35.94	1.04	2	36.76	1.08	2
2	75.00	1.42	5	51.47	1.57	7
3	73.44	1.47	7	69.12	1.79	10
4	65.62	1.26	8	73.53	1.92	9
5	40.62	1.38	7	72.06	1.57	7
6	35.94	1.22	5	54.41	1.62	10
7	54.69	1.89	8	50.00	1.32	7
8	34.37	1.18	4	29.41	1.05	4
9	31.25	1.00	4	13.23	1.00	4
10	12.50	1.00	1	11.76	1.00	3
11	53.12	1.00	2	29.41	1.00	2
12	78.12	1.00	1	69.12	1.00	1
13	56.25	1.00	1	27.94	1.00	1
14	71.87	1.00	1	45.59	1.00	1
15	23.44	1.00	1	2.94	1.00	1

It was possible that factors such as interspecific competition or predation of one species by another may have led to a negative association between species. Calculation of the two-tailed probability using Fishers Exact Test was carried out only on the two most abundant species, *C. vicina* and *M. prolapsa*. The analysis did not reveal any significant associations (P>0.05 in all cases). It would appear that the two species are distributed independently of each other during any one sampling session. When the data for these two species from the whole season were studied, however, it was clear that there was a temporal separation of the species.

3.3.5 Comparison of the *Lucilia* species and *Calliphora* species populations as indicated by the two trapping methods

The results from the larval traps suggested that *Lucilia spp.* only account for a small percentage of the carrion fly community. A total of only 348 individuals were reared during the 16 sampling sessions.

Using the sticky traps, adult flies of two *Lucilia spp.* (*L. caesar* and *L. illustris*) were caught in relatively large numbers (322 individuals for 336 trap days compared with only 30 individuals of *L. caesar* from the carcass traps during the same period for 12936 trap days). The sticky trap data are presented in Table 3.5.

During the first two sticky-trap sessions the two *Lucilia* species were more abundant than the two *Calliphora* species. When using the larval traps *C. vicina* always outnumbered the *Lucilia* species. In addition to these difference in numbers there was also a difference in the Calliphoridae species composition: *C. vomitoria* was caught on the sticky traps but was not reared from any of the carcass traps.

Table 3.5 The numbers of adult flies caught on each transect using sticky traps.

Session (session number using chick traps)	*C. vicina*		*C. vomitoria*		*L. illustris*		*L. caesar*	
	T1	T2	T1	T2	T1	T2	T1	T2
1 (9)	10	1	2	3	2	7	82	98
2 (11)	58	0	2	3	0	0	94	12
3 (12)	33	19	2	4	1	1	14	6
4 (13)	23	14	7	2	0	0	2	2
5 (14)	11	7	2	1	0	0	1	0
6 (15)	11	0	4	0	0	0	0	0
7 (16)	0	0	2	0	0	0	0	0

Differences between the two trapping methods are also evident when the seasonality of the different species are considered. The data collected from the larval traps suggests that there was a peak in the numbers of *Calliphora* during the fourteenth session. The adult trap data showed a peak occurring during the eleventh session. This could, however, simply reflect a natural lag between the peak in adults and the peak in larvae that would follow. The larval traps failed to yield any data for *L. caesar* after the

eleventh session suggesting that this was the end of the season for this species. The adult data showed this species to be present up until the fourteenth session.

3.3.6 Pattern analysis

The pattern analysis was carried out only on *C. vicina* and *M. prolapsa,* which together accounted for 90.8% of the total number of flies found. For *C. vicina* analysis was carried out on all sampling sessions in which this species was found except for the fourth, sixth, and eighth session on Transect 1 and the fourth, fifth, seventh, and eighth sessions on Transect 2. In each of these cases there were insufficient numbers of flies to warrant a full analysis. For *M. prolapsa* the analysis was carried out on all sampling sessions in which this species was found.

The analysis of the *C. vicina* data from Transect 1 showed that during the first (Figure 3.9 a-b) and second (Figure 3.10 a-b) sampling sessions there appeared to be aggregation at a block size of 16 (approximately 400 m). Inspection of the raw data for these sessions showed that this aggregation was evident in the data. In both cases there appeared to be a large aggregation at the start of the transect between traps one and 16, and two less distinct aggregations further down the transect. No pattern was evident in the data from the third session, flies were only reared from three traps. Later in the season, during session nine (Figure 3.12 a-b) when the population of *C. vicina* started to increase again an aggregation at a block size of eight was shown. Again inspection of the raw data showed that this pattern is more evident at the start of the transect. No pattern was revealed for the tenth session (Figure 3.13 a-b). Both the eleventh and twelfth sessions (Figures 3.14 a-b and 3.15 a-b) indicated aggregations over block size of four (approximately 100 m). In each of these two sessions there appeared to be no difference between different regions on the transect. For the remaining three sessions aggregations at a block size of 16 was indicated. The patterns were not very clear in the raw data (Figures 3.16 a-b, 3.17 a-b, 3.18 a-b).

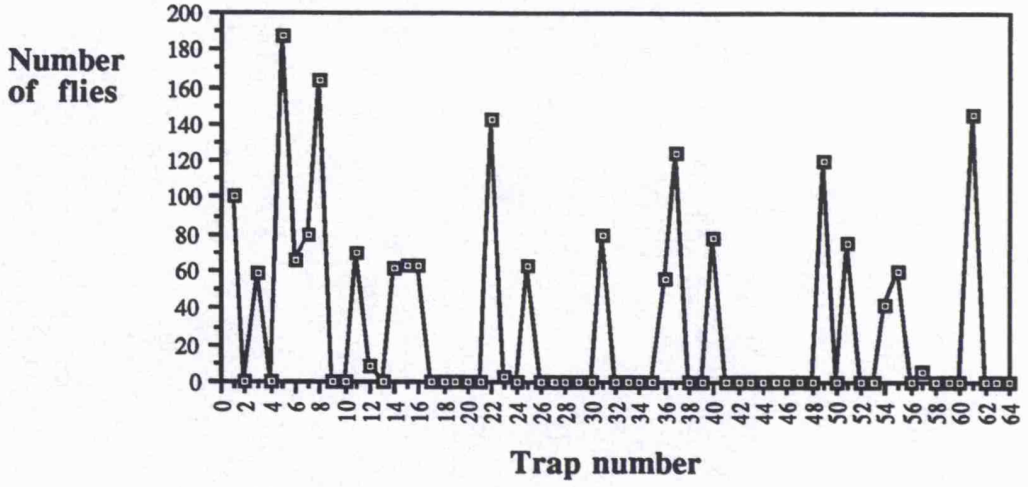
The data collected from Transect 2 gave rise to different patterns from those of Transect 1. The pattern analysis of the data from the first session (Figure 3.19 a-b) indicated aggregations at a block size of four (approximately 100 m) with no frame shift, a block size of two (approximately 50 m) with the first frame shift, and a block size of eight (approximately 200 m) with the second frame shift. The data from the second session (Figure 3.20 a-b) gave rise to aggregations at a block size of 8. However, during this session a number of traps were lost from the middle region of the transect, thought to be due to interference by badgers. The aggregations revealed by the analysis were not reliable. During the third session an aggregation at a block size of 16 (approximately

400 m) was observed (Figure 3.21 a-b) which remained stable with each frame shift. A block size of 16 was also indicated in the ninth session's data but only in the first and second frame shift of the analysis (Figure 3.22 a-b). In the remaining four sessions aggregations were indicated but the frame shift analysis gave varying results, each frame shift giving block sizes tending to disagree with the next (Figures 3.23 a-b, 3.24 a-b, 3.25 a-b, 3.26 a-b, 3.27 a-b). Consistent trends are hard to find.

When the data for *M. prolapsa* are considered the overall picture was much the same. The data from Transect 1 (Figures 3.28 - 3.35 a-b) give rise to aggregations over block sizes of two, four, eight, and 16 (50-400 m) with no consistent trends being observed. The Transect 2 data also showed a range of trends (Figures 3.36 -3.42 a-b). The frame shift analysis showed consistent trends during the second session in the first and second frame shift when a block size of four was indicated in both cases. This may have been due to missing traps as described above The agreement between the frame shifts of the third session (Figure 3.37 a-b) indicates the presence of large aggregations over a block size of 16 (approximately 400 m). During the sixth, seventh and eighth sessions the frame shift analysis did appear to give rise to consistent results within each sampling session. A block size of eight (approximately 200 m) was indicated by all frame shifts in the sixth session (Figure 3.40 a-b). A block size of four was indicated by all frame shifts in the seventh session (Figure 3.41 a-b). A block size of 16 was indicated by all frame shifts in the eighth session (Figure 3.42 a-b). Unfortunately the block size indicted by each session are different.

From these data it is possible to say that aggregations of both species do exist over the block size 2-16. However, neither species gave rise to consistent aggregations. The results of the two-tailed test showed that these aggregations were not stable from one sampling session to the next, $P>0.05$ in all cases except one. The only significant association was shown by *M. prolapsa* between the seventh and eighth session on Transect 2 ($P<0.05$).

a



b

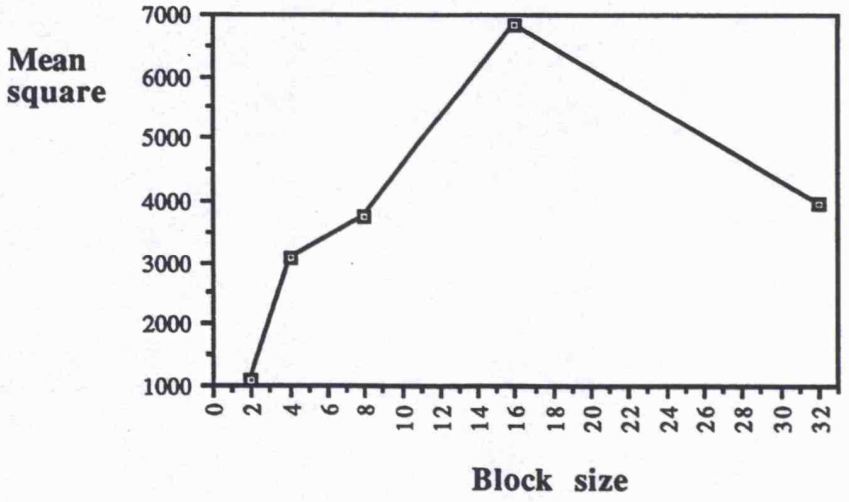
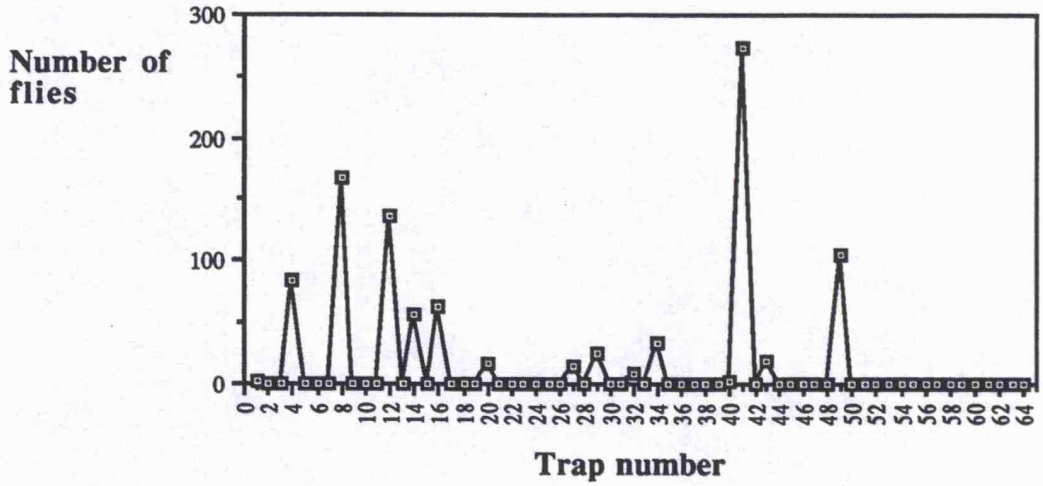


Figure 3.9 a-b) Data from the first sampling session (12th - 26th May 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

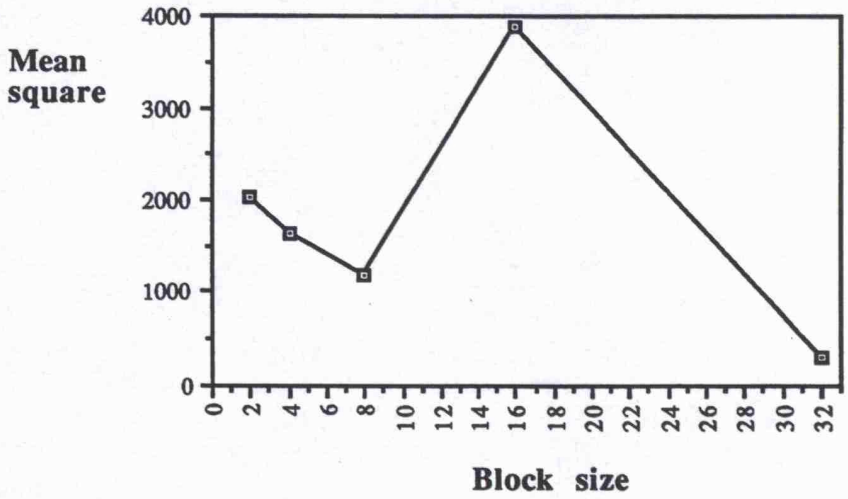
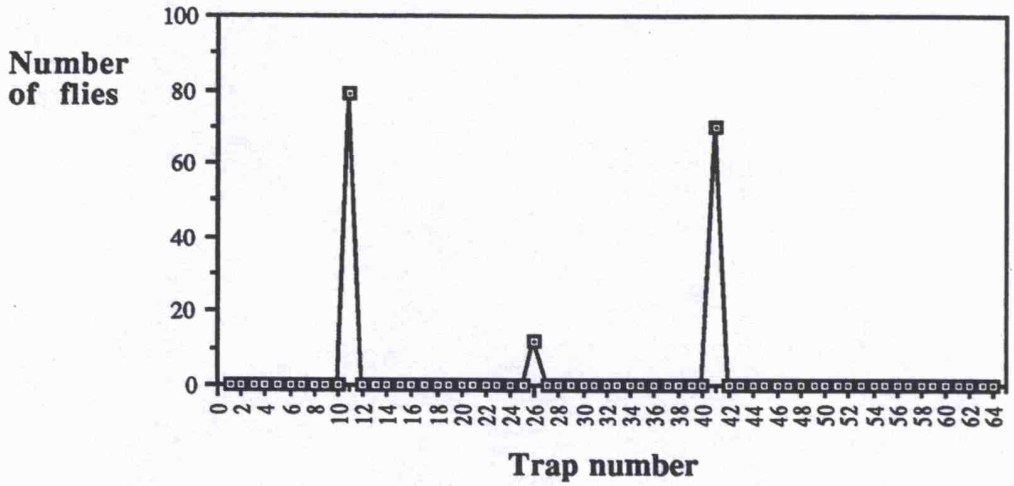


Figure 3.10 a-b) Data from the second sampling session (26th May - 9th June 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

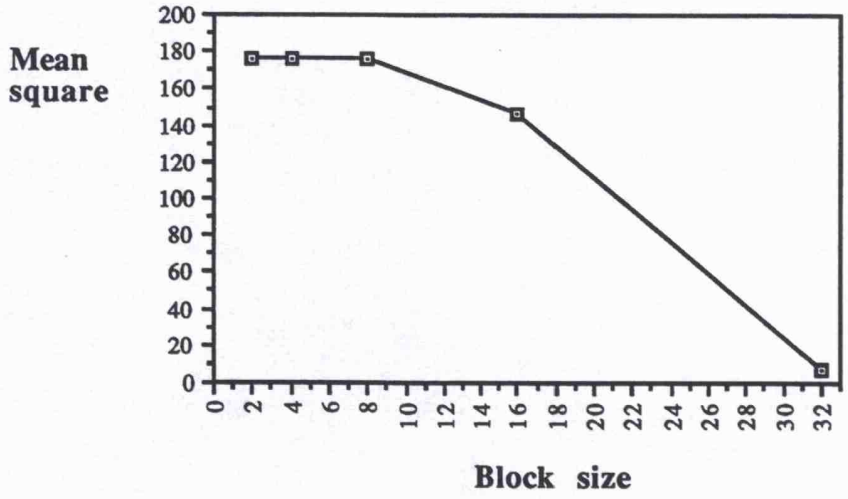
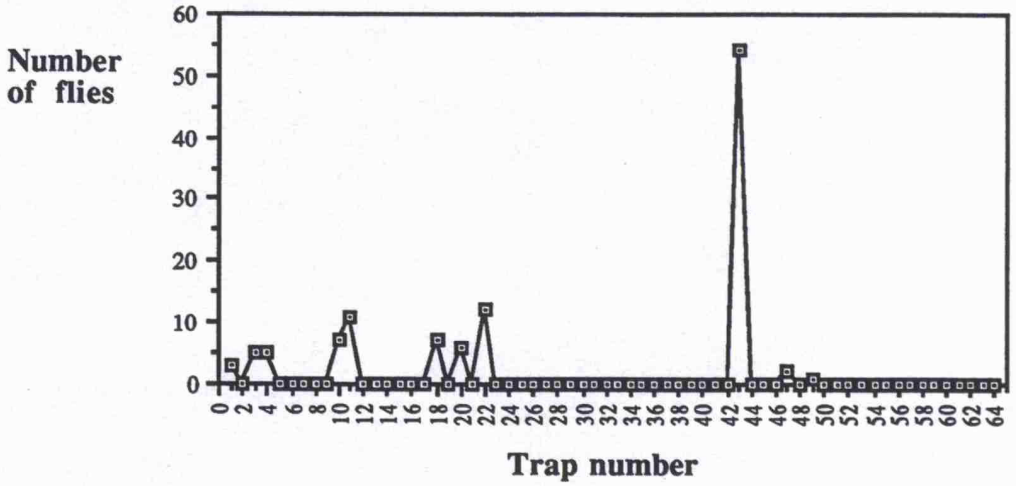


Figure 3.11 a-b) Data from the third sampling session (9th - 19th June 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

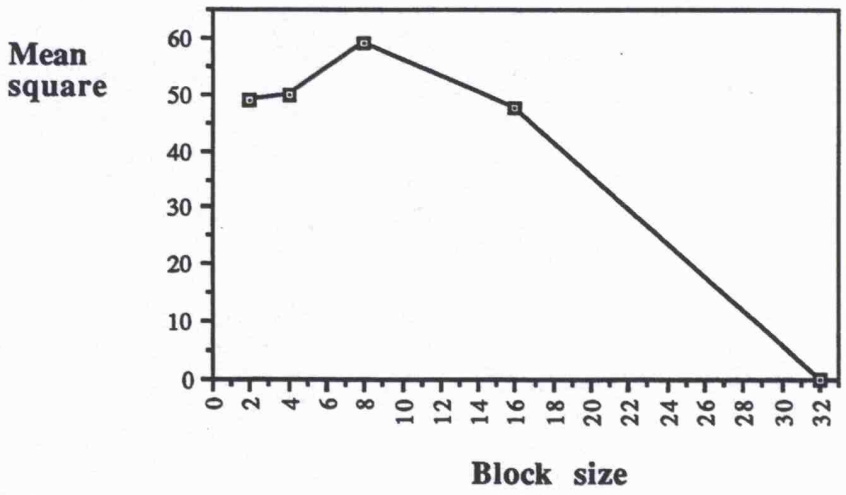
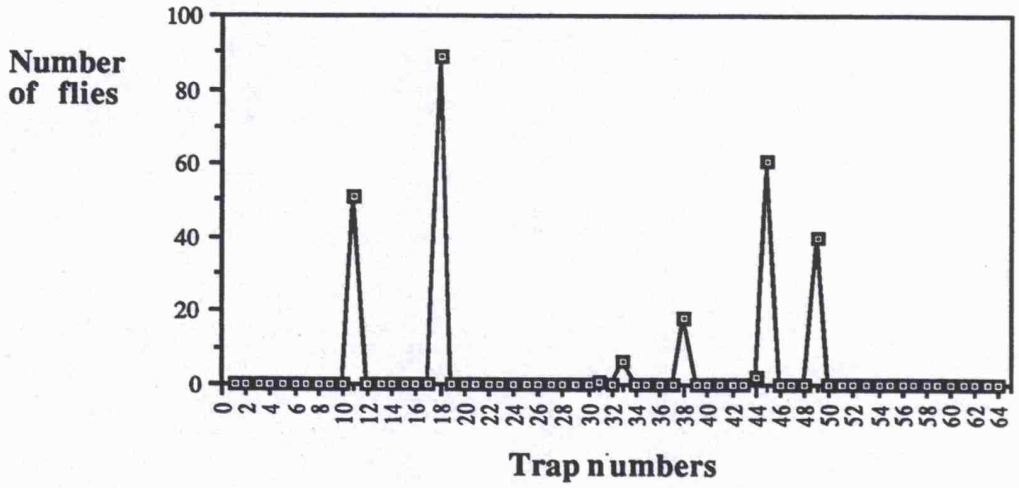


Figure 3.12 a-b) Data from the ninth sampling session (1st - 15th September 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

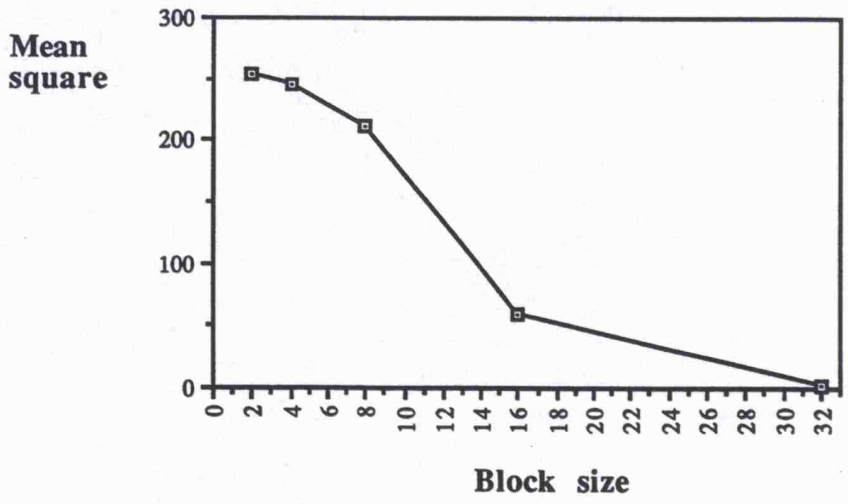
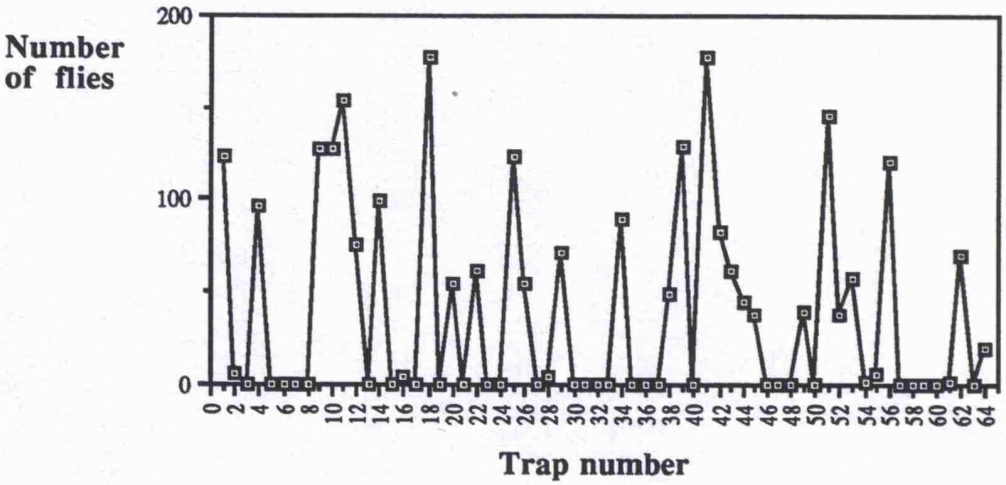


Figure 3.13 a-b) Data from the tenth sampling session (15th September - 1st October 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

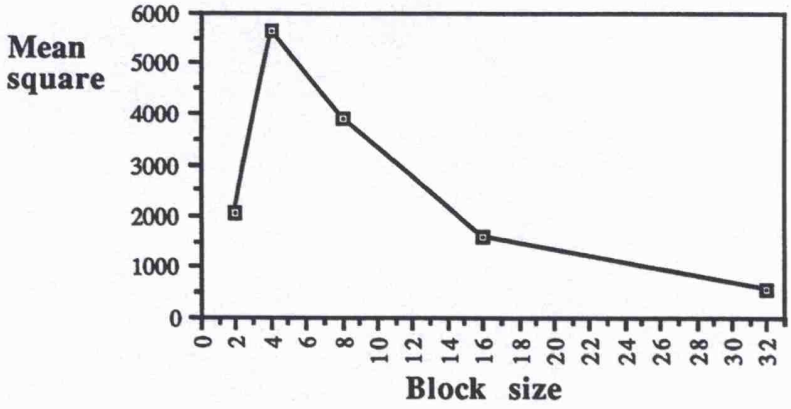
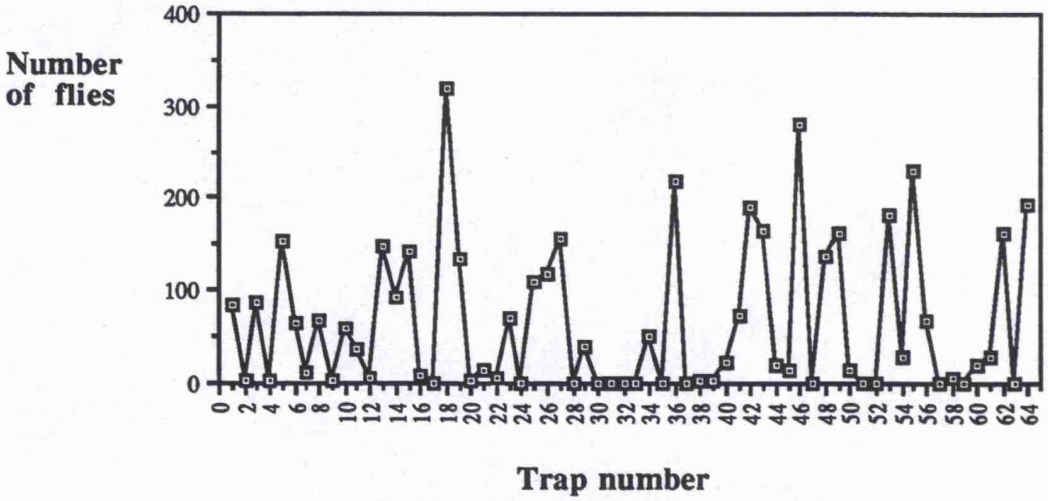


Figure 3.14 a-b) Data from the eleventh sampling session (1st - 13th October 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

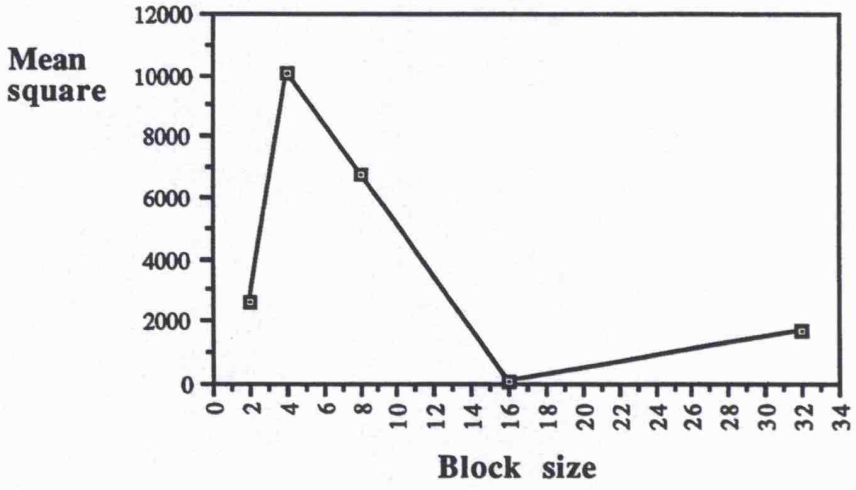
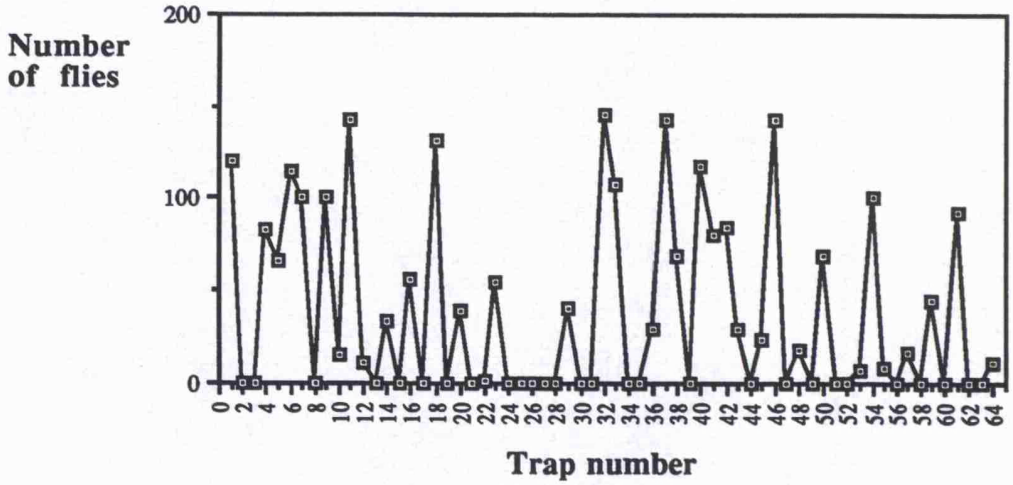


Figure 3.15 a-b) Data from the twelfth sampling session (13th - 27th October 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

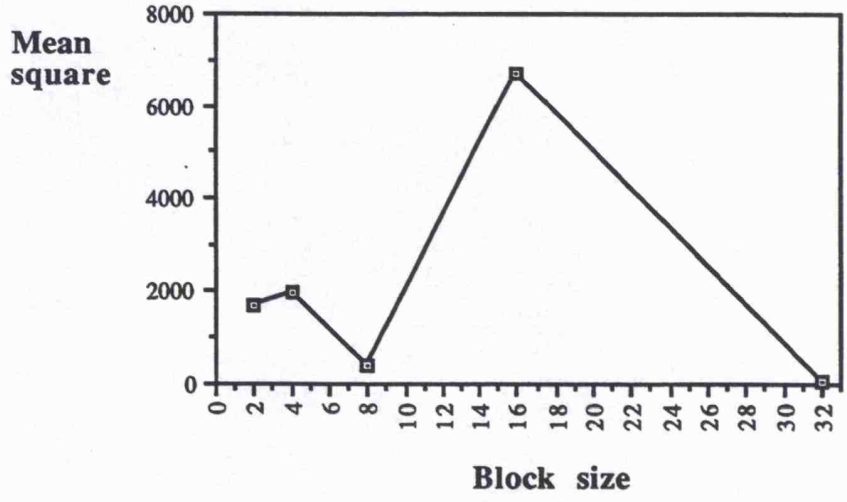
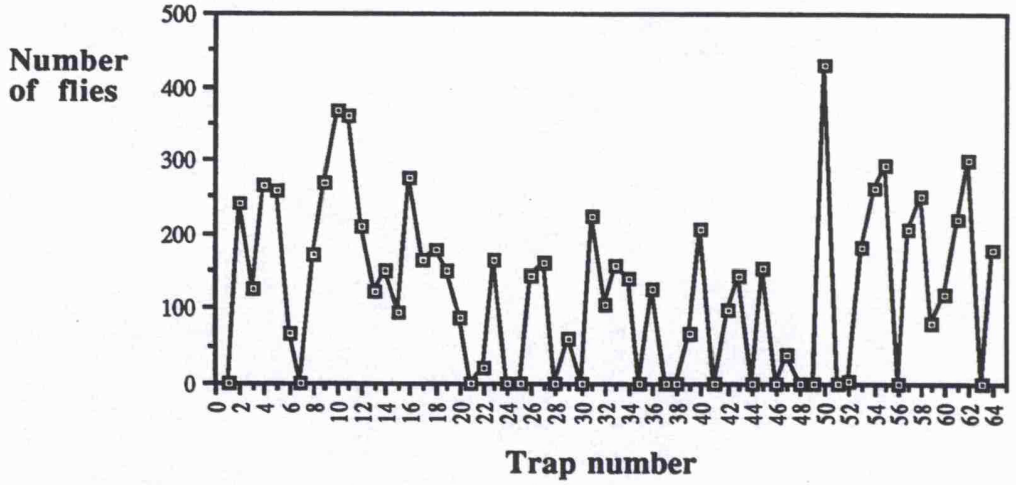


Figure 3.16 a-b) Data from the thirteenth sampling session (27th October - 10th November 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

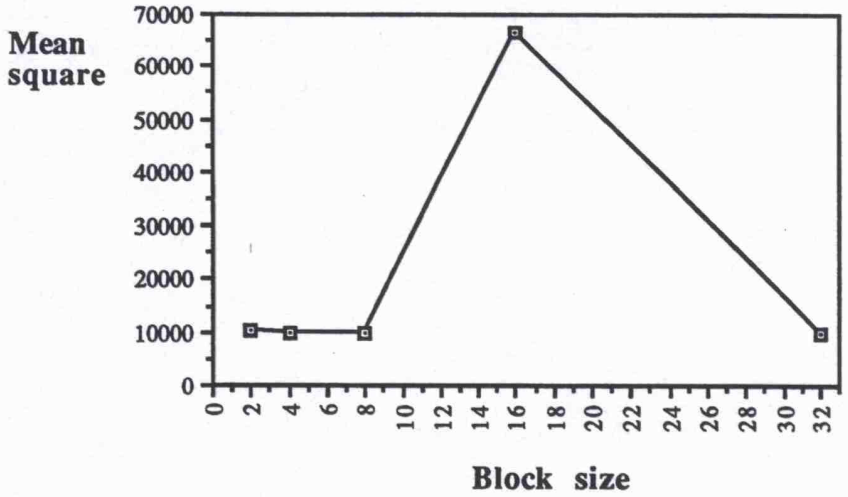
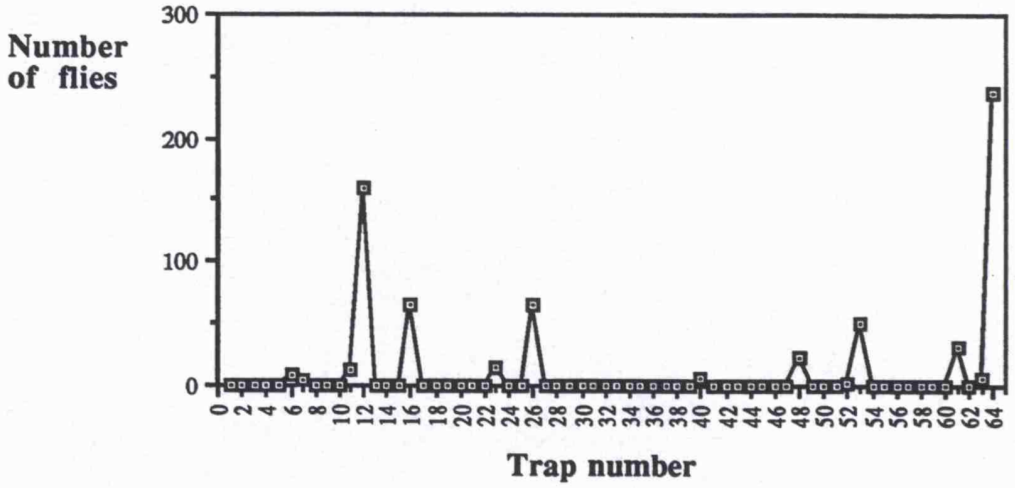


Figure 3.17 a-b) Data from the fourteenth sampling session (10th - 25th November 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data.

a



b

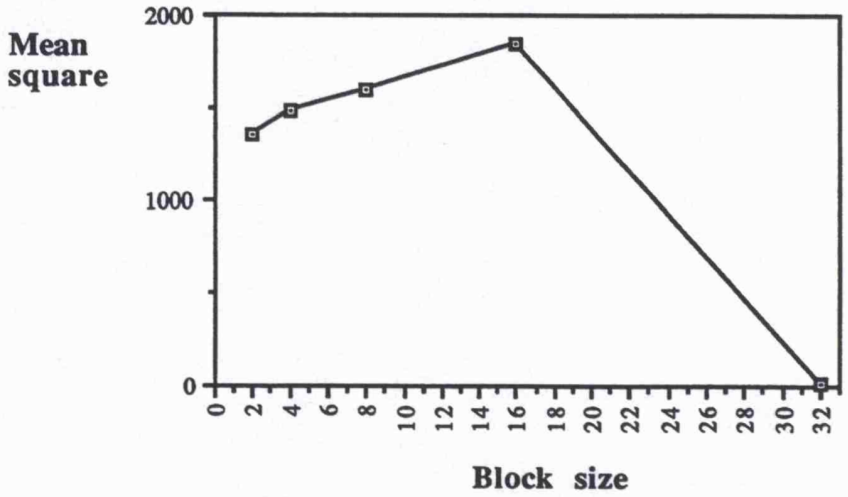
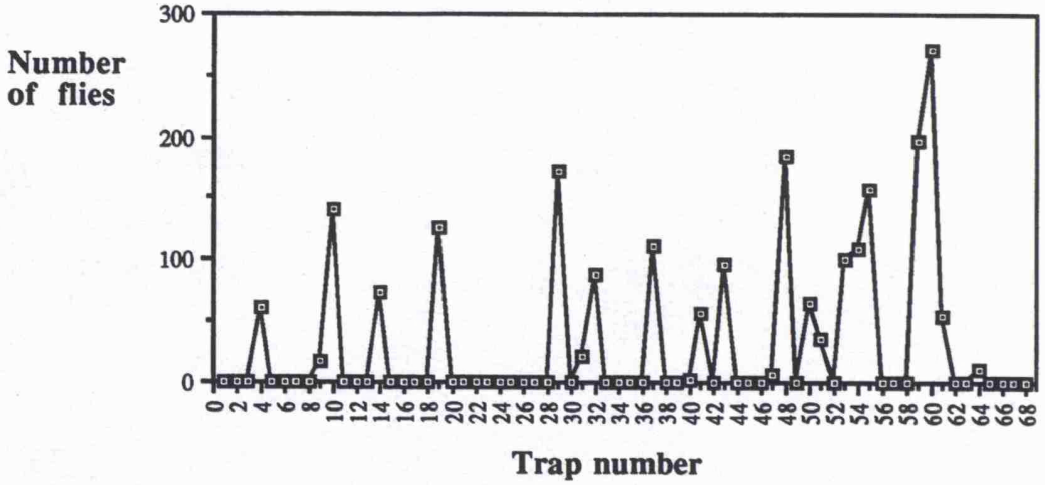


Figure 3.18 a-b) Data from the fifteenth sampling session (25th November - 8th December 1994) on Transect 1 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data..

a



b

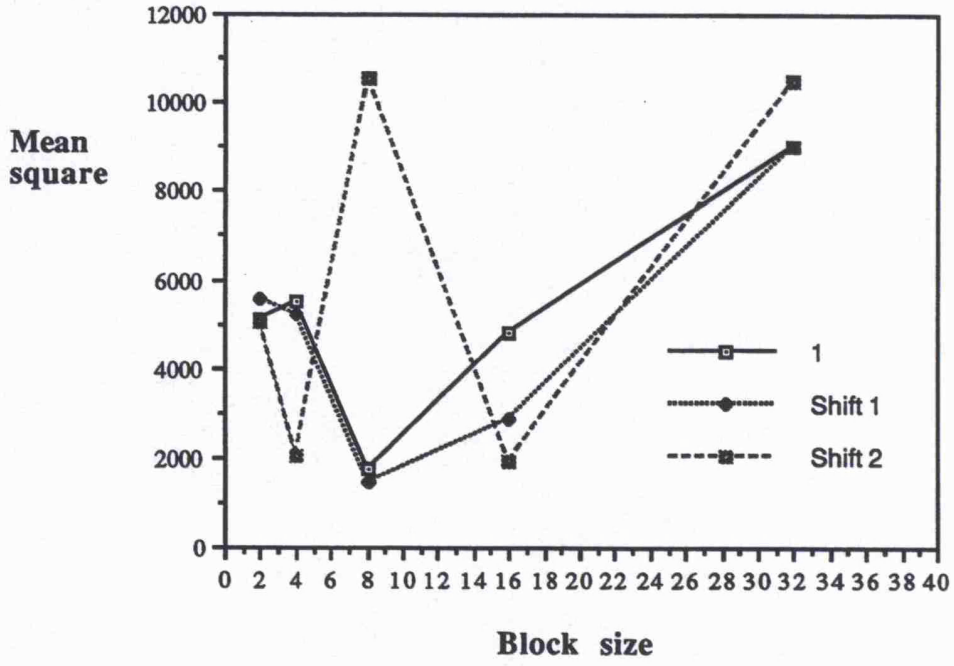
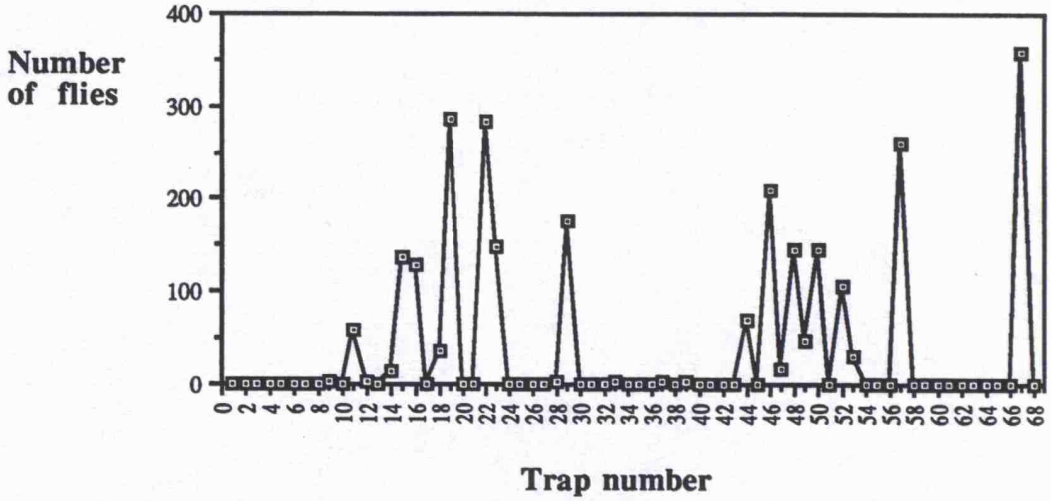


Figure 3.19 a-b) Data from the first sampling session (12th - 26th May) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

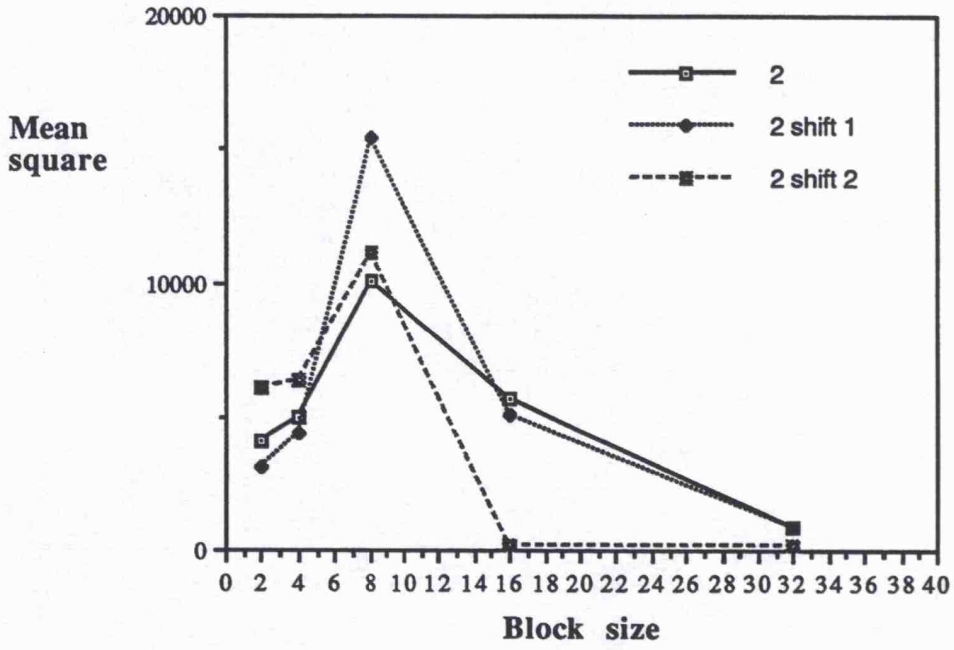
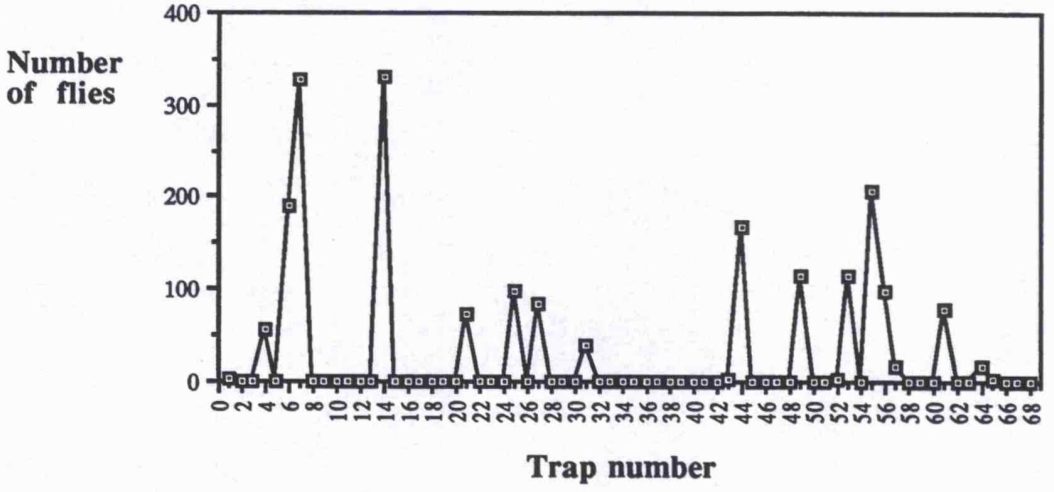


Figure 3.20 a-b) Data from the second sampling session (26th May - 9th June 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

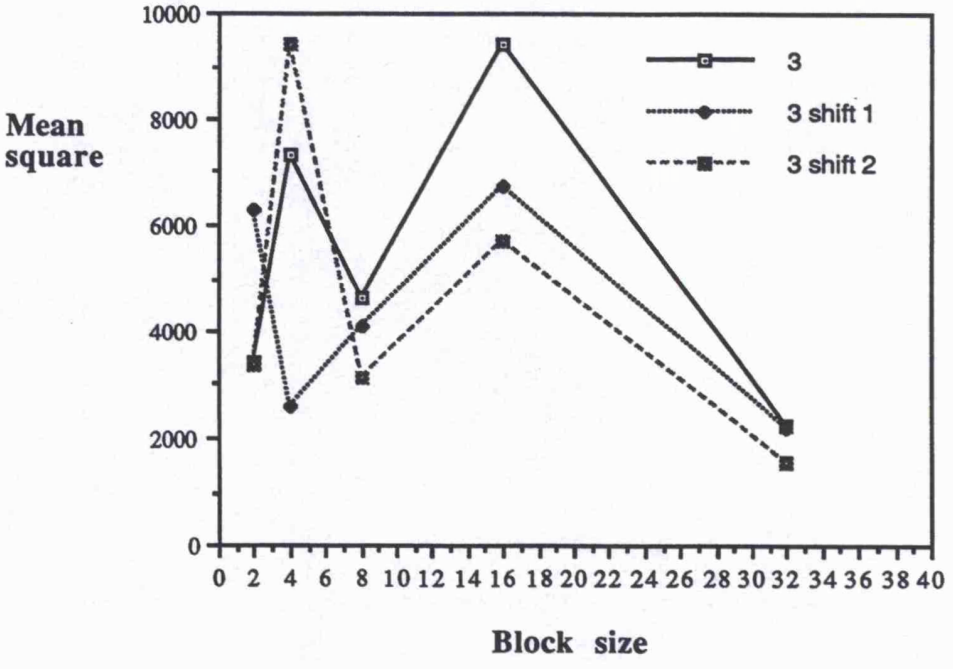
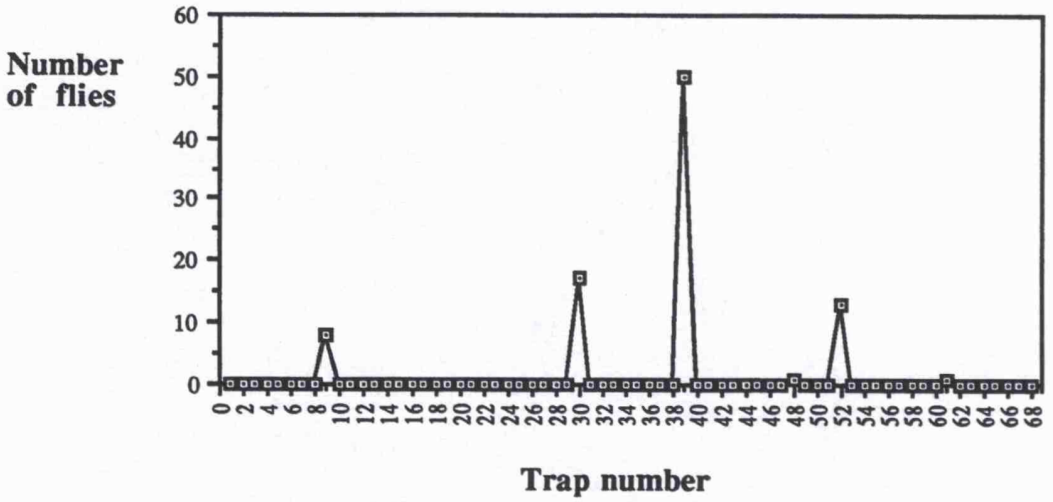


Figure 3.21 a-b) Data from the third sampling session (9th - 19th June 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

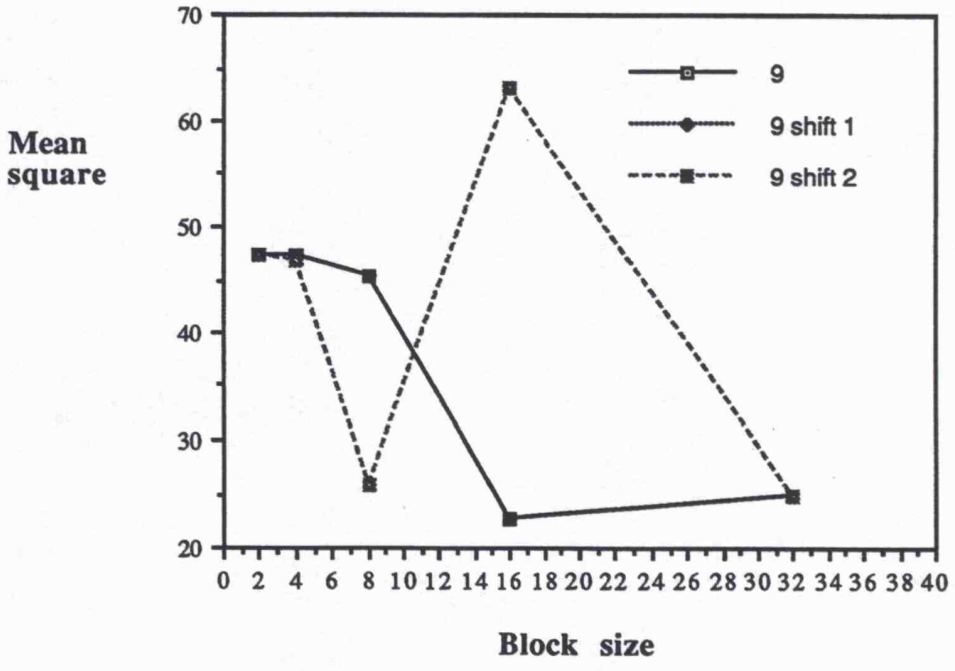
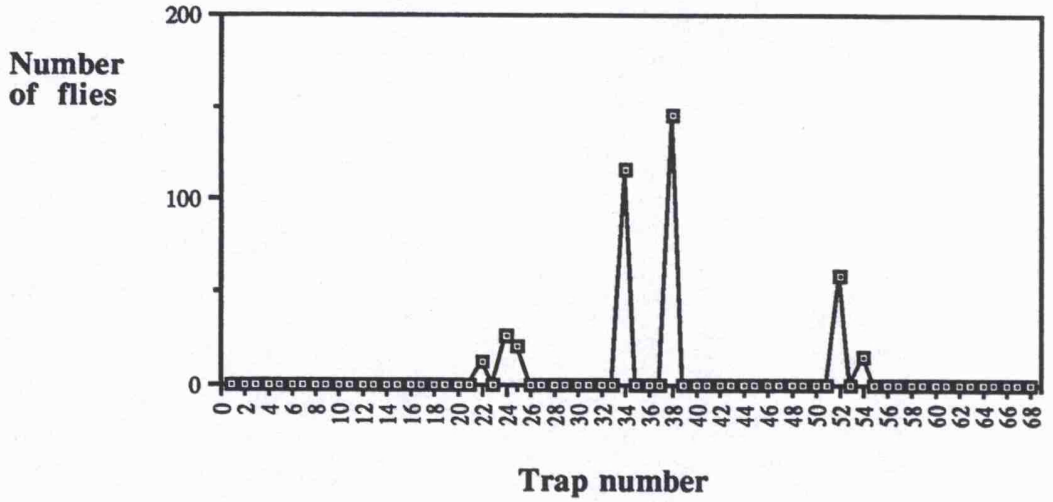


Figure 3.22 a-b) Data from the ninth sampling session (1st - 15th September 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

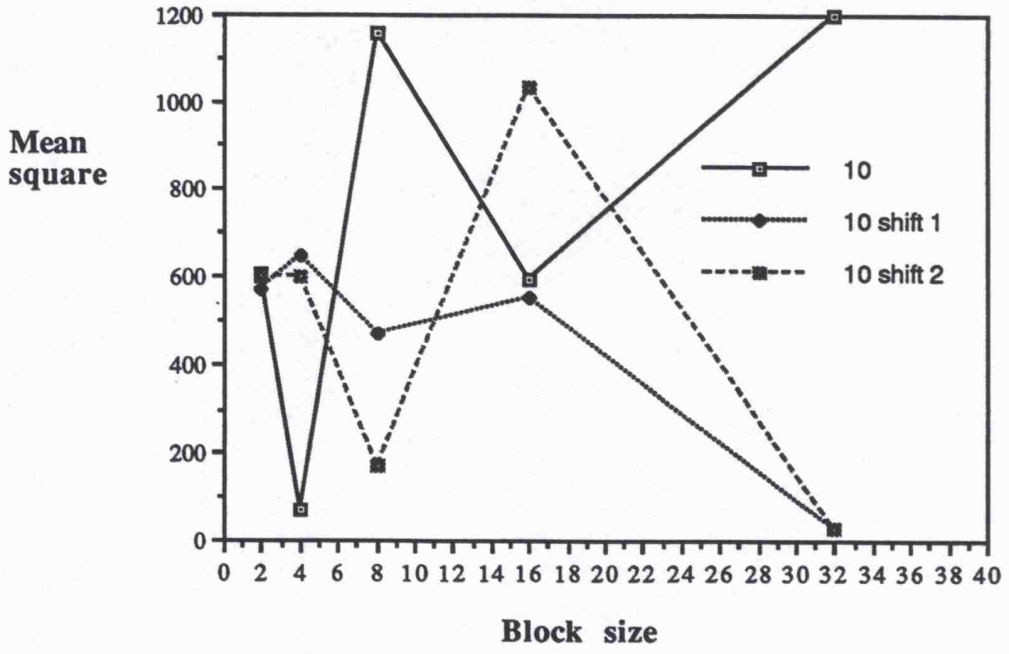
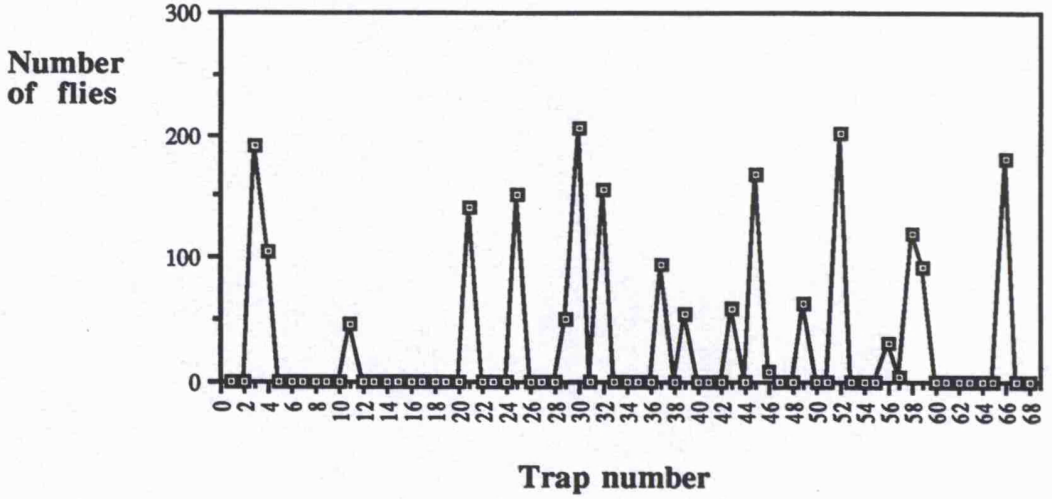


Figure 3.23 a-b) Data from the tenth sampling session (15th September - 1st October 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

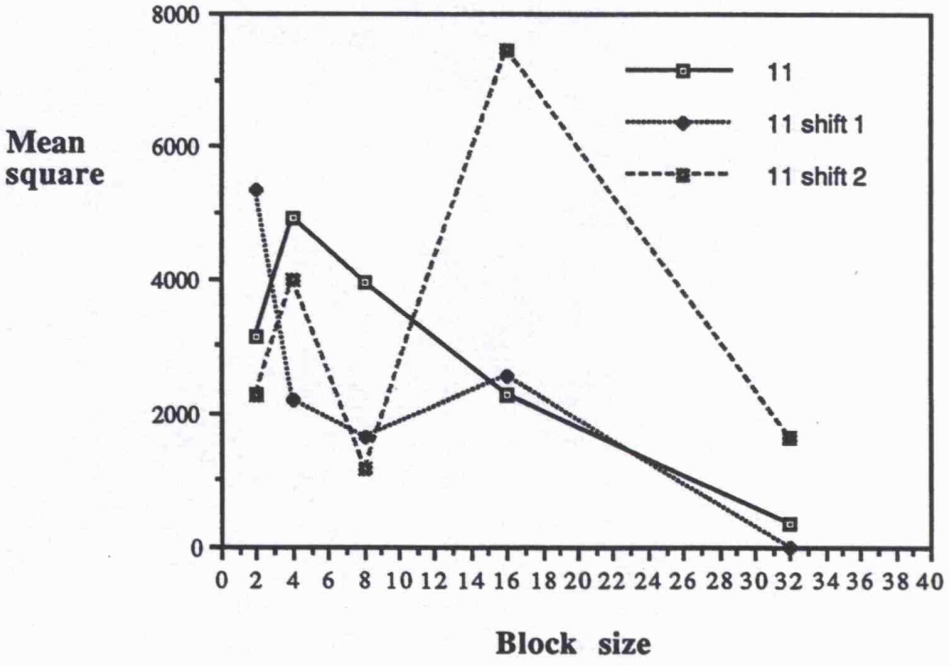
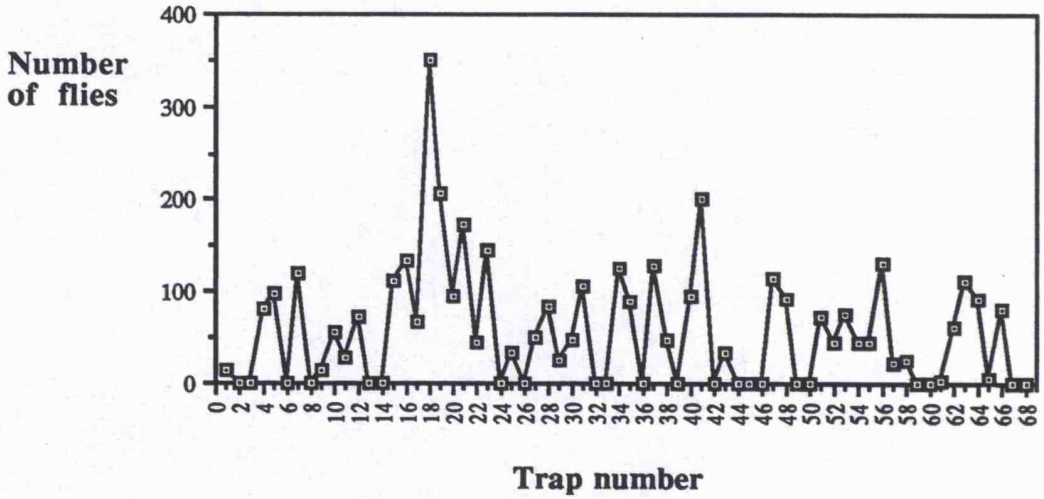


Figure 3.24 a-b) Data from the eleventh sampling session (1st - 13th October 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

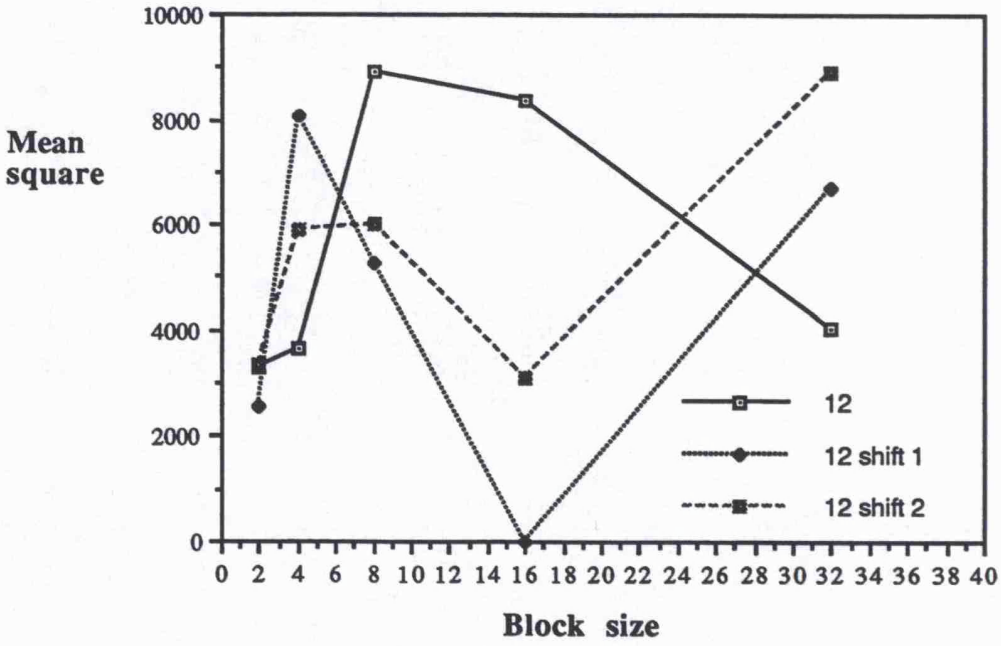
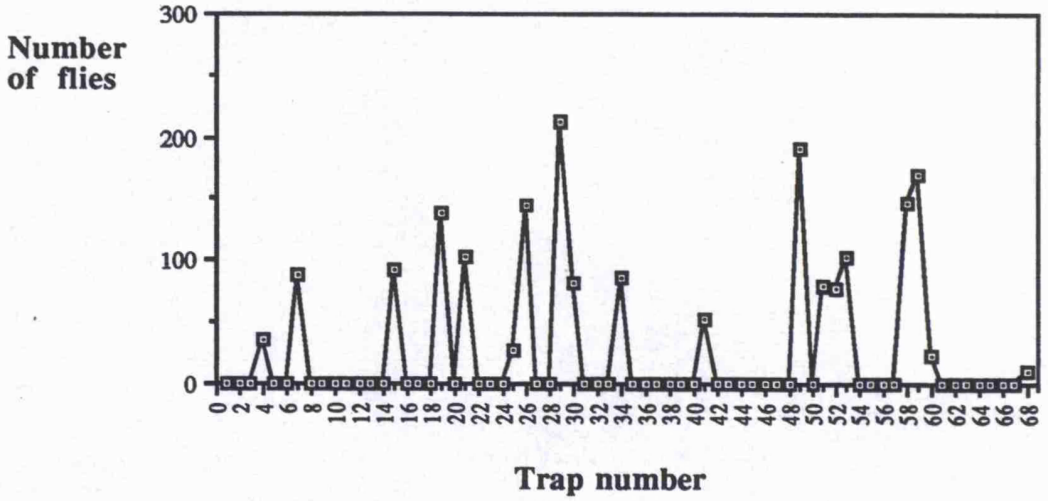


Figure 3.25 a-b) Data from the twelfth sampling session (13th - 27th October 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

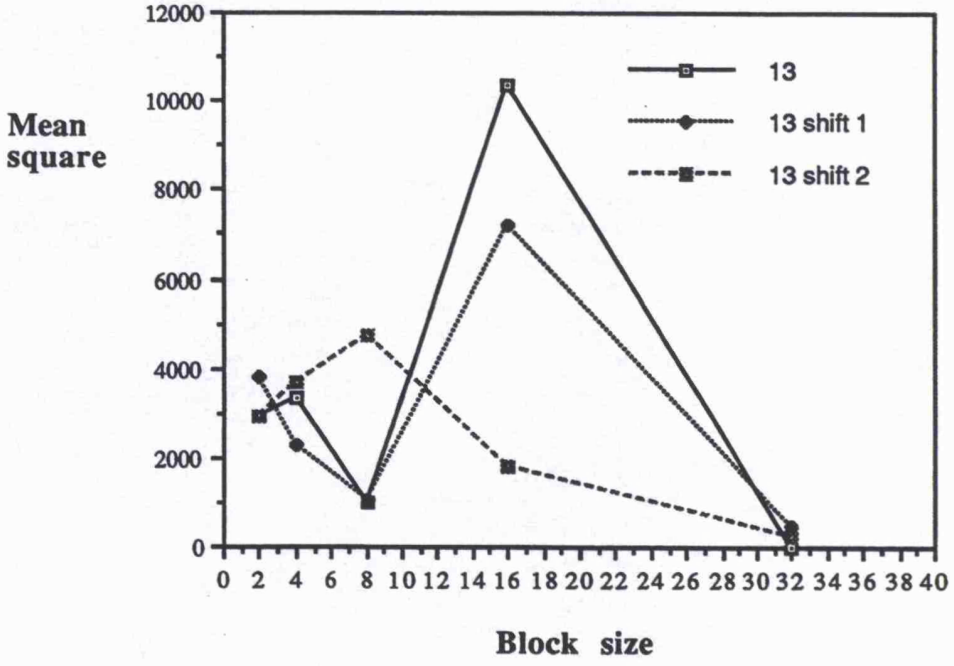
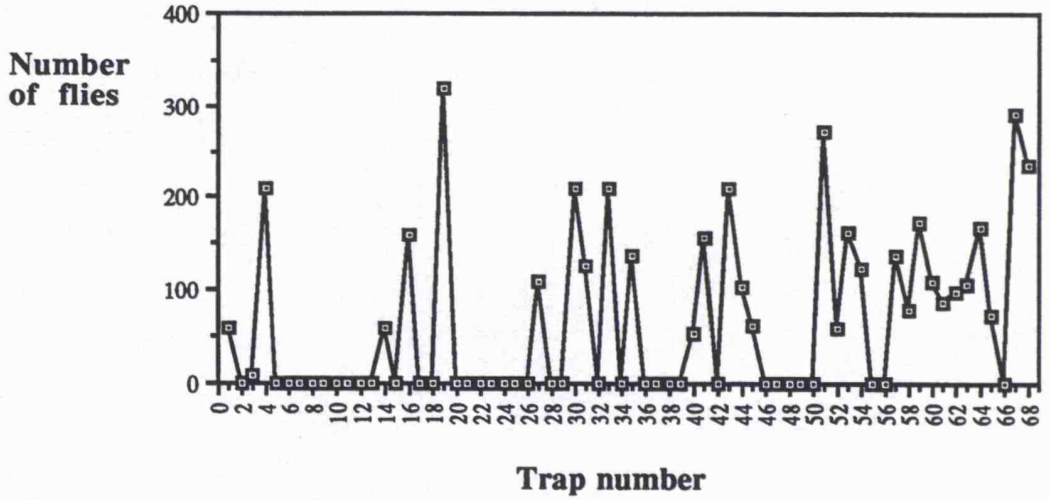


Figure 3.26 a-b) Data from the thirteenth sampling session (27th October - 10th November 1994) on Transect 2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

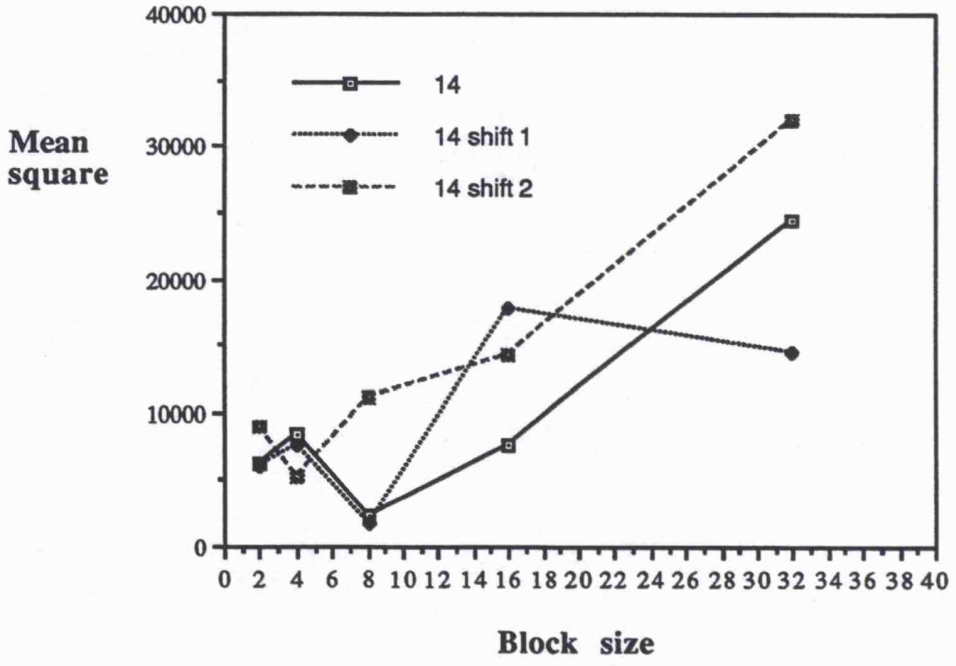
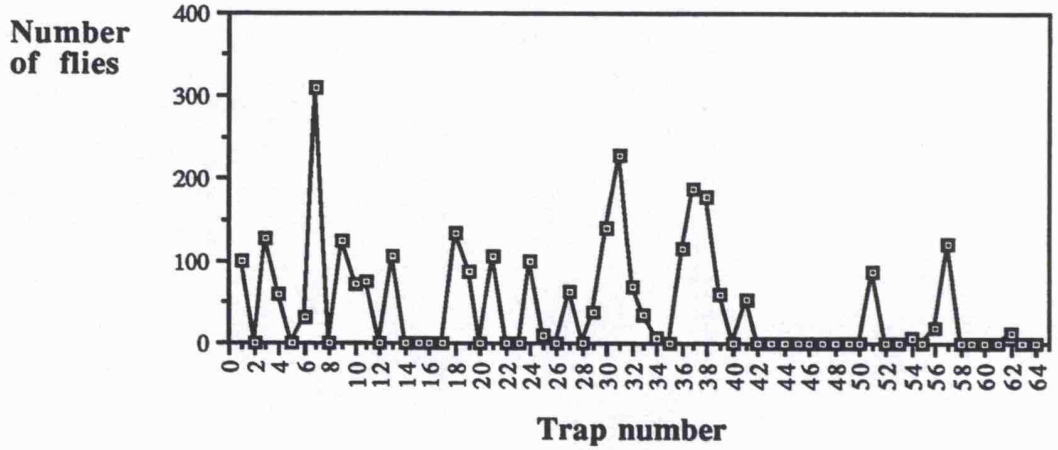


Figure 3.27 a-b) Data from the fourteenth sampling session (10th - 25th November 1994) on T2 a) The number of *C. vicina* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

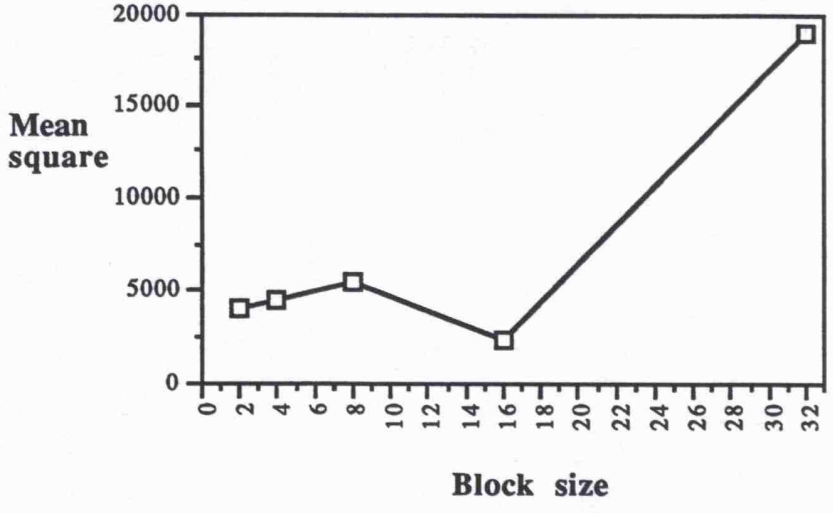
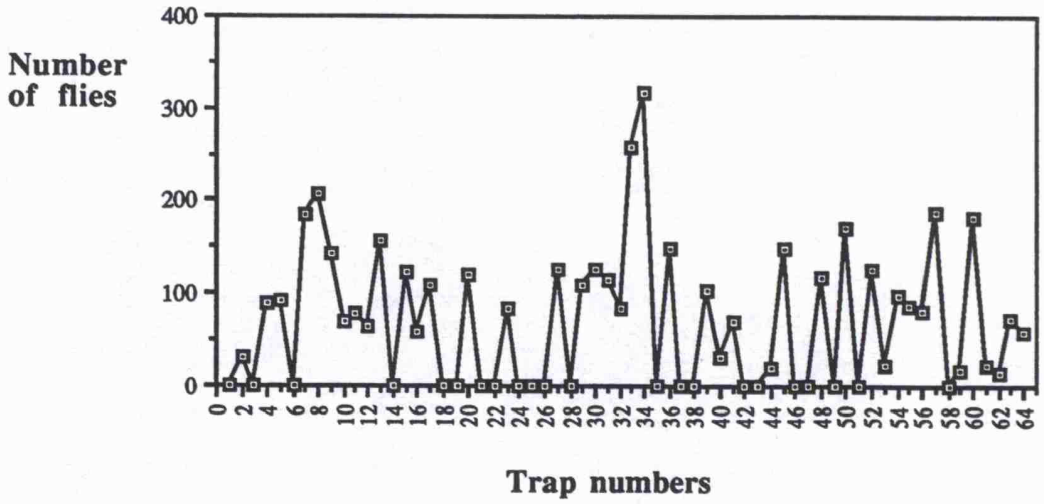


Figure 3.28 a-b) Data from the second sampling session (26th May - 9th June 1994) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

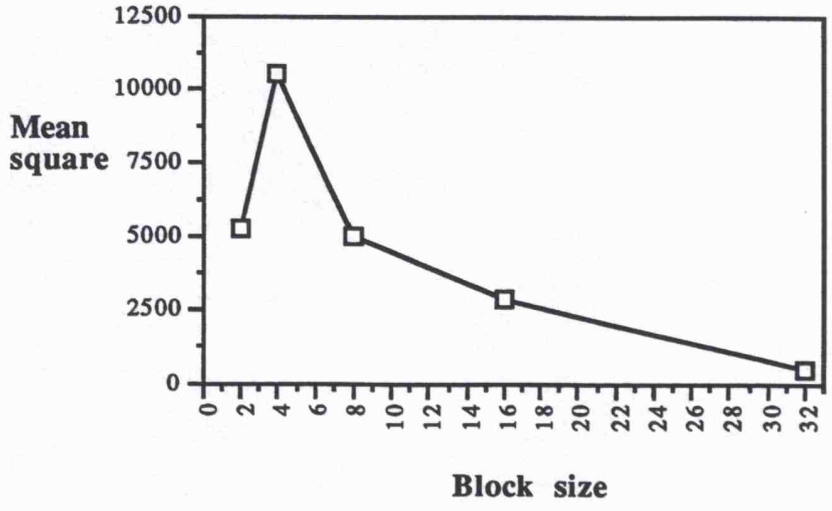
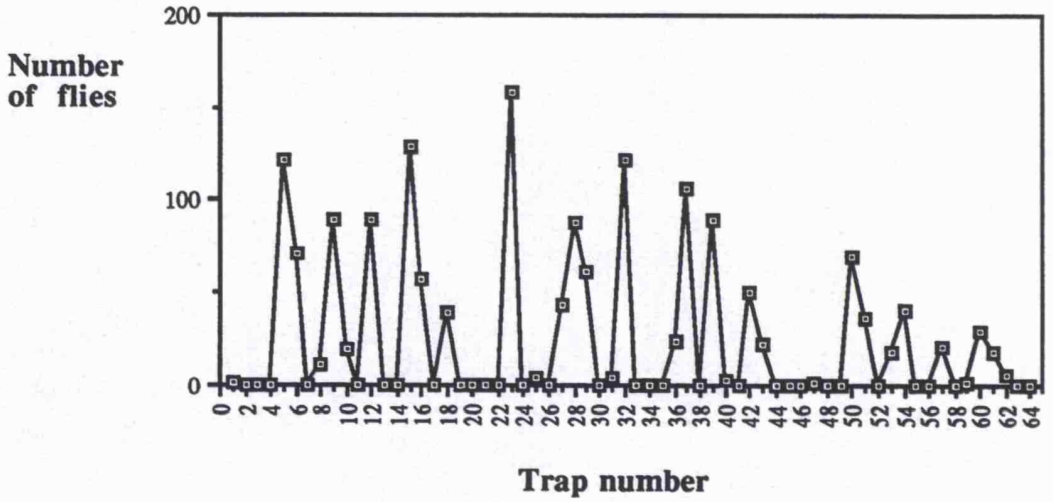


Figure 3.29 a-b) Data from the third sampling session (9th - 19th June 1994) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

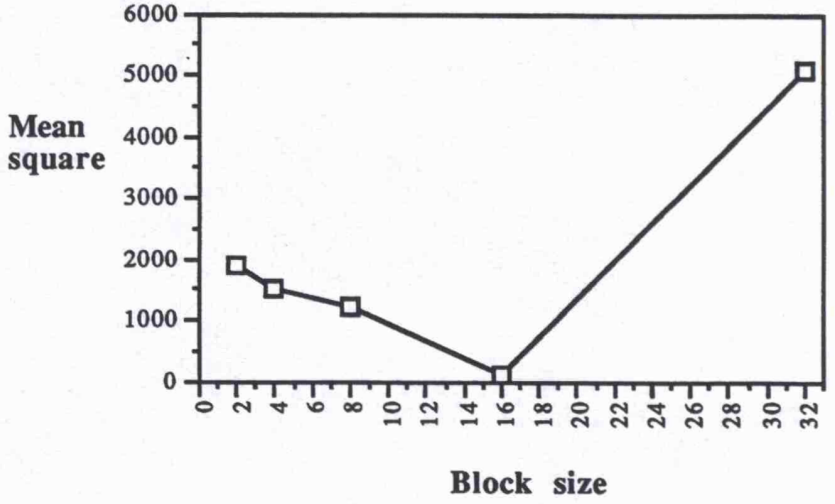
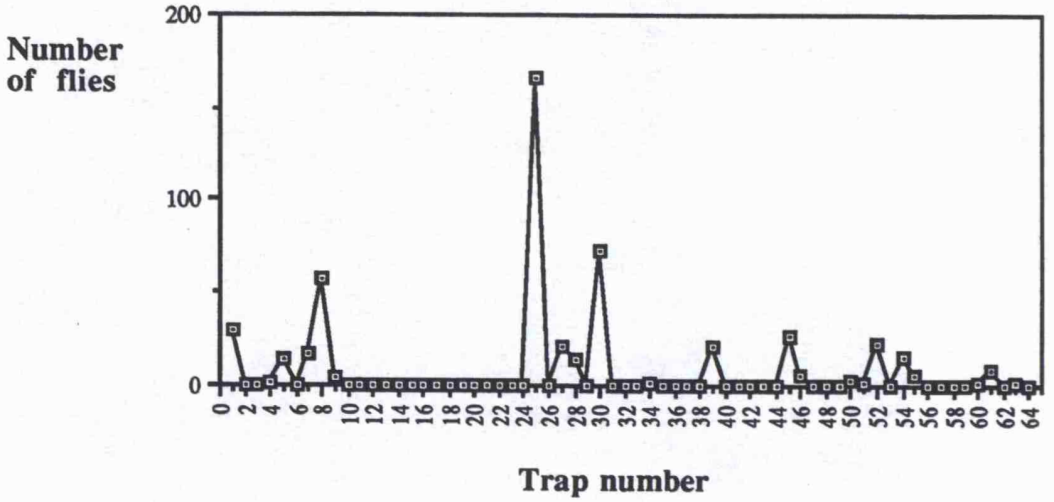


Figure 3.30 a-b) Data from the fourth sampling session (19th June - 4th July 1994) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

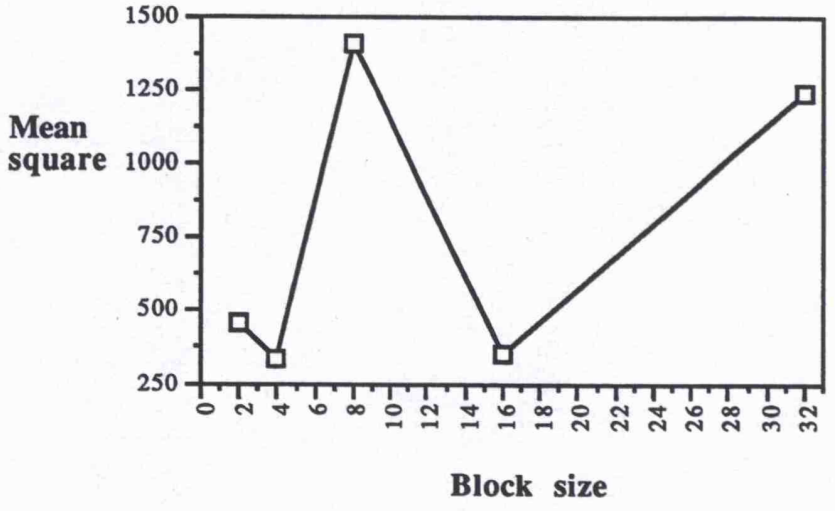
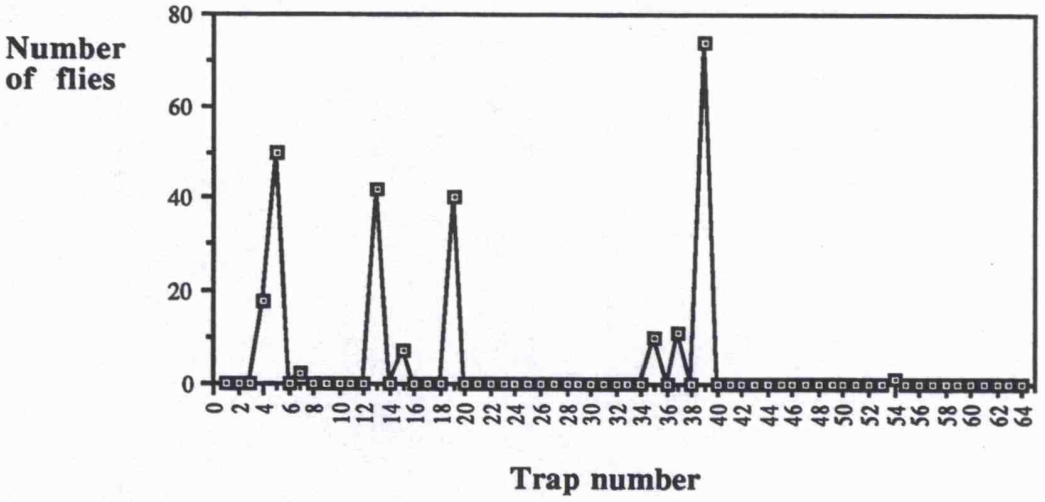


Figure 3.31 a-b) Data from the fifth sampling session (4th - 21st July 1994) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

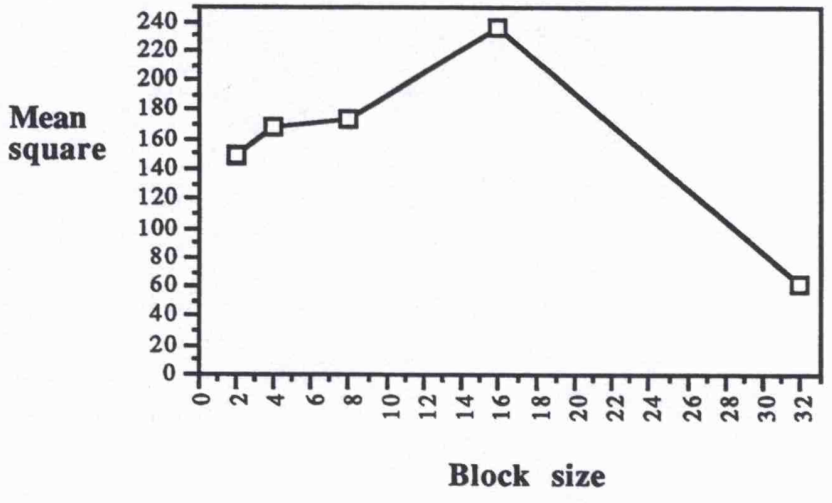
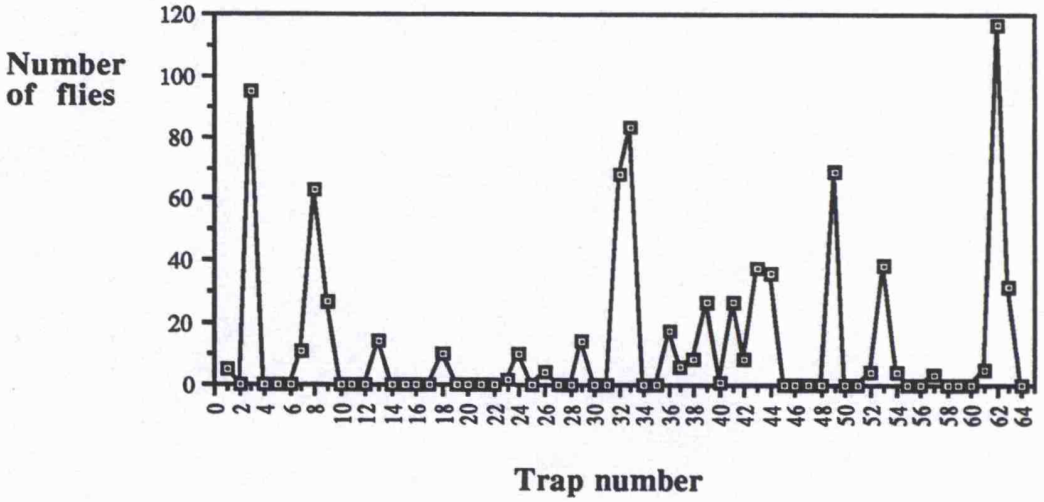


Figure 3.32 a-b) Data from the sixth sampling session (21st July - 4th August 1994) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

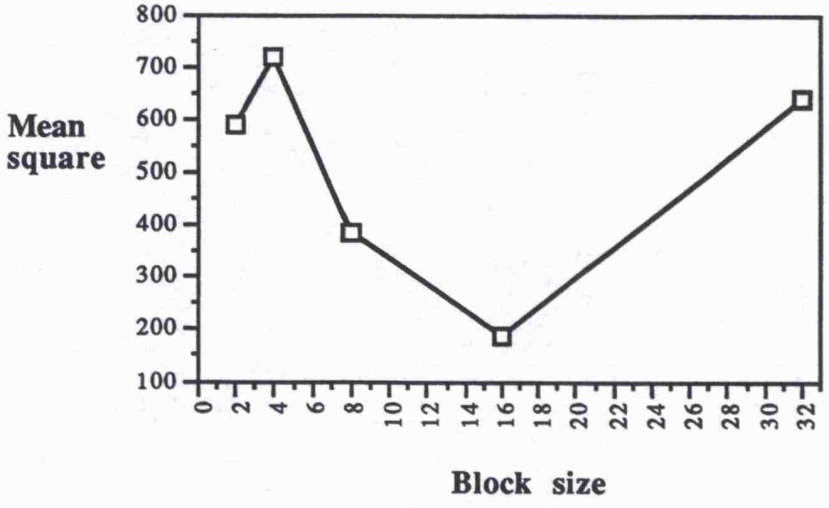
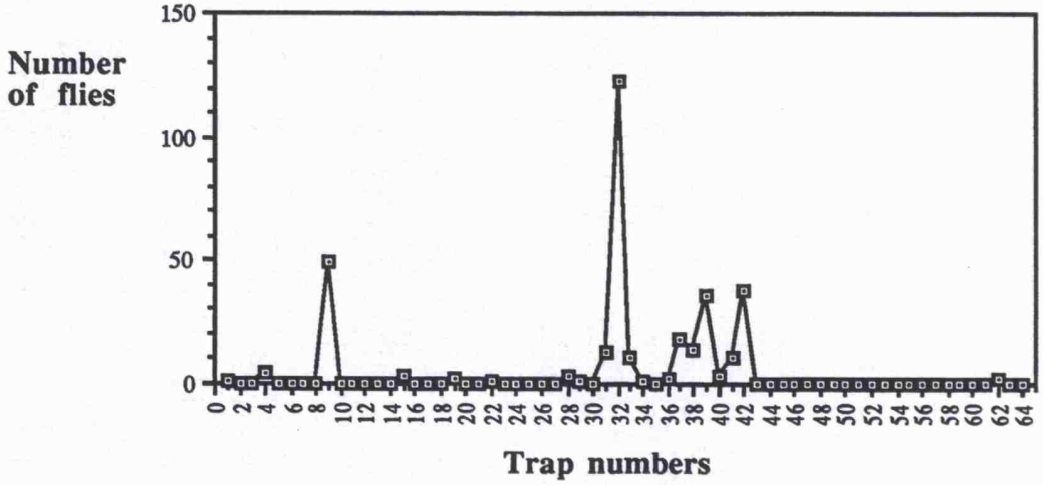


Figure 3.33 a-b) Data from the seventh sampling session (4th - 18th July 1994) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

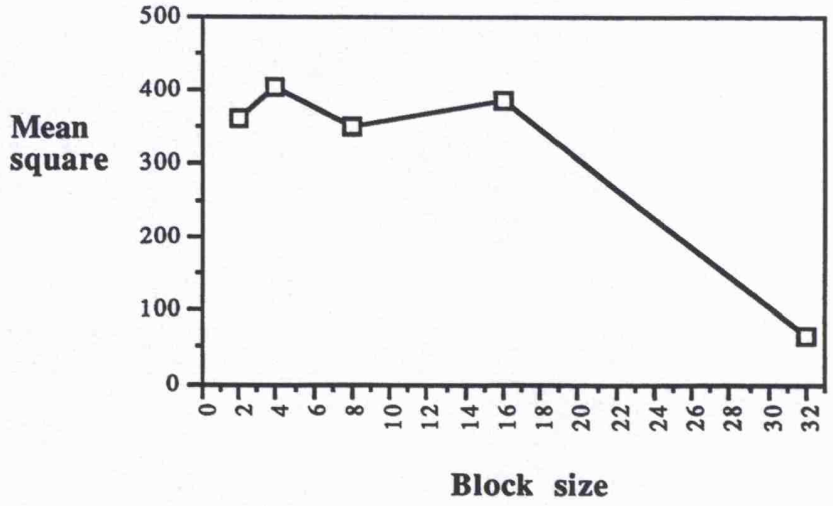
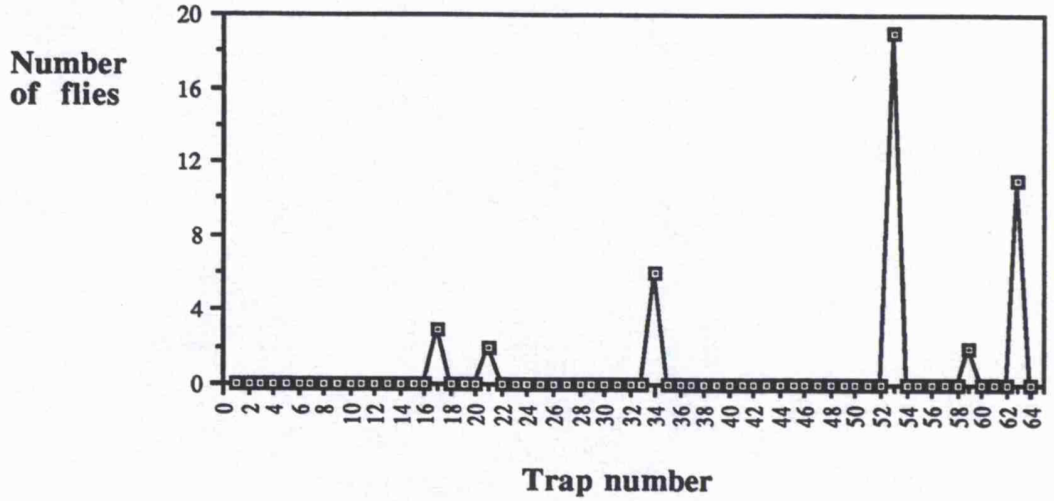


Figure 3.34 a-b) Data from the eighth sampling session (18th August - 1st September) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

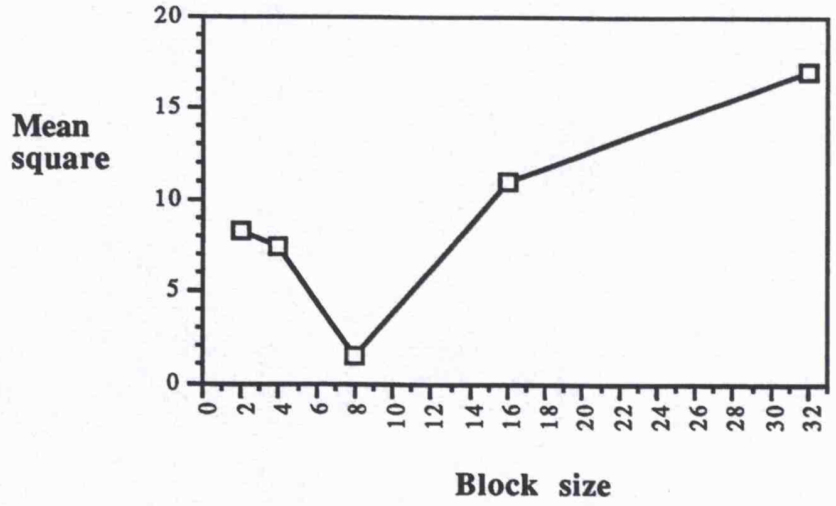
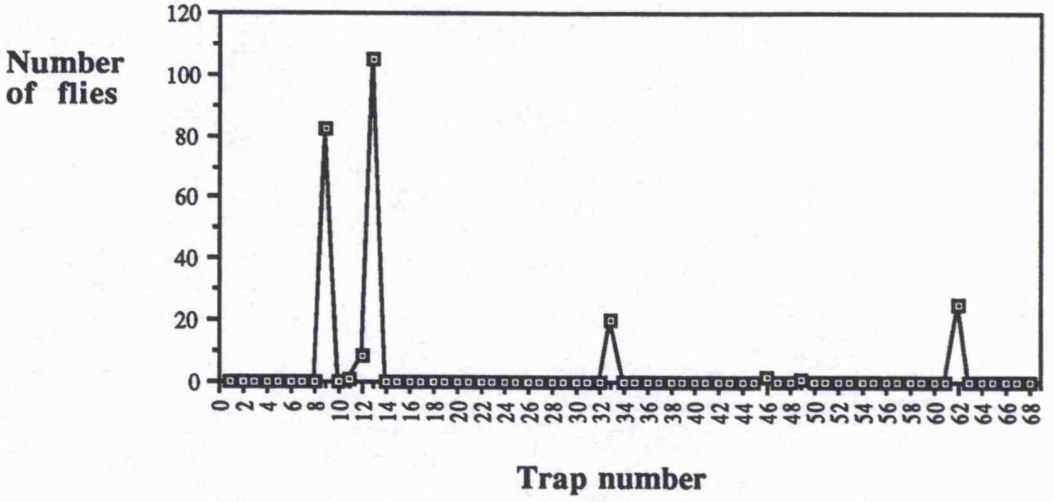


Figure 3.35 a-b) Data from the ninth sampling session (1st - 15th September) on Transect 1 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data.

a



b

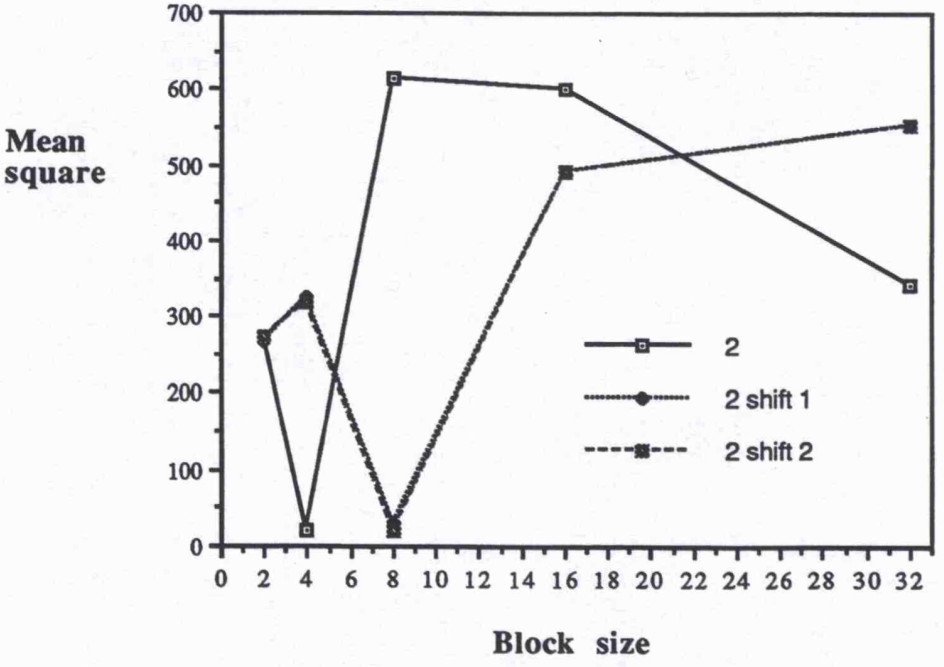
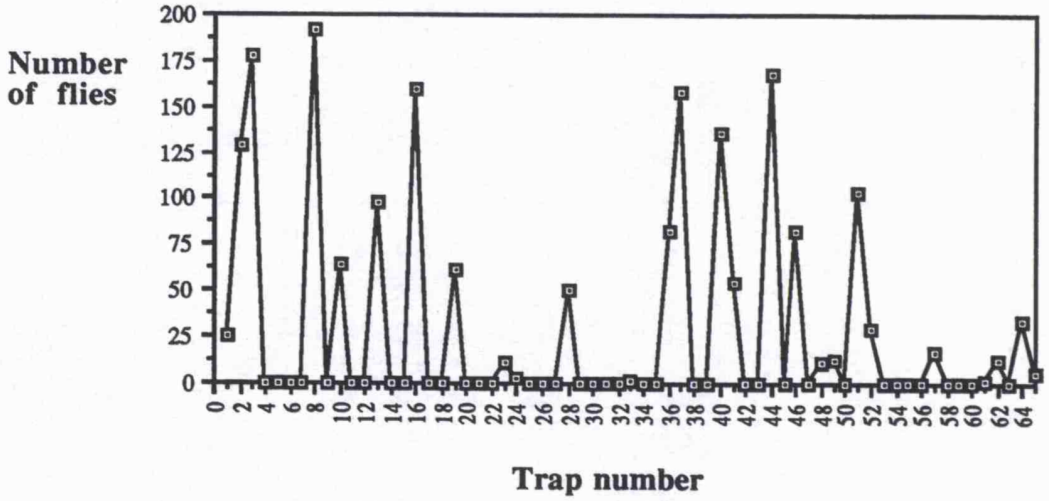


Figure 3.36 a-b) Data from the second sampling session (26th May - 9th June 1994) on Transect 2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

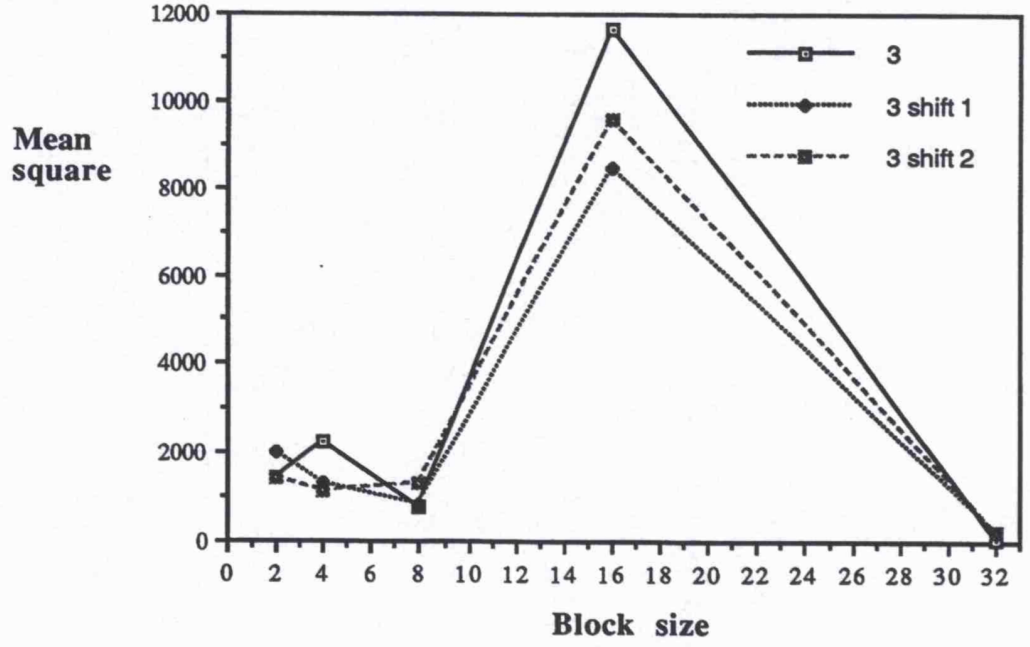
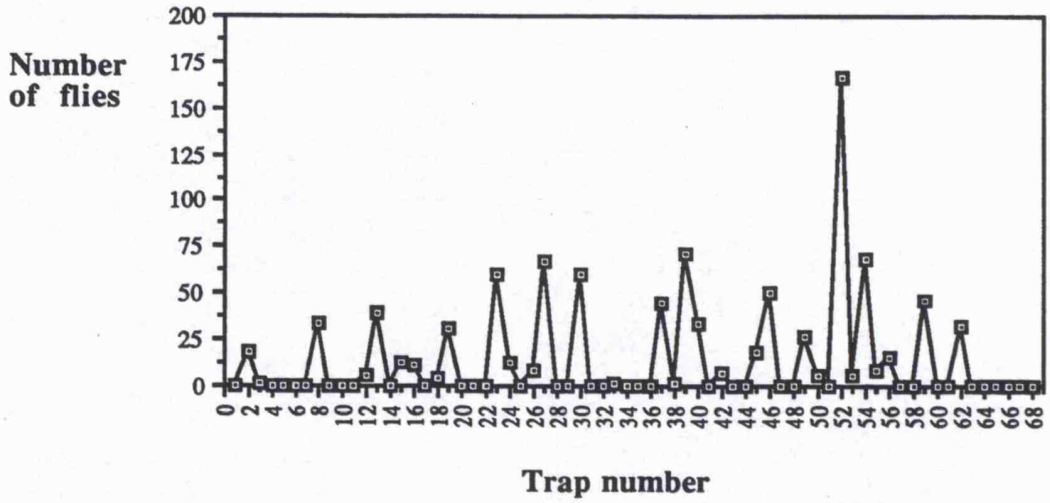


Figure 3.37 a-b) Data from the third sampling session (9th - 19th June 1994) on Transect 2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

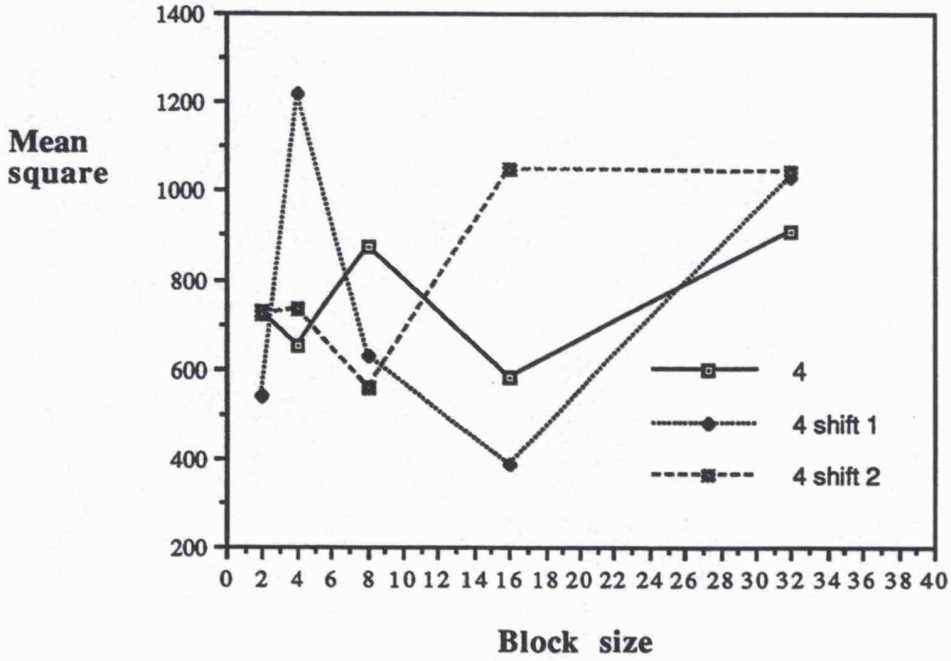
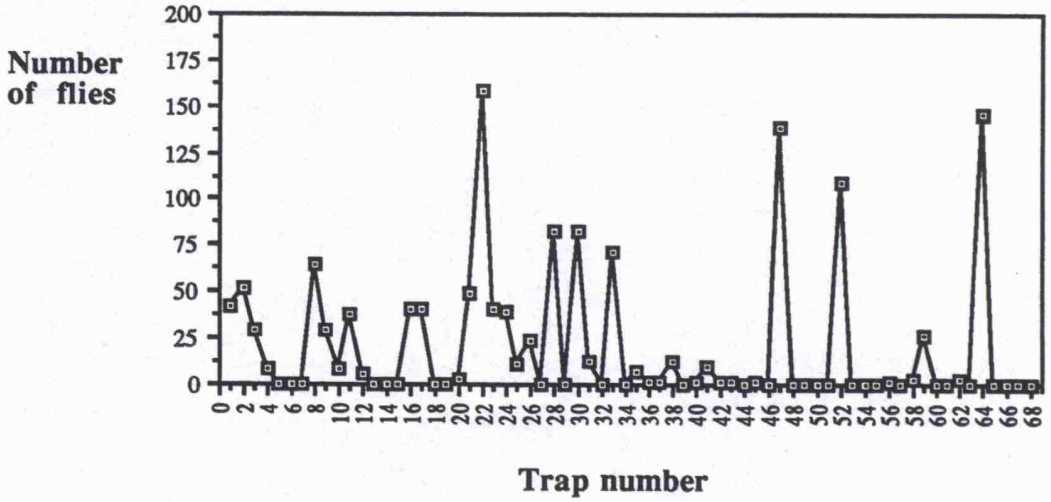


Figure 3.38 a-b) Data from the fourth sampling session (19th June - 4th July 1994) on Transect 2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

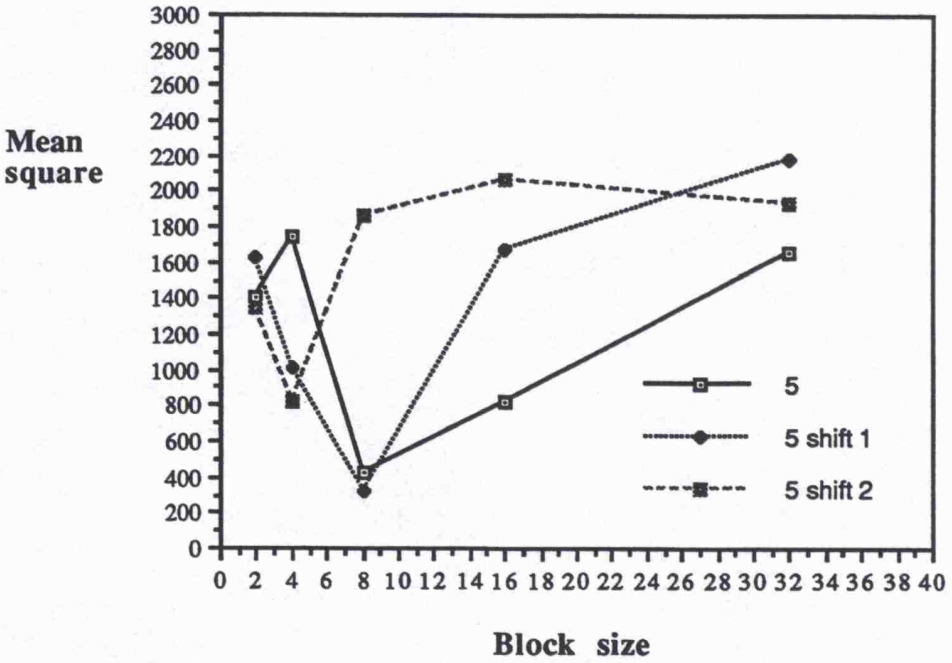
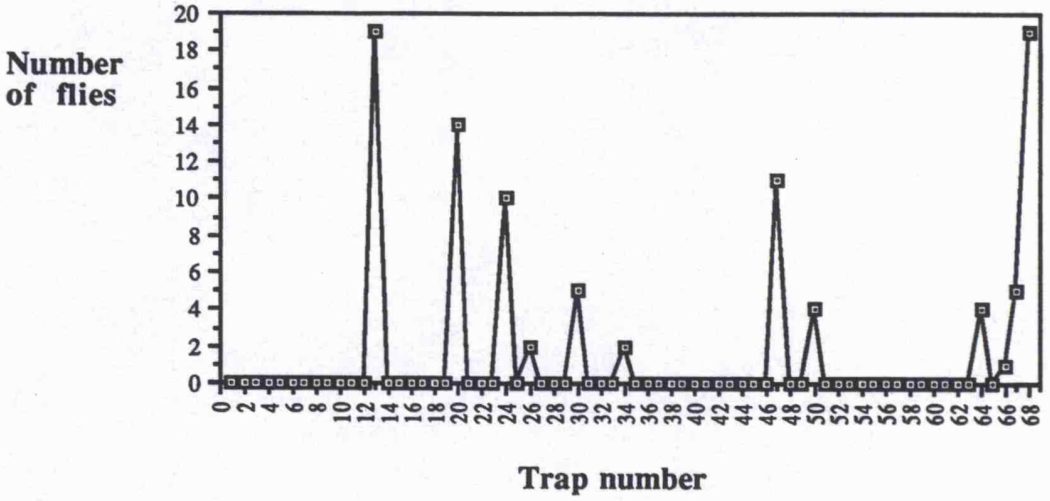


Figure 3.39 a-b) Data from the fifth sampling session (4th - 21st July 1994) on Transect 2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

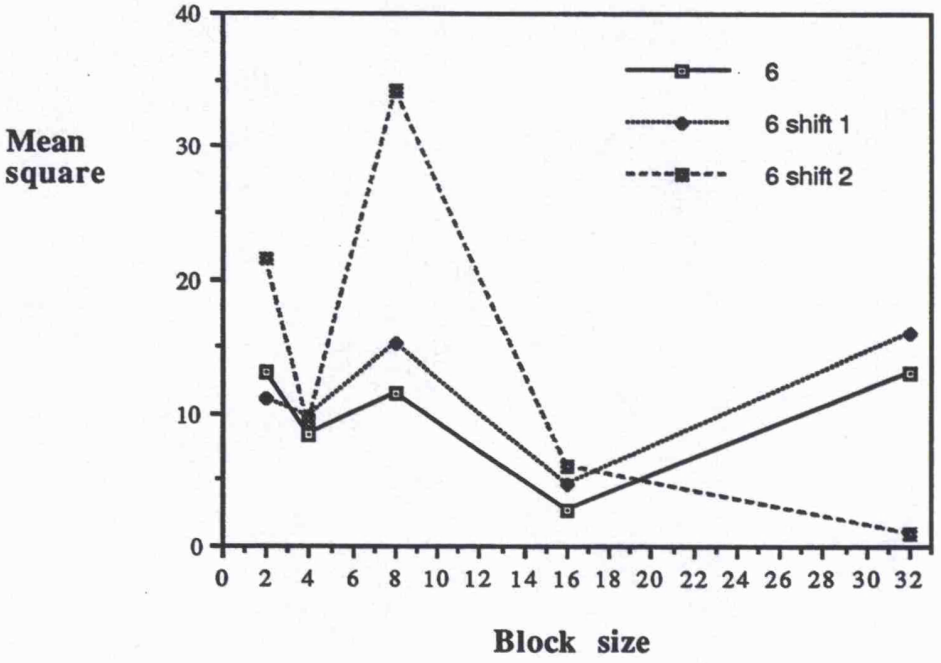
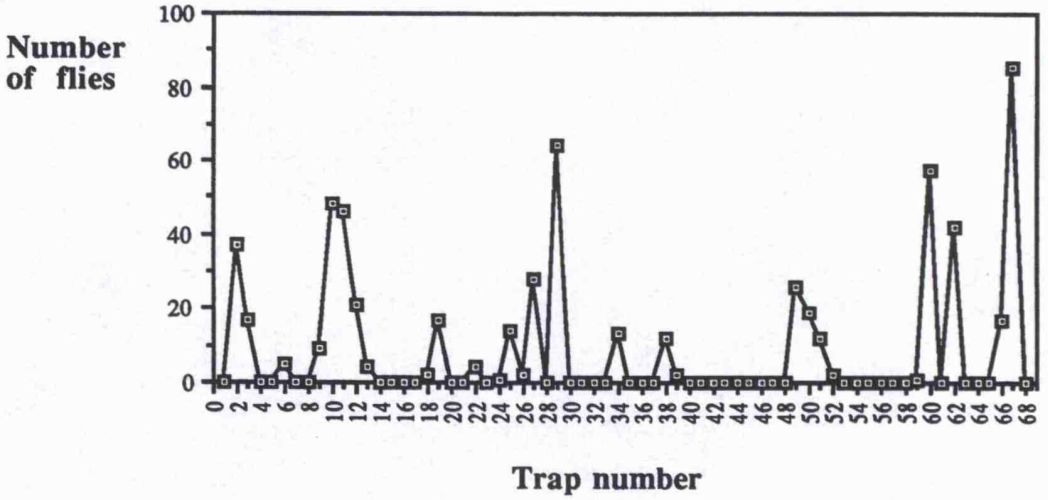


Figure 3.40 a-b) Data from the sixth sampling session (21st July - 4th August) on T2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

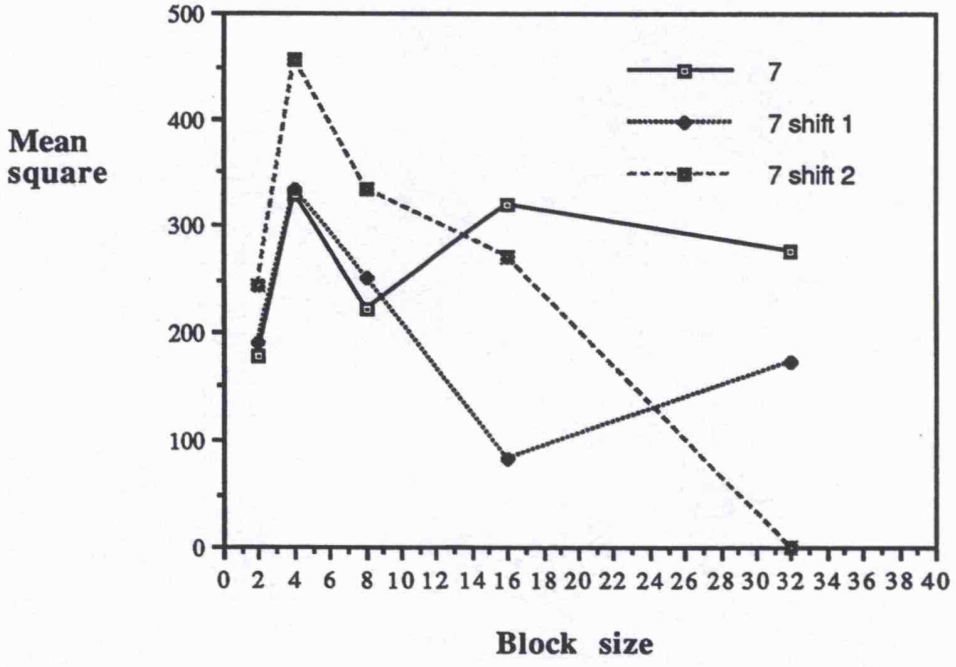
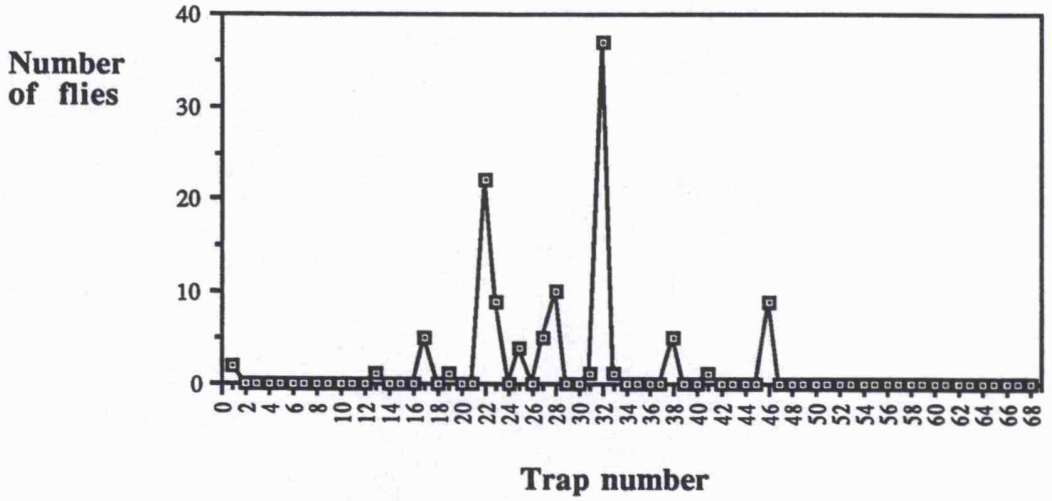


Figure 3.41 a-b) Data from the seventh sampling session (4th - 18th August 1994) on Transect 2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

a



b

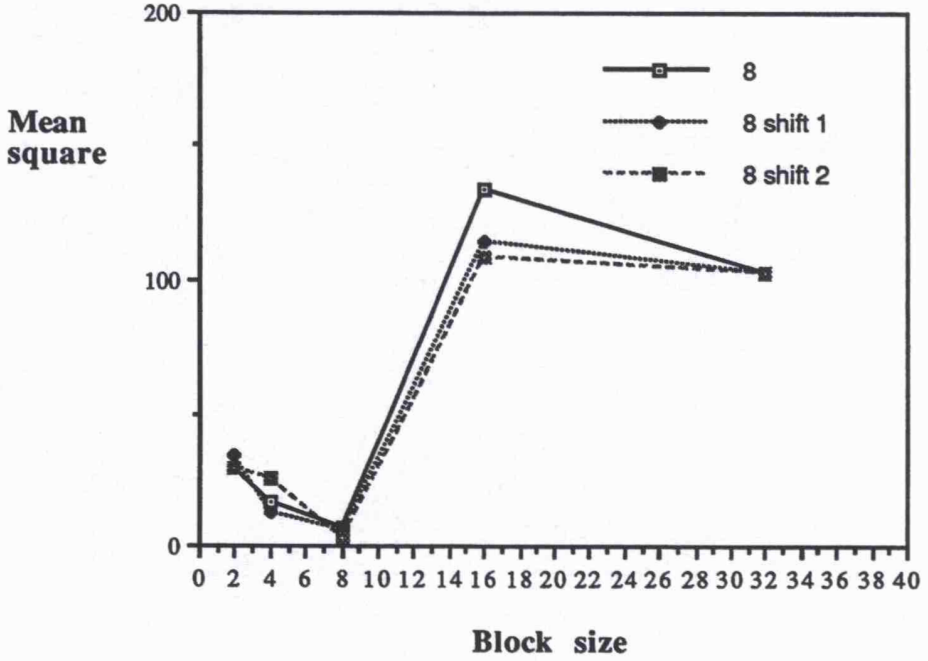


Figure 3.42 a-b) Data from the eighth sampling session (18th August - 1st September) on Transect 2 a) The number of *M. prolapsa* adults reared from each trap; b) pattern analysis of this data including the frame shift.

3.4 DISCUSSION

The field population data can be considered in a number of ways. First they will be considered in terms of the different trapping methods used. Second the species composition of the individual patches and the whole transects can be considered. Finally, the degree of aggregation shown by each species and the possible implications of this to population structure will be considered.

3.4.1 Why were there few *Lucilia* species?

The larval traps collected many *M. prolapsa* and *C. vicina* but very few *L. sericata*. The species of *Lucilia* reared were clearly present in small numbers relative to other species. On the basis of these results one may assume that they were an uncommon species at the study site. However, fly strike of the sheep was known to be a problem at Brooksby and so higher numbers of *L. sericata* were expected. It is possible that myiasis at Brooksby was actually caused by another species of fly. In New Zealand *C. vicina* was found on 1.1% cases of fly strike; the major species involved were *Calliphora stygia* (Fabricius) and *Chrysomya rufifacies* (Macquart) (Dymock, Peters, Herman and Forgie (1991)). In Australia *L. cuprina* is the predominant species involved in myiasis (Vogt, Woodburn, Morton, and Ellem (1983)). In Great Britain *C. vicina* has been identified as a secondary species in fly strike as have *L. caesar*, *L. illustris* and *M. prolapsa*. None of these species, however, is thought to cause strike and *L. sericata* is considered to be the primary species involved in fly strike of sheep (MacLeod (1937)). The low numbers of *L. sericata* in the larval traps may therefore represent a failing of the method. There are two reasons that may explain the low numbers of *L. sericata* in the larval traps.

First the larval traps may create a micro-habitat that is simply unsuitable for oviposition by *Lucilia spp.* Isiche (1990) and Smith (1986) both showed that larvae of *L. sericata* were found upon carcasses exposed to bright sunlight. Carcasses exposed in shaded conditions were more likely to attract bluebottles (*Calliphora spp.*). Greenberg (1990) showed that *Calliphora vicina* will oviposit in the dark. Wall *et al.* (1992) showed that for the larvae of *L. sericata* to complete development and reach pupation a base temperature of around 9°C was required. Temperatures in a shaded area may be frequently below this and so retard development. In contrast, *C. vicina* will develop in low temperatures; for example Davies and Ratcliffe (1994) studied the effect of temperature on the egg, larvae and pupal stages of *C. vicina*. The time taken for the first eggs to hatch decreased from 318 hours at 3.5 °C to 208 hours at 5 °C. The time taken for larvae to reach the wandering phase showed a similar decrease from 36 days at 4 °C

to 16 days at 10°C. Finally the pupation period decreased from 103 days at 5 °C to 13 days at 17-20°C. Such temperature requirements may also be important in the seasonality of some fly species.

An alternative theory, which may explain the apparent low abundance of *L. sericata,* is that they were quite simply out competed by larvae of other species on the carcass. The larval traps worked in such a way that the adult flies recorded were the end product of the intense interspecific competition within the carcass. *L. sericata* is described as a poor competitor on carrion by Cragg and Hobart (1955) and Davies (1990). It is possible that either micro-habitat or competition effects were in action, maybe both to some extent.

Different trapping methods show a different bias, for example the sticky traps were apparently better suited to catching *L. caesar* than the larval traps. The sticky traps showed that *L. caesar* adults were abundant at Brooksby, frequently more so than *C. vicina.* The lack of *L. sericata* on the sticky traps may not be due to a failing of the sticky traps but be due to the seasonality of the insects. The sticky traps were not set up until late in the season (September) when *L. sericata* may have no longer been abundant. The work of Davies (1934) showed that four generations of *L. sericata* occurred in the field between the end of April and September. If future work was to be carried out the use of the sticky traps throughout the season would be more appropriate for the study of *L. sericata.*

3.4.2 Differences between the *Lucilia* species found on each transect

As outlined in the methods both transects had different aspects; Transect 1 was exposed to sunlight and Transect 2 was shaded. On the basis of the works mentioned above (Isiche (1990); Greenberg (1990); Smith (1986)) *L. sericata* was expected to be found on Transect 1 whilst being absent, or at least rarer on Transect 2. The results from the larval traps were not as expected. *L. sericata* was found to be more abundant on Transect 2 whilst *L. illustris* and *L. caesar* were found in approximately equal numbers on both transects from the larval traps. The higher abundance of *L. sericata* on Transect 2 may be due to the presence of sheep along this transect (French *et al.* (1994)).

When the adult trap data are considered the results are again different. No specimens of *L. sericata* were caught, whilst *L. caesar* was more abundant on Transect 1, which may reflect a preference for carcasses exposed to bright sunlight. *L. illustris* was only found in small numbers on the adult traps and so no conclusions can be drawn.

3.4.3 The seasonality of the fly species found

This section will deal only with the common species *C. vicina* and *M. prolapsa.* The data for *C. vicina* are interesting in that the population shows two peaks, one at the start of the season and one at the end. These peaks fall on either side of the hottest part of the year and are also in the times of the year when the numbers of other species were lowest. Frequently *C. vicina* was the only species found.

There may be several explanations for these results. First *C. vicina* may show a seasonal habitat change with the species moving to a less species rich area. There is no evidence, however, to support this. Had traps been set up in different habitats this may have been detected.

The second possibility is that *C. vicina* may only be adapted to the cooler times of the year, the trade off for this being the inability to reproduce during the hottest part of the year. That *C. vicina* is cold adapted has been shown by Davies and Ratcliffe (1994) and Block *et al.* (1990). My results showed *C. vicina* to be present until mid December when temperatures were low. *C. vomitoria,* a closely related species, has also been shown to be cold adapted and has also been shown to have two peaks in abundance during the year, one in the spring and one in the autumn. Greenberg and Tantawi (1993) observed these bimodal peaks when summers were hot, in cooler years the peaks coalesced.

This seasonal pattern has also been observed by Kneidel (1984, 1984 a) in North Carolina. *C. vicina* accounted for 99.4% of the flies reared from carcasses in April and March and again in October. *Phaenicia caeruleiviridis* (Macquart) was the dominant fly from May to September accounting for 96.4% of the flies reared. Kneidel attributes this partly to seasonality and partly to the competitive exclusion of *C. vicina* by *P. caeruleiviridis* as *C. vicina* is capable of breeding in the summer. Kneidel also quotes Putman (1978) who has reared *C. vicina* from mouse carcasses throughout the summer in Great Britain. *P. caeruleiviridis* is absent from Great Britain, but the two peaks in the population of *C. vicina* observed at Brooksby may be caused by competitive exclusion by *M. prolapsa* during the summer. One would expect *M. prolapsa* to have an adverse effect on other fly species as it becomes predatory on other larvae during its third instar (Smith (1986)).

It is possible that both of these explanations are responsible for the bimodal peak observed. The cold adaptation may have arisen through evolutionary pressure to avoid competition with other species. Such an adaptation would allow the species to exploit

resources in both a spatial manner by exploiting shaded carcasses and a temporal manner by exploiting the cooler times of the year.

3.4.4 The species composition in each individual patch and the local community

My results supported the findings of other workers in that not all species in the area were represented by the species arising from one patch. Kneidel (1984a) suggested that small carcasses that decomposed quickly frequently gave rise to one dominant species as the early carcass colonisers depleted the resource and prevented colonisation by species of fly adapted to old carcasses. Smith (1986) presents various examples of the faunal succession on carcasses, both human and other animals. In these examples the early colonisers include the Calliphoridae and Muscidae, the most common families found during this study. The other families found at later stages include Sepsidae, Phoridae, Fannidae, and the Muscidae genus *Orphyra*. These families formed only a small percentage of the total fly catch at Brookbsy. Thus, the predominance of *C. vicina* and *M. prolapsa* may be explained by their early colonisation of the carcass. It is also possible that the carcasses had not aged sufficiently to attract these other families.

The fact that not all carcasses give rise to all species may allow species to coexist in an area through the presence of refuges. Shorrocks (1990) describes three types of refuge that may be of importance in the coexistence of species in a patchy environment. One type is a probability refuge (Shorrocks and Rosewell (1986)). In this case one species may be aggregated into a number of patches, so leaving some open for use by other species. The effects of patchiness of carcasses in relation to such coexistence has also been studied by a number of workers (Kneidel (1985); Shorrocks (1990); Hanski (1987); Kuusela and Hanski (1982)). Hanski (1987) provides an example of such coexistence. Fifteen cages were set up, each initially containing 13 species. Each cage was supplied with 50 g of liver once a week. However, the liver was divided into patches of different sizes (1-16) pieces. After four years only *Lucilia illustris* and two species of *Sarcophaga* remained. *L. illustris* was the most abundant species in all the cages, the *Sarcophaga* species were only found in only five cages, in which the resource had been much divided. Coexistence was possible because *L. illustris* laid large clusters of eggs on a few resource patches. *Sarcophaga* laid fewer first instar larvae that were spread over a large number of patches. Thus, by chance *Sarcophaga* laid larvae on patches with no *L. illustris* and was able to survive. For such a system to work the species need to be independently aggregated. The lack of significant associations between the species in my results suggests that the species are independently aggregated of each other. This, coupled with the presence of unoccupied

carcasses, suggests that probability refuges were present and that they may have contributed towards coexistence.

Another type of refuge is the priority refuge. Each species could resist invasion of a patch that it had colonised first. It is difficult to say whether or not priority effects were occurring on the chick carcasses. It is possible that *M. prolapsa* could exclude other species through its predatory behaviour. Under such conditions, however, one may expect to find negative associations between this and other species. As already mentioned above no such associations were found.

3.4.5 Aggregations and population structure

The pattern analysis showed clearly that aggregations of *C. vicina* and *M. prolapsa* did exist, although the scale over which they existed appeared to be variable. The lack of temporally stable aggregations suggests that there are no stable local populations. If these results are considered in terms of metapopulation theory there are a number of conclusions that can be drawn. The first three metapopulation models proposed by Harrison (1991), described in section 3.1.3, are not applicable to blowfly populations because the patches of food are ephemeral. My results indicated a large mobile population shifting around the transects. The similarity of the seasonal population fluctuations and species composition of the two transects has made it impossible to treat the two transects as representing two different local populations.

Even if the aggregations on either transect had been stable over time they need not correspond to separate populations as the spatial scale involved is well below the distance that these animals could disperse. Cragg and Hobart (1955) showed that *L. sericata* individuals dispersed a distance of 0.7 mile in 24 hours, while Braack and Retief (1986) showed that two Calliphoridae species covered a distance of up to 63.5 km in 1 week. The high dispersal of these animals suggests that their populations will lie well towards the patchy population end of the metapopulation continuum proposed by Harrison (1991). Bearing this in mind it may be more appropriate to consider the data in terms of Doube's (1986) levels of spatial organisation. In this case the species composition of the patch and the local community would have been determined by factors that influence colonisation, survival, and emigration.

The colonisation of a carcass may be affected by the abundance and activity of the species in the area. These two factors will vary with the season and weather conditions. The seasonality which governs which species are available for the colonisation of the carcass has already been discussed and will be considered no further. Weather

conditions may affect colonisation in a number of ways by making the patch unavailable to the flies. This may occur through desiccation of the carcass in hot weather or through flooding - if the carcass was in a ditch for example. Desiccation was not a problem during this study but flooding was. As the chick carcasses were in glass jars they did collect water. Occasionally some jars were flooded rendering the carcass useless to the flies. During the cold spells, especially during the final sampling session when no flies were found, the carcasses were frozen solid which also would exclude the flies.

Colonisation may be affected by the time of day at which the carcass becomes available and the time for which it remains available. As mentioned previously some species will oviposit in the dark and some only in bright sunlight. Thus, a carcass becoming available at night may be colonised by species such as *C. vicina.* The length of time the carcass remains available is obviously critical. Large scavengers may remove the carcass hence making it unavailable for colonisation by flies. This was a problem that I encountered early on in the study.

Finally, the interactions between individuals on each carcass will play a role in determining the patch community. Competition is an important factor in determining the patch community. In addition to these interspecific interactions there will also be intense intraspecific competition. Intense scramble competition between larvae can result in no adults emerging if the competition is extreme. My results only reveal the end product of such competition, so it is possible that more species were originally present than indicated by adult emergence from the chick carcasses. The effects of competition will also be carried forwards into the next generation through the effect upon the resultant body size. The effects of such competition are investigated in the following chapters.

3.4.6 The question of dispersion and future work

As mentioned previously the great similarity between the two transects has made it very difficult to distinguish local populations. This may be because they were not separate populations or it may be due to a failing in the method. The question arising is how much movement was there between the two transects, and how can this movement be measured?

One method of measuring this dispersion may be through mark release recapture methods. Large numbers of flies may be released from a point source and their movements monitored by trapping. A good example of this type of study is provided by Plant and Cunningham (1991). Their work studied the dispersion of sterile fruit flies

released from a point source. Three different methods of analysing the data were studied. These were (1) statistical studies in which parameters such as the mean distance flown are used. In this case the data are not fitted to any kind of model; (2) the observations of dispersion are fitted to a curve such as the exponential curve; (3) the dispersion data may be fitted to a biological model such as the diffusion model.

Studying the degree of dispersion in this manner may give rise to useful data but may not reveal the degree of movement between neighbouring areas which could potentially separate populations. To detect this a slightly different approach would be required. Instead of releasing large numbers of insects from a point source, which might cause an initially high density-dependent dispersal, the movements of the naturally occurring population could be monitored through a system of mark and recapture. The analysis of the resultant data may be based upon the degree of dispersion observed *i.e.* whether flies from a particular region remain associated with that region or occurred randomly throughout the whole sampling region

3.4.7 Summary

The field work has provided an insight into how the carrion feeding communities of flies are organised and how the community varies over the season. In particular this work has highlighted the patch as being the most important feature of such communities. Unfortunately the field study has provided little information regarding the population structure of *L. sericata,* and so it was not possible to study the effects of toxins upon natural populations of this species. Such a study was to form the basis of the next years' work. Consequently rather than spend more time trying to study natural populations I turned my attention to laboratory populations of this species. In the following chapters the effects of toxins were considered from a physiological level to the effects upon the long term population dynamics.

CHAPTER 4 METABOLIC COSTS OF DETOXIFICATION

SECTION INDEX

		Page
4.0	ABSTRACT	78
4.1	INTRODUCTION	79
4.1.1	General aims	79
4.1.2	Physiological ecotoxicology	79
4.1.3	Scope For Growth	83
4.1.4	Metabolism and allometric relationships	83
4.1.5	Summary and hypotheses	85
4.2	METHODS	87
4.2.1	Rearing of experimental animals	87
4.2.2	Respirometer operating procedure	87
4.2.3	Processing of respirometry data	89
4.2.4	Analysis of respirometry data	90
4.3	RESULTS	91
4.3.1	General comments about the results	91
4.3.2	The effects of deltamethrin and cadmium upon respiration rate	91
4.4	DISCUSSION	98
4.4.1	The allometric relationship between mass and respiration rate	98
4.4.2	Future respirometry work	99
4.4.3	The implications of the observed respiratory rates for scope for growth	99

4.0 ABSTRACT

Larvae of *L. sericata* were reared upon diets containing either 0.2 mg/kg deltamethrin or 50 mg/kg cadmium, a control batch of larvae were reared upon a diet containing neither toxin. The respiration rate was measured in the larvae at an age of four days, using a Gilson respirometer. The results showed that although deltamethrin caused an elevation in the respiratory rate the increase was not significant. Cadmium caused a significant decrease in the respiratory rate, K of the allometric equation was significantly reduced.

The respiration rate showed a positive allometric relationship with mass. The allometric coefficient 'b' was not altered by the presence of either toxin when larvae within the control size range were considered. Larvae below the control size range had low respiration rates and were apparently more severely affected than the larger larvae. The results are discussed in terms of the possible implications of the observed metabolic effects for the animals' scope for growth.

4.1 INTRODUCTION

4.1.1 General aims

Although ecotoxicology is supposed to make predictions about long-term effects of toxicants on populations and communities, most effort has gone into monitoring levels of toxicants and into studying the effects on individual physiology without relating these to population dynamics. The energetic cost of detoxification is encompassed in the 'Scope For Growth' concept. The prediction made by the scope for growth theory is that through the costs of detoxification less energy is available for growth. This chapter deals with the physiological effects of two contrasting toxins. The basic question being asked in this chapter is, does the presence of a toxin have a metabolic cost to the animal in question? In later chapters the consequences of the toxins on life history parameters and long term population dynamics will be investigated.

4.1.2 Physiological ecotoxicology

In chapters five and six the effects of the toxins will be investigated at whole animal and population level. A fundamental assumption to any effects observed at these higher levels is that the toxins used must have a physiological effect. In this chapter an effect of the toxins upon the basal metabolic rate will be sought and predictions will be made as to what effect this may have upon the animals in terms of their scope for growth.

Calow (1989, 1991) discussed a range of graded physiological responses that may be observed in animals exposed to toxins. It is useful to give an account of these responses at this stage. These responses can be broken down into three different phases: i) a phase of defence or resistance; ii) a phase of repair; and iii) a phase of exhaustion.

i) Defence/resistance phase

The defence/resistance phase may involve simple responses such as the animal moving away or reducing intake of polluted food. The dietary toxicity of deltamethrin to a

carabid beetle *Nebria brevicollis* (F) was studied by Wiles and Jepson (1993). Their results showed that the consumption of their food (deltamethrin contaminated aphids) was reduced when compared to control animals. 53-80% of the beetles fed contaminated aphids also showed a regurgitation response. In their study of bumble bees *Bombus terrestris,* Tasei *et al.* (1994) showed that dietary contamination (0.2 mg/kg deltamethrin) resulted in a reduction of food uptake by 47-59%. However, when applied topically to the insect (0.08-0.16 mg/kg) food uptake was increased by 40-100%. A similar reduction in intake of food contaminated by cadmium was observed in the alligator-weed flea beetle (Quimby *et al.* (1979)).

Once contaminated food has been consumed the toxin may enter the body across the midgut wall. Metals can enter the cells of the midgut through three routes; ion channels, via pinocytotic vesicles or through the direct passage of the metals through the lipid membrane (Hopkin (1989), Simkiss and Taylor (1989)). In terrestrial invertebrates excess or toxic metals entering the cells may be detoxified by binding them to metal-binding proteins and membrane bound granules; there are four types of membrane bound granule Types A - D. The most important of these membrane bound granules for detoxifying cadmium are the Type B granules. These granules always contain large amounts of sulphur and metals such as cadmium, copper and mercury. Type B granules are thought to be residues of metallothioneins.

Metallothioneins provide a large number of binding sites for the metals which decreases the amount of metal binding to other structures in the cell. Metallothionein production can be induced by the presence of metals. The free metal ions are taken up by a metal-regulating factor which is then able to bind to the metal-regulating element of the metallothionein gene, thus triggering production of the metallothionein and increasing tolerance. Metallothioneins are found in flesh fly *Sarcophagaperegrina* and most, if not all, arthropods, many examples are cited by Posthuma and Van Straalen (1993).

Granules containing metals may be excreted if they are stored in cells which break down during the normal course of digestion. The springtail *Orchesella cincta* is able to tolerate cadmium through exfoliation of the whole midgut epithelium at every moult. The discarded epithelium contains a high concentration of the metal (Posthuma and Van Straalen (1993)). The blowfly *L. sericata* has been shown to lose 80% of the larval cadmium load by depositing it in the pupal case (Simkiss, Daniels and Smith (1993)). Weismann and Reháková (1994) studied the effects of cadmium upon larvae of the lepidoptera *Scotia segetum* (Den. et Shiff.) and *Mamestra brassicae* (L.) They found that 86.2% of the cadmium consumed by the larvae was eliminated from the body in the faeces. Of the remaining 13.8% in the body, 88.39% was bound to the digestive tract

and the remaining 11.61% was found in the integument, haemolymph and body fat. In this species then the majority of the cadmium was eliminated from the body prior to pupation. Of the original 119.4 μg cadmium consumed, 12.86 μg was carried into the pupal stage, and 3.91 μg was lost in the final larval exuvae.

Organic toxins such as deltamethrin are not neutralised by specific binding proteins but can be destroyed through enzymatic processes. Deltamethrin is highly insoluble in water. In order to excrete it from the body it has to be broken down into water soluble compounds. This detoxification has been the subject of much research (Gilbert and Wilkinson (1974); Sahgal, Kumar, and Pillai (1994); Gunjima and Sato (1992); Yamamoto, Kimmel, and Casida (1969); Ishaaya and Casida (1980); Yu, Robinson, and Nation (1984); Riskallah (1983); Jao and Casida (1974)). Throughout all these studies two main enzyme systems that are involved with the metabolism of deltamethrin have been identified, namely esterases and mixed function oxidases. The relative importance of the two systems seems to vary between insect groups but in many cases the activity of both appear to be localised in the gut.

The presence of a detoxification system was illustrated by Tasei *et al* (1994). In their experiments they fed queen bees (*Bombus terrestris*) with a sugar solution contaminated with 0.01-0.2 mg/l of deltamethrin either for a five day period or continuously. None of these treatments reduced the size of the next batch of workers or the development period from egg to adult. They suggested that the detoxification may be due to intestinal enzymes.

Gunjima and Sato (1992) tested the oral and topical toxicity of a range of pyrethroids upon the housefly *Musca domestica* (L.). The oral LD_{50} dose was 5-10 times the strength of the topical LD_{50} dose. The toxicity was increased in the presence of piperonyl butoxide (PB) and s,s,s-tributylphosphorotrithioate (DEF); the synergistic effect was greater for the oral application than the topical application. PB and DEF inhibit mixed function oxidase and esterase respectively, thus implicating these enzymes in the detoxification process. Gunjima and Sato (1992) could not say where this detoxification took place. Ishaaya and Casida (1980) studied the detoxifying effects of esterases taken from the guts of the cabbage looper *Tricoplusia ni* (Hübner), thus localising detoxification through esterases to the gut. Gilbert and Wilkinson (1974) studied the role of microsomal oxidases in the honey bee *Apis mellifera* (L.). Although they found activity in a number of areas in the body, the main centre of activity was in the midgut. No information was available regarding the detoxification of pyrethroids in *L. sericata* but on the basis of these other research papers it would seem reasonable to assume that similar processes are at work and that they are probably in the gut.

ii & iii) Repair and exhaustion phase

The repair phase may involve an increased turnover of damaged cells. The exhaustion phase is reached when the defence and repair phases are finally overloaded. During this phase there may be a number of effects all associated with the deterioration of the animal.

There are energetic costs associated with the resistance and repair phases which may manifest themselves as alterations of the metabolic rate. At a low level of the toxin one would predict an increase in the metabolic rate associated, in the case of cadmium, with an elevated metallothionein production or, in the case of deltamethrin, an increase in enzyme production. Such increases may continue with increases in the toxin level until a point is reached where the detoxification mechanisms are saturated and no longer able to cope. After this point the metabolic processes may become impaired, resulting in a depression in the metabolic rate. In reality, studies of metabolic rate have shown variable results with metabolic rates increased, decreased and unaltered.

Khalil, Donker, and Van Straalen (1995) investigated the sub-lethal effects of cadmium on the isopod *Porcellio scaber* (Latreille). The animals were collected from the vicinity of a zinc smelting plant and an ancient Roman mine and also from two unpolluted reference sites. The energy budgets of these four groups of animals were tested under conditions; one in which they were supplied with uncontaminated food and one in which they were supplied with food contaminated with cadmium at levels of up to 0.5 μmol/g. Even though growth was severely reduced at the highest cadmium concentration there was no significant effect of cadmium upon respiration.

Weismann and Reháková (1994) studied the effect of cadmium upon enzyme activity. Caterpillars of *Scotia segetum* were intoxicated with cadmium chloride to give three different levels, 0.111, 0.221, and 0.332 mg/g living mass. Cell-free extracts of the enzymes xanthin dehydrogenase, which showed up to a 65% reduction in activity with a cadmium concentration of 0.332 mg/g living mass, and succinate dehydrogenase, which showed a reduction of 60.5% at the same dose of cadmium. Succinate dehydrogenase is an important enzyme in the citric acid cycle where it oxidises succinate to fumarate.

Reddy and Bhagyalakshmi (1994) showed that there were major changes in the oxidative metabolism of the edible crab accompanied by a reduced oxygen uptake and a shift towards anaerobic metabolism. The crabs in their study were exposed to cadmium at a concentration of 2.5 ppm for a period of 96 hours.

Le Bras (1987) showed the respiratory rate of *Asellus aquaticus* did increase with increasing levels of the pesticide lindane. Another example of an effect on respiration rates is provided by Widdows and Donkin (1991) who studied the effects of different levels of pentachlorophenol (PCP) on the mussel *Mytilus edulis*. At levels of up to a tissue concentration of 19.3 mg kg wet weight, the respiratory rate increased to 191% of the control. However, at a level of 42.1 mg kg wet weight, the respiratory rate fell dramatically to 45% of the control.

4.1.3 Scope For Growth

During the first few days after hatching from the egg, blowfly larvae undergo a rapid growth phase during which time they consume all the energy that they need to reach the adult stage. These first few days are critical to the rest of the animal's life. Any factor that reduces the amount of energy available to the animal for growth may have consequences on the animal for the rest of its life. As mentioned above, the presence of a toxin may be expected to have some metabolic costs. A metabolic cost may incur a growth penalty on the animal, thus reducing the animal's scope for growth (Figure 4.1).

Scope for growth (Widdows and Donkin (1991); Calow (1989, 1981); Maltby and Naylor (1990); Anderlini (1992)) represents the amount of energy available for growth and reproduction after basal metabolism. Any factor that reduces this amount of energy can be said to reduce the animal's scope for growth. During the growth phase, blowfly larvae must put as much energy as possible into growth as this will affect the size of the resultant adult. In the presence of a toxin will the metabolic energy demands be increased?

It was not feasible during this study to calculate a full energy budget because of the feeding method of blowfly larvae. The larvae live in their food and their faeces are continually being mixed with the remaining food. It is not possible to determine the amount of food consumed and passed through the body undigested in the faeces, nor to determine the energy loss through excretion. It is possible, however, to measure the growth of the larvae and their respiration rates.

4.1.4. Metabolism and allometric relationships

The major statistic used for comparison in this chapter will be the estimated basal metabolic rate. In order to make comparisons between the different treatments the factor of mass will have to be allowed for, as an allometric relationship occurs between mass

and metabolic rate. The amount of oxygen consumed by an individual increases with its body mass but not in direct proportion, because while oxygen uptake is dependent upon surface area, surface area and mass increase at different rates. Thus, if oxygen uptake is proportional to surface area, which is equivalent to body length squared, mass which is equivalent to volume is equivalent to body length cubed. Consequently if oxygen uptake is proportional to surface area it must be proportional to the cubed root of the mass squared, *i.e.* $mass^{0.67}$. This allometric relationship between mass and oxygen uptake is illustrated by the studies of by Webb (1975) and Phillipson and Watson (1965) who studied mites and woodlice respectively.

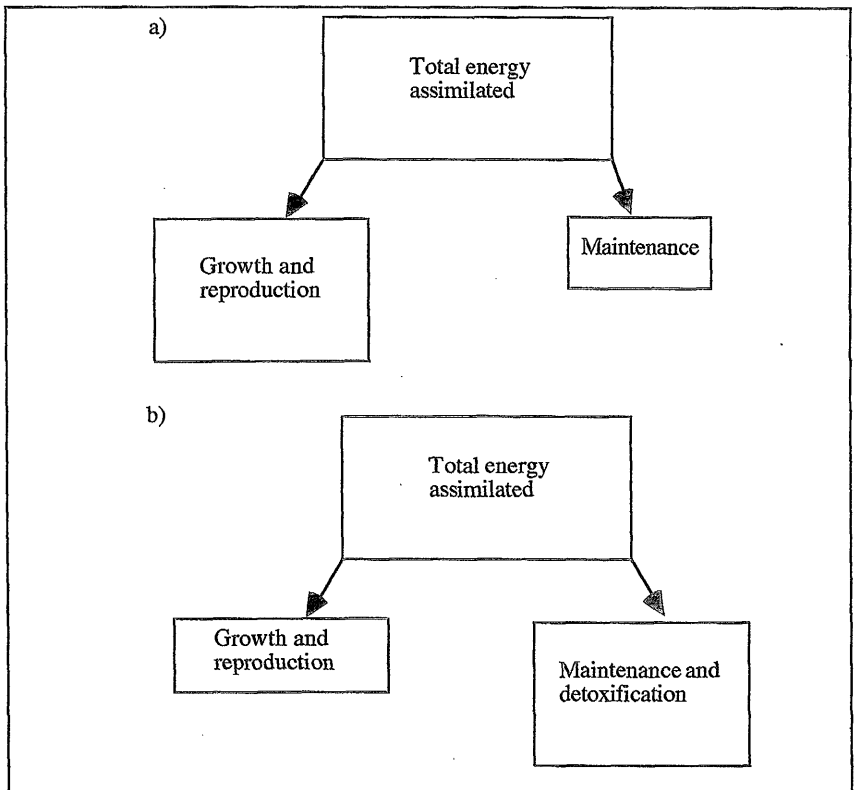


Figure 4.1) Diagrammatic representation of the energy partitioning under a) control conditions under which most of the assimilated energy is used for growth and reproduction and b) in the presence of a toxin the amount of energy available for growth is reduced due to the metabolic demands of detoxification (in both cases the amount of energy is represented by the box size).

The amount of oxygen consumed by individuals with increasing body mass can be described by the following equation.

Log_{10} respiratory rate = K + b ($\log_{10}$ mass)

Where K and b are constants, the allometric coefficient b usually having a value of less than 1. The constant K describes the level of metabolic activity for a given mass.

The mass-specific oxygen consumption is expected to fall as body mass increases. The respiratory rate can be predicted by the following equation;

log (Respiratory rate per unit mass) = K + (b - 1) log mass

As b is usually less than one, b-1 will be negative. Thus, if oxygen consumption is only dependent upon the mass and surface area, b should be 0.67 and b-1 should be -0.33. Values that have been calculated for different animals have given values for b usually lying between 0.67 and 1, presumably because factors additional to the geometrical ones will be involved in determining the size-dependent respiration. The nature of these factors is not considered in this study. The general relationship between mass and respiration rate will be estimated for different experimental treatments and the statistics describing the relationship will be compared.

It has been suggested that an allometric coefficient of 0.67 is a valid figure when considering the variation of metabolic rate within a given species. Khalil, Donker, and Van Straalen (1995) estimated a value of 0.617 for this allometric coefficient for the woodlouse *Porcellio scaber*. When considering this relationship across a range of taxa, however, the value of this exponent is considered to be 0.75. Interestingly, the allometric relationships within and between taxa are the same for both endotherms and ectotherms, the constant K and, hence, metabolic rate is lower for any given size in ectotherms (Reiss (1989); Pough, Heiser, and McFarland (1989)).

4.1.5. Summary and hypotheses

Thus the effect of a toxin upon the metabolic rate may be variable depending upon the concentration of the toxin that the animal is exposed to. The possible effects are illustrated in Figure 4.2. If the toxins are below the threshold concentration then the animals will show an elevated metabolic rate as the detoxification mechanisms deal with the toxins in the case of cadmium through elevated metallothionein production and through elevated enzyme production in the case of deltamethrin. Once these

detoxification mechanisms are unable to deal with the toxins the metabolic rate may fall as the animal reaches respiratory failure.

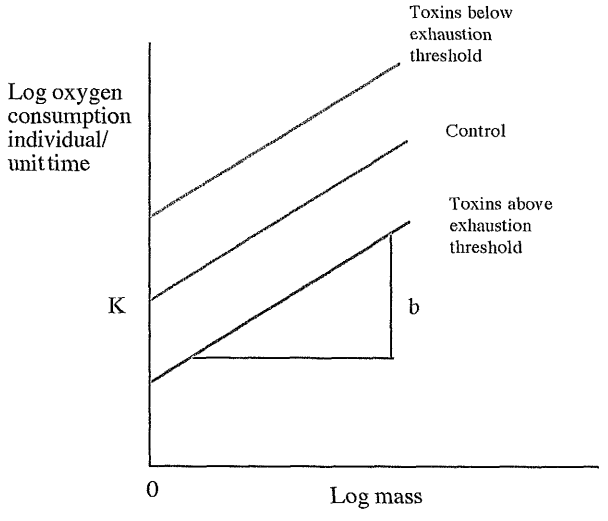


Figure 4.2) The expected metabolic responses under conditions where the level of toxin is below the exhaustion threshold and when it exceeds the exhaustion threshold.

Thus the main hypothesis being tested in this chapter is that the presence of a toxin in the larval diet will alter the metabolic rate for a given body mass, measured by the constant K in the allometric equation. An alteration in the metabolic rate may have consequences for the animals scope for growth.

4.2 RESPIROMETRY METHODS

4.2.1 Rearing of experimental animals

Larvae from three experimental treatments were used;

i) Larvae reared on a control diet.
ii) Larvae reared on a diet containing 50 mg/kg cadmium.
iii) Larvae reared on a diet containing 0.2 mg/kg deltamethrin.

The methods for making these diets is given in Chapter 2.

Eggs were collected from the stock cage by placing a small amount of fresh diet in the cage. The diet was checked regularly and removed when sufficient eggs had been laid. Twenty-four hours later the eggs had hatched and the young larvae could be removed and placed on the experimental diets. In order to generate larvae with a range of sizes, larvae were reared at four population densities (8 larvae on blocks of 32, 16, 8, and 4g of diet). Two replicates of eight larvae at each density were used. For all the respirometry experiments the larvae used were four days old (from the laying of the eggs). This age group was chosen so that the larvae should still be in their growth phase (see Chapter 5) and still actively consuming the contaminated diets. The larger size of the larvae at four days also made it easier to handle them without risk of damaging them.

Limitations of the respirometer meant that all treatments could not be carried out simultaneously. Only a maximum of 14 larvae could be tested at any one time.

4.2.2 Respirometer operating procedure

All respirometry work was carried out using a Gilson respirometer (Figure 4.2). The water bath in the respirometer was maintained at approximately 25°C by two aquarium heaters. The operating procedure for using the respirometer is summarised below.

1) In the central well inside each reaction vessel a few drops of 10% KOH were placed along with a short length of filter paper that acted as a wick. The KOH absorbed any CO_2 produced during the experiment. Control vessels were also set up following this procedure but without the addition of animals.

2) The mass of each larva was recorded and larvae were than kept separately. In preliminary trials the larvae repeatedly climbed up the sides of the reaction vessels into the pipes of the respirometer. To remove the larva the respirometer had to be partially disassembled. The larvae were therefore placed inside a maggot-restraining device that was placed inside the reaction vessel. The restraining devices were made from Gilson pipette tips that had been cut to a length of approximately 1 cm. The narrow end of each tip was plugged with a small piece of rubber tubing. The broad end was covered by a fine nylon mesh, held in place by a small rubber band (made from rubber tubing).

Once the larvae, in their restraining devices, had been installed into the reaction vessels the reaction vessels were connected to the respirometer. The joints between the reaction vessels and the respirometer were lightly greased to improve the seal. Each reaction vessel was held in place on the respirometer by two metal springs. Four vessels were set up as above but excluding any larvae, to serve as controls for the experiment.

3) Once connected to the respirometer, all the vessels were submerged under the water. At this time the reaction vessels were connected via a narrow tube, which at this stage was left open, to a series of reference flasks. The vessels were left for a period of one hour in order to allow the pressure to equilibrate between the reaction vessel and its reference flask. The manometer scales were set to a value of 100 to allow for the readings taken either to increase or to decrease during the course of the experiment.

4) After equilibration for one hour, the connection between the reaction vessel and the reference flask was closed and the experiment began.

5) Readings were taken from the respirometer at 30 minute intervals. To take a reading, the scale on the manometer was adjusted until the pressure in the reaction vessel and reference flask was equal. Equal pressure was indicated by the manometer fluid being in a central position. The readings taken from the control vessels were recorded and a mean value calculated. The control mean was then subtracted from the value recorded from the reaction vessels. At the same time that these readings were taken, the temperature of the water bath was also recorded and the mean temperature during the experiment was calculated.

6) Readings were taken every thirty minutes over a two hour period, after which the connection between the reaction vessel and reference flask was opened and the reaction vessels removed and cleaned.

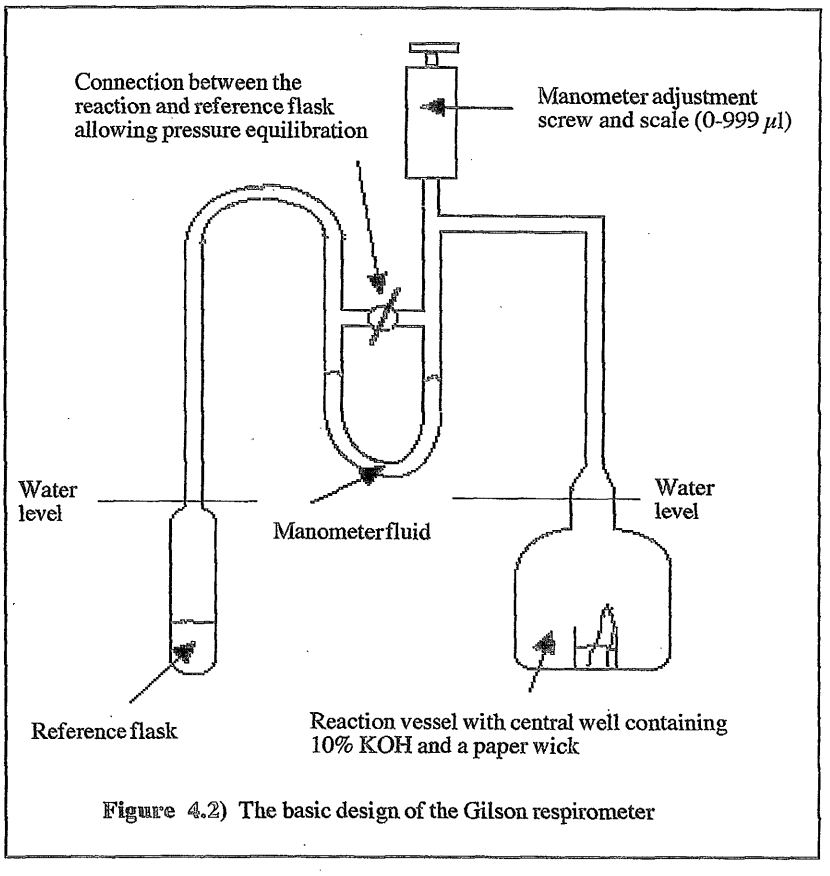


Figure 4.2) The basic design of the Gilson respirometer

4.2.3 Processing of respirometry data

The readings taken from the respirometer were corrected by either the addition or subtraction of the mean values from the control vessels. These adjusted values were plotted on a graph against time using the computer package Cricket graph ®. Linear regression of the data was carried out and the gradient of the resultant line recorded, this value being the amount of oxygen (μl) consumed per individual in one hour. This value was converted to a volume of gas at standard temperature and pressure (STP) using the following formula;

$$STP = \frac{(273)*(P_b\text{-}3\text{-}P_w)}{(273+t)*(760)}$$

Where: t = mean temperature of the water bath (°C)

P_b-3 = operating pressure (mm Hg)-barometric pressure minus three to compensate for mercury specific gravity at room temperature)

P_w = vapour pressure of water (mm Hg)

4.2.4 Analysis of respirometry data

The resultant values gave three regression lines of $\log_{10}$ oxygen consumption against $\log_{10}$ mass. Comparisons of these regression lines were made between larvae from the three treatments using an analysis of covariance. This analysis involved three stages. The first was the calculation of the individual regression coefficients. The second was the calculation of the regression coefficient of the three data sets combined to give one single regression line. The third step was the analysis of covariance of the three data sets, treating them as three separate parallel lines with the same gradient. The analysis carried out tested whether the increase in the residual variance was significant between the different analysis treatments as outlined below.

i) Combined regression *vs.* individual regressions. Could the data be treated as three separate lines or are they better represented by a single line passing through the points produced by all the treatments? A significant increase in the residuals of the combined regression would rule out this possibility.

ii) Individual regressions *vs.* parallel lines. If the data can be treated as three separate lines, could they be treated as three separate parallel lines with the same gradient? A significant increase in the residuals would exclude this possibility.

The regressions and analysis of covariance were carried out using the Minitab® statistical package. These analysis methods could be repeated to make specific comparisons between treatment pairs.

4.3 RESPIROMETRY RESULTS

4.3.1 General comments about the results

Central to these respirometry studies is the assumption that the experiments measured the basal metabolic rate and that differences observed between the treatments were because of the toxins. The larvae were not, however, completely inactive during these experiments. The animals were confined to a small space but they could still move. Thus a small amount of the oxygen consumption measured may have been due to activity, and larvae from the three treatments might have showed different levels of activity. With these limitations in mind the following interpretations have been made.

4.3.2 The effects of deltamethrin and cadmium upon respiration rate

The results for the larvae reared on all diets show the expected allometric relationship between size and respiratory rate *i.e.* larger animals consume more oxygen. The graph in Figure 4.4 shows a scatter plot of the raw data produced by larvae from each of the three treatments. Examination of this graph does not immediately reveal any clear trends. The smaller larvae from the deltamethrin treatment appear to have the lowest respiratory rate whilst the largest larvae from the same treatment would appear to have the highest rate. Similarly, if the cadmium data are examined the regression line produced can be seen to converge with the control treatment at the higher masses. Thus, in both experimental treatments it appears that the allometric relationships observed are different from the control.

The treatments affected body mass differently at the different densities. When the mass ranges of the larvae used are considered, it can be seen that the smallest control larvae have a log mass (in mg) of 1.2 whilst those from the deltamethrin and cadmium treatments have larvae with a log mass of 0.5 and 0.4 respectively. In order to make valid comparisons between the three different treatments, larvae with a similar size range were used. This was achieved by excluding all larvae with a log mass below 1.2. Further justification for their exclusion will be given in the discussion. Exclusion of these smaller larvae gave rise to the scatter plots shown in Figure 4.5, which suggest that the effect of cadmium was to depress the respiratory rate. Deltamethrin appeared to cause an elevation of the rate. Analysis of covariance was used to determine whether or not the respiratory rates were significantly different from each other.

The initial step in this analysis involved determining whether or not the three data sets could be represented by a single line or by three separate lines. The first step of the

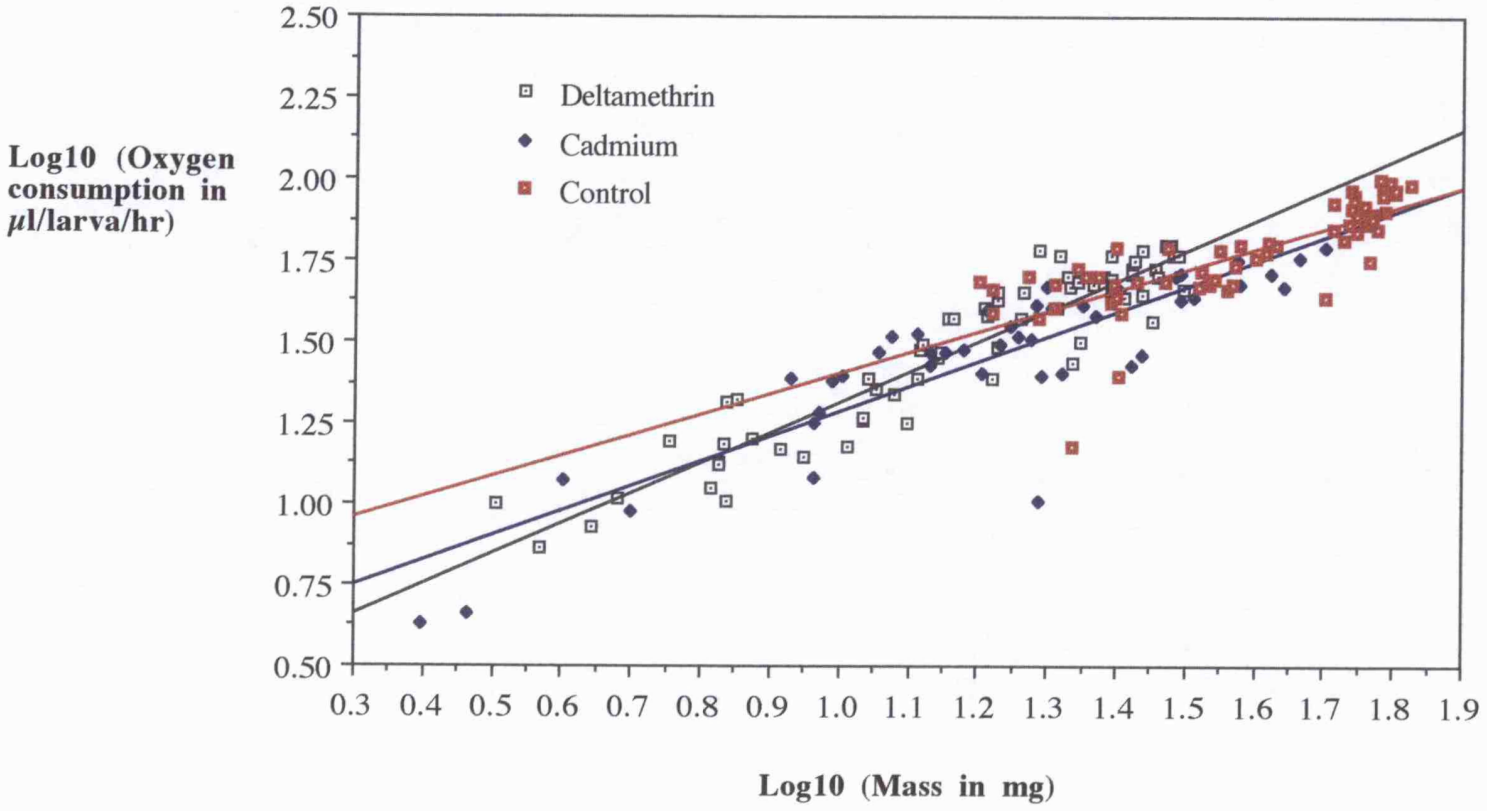


Figure 4.4) Scatter plots of the raw oxygen consumption data of larvae from the three treatments.

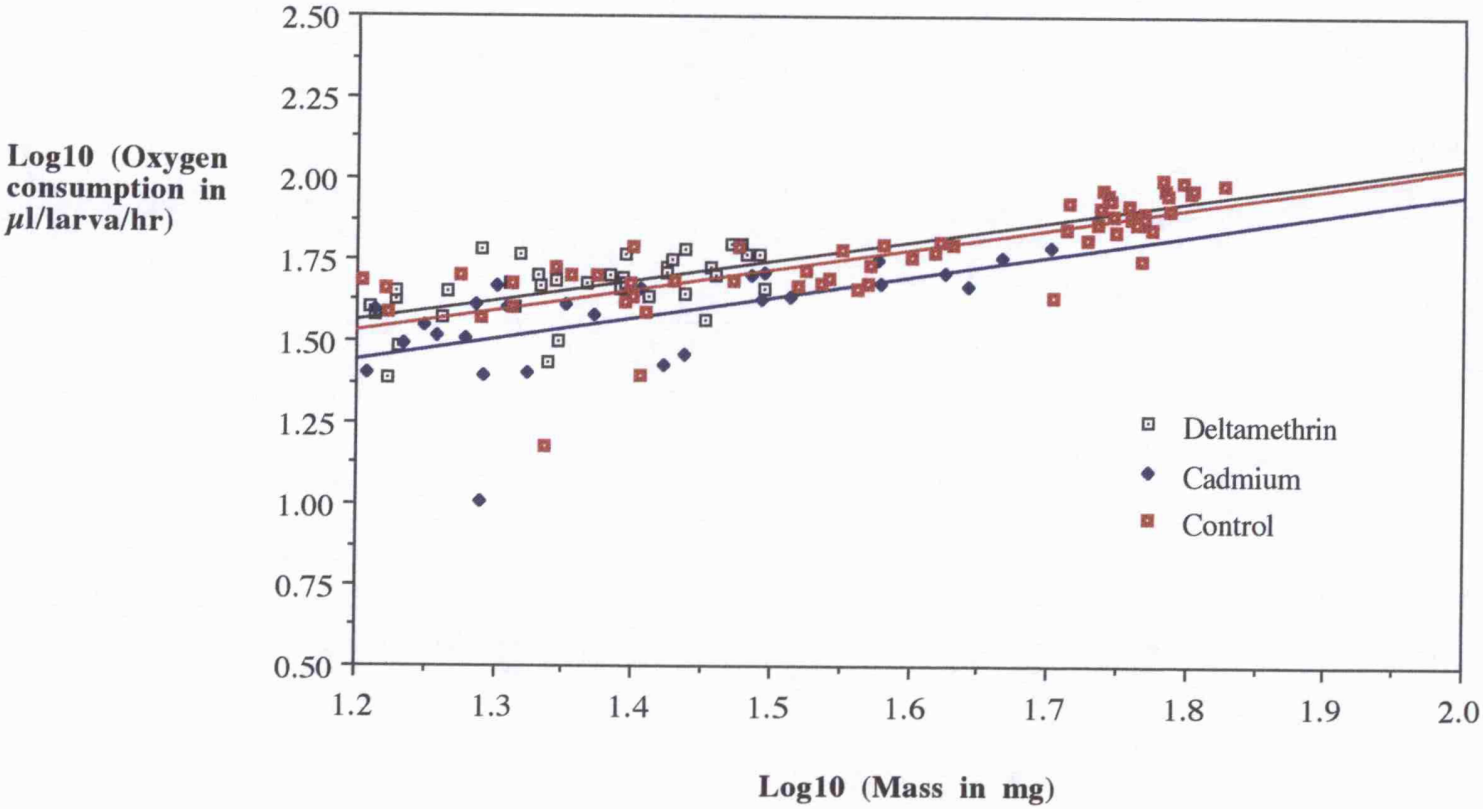


Figure 4.5) The scatter plots and regression lines produced by excluding all larvae with a mass below the minimum mass of the control larvae.

analysis required the regressions of the individual data sets to be calculated. The sums of squares, degrees of freedom, slope and mean square were recorded for each analysis (Table 4.1). *(Note that the residual mean square is calculated by dividing the sums of squares by the degrees of freedom).*

Table 4.1 Regression data from the individual treatments.

Treatment	Sums of squares	Degrees of freedom	Residual mean square	Slope
Control	0.54275	59	0.00920	0.633
Cadmium	0.42348	25	0.01694	0.643
Deltamethrin	0.24734	35	0.00707	0.614
Totals	1.21357	119	0.01020	

Following this the three data sets were combined and a regression carried out on the single data set (Table 4.2).

Table 4.2 Regression data from the combined data sets.

Treatment	Sums of squares	Degrees of freedom	Residual mean square	Slope
Combined data set	1.4365	123	0.0117	0.642

Finally the three data sets were analysed simultaneously as three parallel lines with the same gradient using analysis of covariance (Table 4.3).

Table 4.3 Analysis of covariance of the three treatments.

Treatment	Sums of squares	Degrees of freedom	Residual mean square	Slope
Parallel lines	1.2137	121	0.01003	0.633

The analyses in Table 4.4 shows that the regression line produced by combining the three data sets is significantly different from that of the separate regressions (Df = 4, 119, F = 5.46, P <0.05). This supports the decision to treat the data as three separate lines.

Table 4.4 Tests between combined data and individual regressions.

Test	Sums of squares	Degrees of freedom	Residual mean square	F ratio
Increase	0.22293	4	0.05573	5.46
Individual	1.21357	119	0.01020	

The data in Table 4.5 shows that treating the three lines as parallel lines with the same slope is valid as there is no significant increase of the residual when the three separate regressions are compared with the three parallel lines (Df = 2, 119, F = 0.008, P >0.05). When treated as three parallel lines, the estimated slope was 0.633 (Table 4.5). According to allometric theory if the respiratory rate was dependent only upon surface area to volume ratio, the gradients of these graphs should be approximately equal to 0.67. Thus, this result gives a close approximation to this value.

Table 4.5 Tests between parallel lines and individual regressions.

Test	Sums of squares	Degrees of freedom	Residual mean square	F ratio
Increase	0.00016	2	0.00008	0.008
Individual	1.21357	119	0.01020	

The results presented so far do not indicate which treatments are significantly different from each other. Comparisons were therefore made between the control and deltamethrin treatments combining the deltamethrin and control data and carrying out a regression on the combined data (Table 4.6).

The comparison of the control and deltamethrin data (Table 4.7) shows that the two lines are not significantly different from each other (Df = 94, 2, F = 0.85, P >0.5).

Table 4.6 Regression data from the combined deltamethrin and control data sets.

Treatment	Sums of squares	Degrees of freedom	Residual mean square	Slope
Combined data set	0.8044	96	0.0084	0.587

Table 4.7 Tests between combined control/deltamethrin data and individual regressions.

Test	Sums of squares	Degrees of freedom	Residual mean square	F ratio
Increase	0.79009	94	0.0084	0.85
Individual	0.01431	2	0.00715	

The data in Table 4.6 show that when the control and deltamethrin data sets are combined the estimated slope of the regression line decreases to 0.587. The reason for this is that the respiratory rate of the deltamethrin larvae was slightly higher than the control but the mean mass of the larvae was lower (Figure 4.6). The result when the data are combined is that the smaller larvae of the deltamethrin larvae pull up the bottom end of the curve so decreasing the slope.

The final stage of the analysis compares the regression line of the control/deltamethrin data with the cadmium data. Analysis of covariance showed that the regression line for cadmium was significantly lower than the control/deltamethrin regression line ($Df = 1, 122$, $F = 20.69$, $P < 0.05$). Thus, the results show that larvae reared on cadmium had a depressed mean respiratory rate at any given size when compared with larvae reared on the control or deltamethrin diet. These final results are presented in Figure 4.6. Note that there are a few individuals with very low respiratory rates and low mass; these outliers have not been excluded from the analyses.

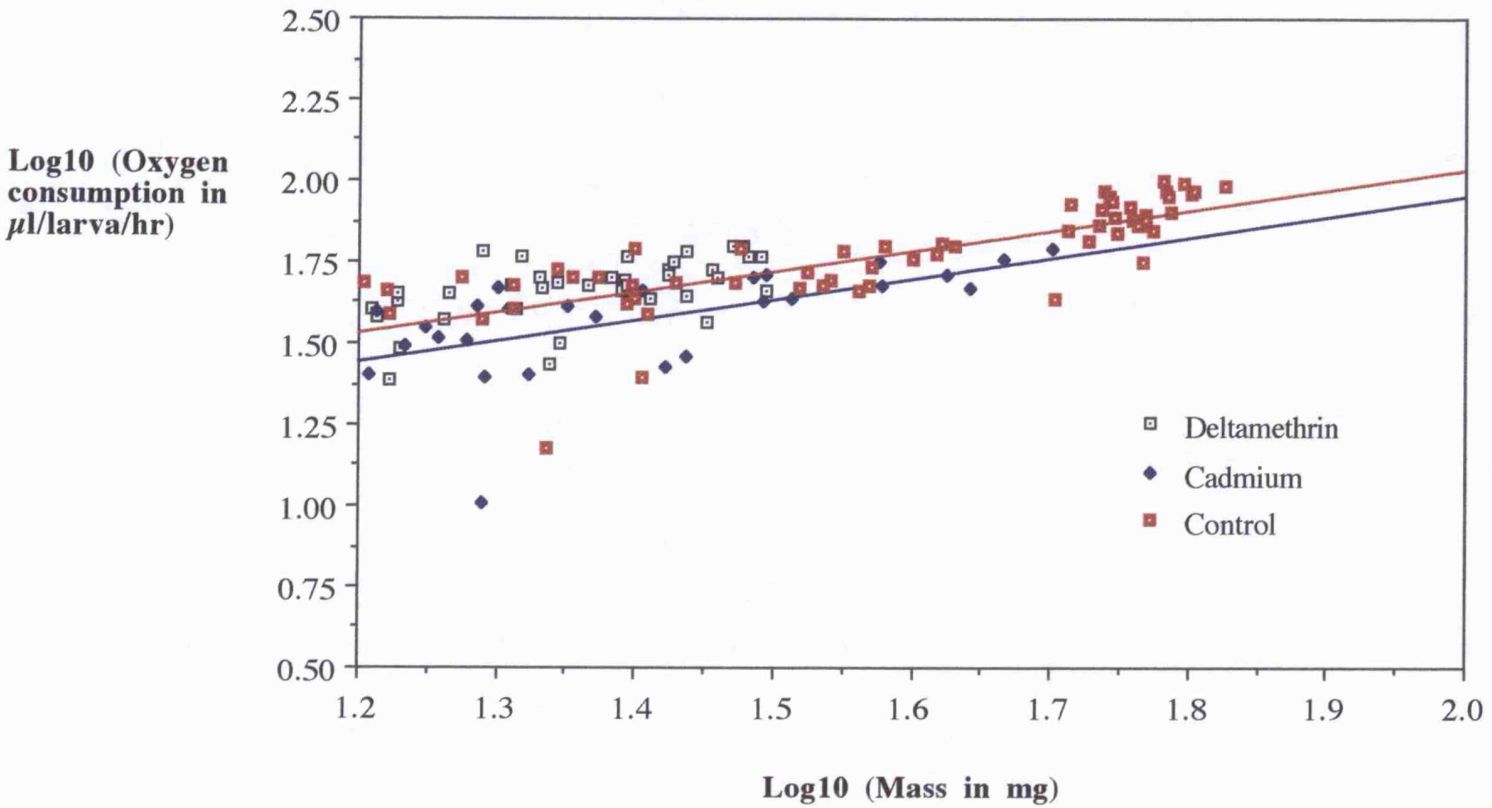


Figure 4.6) The results of the final analysis, the red line represents the deltamethrin and control data sets combined.

4.4 DISCUSSION

4.4.1 The allometric relationship between mass and respiration rate

Allometric theory predicts that smaller individuals should have lower individual respiration rates, as was observed for larvae within each of the three treatments. When the raw data were examined, however, there appeared to be a difference between the allometric relationships of the three treatments. The slopes of the regression line for both the cadmium and deltamethrin treatments seemed to be steeper than for the control, because of the presence of exceptionally small larvae in both of these treatments. The exceptionally small larvae were almost certainly dying; in Chapter 5 daily observations of mass were carried out and larvae of such small sizes at this age always died. Thus, it is reasonable to assume that the exceptionally small larvae had been particularly affected by the toxin and were on the verge of a respiratory failure.

When all larvae with a mass below 15.85 mg (log mass = 1.2) were excluded from the analysis, the resultant regressions gave rise to three lines, which the analysis of covariance showed could be represented by three parallel lines with the same gradient. In other words, when larvae in the same size range as the control larvae were considered the slopes (b) of the allometric relationship between mass and respiratory rate were not significantly different but the intercepts (K) were different. Further analysis showed that the respiratory rates of the control and deltamethrin treatments were not significantly different but that cadmium caused a significant depression in the respiratory rate (estimated K was significantly lower).

These results may be interpreted in terms of the different phases suggested by Calow (1989). The deltamethrin treatment gave an increased metabolic rate though the increase was not significant. The dose might not have been high enough to cause a significant elevation in the metabolic rate. Alternatively, the dose may have bordered on the limit of causing a depression in the rate. As the dose of deltamethrin used was selected for its effect of increased mortality, the second option seems more feasible. Considering cadmium in the same way we may reflect that the dose used is considerably above that required to cause an elevated respiratory rate through increased metallothionein production. The concentration used (50 mg/kg) was shown by Simkiss *et al.* (1993) to have a significant effect on growth and survival. Cadmium is known to decrease the activity of metabolic enzymes as shown by Weismann and Reháková (1994). Increased metallothionein production in itself may only have a small effect on metabolic rate, for example Barber, Baird, and Calow (1990) showed that in daphnids the production of such proteins was responsible for less than 5% of the total energy consumption.

4.4.2 Future respirometry work

This work has raised some interesting questions. In the case of both cadmium and deltamethrin it would be interesting to know exactly how dose level affects the respirometry rate. Do elevated rates occur at certain toxin concentrations? Such a relationship could be sought relatively easily by following the same methods used for this study, using a range of doses.

Another interesting study would be to look at the changes in the respiration rate during development. As the toxin is in the larval diet, are the animals only affected whilst they are consuming it? If so do the effects decrease with time after consumption? It has already been mentioned that *L. sericata* loses 80% of the larval cadmium load in the pupal case (Simkiss, Daniels, and Smith (1993)). Would the effects of cadmium on metabolism persist once the larvae had pupated? In the case of deltamethrin, would all of the toxin have been metabolised? To investigate this, comparisons of the pupal respiration rate would have to be observed. This would not be without difficulties. During pupation the respiration rate follows a "u" shaped curve (Wigglesworth (1972); Taylor (1927)) thus only pupae at the same stage of pupation could be compared. The reasons behind this varying respiratory rate are not clear. It has been suggested that the fall of the curve represents histolysis and the rise histogenesis. If this were the case the curve would represent a measure of the amount of organised tissue present. Wigglesworth (1972) suggests that the curve may reflect the almost complete cessation of mechanical work during pupation. The oxygen consumption then reflects basic metabolic processes. This lack of mechanical work would make the pupae ideal for studying the basal metabolic rate but if the toxins have already been dealt with by this stage they would not be useful for studying their metabolic effects. Finally interspecific comparisons of metabolic rate could be made to investigate further the allometric relationship between mass and metabolic rate, Appendix 3 contains data collected for *C. vicina.*

4.4.3 The implications of the observed respiratory responses for scope for growth

On the basis of the results obtained it is possible to make some broad conclusions and to hypothesise as to how these two toxins may affect the scope for growth of the animals. The results obtained from the deltamethrin treatment did not show any significant effect on the respiratory rate, and so it is difficult to say that there was an increased metabolic demand of the detoxification process that was diverting energy away from growth. However, as mentioned in the Introduction, one of the effects of

deltamethrin may have been to reduce the food intake of the poisoned animal (Wiles and Jepson (1993); Tasei *et. al.* (1994)), the possible consequences of reduced food intake are illustrated in Figure 4.7.

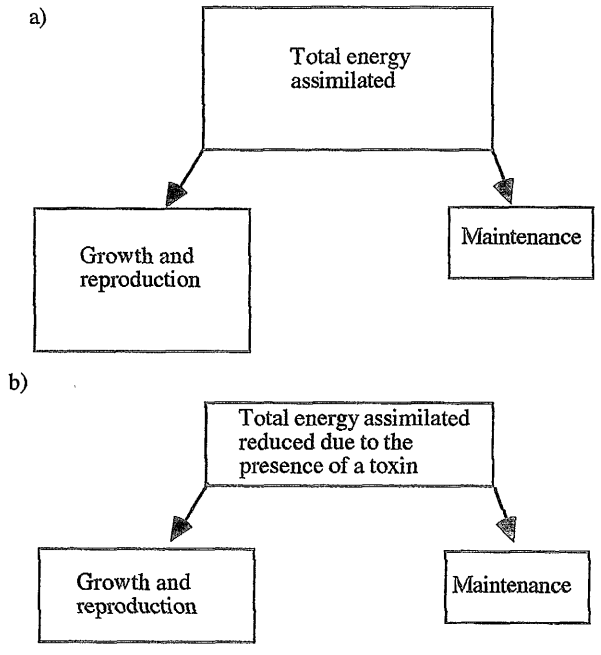


Figure 4.7) Diagrammatic representation of the energy partitioning under a) control conditions under which food intake is not reduced and b) in the presence of a toxin the amount of energy available for growth is reduced due the reduced intake of food (in both cases the amount of energy is represented by the box size).

It was not possible to determine the level of food intake by the larvae in this experiment but a reduced food intake would result in a reduction in the amount of energy available for growth and might result in smaller larvae. In the case of cadmium, similar constraints apply to determining food intake. However, as the respiratory rate was significantly reduced, the growth rate may be a reduced. A reduced growth rate combined with a reduced food intake may result in smaller, slower growing larvae. It is known that smaller larvae are obtained from cadmium treatments (Simkiss *et al.* (1993)) suggesting a reduction in the scope for growth. Such reductions in the scope for growth caused by cadmium and deltamethrin will be investigated fully in Chapter 5.

CHAPTER 5 THE INTERACTION OF POPULATION DENSITY AND TOXINS - THE COSTS TO THE LARVAE AND ADULTS

SECTION INDEX

		Page
5.0	ABSTRACT	102
5.1	INTRODUCTION	102
5.1.1	Introduction and aims	102
5.1.2	The effect of population density upon larval growth	102
5.1.3	The effect of population density and toxins on the immature stages	103
5.1.4	The consequences of larval stress on the adult stage	104
5.2	METHODS	106
5.2.1	Larval population density experiments	106
5.2.2	Measuring adult longevity and fecundity	107
5.2.3	Analysis of the results	107
5.3	RESULTS	108
5.3.1	Changes in larval mass during early development	108
5.3.2	The effects of increasing larval population density and the presence of toxins in the larval diet upon pupal mass	111
5.3.3	The effects of increasing larval population density and the presence of toxins in the larval diet upon adult mass	113
5.3.4	The effects of increasing larval population density and the presence of toxins in the larval diet upon the egg to adult development period	114
5.3.5	The effects of increasing larval population density and the presence of toxins in the larval diet upon the survival to adult emergence	116
5.3.6	Adult longevity	118
5.3.7	Lifetime female fecundity	119
5.4	DISCUSSION	128
5.4.1	The effects of increasing larval population density and the presence of toxins in the larval diet upon the growth and development of the larvae	128
5.4.2	Longevity and fecundity of the adult flies	130

5.0 ABSTRACT

Increasing larval population density was shown to decrease peak larval mass, pupal mass, adult mass, egg-to-adult development time and survival of larvae to the adult stage. The reductions in mass were increased when either deltamethrin or cadmium was present in the larval diet. Both toxins lengthened the egg-to-adult development period. A strong correlation was shown between female body mass, on the day of emergence from the pupae, and life-time egg production. There was no significant difference in this relationship between females, which produced eggs, from the three treatments. The number of females producing eggs, however, was reduced in the presence of cadmium. The overall implication of the results is that the presence of a toxin in the larval diet causes a reduced scope for growth. The ecological implications of these result are discussed.

5.1 INTRODUCTION

5.1.1 Introduction and aims

In chapter 3 the importance of the patch as the fundamental unit of the natural blowfly population was demonstrated. The presence and abundance of an insect species feeding upon such ephemeral resource patches is determined by the presence of such patches and the insect's ability to find and exploit them efficiently. The performance of a species within a patch will depend upon the conditions prevailing, such as the presence of high population densities or the presence of a pollutant in the patch. In this chapter I shall be studying the effects of intraspecific competition, alone and combined with the presence of a toxin (cadmium or deltamethrin) within the patch upon the immature stages of *L. sericata*. The effects upon the larvae which may have consequences that carry through to the adult stage will also be considered. This chapter aims to form a link between the physiological studies carried out in chapter 4 and the observed natural population dynamics studied in chapter 3.

5.1.2 The effect of population density upon larval growth

Within a resource patch there may be intense intraspecific competition which may be scramble competition or contest competition (Nicholson (1945a, b)). *M. prolapsa* may exhibit contest competition as it becomes a facultative predator in its third instar and so actively interferes with larvae of its own and other species. Species such as *C. vicina* or *L. sericata* exhibit scramble competition. Under such conditions the larvae must obtain as much food as they can before the patch becomes depleted. Under extreme scramble

competition there may be no larvae that reach the adult stage. Nicholson (1954a, b) carried out a series of experiments with *L. cuprina* in which the food was limited to either the adult flies or the larvae. When the larval food was limited the number of larvae surviving to reach adulthood decreased.

The recent work of Prinkkilä and Hanski (1995) has shown that even under conditions of very intense competition some individuals are able to reach the adult stage. *L. silvarum* was shown to produce adult flies even when the larvae were kept at a density of 512 larvae/g liver . The ability to survive at increasingly higher population densities is not without its costs. The adult flies emerging from high population density patches are smaller than those from low population densities; this has been demonstrated by Prinkkilä and Hanski (1995), and Simkiss *et al.* (1993).

Many types of flies are highly adapted to developing under intense competition and have evolved to show a plasticity in their ability to pupate at a great range of sizes, allowing them to respond to resource availability. For example the larvae of the fleshfly *Sarcophaga bullata* may weigh up to 120 mg but they are able to pupate and emerge as a fecund adult at a weight of only 20 mg. This plasticity is not seen in all Diptera species; for example larva of tsetse flies develop singularly within the mother's uterus and are not capable of pupation until they are fully fed and expelled from the uterus on the day of parturition. Larvae expelled earlier will not develop into adult flies. Under conditions of food shortage the larval phase will be extended rather than a miniature adult being produced, possibly because of the inability of a small female to carry a full size larva (Delinger and Zdarek (1994)).

A non-dipteran example of a plastic response to food limitation is provided by Banno (1990) who studied the Lycaenid butterfly *Taraka hamada* (Druce). The larvae of this butterfly feed on aphids. As the butterfly population grows through the year, predation pressure on the aphids increases and their numbers fall. The size of the butterfly larvae was found to vary from over 60 mg to 9 mg, under limited food conditions. Larvae with a mass of less than 13-21 mg produced deformed pupae and those under 13 mg usually failed to emerge as adults.

5.1.3 The effect of population density and toxins on the immature stages

The effects of increasing the population density in *L. sericata* were described by Simkiss *et al.* (1993) and a similar reduction in mass was expected in this experiment. The presence of a toxin will provide an additional stress and the effects of the two stresses combined were investigated in this experiment.

In Chapter 4 the effect of cadmium in reducing the respiratory rate of larvae was demonstrated. It was suggested that this reduced respiratory rate combined with a reduced intake of food may result in less energy being available for the growth of the larvae, thus resulting in larvae of reduced size. The effects of population density and cadmium on blowflies have been studied by Simkiss *et al.* (1993). In their experiments the mean pupal and adult mass was decreased with increasing population density. The size was decreased further when the effects of population density and cadmium were combined, the effects of toxin and density on size appearing to be additive. The reduced metabolic rate may also manifest itself through extending the development period. Weismann and Reháková (1994) showed that the growth rate of larval *Scotia segetum* (Den. et Shiff.) was slowed down. The sixth instar stage was slowed down from 32 to 92 days. Only larvae reared on the lowest dose of cadmium pupated and these pupae showed a 37% reduction in their mean mass.

The respiration experiment in chapter 4 did not show a clear effect of deltamethrin on metabolic rate. The respiratory rate was increased, but not significantly, thus making it difficult to comment on the energetic costs of its detoxification. Both Wiles and Jepson (1993), and Tasei *et al.* (1994) showed that deltamethrin has caused a reduction in the amount of food consumed. This reduced food intake may result in a reduction in the amount of energy available for growth of the larvae with the end result of a reduced adult size, and an extended developmental period could also be expected. There was no information in the literature investigating the combined effects of population density and deltamethrin.

5.1.4 The consequences of larval stress on the adult stage

Larvae that survive to adulthood carry with them the costs of stress during the larval period in the form of a reduced size. This reduced size may have a number of negative consequences. Blueweiss *et al.* (1978) presented data for a range of animals (mammals, invertebrates, reptiles, amphibians, birds, and fish) in which they demonstrated positive allometric relationships between body weight and the following parameters; fecundity, longevity, litter weight, life span, and a negative relationship with r_{max}.

Partridge and Farquhar (1981) showed a positive relationship between body size and longevity in male *Drosophila melanogaster*. The same relationship is shown when fecundity is considered. The number of eggs produced by the butterfly *T. hamada* was shown to increase with body size (Banno (1990)). Wall (1993) showed that the number of oöcytes matured by *L. sericata* increased with body size. Philipson and Watson (1965) also demonstrated a mass/fecundity relationship in the woodlouse *Oniscus*

asellus. Pitcairn and Gutierrez (1992) demonstrated a positive allometric relationship between mass, longevity and fecundity in the parasitoid *Tetrastichus incertus* (Ratzburg), though the mass/longevity relationship only held true for the females. Other examples are provided by Chua (1992) and Xue and Ali (1994).

Thus, any factor that reduces the resultant body mass of an individual may also result a reduction in fecundity and longevity. Colegrave (1993) carried out a series of experiments on the beetle *Callosobruchus maculatus* confirming that larval competition did not affect fecundity independently of its effect through reducing size. As described in section 5.1.3 cadmium has been shown to cause a reduction in mass additional to that caused by an increased population density alone. The effect of deltamethrin was not known at this stage but it was hypothesised that a similar quantitative result would be obtained.

It is not just size that will affect the adults emerging from polluted patches. Adults too will be exposed to the toxins, especially the female flies that require a protein meal in order to produce their eggs. In the process of ingesting contaminated food it is possible that energy will have to be diverted away from reproduction into detoxification, or if the contaminated food is avoided, egg production could fall for this reason. When a solution of deltamethrin was applied to the thorax of the alfalfa leaf cutting bee *Megachilerotundata* (F.) it reduced the life span of the animals and also reduced the number of larvae reaching the adult stage. Females showed a 20% reduction in the number of eggs laid (Tasei *et al.* (1988)). In this experiment the toxin was applied topically and so may not give a good representation of the effects of deltamethrin in food. Tasei *et al.* (1994) applied deltamethrin topically in one experiment and through the food in another (in doses of up to 0.2 mg/l) to bumble bees (*Bombus terrestris*). No reduction in the fecundity or longevity was observed.

5.2 METHODS

5.2.1 Larval population density experiments

Three experimental treatments were used:- control diet, diet containing 50 mg/kg cadmium, and diet containing 0.2 mg/kg deltamethrin. The diets were made up by the methods described in Chapter 2. For each of these treatments four population densities were used. In each case eight larvae were placed on blocks of diet with masses of 32 g, 16 g, 8 g, and 4 g. These masses of diet gave inverse densities of 4 g, 2 g, 1 g and 0.5 g of diet per larvae respectively. From here on this nomenclature will be used for the larval densities with 4 g diet/larva being the lowest population density and 0.5 g diet/larva being the highest. Each block of diet was placed into a separate plastic container with a perforated lid and labelled with the density and treatment.

Eggs were collected from the stock cage by placing a fresh block of diet in with the flies. The block was checked regularly and removed as soon as sufficient eggs had been obtained. 24 hours later the newly hatched larvae were transferred to the experimental blocks of diet, and the experiment began.

After a further 48 hours, three days from oviposition, the larvae were removed from the diet and weighed individually to the nearest 0.1 mg. A small foil dish was used to weigh the larvae, which helped to contain the larvae long enough to obtain a measure of their mass. The larvae were prone to crawling around making weighing them a difficult matter. In addition to this the larvae were very prone to desiccation while they were out of the diet. As they dried their mass decreased. On the basis of this mass loss and the activity of the larvae, rapidly weighing the larvae to the nearest 0.1 mg was considered to be precise enough. The animals could have been anaesthetised but it was not desirable to do anything that may interfere with their growth. For the reason of consistency this level of accuracy was maintained for all observations of mass. Larvae were weighed every day until all had either pupated or died. The pupae were weighed on the day they were found only and were transferred to a separate container labelled with the treatment and pupal number. The pupae were retained in these containers and examined every day until the adult fly emerged.

The emergent flies were weighed and sexed on the day of emergence. This experiment was repeated three times. In all cases the adult flies obtained were retained for the next stage of the experiment.

5.2.2 Measuring adult longevity and fecundity

The adult flies emerging from the different treatments were retained and used to measure the adult longevity and fecundity. The male flies were placed individually into small plastic containers (approximately 10 cm * 8 cm * 15 cm) with perforated lids. Each fly was supplied with sugar, water, and a small amount of dried diet (approximately 1 g) containing the test substance. The females were also housed individually in separate containers. These containers were glass jars (11 cm diameter and approximately 10 cm deep). The top of these jars was covered by a fine nylon mesh which allowed access to the jars without allowing the females to escape. Each female was supplied with sugar, water, dried diet + test substance, and also a small amount of fresh diet on which to oviposit, this diet again contained the test substance. Each of the females had a male fly from the stock cage added with which to mate. Males from the stock cage were used in order that any reduction in fecundity of the females was the result of exposure of the females alone to density/toxin stress.

All adult flies were checked daily. Any deaths of the experimental flies was recorded. Any eggs laid were removed and counted. If any of the 'stud' males died they were replaced with fresh ones from the stock cage. The amounts of food and water were also checked daily and the flies were kept with a constant supply of each. The fresh diet was replaced every two days or when eggs had been laid.

5.2.3 Analysis of the results

Comparisons were made between the peak larval mass, pupal mass, adult mass, duration of developmental periods, and the survival to adulthood. Comparisons were made using analysis of variance. This test compared the density means, the treatment means, and also measured the interaction of density and toxin and whether any of the effects changed over time (*i.e.* between different experiments). In each case the mean value for each replicate was calculated and the final analysis was carried out upon the weighted replicate means. Where the data required transforming for the analysis, this has been indicated in the results section. To look for correlations between mass and fecundity (total number of eggs produced), and between mass and longevity, the data from the different densities within each treatment were combined and a regression of the data carried out. All confidence intervals presented were calculated from the pooled error mean square. All analyses were carried out using Minitab®.

5.3 RESULTS

During the first experiment carried out, virtually all the larvae on the deltamethrin diet died. As the diet had been made up from a stock solution that had been retained for some time, the solution may have become concentrated through evaporation. Thus only the data of the second and third experiments are presented. All tables of means are based upon the results of experiments two and three only unless otherwise stated.

5.3.1 Changes in larval mass during early development

The larvae reared on the control diet showed a rapid growth during the first five days of life. The larvae from all densities reached their peak mass at an age of five days (Figure 5.1 a). The peak mass also marks the end of the larval feeding period, which could be observed by the change in colour of the larva's gut (seen as a thick black line in the larvae that were feeding). Following this peak the mass fell steadily until the larvae pupated. This mass loss could be attributed at least in part to the emptying of the gut following the cessation of the feeding period. Increasing the larval density decreased the peak larval mass.

The same general mass changes were observed in larvae reared on the cadmium diet (Figure 5.1 b). The timing of the peak mass, however, was different. The larvae reared at the lowest densities (2 g diet/larva and 4 g diet/larva) both reached their peak mass after six days indicating a longer feeding period. The larvae reared at the higher densities, however, reached their peak mass after five days as did the control larvae. When viewing the mass gain curves from the cadmium treatment it can be seen that the peaks are not as pronounced as in the control experiment. The peaks were flatter because the larvae did not all reach their peak mass on the same day, thus depressing the peak. The larvae reared on the deltamethrin diet showed the same changes as the control larvae but again the peaks were depressed (Figure 5.1 c).

The analysis of variance presented in Table 5.1 shows that there was a significant difference between the four densities and the three treatments. There was no significant difference between the results obtained from experiments one and two. The effects of density and toxin were shown to be additive (the interaction was not significant). The data in Table 5.2 show the density and toxin means with 95% confidence intervals calculated using the pooled error mean square. The mean peak mass of larvae reared on the control diet (Figure 5.2) was significantly higher than that of larvae from the two toxin treatments. The peak mass of the larvae reared on the diet containing cadmium was

significantly lower than that of the larvae reared on the diet containing deltamethrin ($p<0.05$ in all cases as shown by lack of overlap of the confidence intervals).

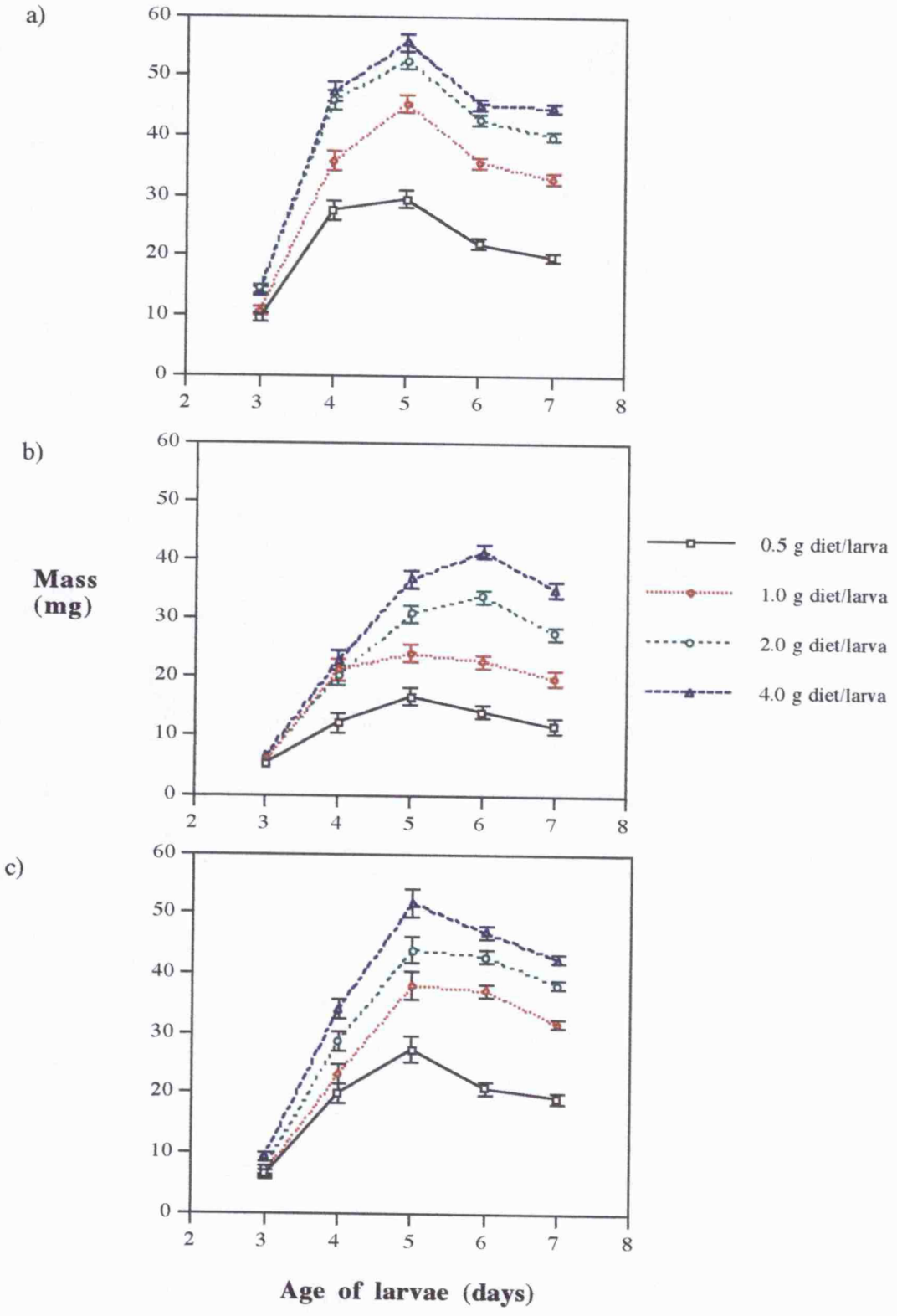


Figure 5.1) The changes in mass recorded in larvae from the three treatments. a) control, b) cadmium, and c) deltamethrin (t_0= day of oviposition).

Table 5.1 Analysis of variance of the peak larval mass of larvae.

Source	DF	Mean square	F	P
Density	3	14421.5	76.56	<0.001
Toxin	2	12209.2	64.82	<0.001
Experiment number (Exp no.)	1	2.3	0.01	ns
Density*toxin interaction	6	197.9	1.05	ns
Density* Exp no. interaction	3	223.2	1.18	ns
Toxin * Exp no. interaction	2	114.2	0.61	ns
Toxin*density*Exp no.interaction	6	306.1	1.63	ns
Error	48	188.4		
Total	71			

Table 5.2 The mean peak larval mass (mg) for different combinations of density and treatment. Density and treatment means have 95% confidence intervals, calculated from the pooled error mean square, in parentheses.

Density (g diet/larva)	Control	Cadmium	Deltamethrin	Mean (±ci)
4.0	55.61	41.33	51.61	49.52 (±0.926)
2.0	52.57	33.86	43.98	43.47 (±0.926)
1.0	45.36	23.95	37.90	35.74 (±0.926)
0.5	29.44	16.59	27.26	24.43 (±0.926)
Mean (±ci)	45.74 (±0.802)	28.93 (±0.802)	40.19 (±0.802)	

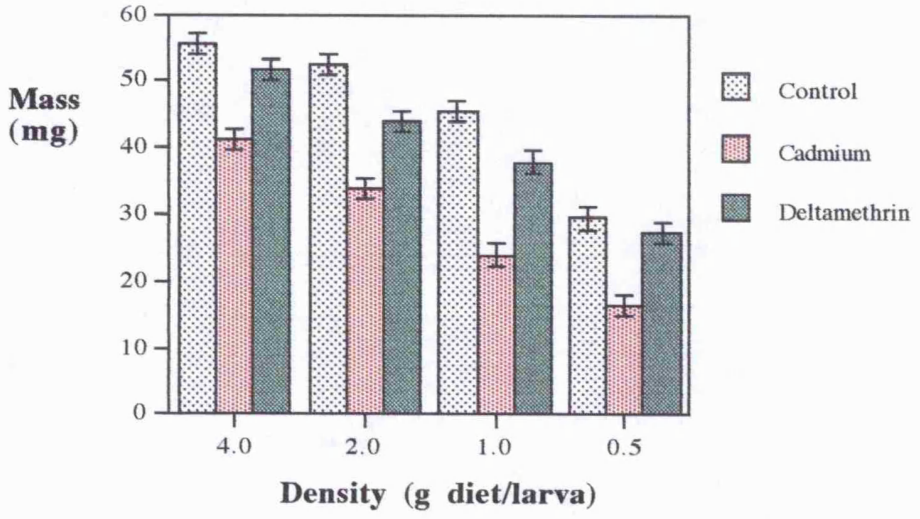


Figure 5.2) The mean peak mass of each density and each treatment (error bars indicate the 95% confidence intervals calculated from the pooled error mean square).

5.3.2 The effects of increasing larval population density and the presence of toxins in the larval diet upon pupal mass

Increasing the larval population density caused the pupal mass to decrease. The mean mass of the control pupae was significantly higher than the means of pupae arising from either the cadmium or deltamethrin treatment at all but the highest density (Figure 5.3). The pupae from the cadmium treatment were significantly lighter than the other treatments at all densities ($p<0.05$ in all cases as shown by lack of overlap of the confidence intervals). The means for each treatment and density are presented in Table 5.3.

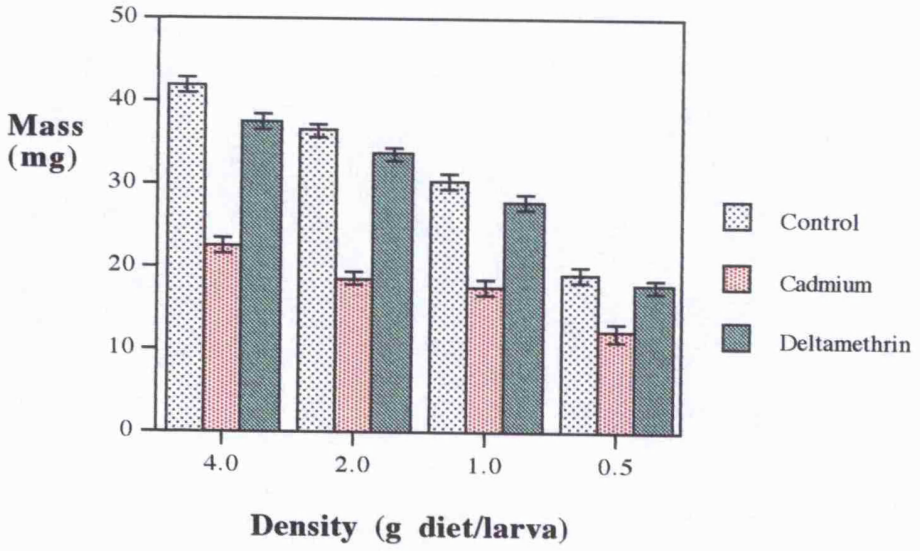


Figure 5.3) The mean mass of pupae from the different treatments and densities (error bars indicate 95% confidence intervals calculated from the pooled error mean square).

Table 5.3 The mean pupal mass (mg) for different combinations of density and treatment. Density and treatment means have 95% confidence intervals, calculated from the pooled error mean square, in parentheses.

Density (g diet/larva)	Control	Cadmium	Deltamethrin	Mean (±ci)
4.0	41.75	22.34	37.37	33.82 (±0.473)
2.0	36.31	18.31	33.47	29.38 (±0.473)
1.0	30.15	17.25	27.69	25.03 (±0.487)
0.5	18.93	11.93	17.54	16.13 (±0.502)
Mean (±ci)	31.79 (±0.409)	17.47 (±0.438)	29.02 (±0.409)	

The analysis of variance of the data (Table 5.4) shows that there was a significant difference between the treatments and between the densities. There was no significant difference between the two experiments. The interaction between density and treatment proved to be significant. This interaction means that the toxins are not acting in an additive manner. Examination of Figure 5.3 shows that the interaction is the result of cadmium having a greater effect on pupal mass at low density than it does at high density.

Table 5.4 Analysis of variance of the pupal mass.

Source	DF	Mean square	F	P
Density	3	3609.4	111.89	<0.001
Toxin	2	4581.8	142.03	<0.001
Experiment number (Exp no.)	1	55.7	1.73	ns
Density*toxin interaction	6	148.8	4.61	<0.01
Density* Exp no. interaction	3	67.5	2.09	ns
Toxin* Exp no. interaction	2	22.4	0.70	ns
Toxin*density* Exp no. interaction	6	37.5	1.16	ns
Error	45	32.3		
Total	68			

Finally comparisons can be made between the pupal mass and the peak larval mass. The mean peak larval mass and pupal mass at each density were used to calculate a mean mass loss, presented below in Table 5.5. These data show that the larvae have lost approximately one third of their peak mass by the time they pupate. The main loss of mass occurs in the day after the mean peak mass has been reached and is probably because of the emptying of the gut, though there may also be loss due to moisture loss.

Table 5.5 The mean mass loss of larvae from the peak larval mass to pupation. The means presented are the overall means of the three treatments.

Density (g diet/larva)	Mean peak larval mass (mg)	Mean pupal mass (mg)	% mass lost
4.0	49.52	33.82	31.71
2.0	43.47	29.38	32.41
1.0	35.74	25.03	29.97
0.5	24.43	16.13	33.98
		Mean % loss	32.02

5.3.3 The effects of increasing larval population density and the presence of toxins in the larval diet upon adult mass

The adult data could not be analysed using a general linear model to estimate interaction effects as the results were not balanced because no flies emerged from the highest density of the cadmium treatment. Consequently one-way analysis of variance was carried out. The analysis showed that there was a significant difference between the mass of adults arising from the different densities (Table 5.6). A further analysis showed that there was a significant difference between the different treatments (Table 5.7). Increasing density caused a reduction in adult mass in all treatments. The presence of either toxin caused a further reduction in mass which was most pronounced in the cadmium treatment (Figure 5.4).

Table 5.6 Analysis of variance of adult mass from the different densities.

Source	DF	Mean square	F	P
Density	10	590.4	37.41	<0.01
Error	251	15.8		
Total	261			

Table 5.7 Analysis of variance of adult mass from the different treatments.

Source	DF	Mean square	F	P
Treatment	2	508.9	14.9	<0.001
Error	259	34.2		
Total	261			

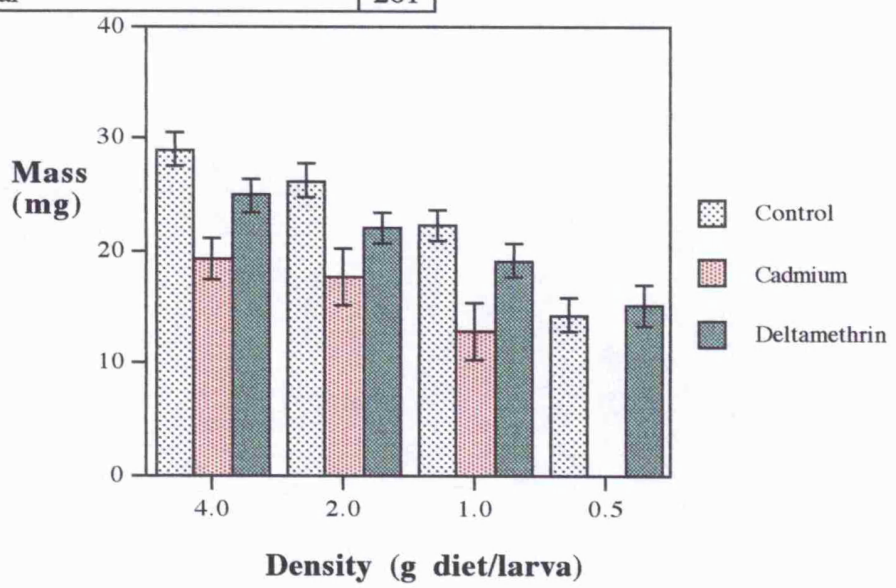


Figure 5.4) The mean mass of adults from the different treatments and densities (error bars indicate 95% confidence intervals calculated from the pooled error mean square).

5.3.4 The effects of increasing larval population density and the presence of toxins in the larval diet upon the egg-to-adult development period

The mean development period from egg to adult of the control animals (Table 5.8) was significantly lower than the development periods of the two toxin treatments; the development period of the cadmium treated animals was significantly longer than that of the deltamethrin animals ($p<0.05$ in all cases as shown by lack of overlap of the confidence intervals). Overall cadmium caused the longest development period. Within each treatment there was the same general trend for the animals reared at the highest densities to develop the quickest, this trend is illustrated in Figure 5.5.

Table 5.8 The mean egg-to-adult development period (days) for adults arising from larvae reared at different combinations of density and treatment. Density and treatment means have 95% confidence intervals, calculated from the pooled error mean square, in parentheses.

Density (g diet/larva)	Control	Cadmium	Deltamethrin	Mean (±ci)
4.0	16.35	18.11	17.31	17.26 (±0.108)
2.0	15.95	17.20	16.97	16.71 (±0.111)
1.0	16.03	16.27	16.80	16.37 (±0.111)
0.5	14.82	16.50	15.17	15.50 (±0.122)
Mean (±ci)	15.79 (±0.093)	17.02 (±0.105)	16.56 (±0.095)	

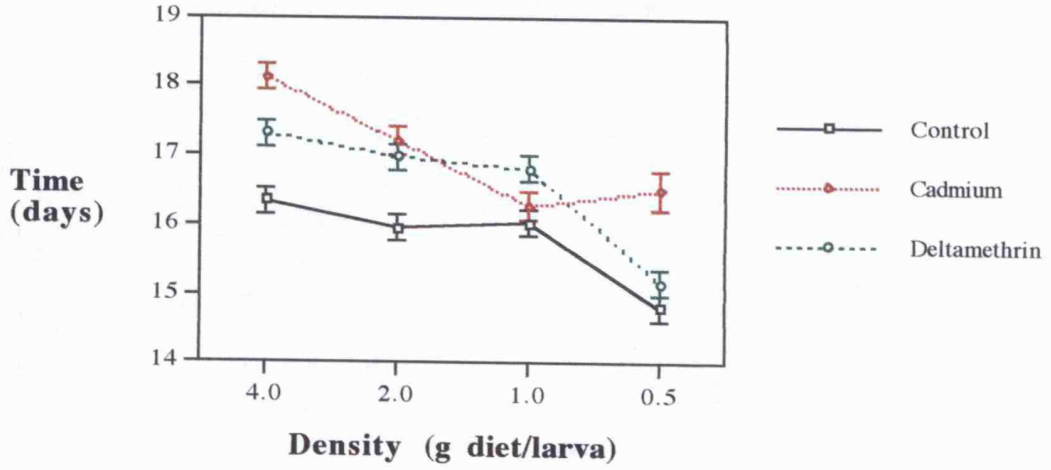


Figure 5.5) The mean egg-to-adult development times of larvae from the three treatments (error bars indicate 95% confidence intervals calculated from the pooled error mean square).

Analysis of variance of the development time data is presented below in Table 5.9. The analysis shows the significant difference between densities and toxins as described on the previous page, but it also shows that there was a significant difference between the two different experiments. The mean development time from the second experiment was lower than the third experiment (15.73 days ± 0.079; 17.18 days ± 0.079 respectively). Analysis of the development periods was possible as the analysis included partially emerged flies that died during emergence, the mass of such adults was not recorded.

Table 5.9 Analysis of variance of the egg-to-adult development times.

Source	DF	Mean square	F	P
Density	3	24.340	25.33	<0.001
Toxin	2	28.375	29.53	<0.001
Experiment number (Exp no.)	1	103.228	107.43	<0.001
Density*toxin interaction	6	2.952	3.07	<0.05
Density* Exp no. interaction	3	1.276	1.33	ns
Toxin * Exp no. interaction	2	8.462	8.81	<0.05
Toxin*density* Exp no. interaction	6	2.830	2.95	<0.05
Error	42	0.961		
Total	65			

Examination of the treatment means shows that development of animals from each treatment took longer during the third experiment (Table 5.10). The results for each treatment are significantly different between the experiments ($p<0.05$ in all cases as shown by lack of overlap of the confidence intervals). The difference was least pronounced in the control animals and highest in the animals from the cadmium treatment. There was a significant interaction between toxin and density and this interaction varied over time.

Table 5.10 The mean differences between the development times (days) of animals from experiment two and experiment three. Treatment means have 95% confidence intervals, calculated from the pooled error mean square are shown in parentheses.

Experiment	Control	Cadmium	Deltamethrin	Means (±ci)
2	15.43 (±0.132)	15.95 (±0.152)	15.82 (±0.132)	15.73 (±0.079)
3	16.15 (±0.132)	18.09 (±0.144)	17.31 (±0.138)	17.18 (±0.079)
Mean (±ci)	15.79 (±0.093)	17.02 (±0.105)	16.56 (±0.095)	

5.3.5 The effects of increasing larval population density and the presence of toxins in the larval diet upon the survival to adult emergence

The effect on survival of increasing the population density is illustrated in Figure 5.6. The control treatment showed a survival peak occurring at a density of 2 g diet/larva, not at the lowest density as may have been expected. A similar trend was observed in the deltamethrin treatment, the difference being that the survival peak occurred at the higher density of 1 g diet/larva. In both treatments, however, these higher survival peaks were not statistically significant as can be seen from the error bars in the graph. There were no significant differences between the survival of the control animals from the different densities. This shows that under control conditions, the range of population densities used did not cause an increased mortality. The treatment means are presented in Table 5.11. These values have been back transformed from the angular transformed data on which the analysis of variance was carried out.

The results for deltamethrin show roughly the same results except that survival at the highest density (0.5 g diet/larva) was slightly reduced when compared with the lower densities, but not significantly. Thus the effects of deltamethrin, in terms of reducing survival to eclosion, appear to be increased at the higher densities. There was no significant difference between the deltamethrin and control treatment at any density. Overall there was no significant difference in survival between the control and deltamethrin treatments.

Table 5.11 The back transformed mean number of larvae to surviving to eclosion from the initial number of eight. The numbers in parentheses show the back transformed 95% confidence interval range.

Density (g diet/larva)	Control	Cadmium	Deltamethrin	Mean
4.0	4.95	3.09	4.85	4.30 (3.25-5.33)
2.0	5.06	1.15	5.48	3.80 (2.77-4.85)
1.0	5.57	1.50	4.91	3.94 (2.90-4.99)
0.5	4.89	0.00	2.76	1.90 (1.08-2.86)
Mean	5.12 (4.22-6.08)	1.08 (0.54-1.78)	4.50 (3.59-5.96)	

The data from the cadmium treatment show a more pronounced effect of density upon survival across the range of densities studied. The highest survival observed was that of the larvae reared at the lowest density (4 g diet/larva). Survival then decreased with increasing population density with no adults emerging from the highest density.

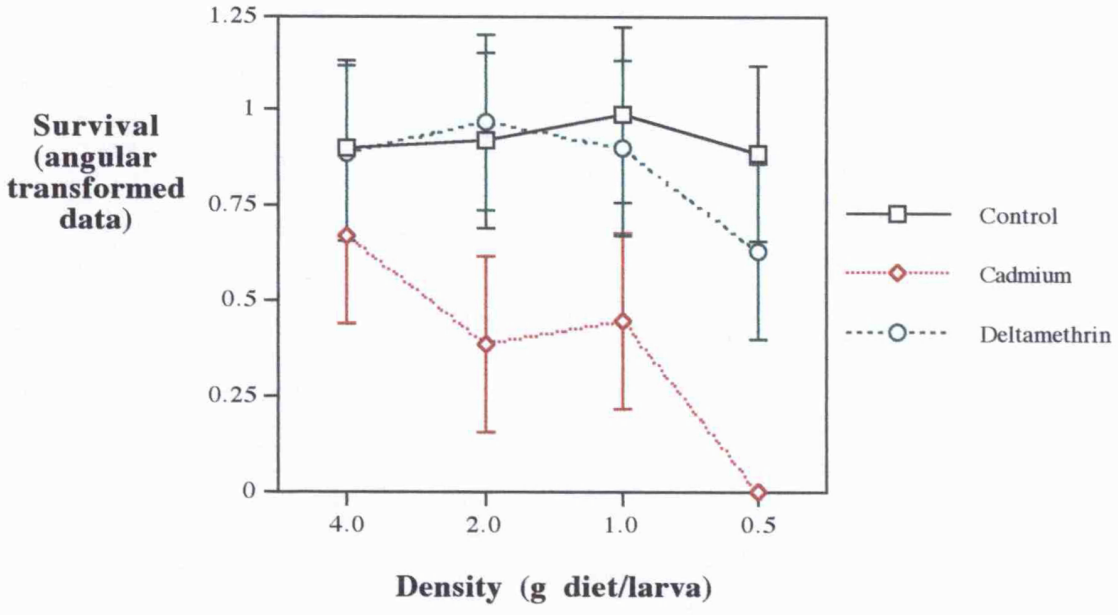


Figure 5.6) The mean number of adults emerging from the three treatments (error bars indicate 95% confidence intervals calculated from the pooled error mean square)

Analysis of variance of the angular transformed data shows that there was a significant difference in the overall effect of the toxins (Table 5.12).

Table 5.12 Analysis of variance of the adult emergence (analysis carried out upon angular transformed data).

Source	DF	Mean square	F	P
Density	3	0.36221	4.65	<0.05
Toxin	2	2.12709	27.33	<0.001
Experiment number (Exp no.)	1	0.08742	1.12	ns
Density*toxin interaction	6	0.12704	1.63	ns
Density* Exp no. interaction	3	0.10741	1.38	ns
Toxin * Exp no. interaction	2	0.12251	1.57	ns
Toxin*density* Exp no. interaction	6	0.06797	0.87	ns
Error	48	0.07784		
Total	71			

Cadmium resulted in the lowest survival. There was a significant effect of density, with the highest density giving the lowest survival. Unlike the analysis for development time, however, there were no significant interactions. The zero values for cadmium, 0.5 g diet/larva, were included in the analysis although their inclusion may not be strictly valid. The trend of survival was not significantly different between the two experiments.

5.3.6 Adult longevity

The data for adult longevity were not split into the larval density categories. Instead they were separated into the three treatments. Analysis of covariance was then carried out using mass as a covariate. There was no relationship between adult mass and longevity ($P>0.05$); the mean longevity varied between experiments. In the second experiment the overall mean age was 21.06 days while in the third the mean was 25.49 days (Table 5.13).

Table 5.13 The mean adult longevity (days) of adult flies resulting from the three treatments. The 95% confidence intervals of the means, shown in the parentheses, were calculated from the pooled error mean square.

Experiment mean	Control	Cadmium	Deltamethrin	Mean (±ci)
2	20.90 (±3.23)	19.57 (±4.62)	22.69 (±3.14)	21.06 (±1.99)
3	26.93 (±2.98)	19.85 (±7.37)	29.70 (±3.27)	25.49 (±2.07)
Mean	23.91 (±2.17)	19.71 (±3.80)	26.20 (±2.24)	

The combined means show that the mean longevity of the third experiment was significantly higher than the second. The significant difference between the treatments is caused by the depression in the mean longevity of the flies from the cadmium treatment, which was significantly lower than the mean longevity of the flies from the deltamethrin treatment. The analysis of variance is presented in Table 5.14.

Dividing the total number of flies from each treatment by the mean longevity gives an estimate of the daily % mortality. The control treatment gave rise to a total of 115 adult flies, cadmium 39 adults, and deltamethrin 108 adults. The mean daily mortality for the three treatments were 4.18%, 5.07%, and 3.08% for the control, cadmium and deltamethrin treatment respectively.

Table 5.14 Analysis of covariance of the adult longevity

Source	DF	Mean square	F	P
Mass	1	47.2	0.34	ns
Toxin	2	537.3	3.91	<0.05
Experiment number (Exp no.)	1	903.1	6.57	<0.05
Toxin * Exp no. interaction	2	146.5	1.07	ns
Error	255	137.5		
Total	261			

5.3.7 Lifetime female fecundity

The initial analysis of lifetime fecundity involved carrying out an analysis of covariance upon the observed egg production, including only females that produced eggs. The analysis showed that there was no significant difference between the three treatments when the effects of mass were removed (Table 5.15). In other words the toxins affected fecundity only through their effects on female body mass at emergence. As there were no significant differences between the data sets, the three were combined and a regression of egg production against body mass carried out. A significant relationship was found between mass and egg production (slope = 6.57, t = 3.17; DF = 1, 82; $p<0.01$) which could be described by the equation shown below and is illustrated in Figure 5.7. This was a positive relationship in which larger females produced more eggs.

Table 5.15 Analysis of covariance of log transformed fecundity data.

Source	DF	Mean square	F	P
Mass	1	0.7871	5.20	<0.05
Toxin	2	0.0231	0.15	ns
Experiment number (Exp no.)	1	0.0017	0.01	ns
Toxin * Exp no. interaction	2	0.1269	0.84	ns
Error	77	0.1513		
Total	83			

Egg production = 53.1 + 6.57 * Mass

Regression analysis of the mean number of eggs per batch also showed a significant relationship with size ($t = 3.08$; $Df = 1, 82$; $p<0.01$). Thus the larger females produced more eggs in total and also produced more eggs per batch than smaller females.

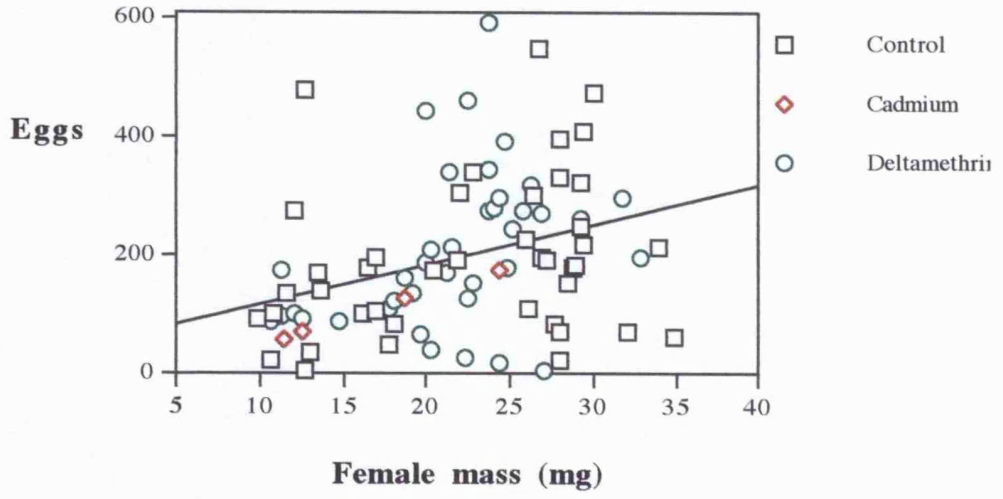


Figure 5.7) The relationship between female mass at emergence and lifetime egg production of female flies reared under the three experimental treatments

Despite the lack of significance between the mean number of eggs per breeding female there did appear to be a difference in the number of females producing eggs. In the case of the control and deltamethrin treatments, just under sixty percent of the females reared produced eggs. The figure for cadmium was much lower than this (18.18%). A Chi-squared test was carried out to test for significant difference (Table 5.16). This analysis gave a significant result (Chi-squared = 12.58, DF = 2, $P<0.05$).

Table 5.16 Chi-squared analysis of the number of females, combined from experiments two and three, from each of the three treatments producing eggs.

	Control	Cadmium	Deltamethrin
Observed number of females laying eggs (expected number)	42 (38.28)	4 (11.70)	38 (34.03)
Observed number of females not laying eggs (expected number)	30 (33.72)	18 (10.30)	26 (29.97)

In the case of both the control and deltamethrin treatments more females than expected produced eggs whilst in the cadmium treatment fewer females than expected produced eggs. Thus, whilst not significantly reducing the mean number of eggs per breeding

female, the number of breeding females was significantly reduced.

Further analyses, using general linear models, were carried out upon log transformed data of mean number of egg batches per laying female, mean number eggs per batch and the mean time to production of the first egg batch. No significant differences were found. The simple means of these fecundity measurements are presented in Table 5.17 along with other descriptive statistics.

Table 5.17 The mean lifetime fecundity of the females from the three treatments of both experiments averaged over larval diet and experiment. Means are simple means, not fitted means from a general linear model.

	Control		Cadmium		Deltamethrin	
	Exp 2	Exp 3	Exp 2	Exp 3	Exp 2	Exp 3
Total number of females	33	39	16	6	31	33
Number of females laying eggs	16	26	3	1	14	24
% females laying eggs	48.48	66.67	18.75	16.66	45.16	72.72
Total number eggs	3202	5000	361	70	1982	5859
Mean number of eggs per laying female	200.12	192.31	120.33	70	141.57	244.12
Mean number of egg batches per laying female	1.87	2.5	1.33	2	2.14	2.58
Mean number of eggs per batch	106.73	76.92	90.25	35	66.07	94.50
Mean time to production of first egg batch after adult emergence	16.67		16.00		15.50	

The mean time to production of the first egg batch was similar in all three treatments. The first batches were produced five days after the adults emerged in both the control and deltamethrin treatments. In the cadmium treatment the first batches were produced after six days. The last egg batches were produced after approximately 60 days for both the control and deltamethrin treatments. The last batch from the cadmium treatment was produced after 39 days.

Using the figures in Table 5.17 a mean daily egg production per laying female can be calculated based upon the mean longevity of the flies from each treatment. The control flies had an overall mean longevity of 23.91 days giving a mean daily egg production of 8.21 eggs/laying female/day; the flies from the cadmium treatment had an overall mean longevity of 19.71 days and a mean daily egg production of 4.83 eggs/laying

female/day; the deltamethrin treatment flies had an overall mean longevity of 26.20 days and a mean daily egg production of 7.36 eggs/laying female/day.

This gives a very simple overview of egg production by predicting the average number of eggs produced each day by a given percentage of the female flies. The reality of the situation is far from this but is difficult to quantify. On the following pages are graphs that illustrate the observed egg production from flies of the different treatments during the two different experiments. Figure 5.8 illustrates the egg production observed from the control treatment during the second experiment. It is clear that there is not a constant daily production of eggs over the course of the experiment (Figure 5.8 a, b). The majority of egg production can be seen to occur between days 20 and 40 (Figure 5.8 c); day 0 is the day on which the egg from which the female arose was laid. Eggs were not produced every day and, when eggs were produced, the number of flies laying them was always low (Figure 5.8 d). This same general trend can be seen for the cadmium treatment (Figure 5.9 a-d) and the deltamethrin treatment (Figure 5.10 a-d).

The results for the control treatment of experiment three (Figure 5.11 a-d) and deltamethrin treatment (Figure 5.12 a-d) show much the same pattern except that the onset of egg laying is slightly later. The data for the cadmium treatment of experiment two are not presented as only one female produced eggs. Another way of describing this egg laying behaviour would be to calculate a probability of eggs being produced on any given day, by how many flies and of how many eggs. These parameters are required for the next chapter in which the long-term population dynamics of the blowflies, under control conditions and exposed to cadmium, will be modelled.

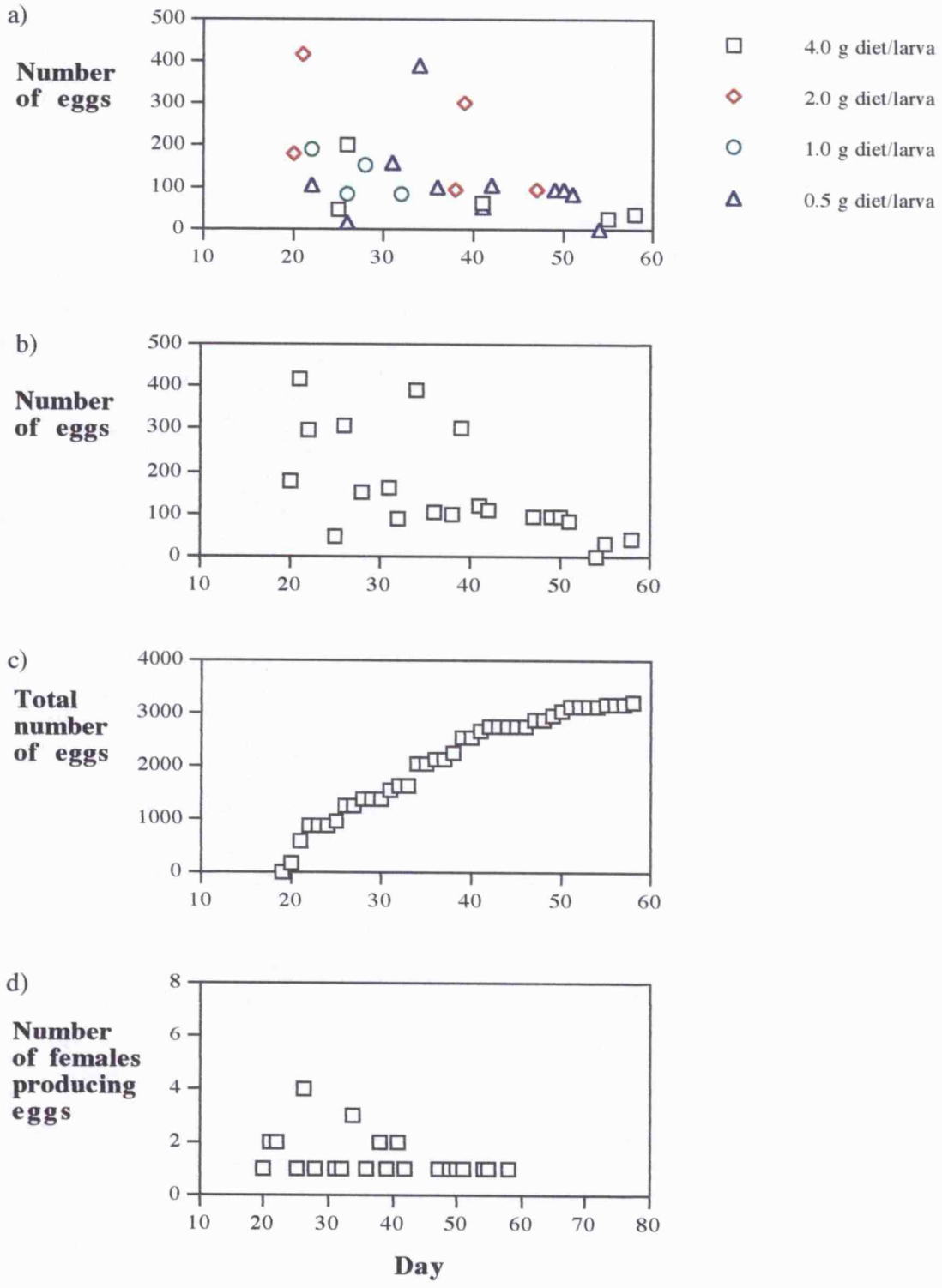


Figure 5.8) The fecundity data from the control treatment of experiment two during which 16 females produced eggs. a) The number of eggs produced by females arising from each population density; b) the total daily egg production; c) the cumulative egg production; d) the number of females producing eggs on any given day. Day '0' was the day of oviposition.

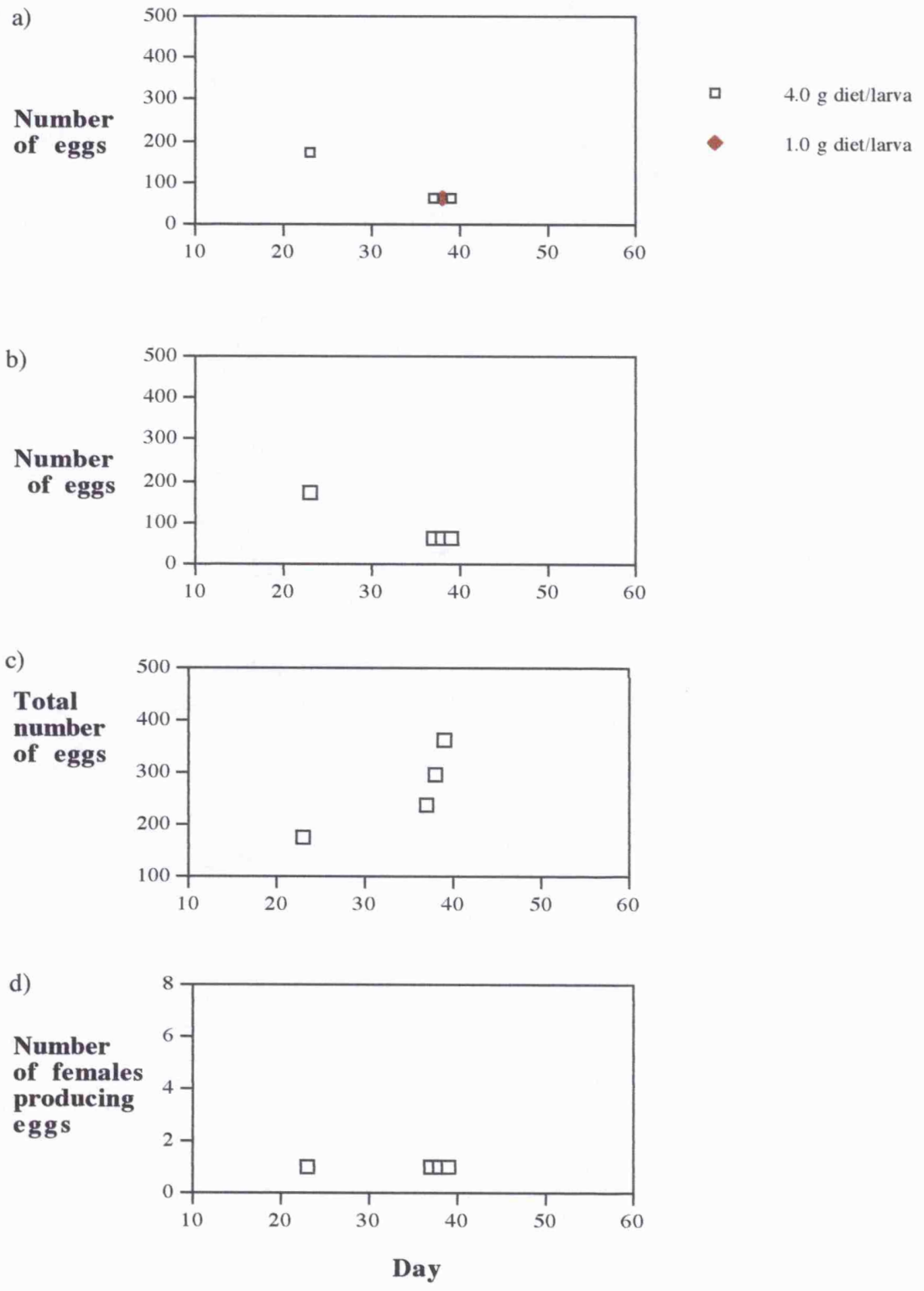


Figure 5.9) The fecundity data from the cadmium treatment of experiment two during which only three females produced eggs. a) The number of eggs produced by females arising from each population density; b) the total daily egg production; c) the cumulative egg production; d) the number of females producing eggs on any given day. Day '0' was the day of oviposition.

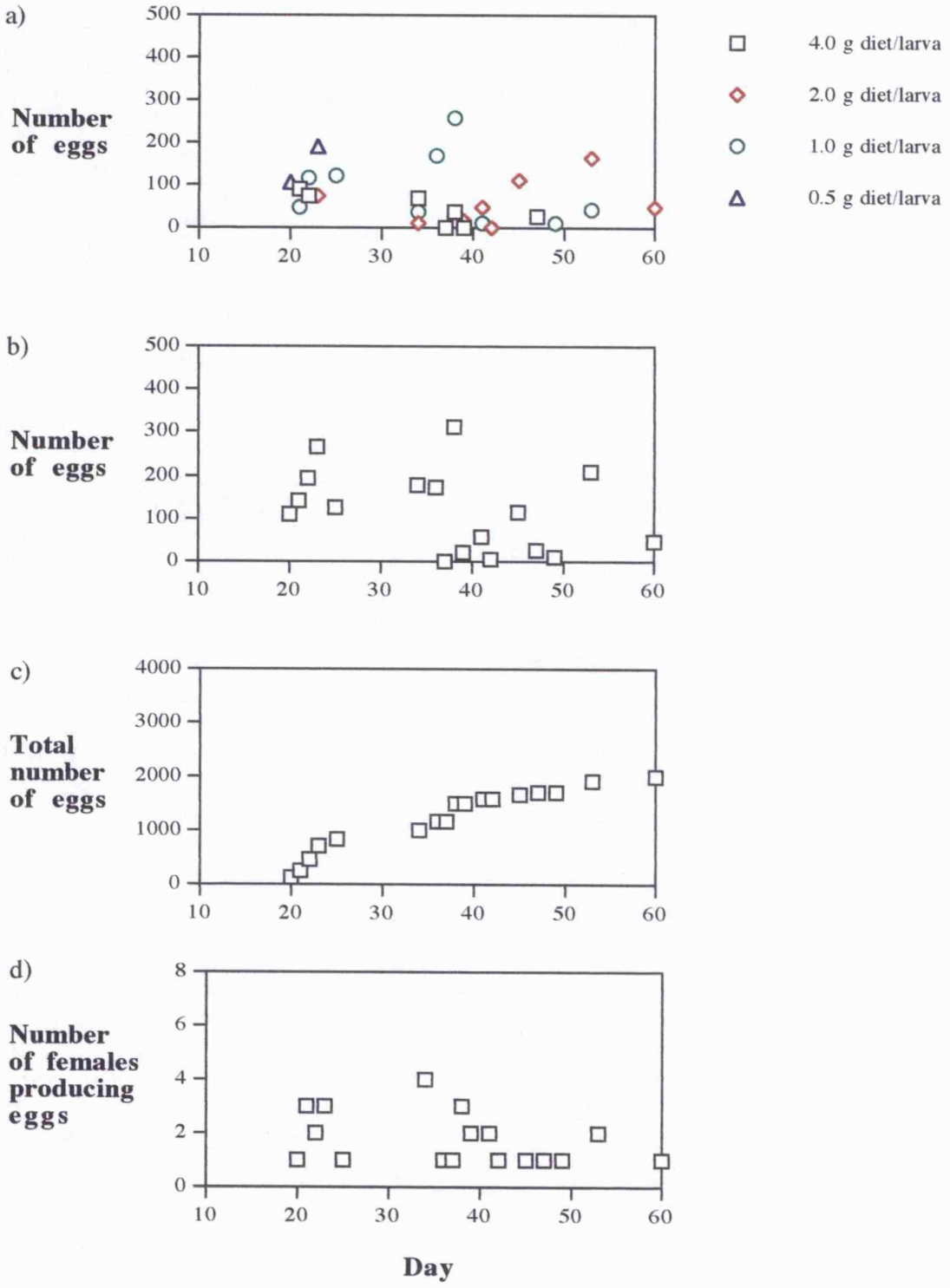


Figure 5.10) The fecundity data from the deltamethrin treatment of experiment two during which 14 females produced eggs. a) The number of eggs produced by females arising from each population density; b) the total daily egg production; c) the cumulative egg production; d) the number of females producing eggs on any given day. Day '0' was the day of oviposition.

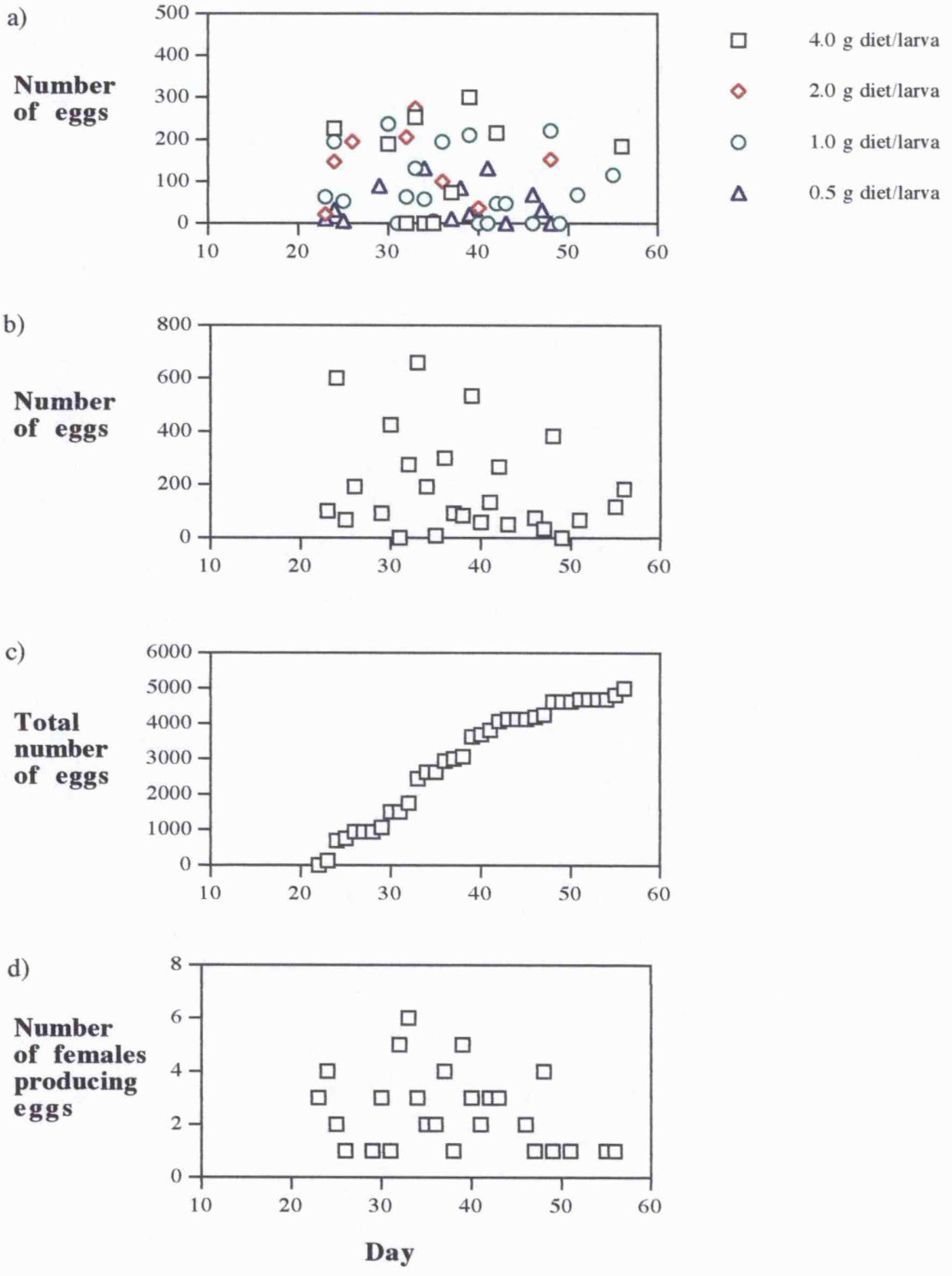


Figure 5.11) The fecundity data from the control treatment of experiment three during which 26 females produced eggs. a) The number of eggs produced by females arising from each population density; b) the total daily egg production; c) the cumulative egg production; d) the number of females producing eggs on any given day. Day '0' was the day of oviposition.

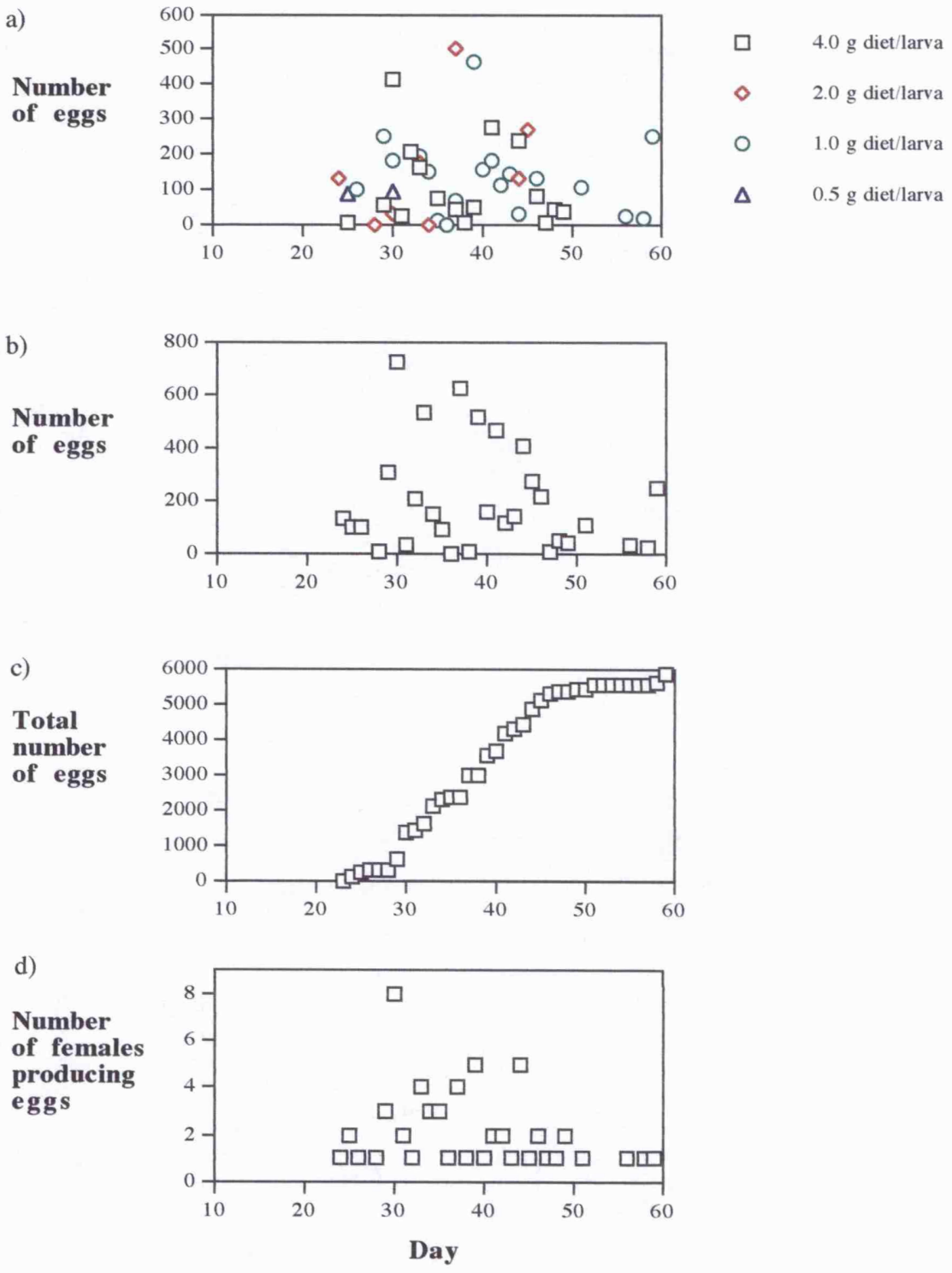


Figure 5.12) The fecundity data from the deltamethrin treatment of experiment three during which 24 females produced eggs. a) The number of eggs produced by females arising from each population density; b) the total daily egg production; c) the cumulative egg production; d) the number of females producing eggs on any given day. Day '0' was the day of oviposition.

5.4 DISCUSSION

5.4.1 The effects of increasing larval population density and the presence of toxins in the larval diet upon the growth and development of the larvae

The daily measurements of larval mass revealed clear trends within and between treatments. The control larvae from all densities acted as expected, the larvae all reaching their peak mass five days after oviposition. Peak mass decreased with increasing population density, which can be explained in terms of scramble competition, reducing the amount of food available to each larva. The depression in the peak mass of the larvae demonstrates a reduction in the scope for growth, caused by the reduction in food intake.

The larvae reared on the cadmium diet showed depressed larval peak masses. These larvae were subject to scramble competition and also had the additional stress of cadmium in the diet. The depression in peak mass was greater than expected from competition alone. Cadmium reduces the metabolic rate (Chapter 4) and also slows down development so that the peak mass was not reached until day six of the experiment at the lower population densities. At the two highest densities the peak mass was reached on day five. The growth period may have been cut short by depletion and desiccation of the food. Had the larvae grown more quickly they may have been able to make maximum use of the resource. The lower peak mass may also be partly due to a reduced food intake caused by high levels of cadmium in the diet.

The larvae from the deltamethrin treatment showed the same general trend as the control larvae but at all densities their mass was reduced. In chapter 4, I did not detect a physiological difference caused by deltamethrin. Based on the peak mass results, it would seem likely that although no significant increase in the respiration rate was found, there may have been an alteration in the energy budget of the larvae. As the peak mass of these larvae was reduced, there would appear to have been less energy used for growth. It is possible that food intake was reduced, or that energy may have been diverted from growth to detoxification. The respiratory rate observed in the deltamethrin treatment was higher, though not significantly, so there is some suggestion of a metabolic cost of detoxifying deltamethrin.

The peak mass of the control larvae was significantly higher than the mass of larvae from the same density on the following day, and all larvae ceased feeding at approximately the same time. In the case of both the cadmium and deltamethrin this was

not true at all densities. The curves produced showed that the peaks in larval mass were less marked because of variability in the duration of the feeding phase; in both cases there were some larvae that were still feeding on day six and seven of the experiment. Thus it would appear that both toxins had some effect in slowing down larval growth. This adds further support to the idea that the toxins reduce the ability of larvae to exploit the resource as efficiently as the control larvae.

The decreased rate of development could have implications for the ecology of these larvae under natural conditions. *L. sericata* is an early coloniser of carcasses, arriving while the carcass is still reasonably fresh. By arriving at a carcass early the larvae may avoid competition with species that arrive at a patch later on. For example *Sarcophaga* species have been shown to have a preference for carcasses that are 4-6 days old. At this stage, larvae of *L. sericata* could be at the end of their growth phase, depending upon ambient temperature, and might no longer be feeding when the competing species arrives. Any factor that prolonged their feeding phase could increase the levels of interspecific competition they are exposed to and so lower their chances of survival.

The results for peak mass were repeatable with no significant difference occurring between the two experiments in terms of either the effects of density, toxin, or the density/toxin interaction. In contrast, estimates of some other parameters changed between experiments carried out at different times.

The mass of pupae, not surprisingly followed the same trend as the peak larval mass with cadmium giving rise to the smallest pupae and those of the control and deltamethrin being closer, though again the control pupae had the highest mass. The results obtained regarding size are largely in agreement with the results of Daniels *et al.* (1991) and Simkiss *et al.* (1993). The same explanation for reduction in peak larval mass may be applied here.

The suggestion above is that the toxins slow larval development down which should be reflected in the egg to adult development period. The results show that overall the control larvae and pupae developed the quickest, cadmium the slowest and deltamethrin again giving values between the two. The effect of increasing population density in all treatments was to decrease the total development time. Those larvae at a density of 0.5 g diet/larva developed the most quickly. This again supports the idea that at high densities, or on a small resource patch, rapid development is required along with the plasticity in the life history to allow pupation at a range of sizes. The emergence data showed that the presence of cadmium or deltamethrin also decreased the numbers of adults emerging at the higher densities.

The analysis of variance showed that the development time was variable and differed significantly between experiments. A small difference between the two experiments may be attributed to the collection time of the eggs. For example eggs collected in the morning in one experiment and during the afternoon in the next would still be recorded as one day old the next day. This may allow for a small degree of difference (± 6 hours) but not for the large differences observed between the results from the two experiments. A possible explanation may be that the egg batches collected for use in the two experiments had varying degrees of 'fitness'. Certainly the parentage of the eggs may be different and the age of the parents may be different. These results show that the development rate of the flies cannot be predicted reliably.

5.4.2 Longevity and fecundity of the adult flies

The effects of population density and toxin were to reduce the mass of the resultant adult flies. An allometric relationship was expected between mass and longevity, which might differ between the three treatments. No relationship was found between mass and longevity, however, indicating that mortality of adults must have been primarily due to some other cause. There may be no relationship between mass and longevity in blowflies under the conditions used in these experiments.

The longevity of the adult flies was reduced when the larvae had been reared on a diet containing cadmium, although the longevity was only significantly different from that of the deltamethrin treatment. The longevity data, like the development period data was variable between the two different experiments. The overall means for both the control and deltamethrin treatments were significantly higher during the second experiment whilst those from the cadmium treatment were not significantly different. This may again reflect a variability in fitness from one batch of eggs to another and possibly even a variance in the tolerance of the flies to deltamethrin.

The measurements of fecundity failed to show any difference between the treatments when body size were removed as a covariate. The strong correlation of lifetime fecundity with size does have ecological implications. The effect of the toxins in reducing the adult mass and especially the effect of cadmium in reducing the survival to the adult stage were discussed earlier. If these data on growth and survival to emergence are now combined with fecundity data, the full potential impact of toxins on natural populations can be considered. In the case of cadmium, for example, a contaminated carcass may give rise to only a few small individuals. The majority of the flies arising may not produce eggs and the egg production in females producing eggs would be limited by their small size. The overall effect may be a reduction in the

abundance of that fly species in a contaminated area. The effects upon the long term population dynamics will be considered in chapter six.

A general overview of the fecundity data shows that the fecundity values observed even for the control flies were much lower than some published data. Mackerras (1933) studied fecundity in a single pair of *L. sericata* supplied with sugar, water and liver. The first batch of eggs was produced after six days, as did some flies from my experiment. A total of thirteen egg batches were produced giving rise to a total of 2219 adult flies, almost as many as the total number of eggs produced from one of the experimental treatments in this work. Similar high values are given by Smith (1986). Daniels *et al.* (1991) showed that a single female *L. sericata* may produce up to 2000 eggs in its life; these females were fed upon lamb. Why were the fecundity values observed in my experiment so much lower than these two examples?

One explanation may be that the parents of these eggs had a lower fecundity caused by generations of inbreeding in the stock cage. To test for this comparisons with a wild stock would need to be made. Alternatively the lowered fecundity may be due to the artificial fly diet that they were given. In these other works where high fecundity values are given the flies were fed on liver. It is possible that although the diet is sufficient to raise the larvae, it is in some way deficient for egg production. Comparisons would need to be made between flies supplied with the artificial diet and those supplied with liver to test for this.

CHAPTER 6 POPULATION DYNAMICS

SECTION INDEX

		Page
6.0	ABSTRACT	133
6.1	INTRODUCTION	133
6.1.1	Introduction and aims	133
6.1.2	Basic population dynamics	134
6.1.3	Nicholson's blowflies	136
6.1.4	Daniels blowflies	136
6.2	METHODS	138
6.2.1	Life-table analysis	138
6.2.2	Measurement of the density-dependent mortality	139
6.2.3	Autocorrelation analysis	140
6.2.4	Assumptions used in computing the population-dynamics simulation model	140
6.3	RESULTS	142
6.3.1	Life-table analysis	142
6.3.2	Summary of the fecundity values measured in the restricted density experiments carried out in Chapter 5 that are used as parameters in the population model	144
6.3.3	Calculation of the density-dependent mortality during the development period	144
6.3.4	The egg-to-adult developmental period	145
6.3.5	The relationship between larval population density and mean pupal mass	146
6.3.6	The population simulation model	148
6.3.7	The deterministic simulation model of the control population dynamics with estimates of parameters calculated from the experiments	153
6.3.8	The effect of varying the mean pupal mass cut-off	154
6.3.9	The effect of varying mean adult longevity	158
6.3.10	The effect of varying egg production	161
6.3.11	The effect of varying the strength of density-dependence	164
6.3.12	The effect of varying the egg-to-adult developmental period	167
6.3.13	The population dynamics predicted by the stochastic model and comparisons of the control and cadmium populations	170

6.3.14 Comparisons of the models using the mean number of adults present, mean pupal mass, and pupal cohort biomass predicted by the control and cadmium models..... 173

6.4 DISCUSSION..... 178
6.4.1 The development time and density-dependent mortality..... 178
6.4.2 The parameter estimates used in the model..... 178
6.4.3 The driving forces of the dynamics..... 180
6.4.4 The performance of the stochastic models..... 182

6.0 ABSTRACT

Construction of a deterministic population simulation model allowed the dynamics underlying the population fluctuations of *L. sericata* under conditions where the larval food was limited to be identified. The basic dynamics were shown to be stable two point limit cycles. Factors important in determining the features of these cycles were identified and these included the mean pupal mass cut-off, adult longevity, egg-to-adult development time, fecundity and the strength of the density-dependent mortality of larvae during their feeding phase. The model was then expanded to include a stochastic element, replacing the constant daily production of eggs, which made the egg laying events less regular. The stochastic element disrupted the stable limit cycles and generated dynamics that agreed very closely with the observations made in the previous studies of Daniels (1994) in terms of both adult numbers, mean mass of individual pupae, and period of the cycles. When the effects of cadmium in the larval diet were modelled the results showed that the cycles were virtually destroyed. The predictions of mean individual pupal mass and cohort biomass gave rise to values higher than those predicted by the control model and as such contradicted the predictions made by scope for growth theory.

6.1 INTRODUCTION

6.1.1 Introduction and aims

In Chapter 4 the effects of the toxins upon metabolic rate were demonstrated, and the way in which these metabolic effects manifest themselves in individual larvae and adults were demonstrated in Chapter 5. In this chapter the effects of the toxins were considered at the next level, the long-term population dynamics.

Based upon the predictions made by the 'Scope For Growth' theory, the cost of detoxifying or otherwise dealing with a toxicant reduces the scope for growth, and therefore mean biomass averaged over population fluctuations should be reduced in the presence of a toxicant. This was not the case, however, in the long-term laboratory populations of *L. sericata*. Daniels (1994) showed that the mean biomass of pupal cohorts in populations maintained on a diet containing cadmium was significantly higher than that of the control populations; in addition the mean mass of pupae from the cadmium populations was also significantly higher than the control populations.

In this chapter a simulation model of the population dynamics was developed, using life-history parameters estimated in this chapter and Chapter 5. The model was used to probe the population dynamics. First a deterministic model was used to identify the underlying processes driving the dynamics. Second a stochastic model was used to try to reproduce the type of population dynamics observed in long term population studies. Once the model had been constructed and tested, the effect of introducing a toxin into the system was investigated. During this chapter the populations considered were control populations and populations exposed to a diet containing 50 mg/kg cadmium. These treatments were used since data relating to the long term dynamics were available from the work of Daniels (1994).

6.1.2 Basic population dynamics

At its most basic level, a population might grow in a geometric manner with a constant growth rate. Under such conditions the population would grow exponentially without limit to an infinite size. This is not the case with real populations. Limits do occur and growth of the population cannot occur continuously. A simple way of describing such limited population growth is by a form of the logistic equation (equation 1).

$$N_{t+1} = (N_t * R) / (1 + aN_t) \quad \ldots\ldots 1$$

Where N_t = the number of individuals at time t
R = the net reproductive rate
a = (R-1)/ the carrying capacity

Using this equation population growth occurs rapidly whilst the population density is low and a population decreases when the density is high. Population increase will continue until the carrying capacity is reached, at which point a stable equilibrium is reached between births and deaths *i.e.* there is an exact compensation for any fluctuations in the population number. The resultant population growth curve produced

is the well known 'sigmoidal curve'. Thus, the growth of the population is density-dependent. This simple view of the dynamics assumes that the response to population density is not delayed and it also only allows for one type of competition, which gives rise to exact compensation.

The model can be expanded to allow for different types of competition by raising the second part of the equation to the power of 'b' (equation 2), . This value describes the type of compensation that occurs. If b = 1 then there would be an exact compensation for any population fluctuation. This would result if there was pure contest competition which would give rise to a constant number of survivors. In contrast if b >> 1 then the competition may be of the pure scramble type in which, at high densities, no animals gain sufficient resources to survive, there is an over compensation.

$$N_{t+1} = (N_t * R) / (1 + aN_t)^b \quad \text{.....2}$$

By incorporating b into the equation the resultant curves can show a wide variety of dynamics. May (1975) described the dynamics observed when different values of R and b are used. When b = 1 the population shows 'monotonic damping' in which the population gradually approaches the carrying capacity and then exists at a constant equilibrium. When the values of R and b are increased the dynamics change first to show 'damped oscillations' which gradually approach the carrying capacity. At higher values 'stable limit cycles' are obtained, the population fluctuates around the carrying capacity in a regular manner. Finally, with high values of R and b the populations fluctuate in a chaotic manner.

Hassell, Lawton and May (1976) cited data for 26 insect species and fitted these data to a form of equation 2 discussed by Hassell (1975). 23 of these species seemed to show monotonic damping. Parameter estimates for the mosquito *Aedes aegypti* (L.) showed damped oscillations and stable limit cycles for the colorado beetle *Leptinotarsa decemlineata* (Say). A population of *Lucilia cuprina* (Weid.) gave parameter estimates that were within the chaotic region. Thus it is clearly demonstrated that the reproductive rates and type of competition are very important in driving the population dynamics.

Another important feature of population dynamics is that there may be a delay between the cause of a response and the response itself. For example an abundance of food in one generation may lead to a great increase in the size of the next generation. This may result in an over crowding of the food source and subsequently a population crash. Such a delayed density-dependent factor may also result in population fluctuations.

6.1.3 Nicholson's blowflies

Nicholson (1954 a, b) studied the population dynamics of the blowfly *L. cuprina*. In a series of experiments Nicholson exposed populations to different stresses and showed that they could respond to these stresses and maintain themselves in a state of balance. In one experiment the larvae were given excess food whilst the adult flies were only supplied with 0.5 g liver per day (sugar and water were not limited). Nicholson found that by killing different proportions of the emerging adults, thus altering the adult population density, the number of pupae could be varied. When 90% of the emerging flies were killed the maximum number of pupae was obtained, while the minimum number of pupae was obtained when none of the emerging flies were killed. In order to produce eggs the females needed to obtain sufficient protein. With the protein source being limited the number of females gaining sufficient protein to mature oöcytes was reduced when the population density was high, hence fewer pupae were produced.

In another experiment Nicholson gave the adults unlimited liver but limited the larval food to 50 g liver per day. Again adult flies were killed. When no adults were killed the number of hatching larvae per day was highest (8794) but the number of resultant adults was the lowest (157). When adults were killed the number of eggs laid was reduced and larval competition for the food was reduced; consequently the number of resultant adults increased as more larvae could gain sufficient food to complete development.

Nicholson then went on to consider the long term dynamics of a population in which the adult protein source was limited to 0.5 g liver per day. The populations showed regular oscillations. The fall in numbers of the adult population was due to the fall in egg production and hence adult recruitment. Nicholson recognised that the cycles were at least in part due to the time lag between the stimulus and the reaction caused by the long development period. He stated that if the adult flies were to come into being immediately that the system would be non-oscillatory as the population growth would respond immediately to the prevailing population-density conditions. Thus from the work of Nicholson it can be seen that competition in both the larval and adult stages may be responsible for causing population fluctuations.

6.1.4 Daniels' blowflies

Daniels (1994) maintained replicate populations of *L. sericata* in closed cages under conditions in which the larval food only was limited. Larvae in one series of six cages were fed on a control diet, as used throughout these experiments (see Chapter 2), and

in another series of six cages diet containing cadmium at a concentration of 50 mg/kg was used. The number of larvae and adults was recorded over a period of 768 days. The results for the control experiments showed that the populations fluctuated greatly, and autocorrelation analysis showed a periodicity of around 68 - 70 days. In none of the population cages were double peaks in the adult numbers observed. In Nicholson's work the adult numbers showed double peaks that were explained by age-specific variations in adult survival. Gurney, Blythe and Nesbit (1980) attributed the double peaks to the presence of two discrete generations per cycle. Daniels (1994) explains the absence of the double peaks from her data by the difference in periodicity, Nicholson's populations cycled over 35-40 days. The long-term changes in the adult numbers are illustrated in Appendix 5.

It had been predicted that the populations maintained on the cadmium diet would show damped oscillations because cadmium would reduce the per capita rate of increase. The presence of cadmium, however, appeared to have destroyed the cycles that were clearly evident in the control populations. The number of adults in the polluted populations fluctuated around a lower mean than that of the unpolluted populations. Interestingly, the mean mass of individual pupa obtained from the cadmium treatment (20 mg) was significantly higher ($P<0.05$) than that of the control treatment (18 mg); similarly the mean biomass of the pupal cohorts was significantly higher in the polluted cages.

The aim of this chapter was to construct a simple spread-sheet model, that incorporated all aspects of the blowflies life-history, to study the main driving forces underlying the long-term population dynamics of this species. By constructing a model in this manner the effects of toxins upon the dynamics, through their effects upon the larval and adult stages, could be investigated.

6.2 METHODS

6.2.1 Life-table analysis

In Chapter 5 the results from two experiments were reported. These experiments examined the response of larvae to the presence of toxins in their diet and to increasing population density. The population densities used were very limited in comparison to those used in this chapter (see section 6.2.2). At the start of the results section in Chapter 5 reference was made to a third experiment in which the deltamethrin gave unexpectedly high mortalities, possibly due to concentration of the stock solution through evaporation. The data for the control and cadmium treatments of that experiment were not included in the results section. In this chapter the control and cadmium treatment results for all three experiments were used for life-table analysis (Andrewartha and Birch (1954)). Estimates were made of the generation time (T), the net reproductive rate (R_0) per female and the intrinsic rate of increase per generation (r). The definitions of these parameters and their derivation are given below.

Generation time (T). This is the mean time from the birth of the parents to the birth of their offspring.

$$\textbf{Generation time (T)} = \frac{\sum l_x m_x x}{\sum l_x m_x}$$

Net reproductive rate (R_0). This is the multiplication rate per generation.

$$\textbf{Net reproductive rate } (R_0) = \sum l_x m_x$$

Intrinsic rate of increase per generation (r). This is approximated by the natural logarithm of the net reproductive rate (Andrewartha and Birch (1954).

$$\textbf{Intrinsic rate of increase per generation } (r) = \ln (R_0)$$

Where:

- x = age
- l_x = the proportion of individuals alive of age x
- m_x = the number of female eggs produced per female of age x

The analysis was carried out upon the combined data of all densities for each treatment from each experiment. Thus for experiment 1, life-table analysis was carried out upon all of the control data (four densities combined) and all of the cadmium data (four densities combined). This procedure was repeated on the data from all three experiments. The data were not split into individual densities as there were insufficient numbers of individuals to do this (each density was represented by three replicates of eight individuals). The life-table analysis was carried out using a spread sheet in Microsoft Excel®. Comparisons between the control and cadmium treatments were made using one-way analysis of variance in Minitab®.

6.2.2 Measurement of the density-dependent mortality

The aim of the model developed later in this Chapter was to simulate the population dynamics of blowflies kept under constant conditions under which the larval diet was replaced every two days with a fresh 20 g block of fly diet (see Chapter 2 for method of making the diet). In order to develop the model it was necessary to study how mortality varied with increasing population density. To investigate this replicates were used in which 25 larvae were placed upon blocks of diet with a mass of 40 g, 20 g, 10 g, 1 g, 0.5 g, 0.25 g and 0.1 g, which were replaced every two days whilst larvae were still present. Using blocks of diet with these masses allowed population densities of 12.5, 25, 50, 500, 1000, 2000 and 5000 larvae per 20 g block of diet per two days to be simulated. These blocks of diet were placed into plastic tubs (10 cm * 5 cm) each with a perforated lid. As small blocks of diet were being used, a 5 ml beaker containing water and tissue paper was placed inside to humidify the air to reduce the risk of the smaller blocks of diet from drying out. The experiment was carried out five times. In each experiment one replicate of each of the seven population densities was tested for both control and cadmium diet. At each diet change the larvae were counted and the number and mass of any pupae recorded. The pupae were placed into a separate container and checked daily, the day of adult emergence was recorded.

The proportions of flies surviving from each replicate and treatment were compared using a general linear model analysis of variance to see if there was a significant difference between the survival of the control and cadmium treatments. In the absence of a difference between the treatments the survival data of the two treatments would be combined. In order to describe the density-dependent mortality the best fit linear regression was sought using different transformations of the data.

The pupal mass data collected for each replicate could be treated in a similar manner, except that the mass data were $\log_{10}$ transformed. Again the best fit linear regression

was sought. The inclusion of this regression in the model allowed the mean pupal mass to be estimated at any given larval population density.

6.2.3 Autocorrelation analysis

Autocorrelation analysis was carried out upon the time-series data generated by the models. This analysis detects cyclic behaviour in time-series data. This is achieved by comparing data points at increasingly distant points in the data set with each other. The maximum distance between data points is set by determining a 'lag' in the analysis. For example with a lag of 70, the first data point would be compared with the 70th, the second with the 71st *etc.* until the whole data series has been covered. For each comparison made an autocorrelation function (ACF) is stored. This is a measure of the strength of the correlation between lagged points points. An ACF of 1.0 would indicate the strongest correlation whilst weak correlations approach 0.

Plotting these ACF values against the lags gives rise to a curve. If the data showed stable limit cycles the curve would resemble a sinusoidal wave. The peaks of the curve represent periodicities. If the peaks of the curve were at 60, 120 and 180 lag units, a fundamental period of 60 lag units would be indicated (120 and 180 would be harmonics of the fundamental period). The lag units used in this chapter were days and in this example the period of the cycles would thus be 60 days. The steepness of the curve from the maximum value to a value of 0 reflects the strength of the periodicity.

6.2.4 Assumptions used in computing the population-dynamics simulation model

The model was constructed in a spreadsheet format using Microsoft Excel® with different columns assigned to calculating different values. The model is described in the results section once all of the parameter estimates have been made. A brief account is given here of the assumptions used in the model.

a) The adult population will be subject to a constant daily mortality. The daily mortality rate was calculated using the longevity data from the experiments described in Chapter 5. These are summarised in this chapter in Table 6.6.

b) On any given day, once the female flies have reached sexual maturity, there is a chance that the females will lay eggs. On days that eggs are produced a certain percentage of sexually mature flies will produce eggs. The probability of egg-laying events, the number of females laying eggs and the mean number of eggs in a batch were

calculated using the data from the experiments carried out in Chapter 5, again these are summarised in Table 6.6.

c) Larvae will be exposed to intense scramble competition during their feeding phase and will suffer density-dependent mortality. The duration of the feeding phase was taken from the experiments in Chapter 5. The density-dependent mortality factor was estimated using the method described in section 6.2.2.

d) There will be a fixed development period before the adults emerge. The egg-to-adult development period was estimated during the experiments described in section 6.2.2.

6.3 RESULTS

6.3.1 Life-table analysis

Although the experiments carried out in Chapter 5 were over a restricted range of population densities, in comparison to those used in this chapter for measuring the density-dependent mortality of the larvae (section 6.2.2), it is useful to include life-table analysis of the data from Chapter 5 as it gives estimates of the generation time and intrinsic rate of increase per generation (see Appendix 4). These parameters are important for the population dynamics. The intrinsic rate of increase was an approximation based on the net reproductive rate rather than by iteration of the Euler-Lotka equation (Chapter 7).

Analysis of variance of the generation-time data (Table 6.1) showed that there was no significant difference between the cadmium and control treatments, the mean generation times are given in Table 6.2. Analysis of variance of the estimated intrinsic rate of increase per generation data was not appropriate as the variance was not equal between the treatments. To overcome this problem the analysis was carried out upon the net reproductive rate data after they had been square root transformed. The analysis of variance of these data (Table 6.3) showed that there was a significant difference between the two treatments. The mean value for the cadmium treatment was significantly lower than the control (Table 6.4).

Table 6.1 The analysis of variance of the generation time of flies reared from different larval population densities on the control and cadmium diets.

Source	DF	Mean square	F	P
Treatment	1	2.7	0.16	>0.5
Error	4	17.1		
Total	5			

Table 6.2 The mean generation times (days) calculated for flies reared on the cadmium and control diet. The standard error based upon the pooled error mean square is 1.17 for each mean.

Treatment	N	Mean
Control	3	36.026
Cadmium	3	34.682

Table 6.3 The analysis of variance carried out upon square root transformed net reproductive rate from the control, and cadmium experiments.

Source	DF	Mean square	F	P
Treatment	1	20.82	11.49	<0.05
Error	4	1.81		
Total	5			

Table 6.4 The means of the square root transformed net reproductive rate from the control, and cadmium experiments. The standard error based upon the pooled error mean square is 0.67 for both means.

Treatment	N	Mean
Control	3	5.792
Cadmium	3	2.067

A summary of the life-table parameters calculated from the three experiments carried out in Chapter 5 is given below in Table 6.5. The highest net reproductive rate was demonstrated by the control data in experiment 3, *i.e.* over one generation the population could increase by a factor of 52. This provides an especially sharp contrast with the cadmium data from the same experiment, which predicts that the population would decrease in size over the same period.

Table 6.5 A summary of the estimated values of life-table parameters calculated from the restricted density experiments carried out in Chapter 5.

CONTROL	Experiment 1	Experiment 2	Experiment 3
Generation time (days)	39.757	32.461	35.859
Net reproductive rate	19.292	33.348	51.987
Intrinsic rate of increase per generation	2.960	3.507	3.951
CADMIUM			
Generation time (days)	33.567	30.778	39.700
Net reproductive rate	11.604	3.760	0.729
Intrinsic rate of increase per generation	2.4514	1.3245	-0.3159

6.3.2 Summary of fecundity values measured in the restricted density experiments carried out in Chapter 5 that are used as parameters in the population model

In Chapter 5 only the results of the second and third experiments were presented due to the high mortality in the deltamethrin treatment of the first experiment. Table 6.6 gives an overview of the three experiments, giving only the data for the control and cadmium treatments, and the final mean values used in the population model. The data labelled experiment one represent the data excluded in Chapter 5.

Table 6.6 The fecundity data from the control and cadmium experiments carried out in Chapter 5 used to estimate the parameters used in the population model. The mean mortality rates were fitted using a general linear model of analysis of variance.

CONTROL	Experiment 1	Experiment 2	Experiment 3	Mean
% of days on which eggs were laid after maturity was reached (5 days after emergence)	40.00	42.86	54.16	45.67
% mature females laying eggs on days when eggs were laid	3.25	4.33	6.41	4.66
Mean no. eggs per batch	80.53	106.73	76.92	88.06
% Daily adult mortality	3.90	4.76	3.70	4.07
CADMIUM				
% of days on which eggs were laid after maturity was reached (5 days after emergence)	28.28	11.76	7.41	15.82
% mature females laying eggs on days when eggs were laid	6.23	6.25	16.67	9.72
Mean no. of eggs per batch	65.53	90.25	35.00	63.59
% Daily adult mortality	4.06	5.13	5.08	4.70

6.3.3 Calculation of the density-dependent mortality during the development period

The data analysis in the following sections (to section 6.3.5) refers exclusively to the experiments described in section 6.2.2. Analysis of variance of the angular transformed survival data showed that there was no significant difference between the survival of

larvae reared under the different treatments. Population density did, however, have a significant effect upon survival (Table 6.7). As there was not a significant difference between the cadmium and control treatments a single survival calibration curve was sought. The best fit was obtained by transforming the proportion surviving to a natural log of the percentage surviving + 1. Regression of these transformed data showed a highly significant relationship between density and survival (DF = 1, 48; t = -20.30; P <0.001) and gave the regression equation (1) which was used to predict survival in the models for control populations and cadmium populations (in Chapter 5 survival was significantly different between the treatments).

$$\text{Natural log (\% surviving + 1)} = 4.48 - 0.00394 * \text{Larval density} \quad \ldots\ldots(1)$$

Table 6.7 The analysis of variance of the angular transformed survival data of larvae reared upon the control diet and the diet containing cadmium.

Source	DF	Mean square	F	P
Density	4	2.5277	95.23	<0.001
Treatment	1	0.0840	3.17	>0.05 <0.10
Density*Treatment	4	0.0044	0.16	>0.5
Error	40	0.0265		
Total	49			

6.3.4 The egg-to-adult developmental period

Analysis of variance of the egg-to-adult development period showed that there was no significant difference between the development times of animals from either treatment (Table 6.8).

Table 6.8 The analysis of variance of the natural log transformed data of the egg to adult development times.

Source	DF	Mean square	F	P
Density	4	0.31655	10.54	<0.001
Treatment	1	0.02029	0.68	>0.10
Density*Treatment	4	0.08144	0.68	>0.10
Error	33	0.99145		
Total	42			

Examination of the means (Table 6.9) showed that duration of the developmental period increased with increasing density. The mean development period of the control treatment was 18.4 days (rounded down to 18 in the model) and the mean of the cadmium treatment was 19.1 days (rounded down to 19 days in the model). These results differed from the results in Chapter 5 in which the highest population densities had the shortest development periods and in which there was a significant difference between the development periods of the two treatments.

Table 6.9 The mean egg to adult development time (ln days) of larvae reared upon the control and cadmium diet. The 95 % confidence intervals were calculated using the pooled error mean square.

Density (larvae/20 g diet)	Control	Cadmium	Mean (±ci)
12.5	2.83	2.86	2.85 ($\pm 3.97*10^{-5}$)
25	2.82	2.85	2.84 ($\pm 4.06*10^{-5}$)
50	2.82	2.89	2.85 ($\pm 3.93*10^{-5}$)
500	2.99	3.05	3.02 ($\pm 9.06*10^{-5}$)
1000	3.10	3.09	3.10 ($\pm 2.79*10^{-4}$)
Mean (±ci)	2.91 ($3.05*10^{-5}$)	2.95 ($3.25*10^{-5}$)	

6.3.5 The relationship between larval population density and mean pupal mass

Analysis of variance of the mean pupal mass, using $\log_{10}$ transformed data, showed that there was a significant difference between the control and cadmium treatment and that there was a significant difference between the different population densities (Table 6.10), the means are shown in Table 6.11. As there was a significant difference between the treatments separate linear regressions were carried out upon the data sets. The best fit was provided by plotting $\log_{10}$ mass against the cube root of the population density. For the control data (DF 1, 20; $t = -17.46$; $P<0.001$) the following regression equation was obtained.

Log_{10} mean pupal mass = 1.7699 - 0.076367 * (larval population density$^{0.33}$).....(2)

Regression of the data for the cadmium treatment gave the following regression equation (DF 1, 25; t = -15.31; P<0.001).

Log_{10} mean pupal mass = 1.7679 - 0.082463 * (larval population density$^{0.33}$).....(3)

Table 6.10 The analysis of variance of mean pupal mass of pupae from larvae reared upon the control diet and the diet containing cadmium.

Source	DF	Mean square	F	P
Density	4	4.4089	166.17	<0.001
Treatment	1	0.1441	5.43	<0.05
Density*Treatment	4	0.0503	1.90	>0.10
Error	35	0.0265		
Total	44			

Table 6.11 The mean log_{10} pupal mass (mg) of pupae from larvae reared upon the control diet and the diet containing cadmium.

Density (larvae/20 g diet)	Control	Cadmium	Mean (±ci)
12.5	1.597	1.581	1.589 ($\pm 3.13*10^{-5}$)
25	1.556	1.558	1.557 ($\pm 3.19*10^{-5}$)
50	1.483	1.436	1.459 ($\pm 3.10*10^{-5}$)
500	1.154	1.043	1.098 ($\pm 5.25*10^{-5}$)
1000	1.092	1.042	1.067 ($\pm 1.07*10^{-4}$)
Mean (±ci)	1.376 ($\pm 2.34*10^{-5}$)	1.332 ($\pm 2.45*10^{-5}$)	

In the model the larval population density was only considered to be important during the feeding phase of the larvae. In the control experiment the feeding phase lasted for four days. In the above equation then the larval population density is taken as the mean of the number of larvae present on the four days following emergence from the egg. In the cadmium model the feeding period was slightly longer and lasted for 5 days.

6.3.6 The population simulation model

Before illustrating the results obtained by running the model a brief description of how the model works is given. This includes the estimates of the parameters described in the previous sections. An example of the spread sheet used in the stochastic model is given in Table 6.12, and is used to give a worked example of how the calculations were carried out within the models.

Column 1 Day

This simply refers to the number of the day.

Column 2 Number of adults

This calculates the number of adult flies (N_t) alive on any given day t. The number present on the previous day is reduced by a constant daily mortality factor and increased by the number of newly emerged adult flies (Ne) predicted by column 8.

Number of adults (N_t) = (N_{t-1} * 0.9593) + Newly emerged flies (Ne_t)

For example the number of adult flies present on day 11 was 138. This figure was reduced by 4.07% on day 12 to 132.38, there were 19 new adult flies predicted by column eight on day 12 giving a total of 151.38 flies. The numbers of flies presented in Table 6.12 are rounded to integers.

In the cadmium model the daily mortality rate was 4.70%, thus on any given day the proportion of the flies alive from the previous day was 0.9530.

Column 3 The probability of egg production

This value calculates a random figure between zero and one. Eggs were produced on 45.67% of the days for the control model and 15.82% of the days in the cadmium model.

Column 4 Determines whether or not eggs are laid

The proportion of days on which eggs were laid was 0.4567. Thus, for eggs to be produced the value in column three must exceed a critical value 0.5433, in which case a value of one is given, otherwise it gives a value of zero.

In the cadmium model the proportion of days on which eggs were laid was 0.1582. Thus, for eggs to be laid the random number in column three had to exceed 0.8418.

Column 5 The number of eggs laid

This calculates the number of sexually mature females alive, assuming that the adult flies need to reach an age of five days to reach sexual maturity, and the number of females producing egg batches. This value is then multiplied by the mean number of eggs per batch to give a total number of eggs. The final figure is multiplied by column four.

This can be illustrated using Table 6.12. On day six eggs were produced (see column three and four). The number of females producing eggs was calculated first by calculating the number of sexually mature flies alive on day six. The only flies that could be at sexual maturity were already alive, or emerged, on day 1. The number of these flies alive on day six was calculated by multiplying the number of flies present on day 1 by the proportion of flies expected to be alive on day 6 *i.e.* 0.9593^5 (0.8124). The number of flies calculated by this term was divided by two to give the number of females. Of the females that were still alive only 4.66% were expected to produce egg batches with a mean number of 88.06 eggs. This was then multiplied by the value in column four, which was either 1 or 0.

Number of eggs (E) = (((Nt-5 * Daily survival^5) / 2) * proportion of females expected to lay eggs * mean number of eggs per batch) * Column 4.

Substituting data from Table 6.12

Number of eggs = (((197 * 0.8124) / 2) * 0.0466 * 88.06) * 1
= 328.375 eggs

In the cadmium model the term used to calculate the number of eggs was the same except that the number of sexually mature flies alive was given by 0.9530^5 and the mean number of eggs per batch was 63.59.

In the deterministic model the term column 4 is replaced by the term 1 - 0.5433. This term makes all fecund females lay the same number of eggs every day that they are alive after they have reached sexual maturity.

Column 6 The number of competing larvae

This calculates the total number of larvae feeding on any given day. It increases by the number of eggs laid on the previous day and decreases by the number of larvae that have reached the end of their feeding period. A feeding period of four days was used for the control animals and five days for the cadmium treatment. Thus, the eggs laid on day six hatch start feeding on day seven. There were already 718.42 larvae present on day seven, from previous egg batches, making the total number of feeding larvae 1046.80. On day eight the number of feeding larvae reduces as the larvae that began their feeding period on day four enter their wandering phase. Thus, the number of larvae feeding varies from day to day and can be calculated as follows.

$$\text{Number of larvae feeding at time } t = E_{t-1} + E_{t-2} + E_{t-3} + E_{t-4}$$

Using the data from Table 6.12 the number of feeding larvae present on day 6 can be calculated.

$$\text{Number of larvae feeding on day } 6 = 343.37 + 0 + 375.05 + 0 = 718.42$$

In the cadmium model the larvae were assumed to feed over a period of five days therefore the term E_{t-5} was added to the above expression.

Column 7 The proportion surviving

This calculates the proportion of larvae surviving to adulthood, from eggs laid in the time period t-x (where x = the egg to adult development period and t = time), based upon the mean larval population density that they have been exposed to during the feeding period. Thus, larvae from eggs laid on day six will feed on days seven, eight, nine and ten and compete with any other larvae present on these days, so the mean density that they are exposed to is simply the average of the larval densities present on these four days. The larvae from the eggs laid on day six were be ready to emerge as adults on day 24 (an 18 day development period). It was on day 24 that the proportion of these larvae surviving to adulthood was calculated.

$$\text{Proportion surviving} = \text{Exp}\left(\left(4.48 - 0.00394 * \left((\Sigma\ Nt\text{-}17 : Nt\text{-}14)/4\right)\right) - 1\right)/\ 100$$

Using the data from Table 6.12 the proportion of the eggs laid on day six that gave rise to adults on day 24 can be calculated

$$\text{Proportion surviving} = \text{Exp}\left(\left(4.48 - 0.00394 * ((1046.80 + 671.75 + 671.75 + 643.41)/4)\right) - 1\right)/ 100$$

$$= 0.0344$$

As no significant difference was observed between the survival from either treatment the proportion surviving was calculated using the same equation in both models.

Column 8 The number of adults emerging

The number of eggs laid in the time period t-x is multiplied by the proportion surviving (column seven) giving the number of new emergent adults. Thus, from the eggs laid on day six 11 adults were expected to emerge. This value is multiplied by the value in column ten. Again this was the same for the control and cadmium models.

Column 9 The mean pupal mass

This calculates the mean mass of pupae arising from eggs laid in the time period t-x. The mass is calculated by linear regression using the cube root of the mean larval population density as a predictor. Thus the eleven adults emerging from the eggs laid on day six arose from pupae with a mean mass of 11.84 mg. This figure is multiplied by column four so that the mean mass is representative of eggs laid on a particular day. In the deterministic model eggs were produced every day so the random term generated by columns three and four was not included in the equation.

$$\text{Mean pupal mass} = \left(10^{1.7699} - 0.076367 * (\sqrt[3]{((\Sigma\ Nt\text{-}17 : Nt\text{-}14)/4)})\right) * \text{column } 4_{t\text{-}x}$$

Using data from Table 6.12

$$\text{Mean pupal mass} = \left(10^{1.7699} - 0.076367 * (\sqrt[3]{((1046.80 + 671.75 + 671.75 + 643.41)/4)})\right) * \text{column } 4_{t\text{-}x}$$

$$= 11.84 \text{ mg}$$

There was a significant difference between the mean pupal masses predicted by the two models. The following equation was used in the cadmium model.

$$\text{Mean pupal mass} = \left(10^{1.7679} - 0.082463 * (\sqrt[3]{((\Sigma\ Nt\text{-}17 : Nt\text{-}14)/4)})\right) * \text{column } 4$$

Table 6.12 An example of the data from the control stochastic population model

Day	Number of adults	Probability of egg production	Are eggs laid?	Number of eggs	Number of competing larvae	Proportion surviving	Number of emerging adults	Mean pupal mass (mg)	Pupal mass cut-off.	Viable biomass (mg)
1	197	0.1487	0	0	0	0.02356913	0	0	0	0
2	188	0.0769	0	0	0	0.07308992	0	0	0	0
3	180	0.9256	1	375.048156	0	0.06654122	0	0	0	0
4	189	0.4070	0	0	375.048156	0.03415916	17	11.8293205	1	201.098448
5	181	0.6931	1	343.377423	375.048156	0.01671929	0	0	0	0
6	173	0.9506	1	328.375497	718.425579	0.00616699	0	10.0553625	0	0
7	165	0.0154	0	0	1046.80107	0.00611398	0	0	0	0
8	158	0.5224	0	0	671.752920	0.00606116	0	10.0456461	0	0
9	151	0.5651	1	315.040451	671.752920	0.00678918	0	0	0	0
10	144	0.5905	1	301.705405	643.415948	0.00755020	0	10.1785329	0	0
11	138	0.3450	0	0	616.745857	0.02022069	0	0	0	0
12	151	0.3579	0	0	616.745857	0.04203873	19	12.1881108	1	231.574106
13	144	0.2215	0	0	616.745857	0.12553133	0	0	0	0
14	138	0.5655	1	251.698985	301.705405	0.34298213	0	0	0	0
15	132	0.7528	1	240.030820	251.698985	0.54807941	0	0	0	0
16	126	0.0730	0	0	491.729805	0.87234672	0	0	0	0
17	120	0.4055	0	0	491.729805	0.87234672	0	0	0	0
18	115	0.5785	1	240.030820	491.729805	0.59981928	0	0	0	0
19	110	0.2200	0	0	480.061640	0.41146647	0	0	0	0
20	105	0.6771	1	220.028251	240.030820	0.19769923	0	0	0	0
21	124	0.1943	0	0	460.059071	0.06406862	24	13.0508884	1	313.221321
22	118	0.9024	1	200.025683	460.090719	0.04529805	0	0	0	0
23	123	0.6296	1	191.691279	420.053935	0.03128435	10	11.6889765	1	116.889765
24	128	0.6625	1	183.356876	611.745215	0.03445013	11	11.8432154	1	130.275370

Column 10 Pupal mass cut-off

If the pupal mass is less than a critical value then a value of 0 is given. This prevents unrealistically small flies from surviving. In Table 6.12 the cut-off value has been set as 11.01 mg (the lowest mean mass recorded from the cadmium experiments described in section 6.3.5), this value was used in both the cadmium and control models. Thus, when the number of adults predicted by column eight is multiplied by this column exceptionally small flies are prevented from coming into existence.

Column 11 The total biomass of all pupae in a cohort

This is the number of emergent adults multiplied by the mean pupal mass to give an estimate of total biomass. The figure predicted here may be lower than the actual total biomass as mean pupal mass is multiplied by the number of adults emerging, not all pupae give rise to adults and their mass is not included in this estimate of total biomass. Dividing the total of this column by the total of column ten gives an estimate of the mean total biomass mass of pupae in a cohort.

The model was tested in two ways. First a deterministic simulation model was used in which the stochastic element generated by columns two and three was removed and replaced by a constant daily egg production. The properties of the model were then investigated by varying different parameters and studying the effect of them upon the resultant dynamics of the population. The stochastic element was then replaced into the model and again tested making comparisons with the cadmium simulation model.

6.3.7 The deterministic simulation model of the control population dynamics with estimates of parameters calculated from the experiments

The deterministic model, using the parameters described in the previous section, predicted stable limit cycles (Figure 6.1a) with the numbers of adults cycling between a maximum of 320 and a minimum of 82 (mean 202.54). The length of the cycle was 70 days (Figure 6.1b), which is approximately two times greater than the generation time calculated in section 6.3.1. With stable limit cycles maximum ACF values of 1.0 would be expected, showing a perfect correlation. As the Autocorrelation analysis was carried out upon the whole time series generated by the model the ACF values do not actually reach a value of 1.0 as the initial period of settling was also included in the analysis. These cycles are taken to represent the underlying dynamics of the population; the effect of introducing a stochastic element upon these cycles will be investigated later. On the following pages the effect of varying the different parameters in the model will be

investigated. When the cadmium model was run as a deterministic model the population showed damped oscillations and reached a stable equilibrium of 185.44 adults.

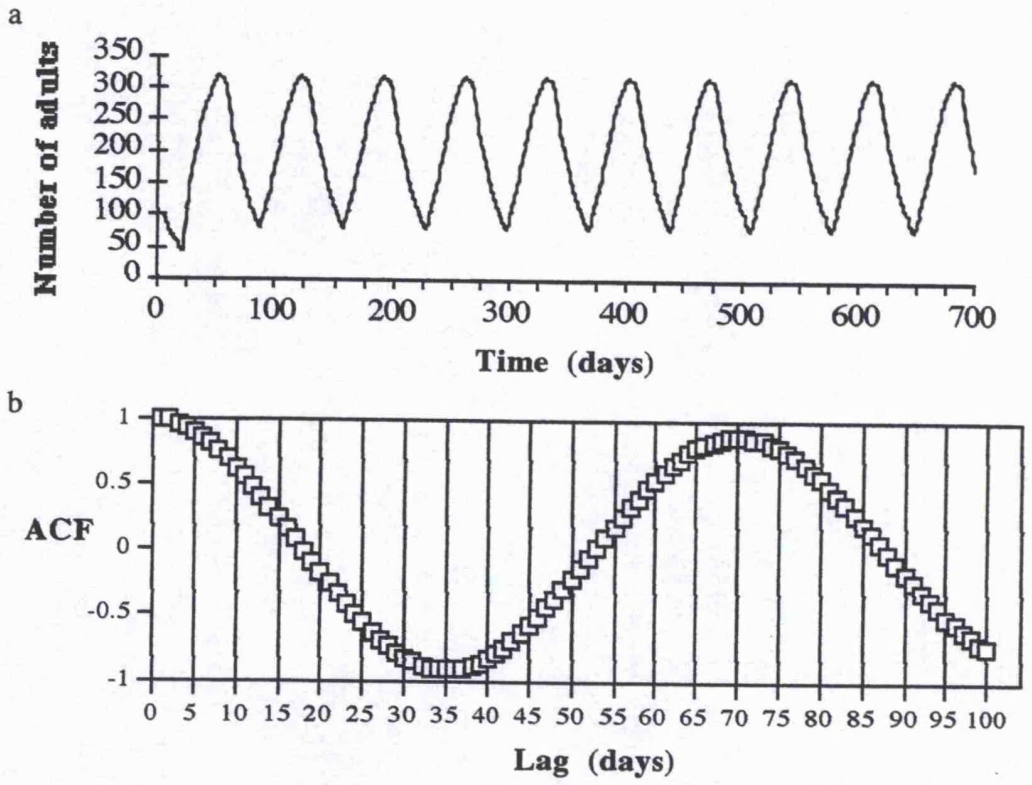


Figure 6.1a-b) a) The population cycles of the adult flies predicted by the deterministic model governed by the parameters estimated through the experiments; b) the results of the autocorrelation analysis of the cycles.

6.3.8 The effects of varying the mean pupal mass cut-off

In the standard deterministic model described in section 6.3.7 only pupae with a mean mass of equal to or greater than 12.36 mg were assumed to give rise to adult flies, based upon the control experiment results presented in section 6.3.5, Table 6.11. In this section the effects of varying this cut-off were investigated. The cut off values used were 0 mg, 11 mg, 20 mg and 30 mg (when using the standard parameters the mean pupal mass predicted by the deterministic model was never below 10 mg).

When the mean pupal mass cut-off was set to 0 mg there were no mortalities due to a small pupal size. The effect of this upon the population dynamics was to lead to a series of damped oscillations (Figure 6.2a). Initially the numbers of adults present varied between a maximum of 320 to a minimum of 160. Towards the end of the 700 day test period the number of adults present varied between a maximum of 222 and a minimum

of 197 (mean 208.33). The cycle of these fluctuations was over a period of 73 days (Figure 6.3a).

When the mean pupal mass cut-off was 11 mg the dynamics of the population fell into a series of damped oscillations (Figure 6.2b). The damping of the population cycles, however, was not as pronounced as when the cut-off was 0 mg. At the start of the 700 day period the population cycled between a maximum of 320 to a minimum of 115. Towards the end of the period the cycles had damped slightly to give a maximum of 286 and a minimum of 135 (mean 208.85). The length of these cycles was 71 days (Figure 6.3b). The peak of the ACF graph showed a stronger correlation between the lags and a taller peak this reflecting a decrease in the dampened nature of the cycles.

With a cut-off at 20 mg, stable two point limit cycles were produced (Figure 6.2c). The number of adults present fluctuated between a maximum of 249 and a minimum 22 (mean 123.41). The length of these cycles was 75 days (Figure 6.3c).

When the cut-off was increased to 30 mg the population still produced stable limit cycles (Figure 6.2d) with adult numbers fluctuating between a maximum of 56 and a minimum of 0 (mean 28.70). The peaks in adult numbers showed small double peaks. The length of these cycles was 65 days (Figure 6.3d). It is interesting to note that increasing the cut-off did not result in a simple linear response in the period of the cycles. Increasing the cut-off from 0 mg to 11 mg, 12.36 mg, 20 mg and 30 mg gave the following cycle lengths respectively 73, 71, 70, 75 and 65 (days).

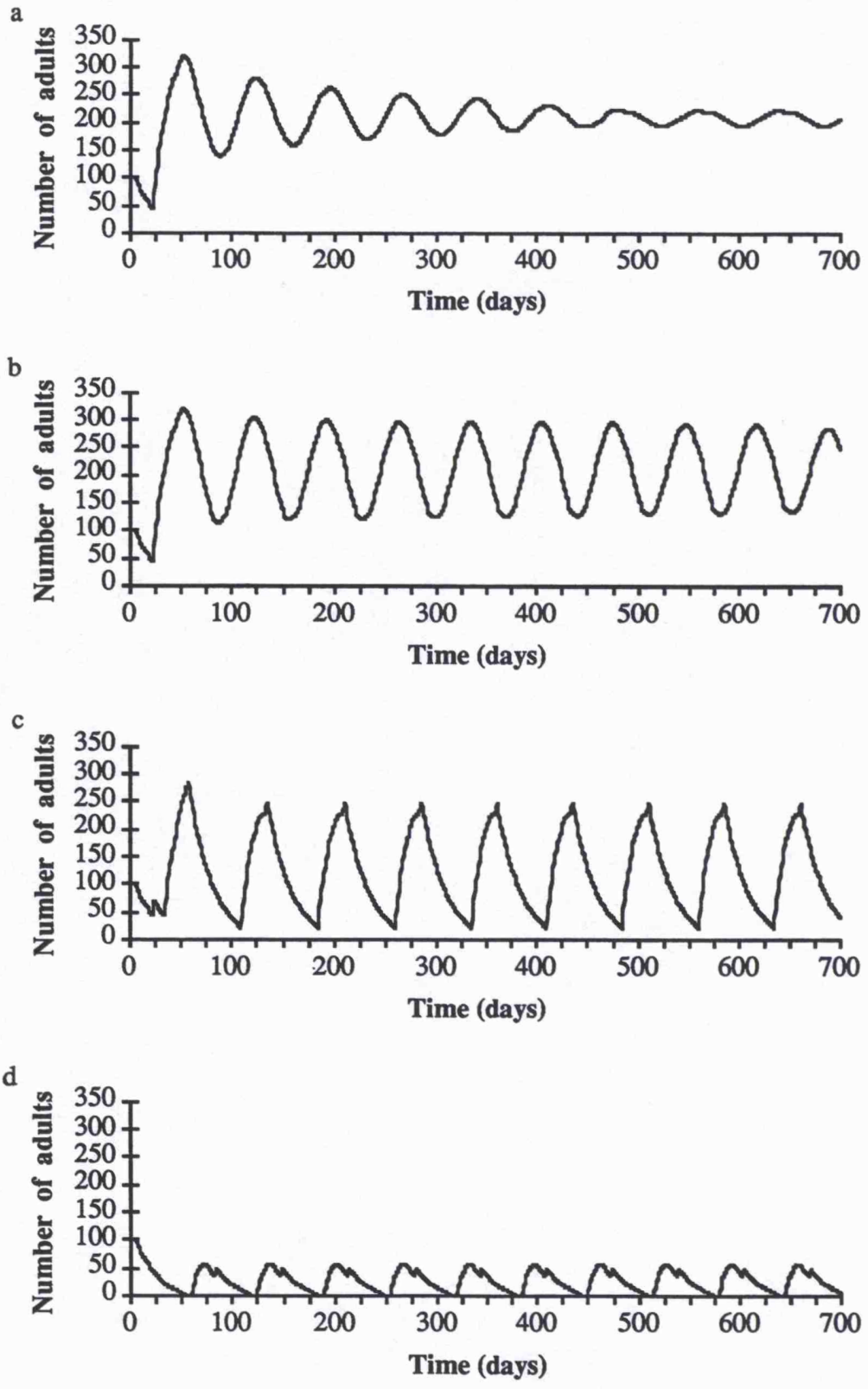


Figure 6.2a-d) The effects of varying the mean pupal mass survival cut-off upon the population dynamics predicted by the deterministic model a) 0 mg, b)11 mg, c) 20 mg, d) 30 mg.

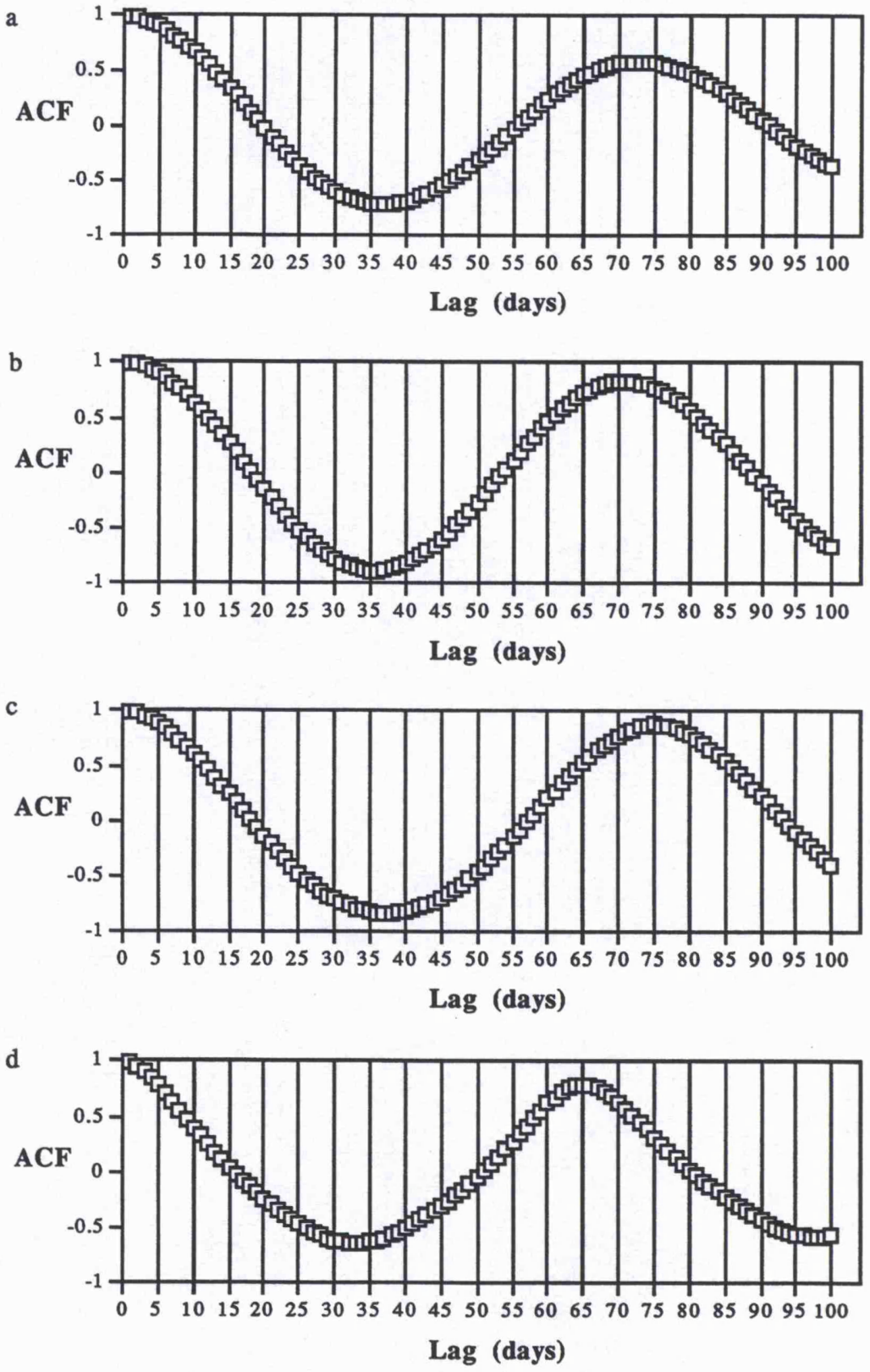


Figure 6.3 a-d) The autocorrelation functions calculated from the population cycles predicted by the deterministic model with varying values for mean pupal mass cut-off a) 0 mg, b) 11 mg, c) 20 mg, d) 30 mg.

6.3.9 The effect of varying mean adult longevity

In order to test the effect of varying the mean adult longevity upon the population cycles four different longevities were used (10, 15, 17.5, and 20 days). Each of these longevities resulted in different daily mortalities. In the standard model a mean longevity of 24.57 days was used which gave a daily mortality rate of 4.07%. (Note that when the daily mortality was altered the number of breeding females predicted was also altered).

The lowest mean longevity, 10 days, gave rise to a population that reached a stable equilibrium, of 170 adults, after a period of 93 days (Figures 6.4a, 6.5a).

When the mean longevity was increased to 15 days the population showed damped oscillations which soon reached a stable equilibrium point, of 206 adults, after a period of 120 days (Figures 6.4b, 6.5b).

When the mean longevity was increased to 17.5 days the same pattern of damped oscillations reaching a stable equilibrium was again observed. The time taken to reach the equilibrium had increased to 366 days. The equilibrium point had altered slightly to 193 adults (Figure 6.4c). The ACF graph shows a periodicity about 70 days during the settling phase (Figure 6.5c).

Finally when the mean longevity was increased to 20 days the population fell into stable two point limit cycles (Figure 6.4d) with the number of adults fluctuating between a maximum of 292 and a minimum of 72 (mean 186.46). The ACF graph shows that the period of these cycles was 68 days (Figure 6.5d). (Note that the mean longevity obtained from the experiments was 24.57 days and this gave rise to a cycle period of 70 days.)

Increasing the mean longevity thus has two effects; first it drives the population dynamics from a stable equilibrium to stable limit cycles and second it causes the period of the cycles to increase. Unlike the effect of varying the mean pupal mass cut-off the effect of increasing mean longevity was always to increase the length of the period of the limit cycles. Increasing the mean longevity will increase the mean generation time. Although not presented here, mean longevity was varied up to 50 days and with each increase the length of the cycle increased.

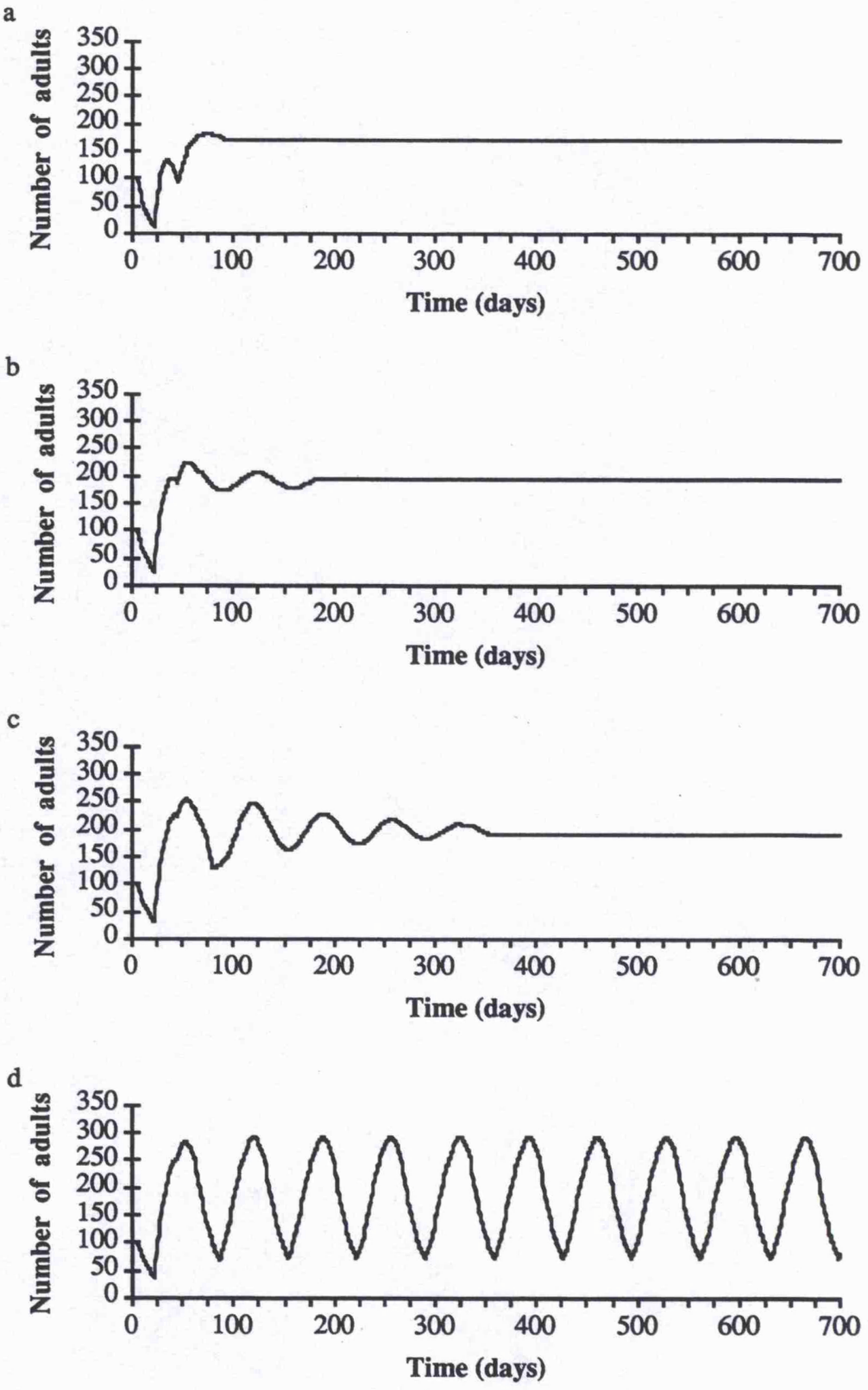


Figure 6.4 a-d) The effects of varying the mean adult longevity upon the population dynamics predicted by the deterministic model a) 10 days, b) 15 days, c) 17.5 days, d) 20 days.

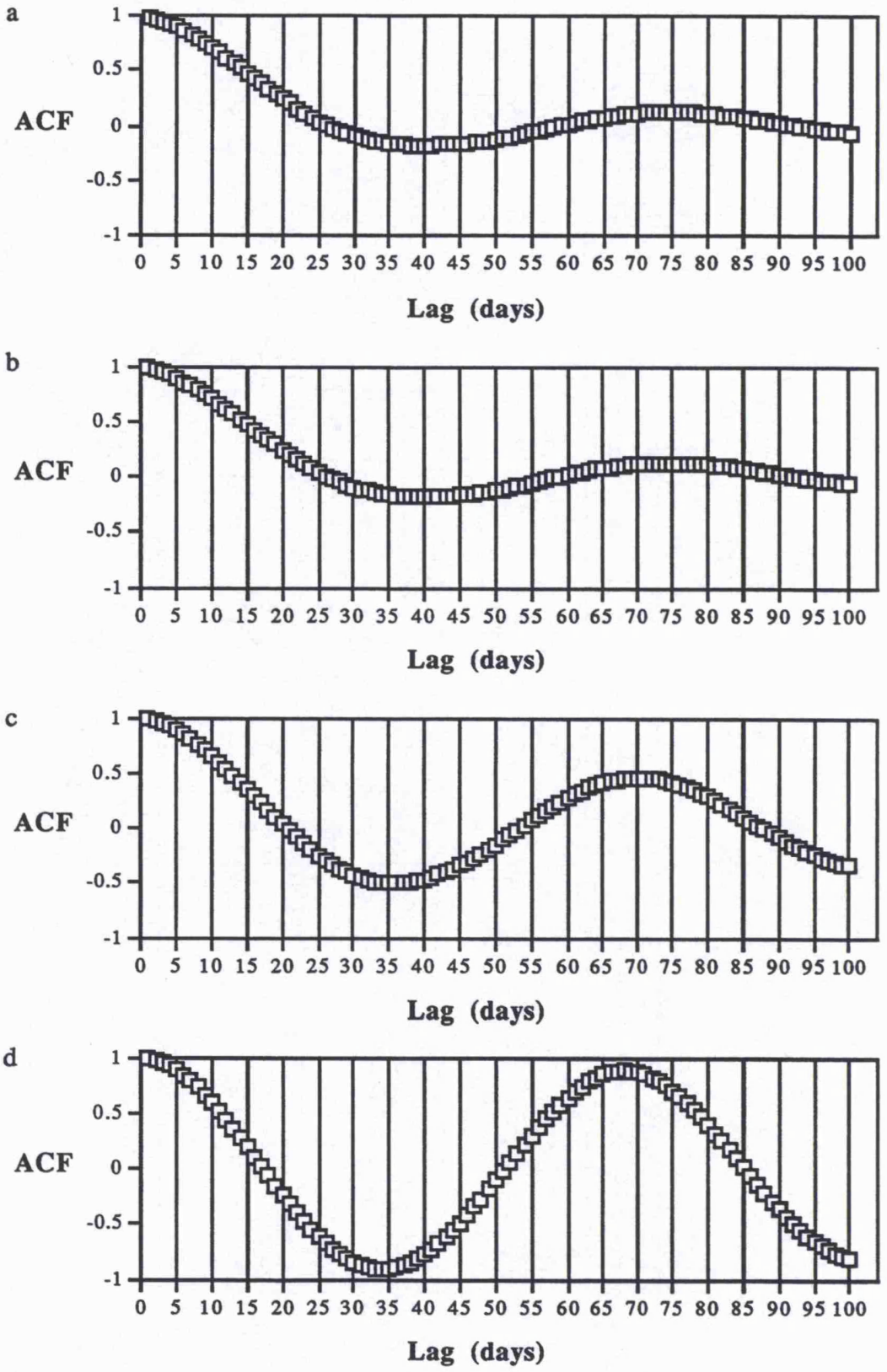


Figure 6.5 a-d) The autocorrelation functions calculated from the population cycles predicted by the deterministic model with varying values for mean adult longevity a) 10 days, b) 15 days, c) 17.5 days, d) 20 days.

6.3.10 The effect of varying egg production

In this section the mean number of eggs per batch was varied. The model was modified to calculate the mean number of eggs produced per day from this value (mean number of eggs per batch * the proportion of days on which eggs were laid). It should be noted that this could be thought of either as an increase in the number of females producing eggs or as an increase in the proportion of days on which eggs were laid. In the standard model a mean batch size of 88.06 eggs per batch was used.

When the mean number of eggs per batch was set to 50 the population dynamics showed damped oscillations to reach a stable equilibrium of 279 adult flies after a period of 107 days (Figures 6.6a, 6.7a).

When the mean number of eggs per batch was increased to 150, the population fell into stable two point limit cycles (Figure 6.6b). These cycles varied between a maximum of 288 and a minimum of 46 adult flies (mean 156.01) The period of these cycles was 72 days (Figure 6.7b).

Increasing the mean number of eggs per batch to 200 (Figure 6.6c) or 1000 (Figure 6.6d) resulted in stable two point limit cycles. The amplitude of these cycles, however, were different. With a batch size of 200 eggs the maximum number of adults was 277 and the minimum 32 (mean 135.44), compared with a batch size of 1000 eggs which gave a maximum of 145 adults and a minimum of 0 (mean 47.86). Increasing the batch size also affected the length of these cycles (Figure 6.7c-d), 75 days for a batch size of 200 eggs and 82 days for a batch size of 1000 eggs.

The mean batch size was increased further, up to 7000 eggs per batch. With each increase the resultant dynamics were always stable limit cycles with decreasing maximum numbers of adults. Interestingly the length of the cycles did not continue to increase, for example with a batch size of 7000 eggs there were approximately 14 complete cycles of the 700 day period modelled, *i.e.* a 50 day cycle. Such large batch sizes are unrealistic, though a mean value of 200 eggs per batch is a realistic value.

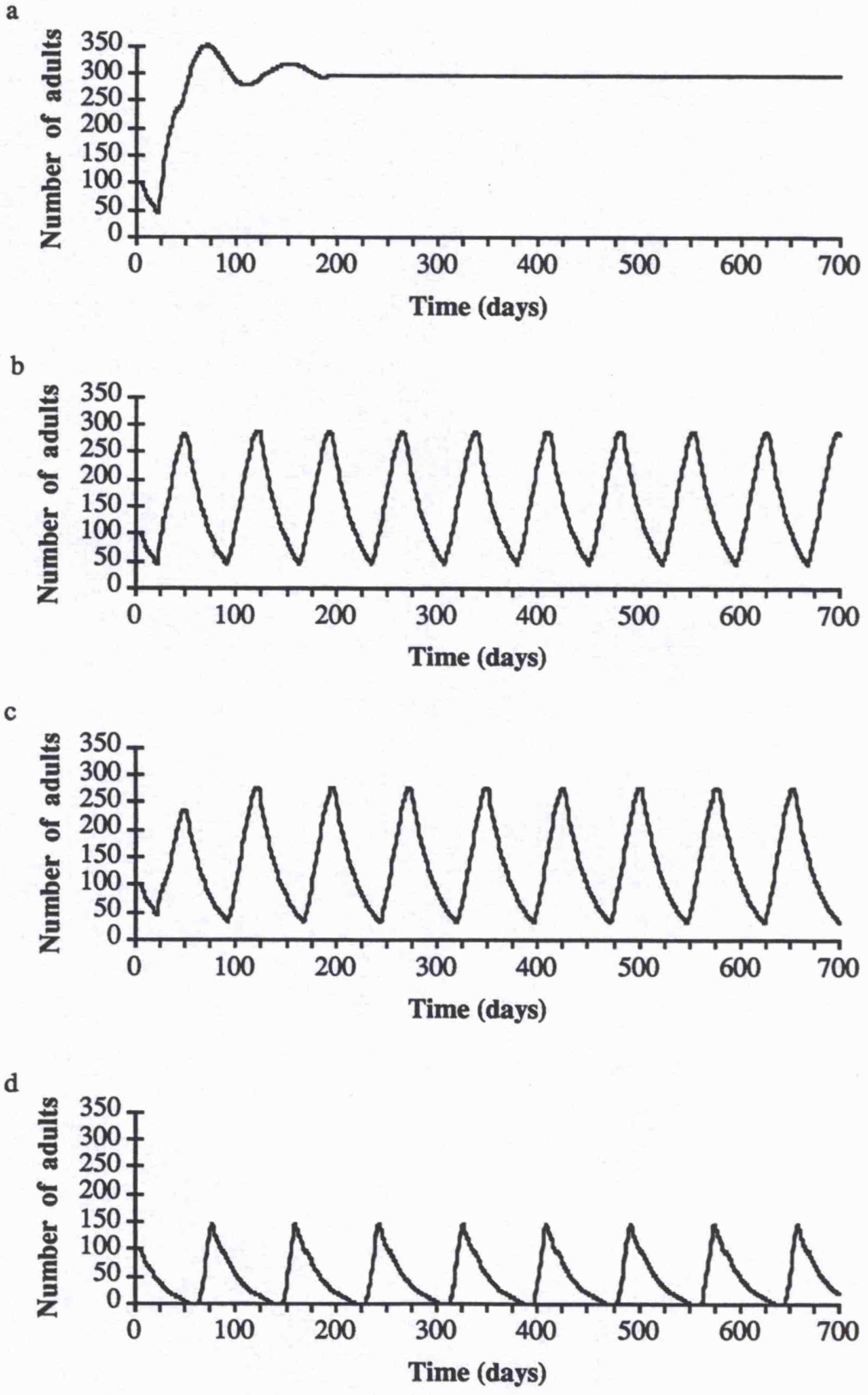


Figure 6.6 a-d) The effects of varying the mean number of eggs per batch upon the population dynamics predicted by the deterministic model a) 50 eggs b) 150 eggs, c) 200 eggs, d) 1000 eggs.

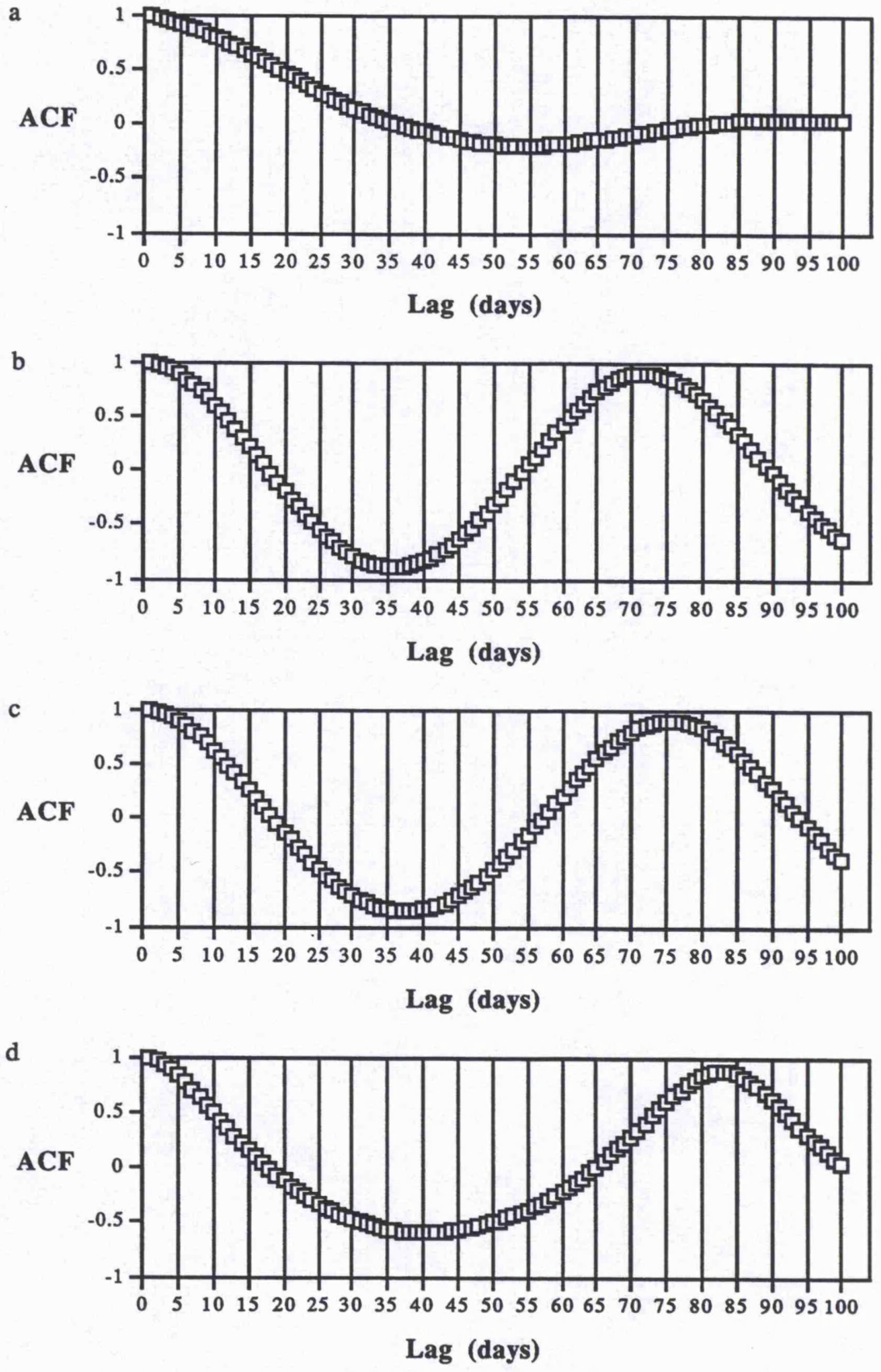


Figure 6.7 a-d) The autocorrelation functions calculated from the population cycles predicted by the deterministic model with varying values for the mean number of eggs per batch a) 50 eggs b) 150 eggs, c) 200 eggs, d) 1000 eggs.

6.3.11 The effect of varying the strength of density-dependence

In this section the value of the regression coefficient describing density-dependence was varied from a minimum of 0.002 to a maximum of 0.01. In the standard model the value used was 0.00394 *i.e.*

Natural log (% surviving + 1) = 4.48 - **0.00394** * Larval density

Decreasing the coefficient to 0.002 gave rise to stable six point limit cycles (Figure 6.8a) in which the maximum and minimum peaks of adult numbers are as follows 620 - 81- 619 - 85 - 626 - 82 (mean 314.71). These cycles were established after 119 days. The differences in these peaks and troughs were only evident when the raw data were examined and the six point cycle consists of a fundamental two point cycle with superimposed variation in amplitude. The ACF graph (Figure 6.9a) shows that the period of these fundamental two point cycles was 72 days.

Increasing the coefficient to 0.006 resulted in stable two point limit cycles (Figure 6.8b) after about 400 days in which the maximum number of flies was 148 and the minimum was 122 (mean 135.12). The ACF graph shows the period of the cycles to be 72 days (Figure 6.9b).

When the coefficient was set to 0.008 the trend shown by the dynamics was much the same with stable two point limit cycles (Figure 6.8c) after about 400 days (mean 100.41). The maximum number of adults, during this stable phase, was 115 and the minimum 87. The ACF graph (Figure 6.9c) showed the period of these cycles was 71 days.

The highest mortality factor, 0.01, also gave a series of damped oscillations that reached a stable two point limit cycle after about 320 days (Figure 6.8d). The maximum number of adults was 94 and the minimum 65 (mean 79.05). The ACF graph (Figure 6.9d) shows that the period of these cycles was 72 days.

Thus, increasing the coefficient of density-dependence reduced the numbers of adult flies present and reduced the amplitude of the population cycles. There did not appear to be a significant effect upon the period of the cycles.

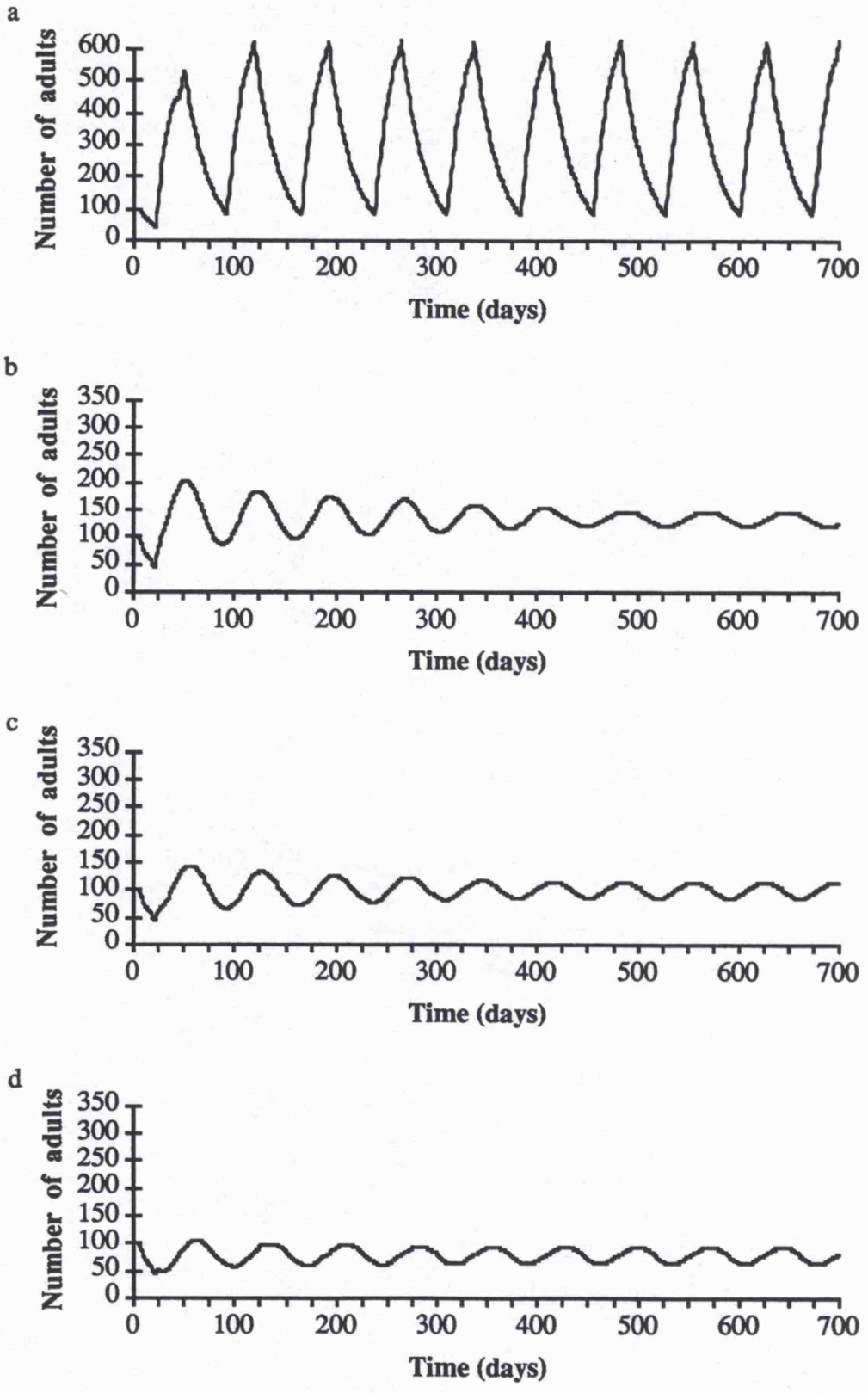


Figure 6.8 a-d) The effects of varying the coefficient of density-dependence upon the population dynamics predicted by the deterministic model a) 0.002, b) 0.006, c) 0.008, d) 0.01.

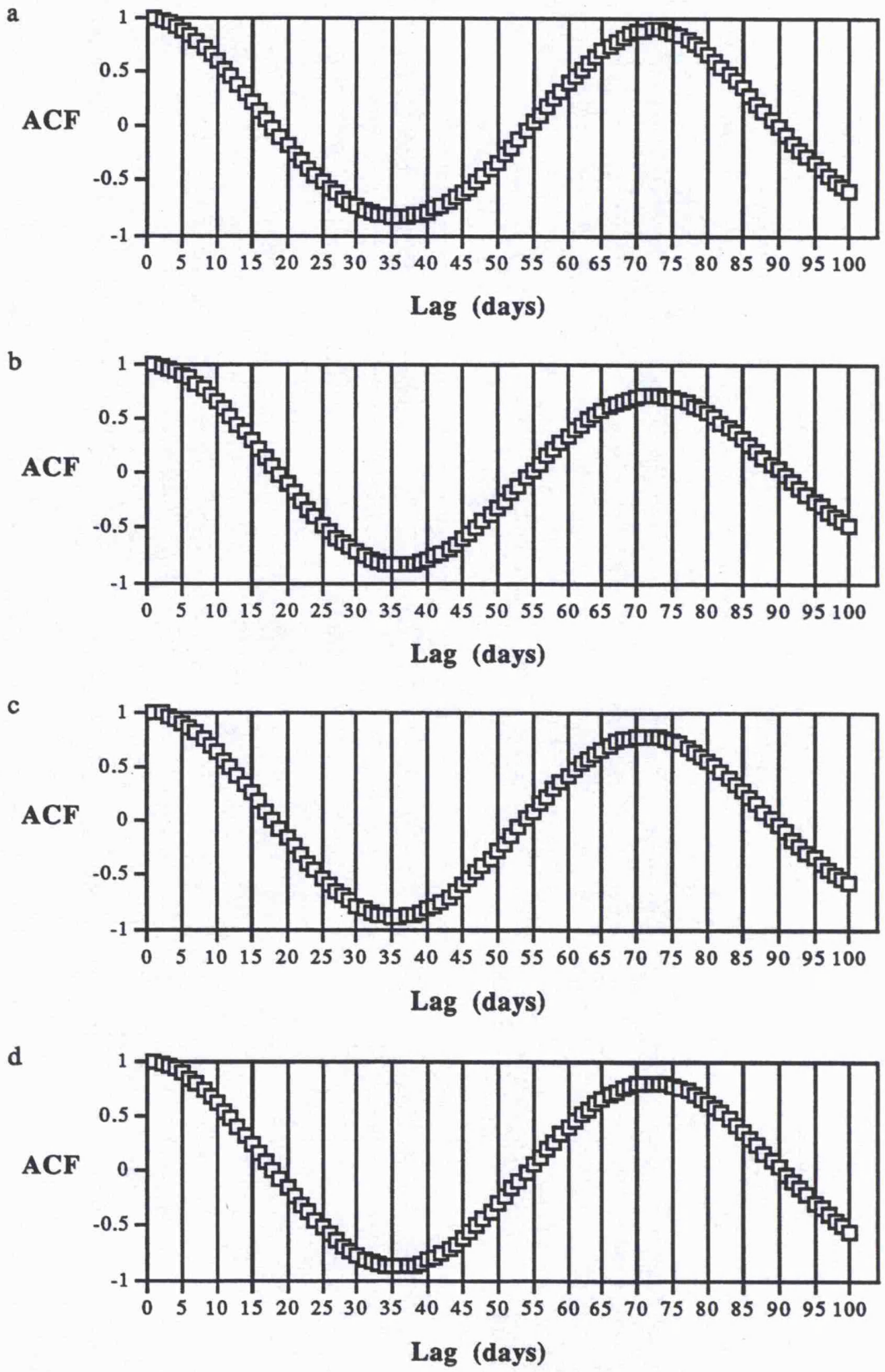


Figure 6.9 a-d) The autocorrelation functions calculated from the population cycles predicted by the deterministic model with varying values for the coefficient of density-dependence a) 0.002, b) 0.006, c) 0.008, d) 0.01.

6.3.12 The effect of varying the egg-to-adult development period

In the standard model the egg to adult development time was 18 days. In this section values of 5, 10, 15 and 25 were used. Development time will contribute to mean generation time. When the development time was only five days the population rapidly reached a stable equilibrium of 209 adult flies after a period of 81 days (Figures 6.10a, 6.11a).

Increasing the development period to 10 days caused the population dynamics to enter a stable two point limit cycle (Figure 6.10b) with the number of flies varying between a maximum of 264 and a minimum of 119 (mean 196.20). The ACF graph (Figure 6.11b) shows the period of these cycles to be 49 days.

A development period of 15 days also resulted in stable two point limit cycles (Figure 6.10c) with the number of adult flies varying between a maximum of 299 and a minimum of 96 (mean 198.47). The ACF graph (Figure 6.11c) shows these cycles to have a period of 62 days.

A development period of 25 days also resulted in a stable four point limit cycle (Figure 6.10 d) which settled after a period of 300 days with the maximum and minimum numbers of flies being 350, 61, 351, 59 (mean 202.97). The ACF graph (Figure 6.11d) shows that the period of these cycles was 86 days.

The effect of extending the development period was two fold. First extending the development period caused the population to show stable limit cycles rather than the stable equilibrium. Second increasing the development period also increased the length of the cycles. The populations in each case had a mean number of adults of about 200, which did not seem to be affected by the development time.

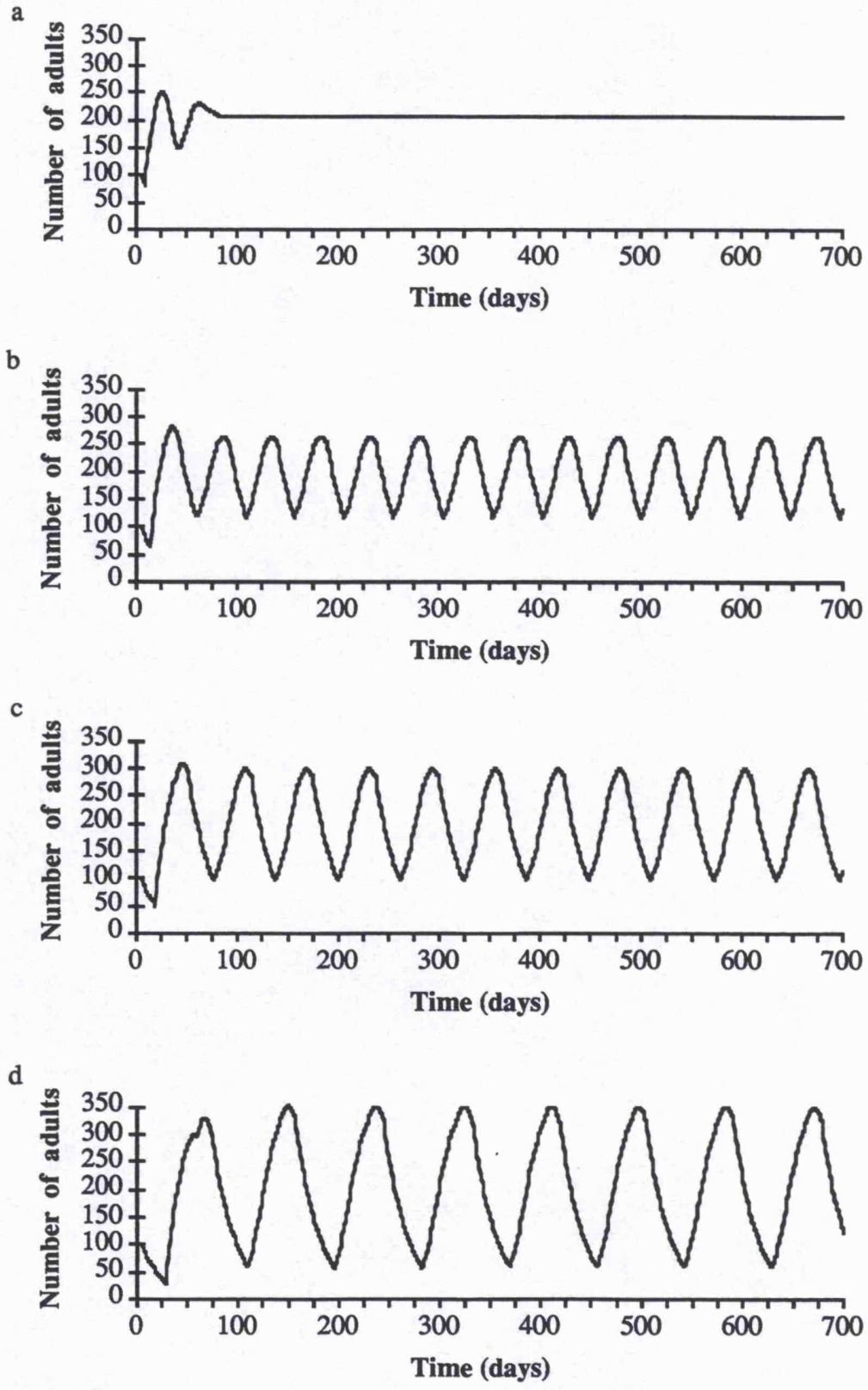


Figure 6.10 a-d) The effects of varying the egg-to-adult development time upon the population dynamics predicted by the deterministic model a) 5 days, b) 10 days, c) 15 days, d) 25 days.

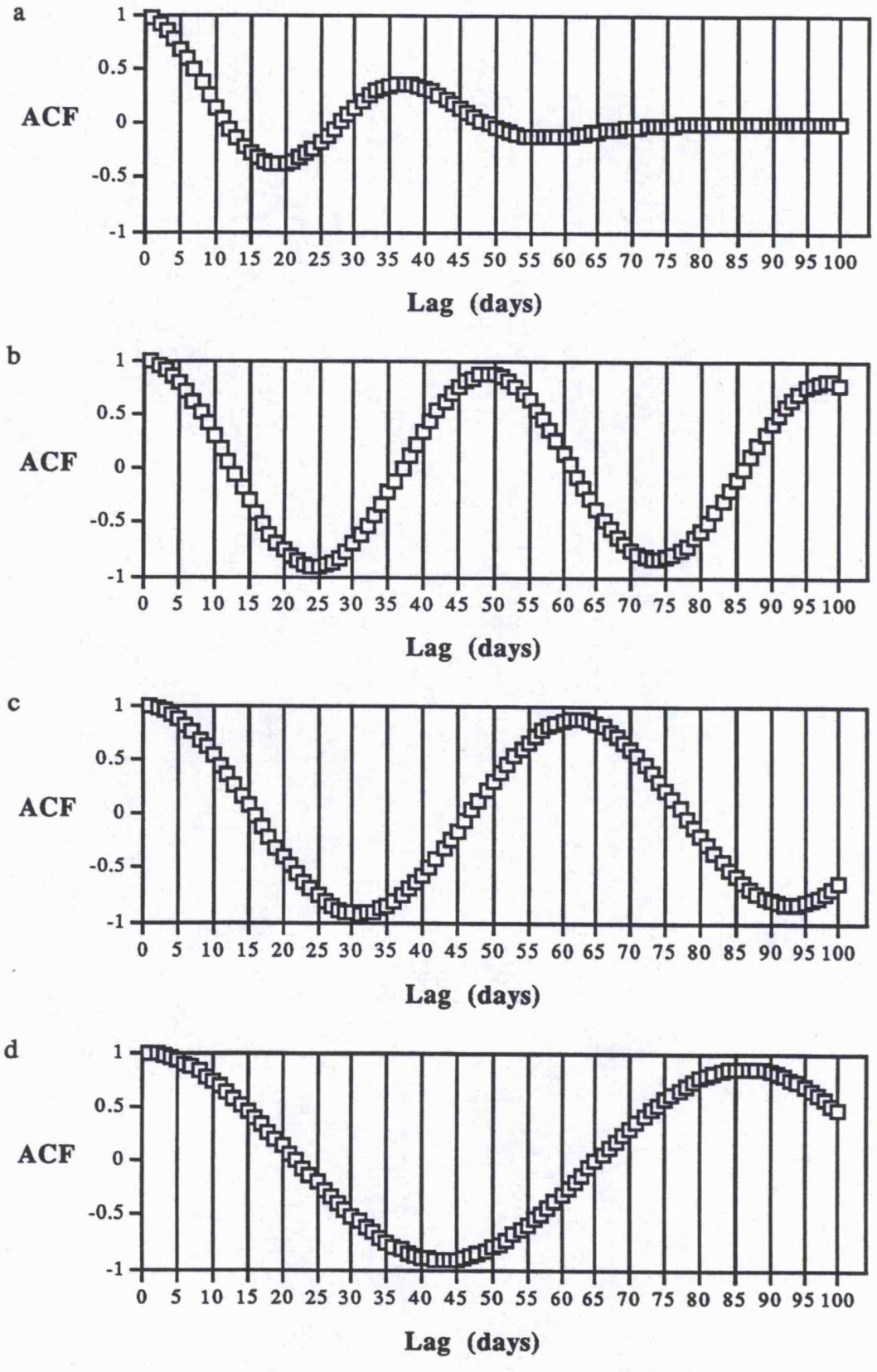


Figure 6.11 a-d) The autocorrelation functions calculated from the population cycles predicted by the deterministic model with varying values for the egg-to-adult development time a) 5 days, b) 10 days, c) 15 days, d) 25 days.

6.3.13 The population dynamics predicted by the stochastic model and comparisons of the control and cadmium populations

In the previous sections, the behaviour of the model under deterministic conditions was studied. Under natural conditions the egg laying behaviour would not be so constant and predictable. My own observations, whilst waiting for eggs to set up the experiments, showed that eggs were not laid every day. Sometimes eggs were not laid for days at a time whilst at other times they may have been laid on consecutive days. This variability must be included to make the simulation model of blowfly population dynamics more realistic. In this section the pupal mass cut-off used in the control model was altered to 11.01 mg, which was the lowest mean mass recorded from the cadmium experiments (section 6.3.5). This value was used in both models for the sake of consistency. The effect of using this cut-off value in the deterministic model is illustrated in section 6.3.8 where a value of 11.0 mg was used. The effect was to reduce the amplitude of the cycles slightly.

The first model to be studied was the control population model. The stochastic element in this model predicted that eggs would be laid on 45.67% of the days after the flies had reached sexual maturity (see Table 6.8 in section 6.3.2). The effect of introducing this stochastic element into the model was to mask the regular cycles (Figure 6.12a-d). Visual examination of these graphs showed that cycles still appeared to be present, at least in some parts of the time series. In Figure 6.12c, for example, there were clear fluctuations of the population for the first 300 days. The dynamics then appeared to become dampened for a period of about 250 days after which the cycles seem to be re-establishing themselves.

Autocorrelation analysis of the data revealed the cyclic nature of these fluctuations (Figure 6.13a-d). The first graph (Figure 6.13a) shows that the population cycles in Figure 6.12a are only weak cycles as indicated by the low ACF values, 0.1647 was the strongest correlation observed. The length of these cycles was 65 days. The cycles predicted in Figure 6.12b show much stronger cycles. The ACF graph (Figure 6.13b) supports this with a maximum autocorrelation of 0.4319. The length of the cycles was again 65 days. That these cycles were strong and consistent was also reflected by the second peak in the ACF graph at a lag of 136 days. The ACF value at this point was 0.3247 showing that correlation values were decreasing. The situation was much the same for the final two graphs. The ACF analysis revealed a cycle length of 67 and 71 days. Thus it would appear that varying the egg production randomly also has an effect upon cycle length. The mean length of the cycles was 67 days.

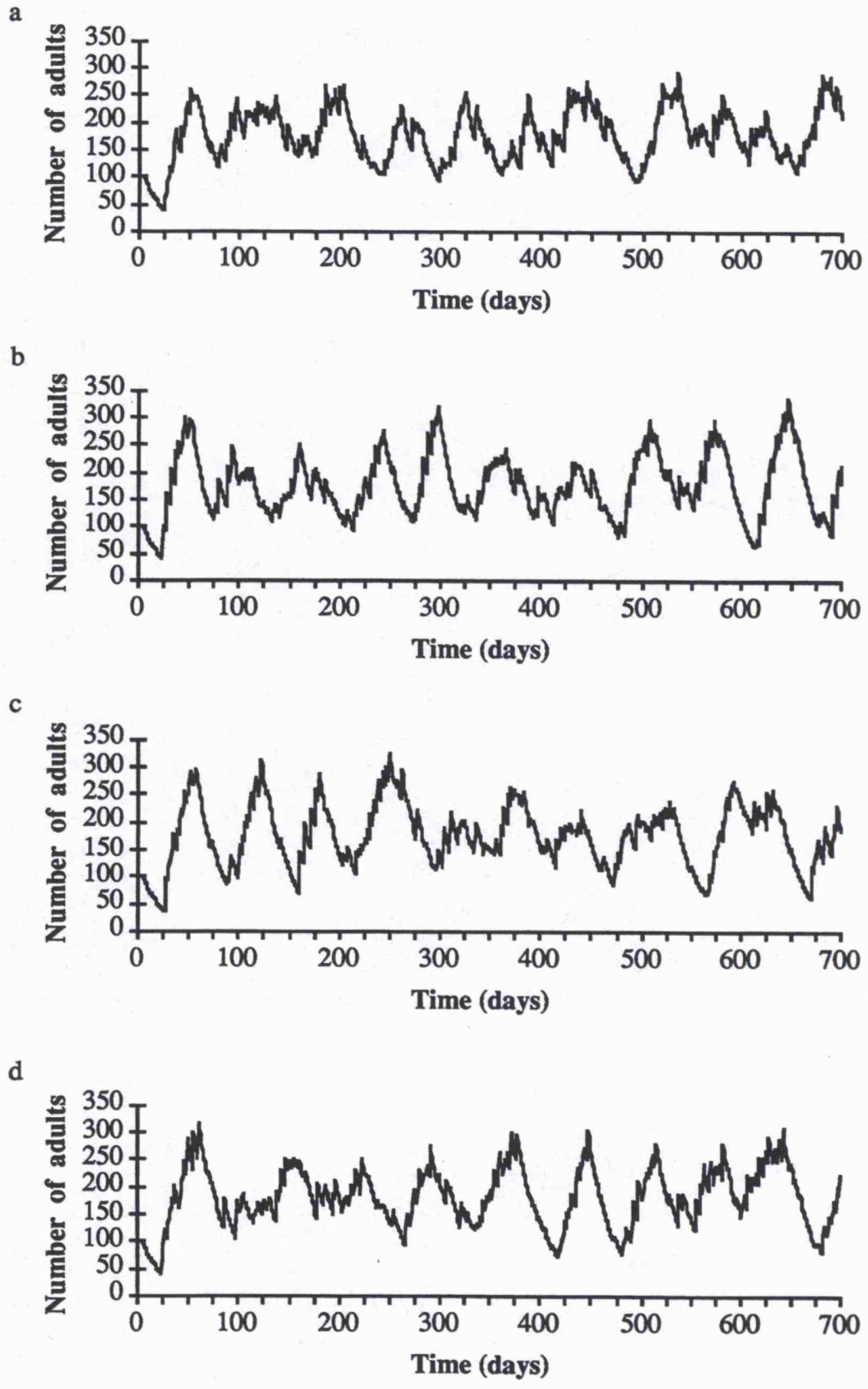
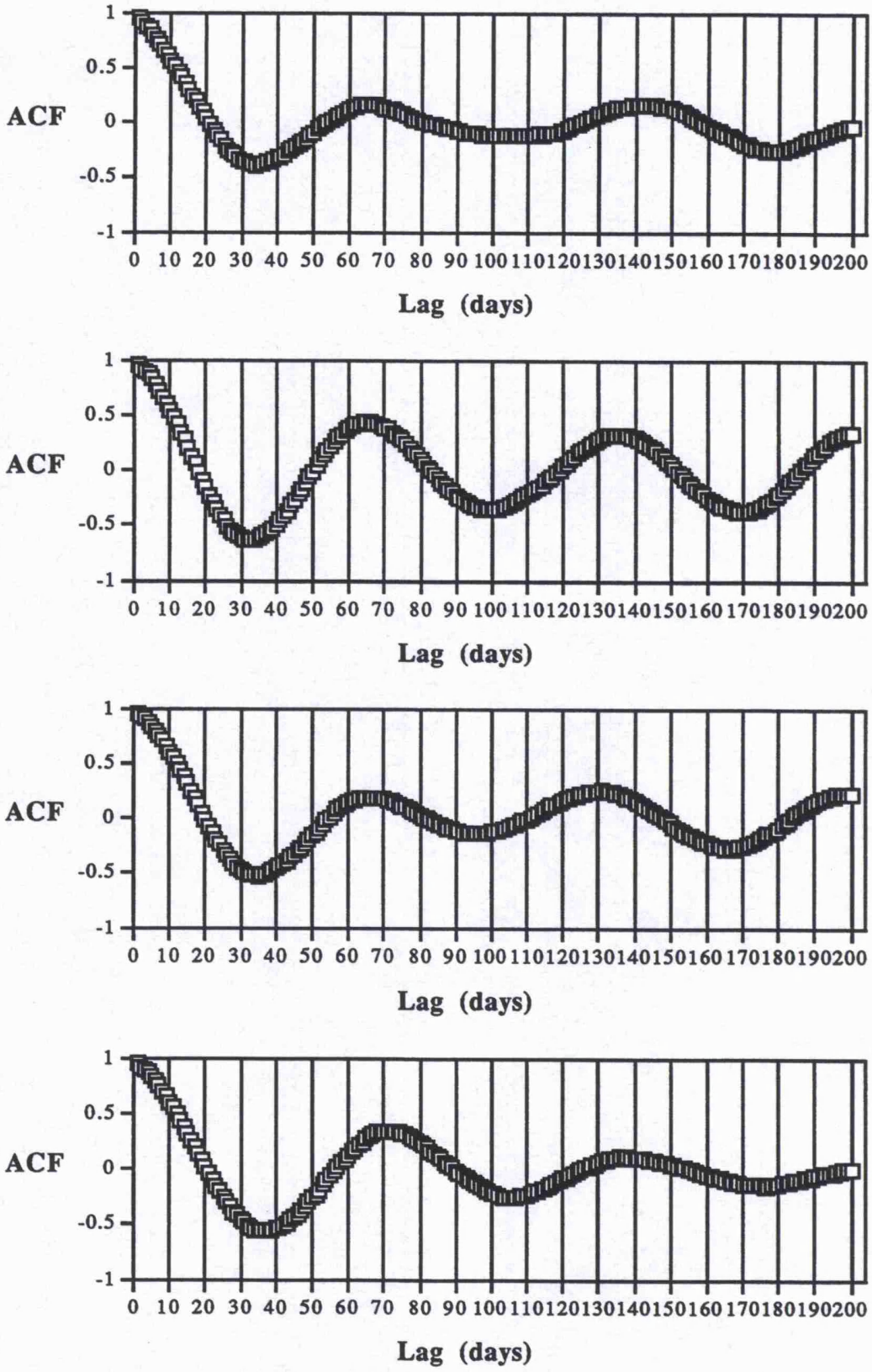


Figure 6.12 a-d) Fours realisations of the dynamics of the control population predicted by the control stochastic model. The parameter values used are the same in each case.



6.13 a-d) Autocorrelation analysis of the control population dynamics predicted using the stochastic model. The parameter values used are the same in each case only the pattern of egg production has changed.

The same procedure was then carried out upon the cadmium population dynamics model. This model differed from the control model in that there was a slightly longer egg to adult development time (19 days), smaller pupae were predicted, the feeding period was five days, and in that the egg production was lower than the control model.

The graphs shown in Figure 6.14a-d show the dynamics predicted by this model. In each of the graphs the population cycles illustrated appear to be greatly dampened when compared with the control population graphs (Figure 6.12a-d). The populations also appear to be fluctuating around a lower mean number of adults.

Calculation of the ACF did not show any clear cyclic behaviour of the populations. The population dynamics in Figure 6.14a did not show any discernible cycle. The ACF graph Figure 6.15a shows only very weak correlations and no cycles. Figure 6.14b shows slightly clearer cycles. The ACF graph (Figure 6.15b) shows weak correlation at lags of 59 days (ACF = 0.061856) and again at 117 days (ACF = 0.190453) suggesting a cycle of about 58.5 days. The clearest cyclic behaviour was shown by the graph in Figure 6.14d. The ACF graph of this data showed a peak at a lag of 64 days (ACF = 0.261603).

6.3.14 Comparisons of the models using the mean number of adults present, mean pupal mass, and pupal cohort biomass predicted by the control and cadmium models

In order to make comparisons between the two models each was run 15 times and the mean number of adults, mean pupal mass and biomass per pupal cohort were recorded. Comparisons were made between the two sets of data using one-way analysis of variance. Analysis of variance of the mean number of adults present (Table 6.13) showed that the mean number present in the control model (182) was significantly higher than in the cadmium model (93.86). The mean numbers of adult are presented in Table 6.14.

Table 6.13 Analysis of variance of the mean number of adults present predicted by each model.

Source	DF	Mean square	F	P
Treatment	1	58269.4	2429.59	<0.001
Error	28	24.0		
Total	29			

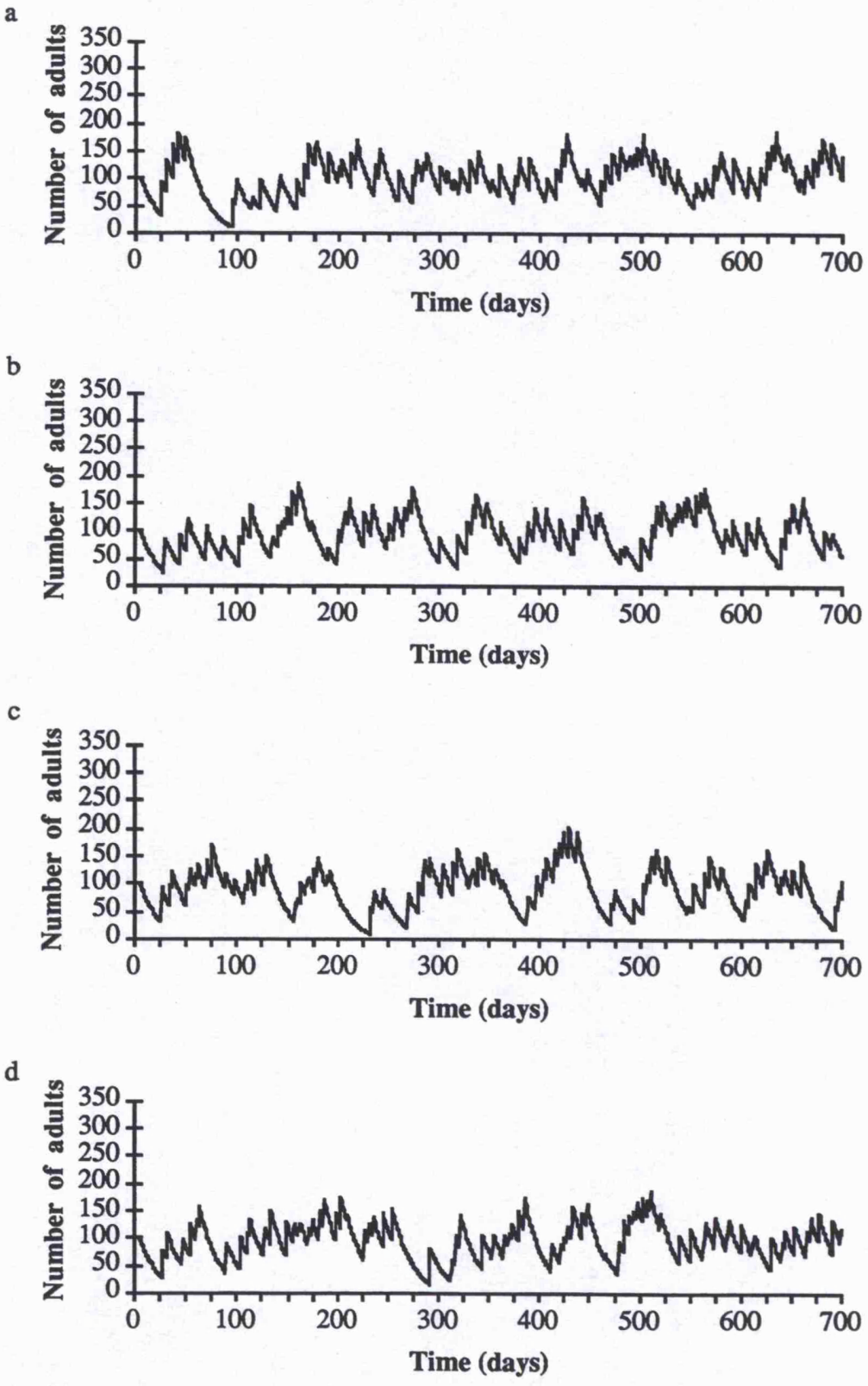


Figure 6.14 a-d) The cadmium population dynamics predicted by the stochastic model. The parameter values used are the same in each case only the pattern of egg production has changed.

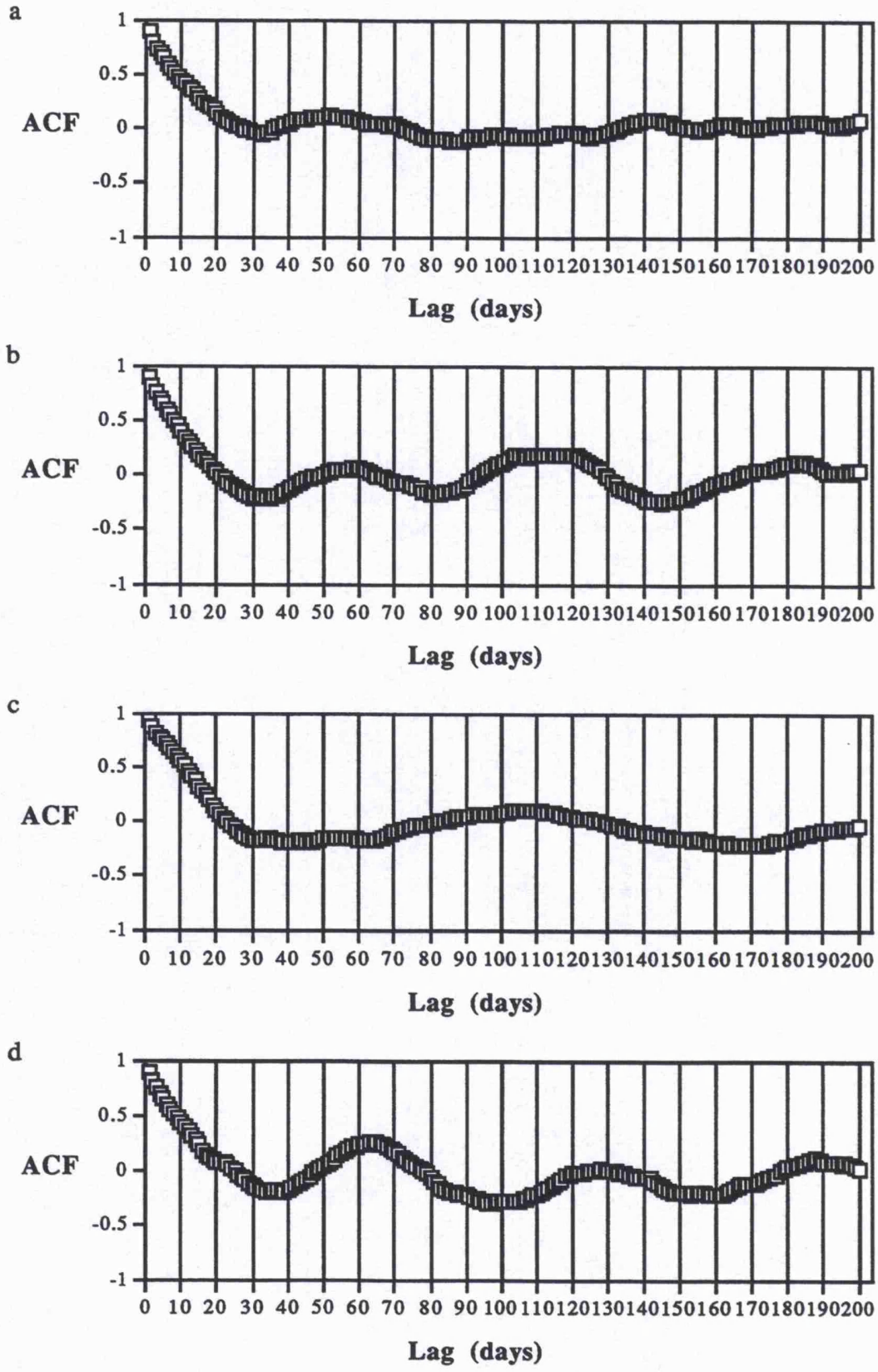


Figure 6.15 a-d) Autocorrelation analysis of the cadmium population dynamics predicted using the stochastic model. The parameter values used are the same in each case; only the pattern of egg production has changed.

Table 6.14 The mean number of adults present per day predicted by the two stochastic models. The standard error based upon the pooled error mean square is 0.57 for each mean.

Treatment	N	Mean
Control	15	182.00
Cadmium	15	93.86

Analysis of variance of the mean mass of individual pupae predicted by the models showed that there was a significant difference between the mean mass predicted by each (Table 6.15). The mean mass of individual pupae from the cadmium model was significantly higher than that of the control model (Table 6.16).

Table 6.15 Analysis of variance of the mean mass of individual pupae predicted by the two stochastic models.

Source	DF	Mean square	F	P
Treatment	1	3.759	15.36	<0.001
Error	28	0.245		
Total	29			

Table 6.16 The mean mass (mg) of individual pupae predicted by the two stochastic models. The standard error based upon the pooled error mean square is 0.18 for each mean.

Treatment	N	Mean
Control	15	15.690
Cadmium	15	16.398

Estimates of the total biomass per pupal cohort were made by multiplying the number of adults emerging on a particular day by the mean mass of the individual pupae from which they emerged. By doing this the estimated biomass is really an estimate of the total viable pupal biomass per cohort. Analysis of variance of these data (Table 6.17) showed the mean total biomass of a pupal cohort was significantly different in each model. The mean total biomass of a pupal cohort (Table 6.18) from the cadmium model (655.85) was significantly higher than the mean total biomass of a pupal cohort predicted by the control model (406.68). A pupal cohort is all the eggs laid on one day that survive to pupate on a later day.

Table 6.17 Analysis of variance of the mean total biomass of all the pupae in a cohort predicted by the two stochastic models.

Source	DF	Mean square	F	P
Treatment	1	465648.0	1408.00	<0.001
Error	28	2002		
Total	29			

Table 6.18 The mean total biomass (mg) of all the pupae in a cohort predicted by the two stochastic models. The standard error based upon the pooled error mean square is 1.73 for each mean.

Treatment	N	Mean
Control	15	406.68
Cadmium	15	655.85

Estimates of average daily biomass production were made by dividing the total biomass produced over the whole time series by the number of days in the period over which this production took place (days 25-701). Analysis of variance of these data (Table 6.19) showed that the mean daily pupal biomass production predicted by the control model was significantly higher than that predicted by the cadmium model. The means are presented in Table 6.20.

Table 6.19 Analysis of variance of the total biomass production of pupae per day (averaged over days 25-701) predicted by the two stochastic models.

Source	DF	Mean square	F	P
Treatment	1	16576.9	1408.00	<0.001
Error	28	11.8		
Total	29			

Table 6.20 Means of total pupal biomass production (mg) of pupae per day (averaged over days 25-701) predicted by the two stochastic models. The standard error based upon the pooled error mean square is 0.48 for each mean.

Treatment	N	Mean
Control	15	129.38
Cadmium	15	82.37

6.4 DISCUSSION

6.4.1 The development time and density-dependent mortality

The measurements of the egg to adult development period and density-dependent mortality gave some interesting and unexpected results when compared with the results from Chapter 5. In Chapter 5 the experiments clearly showed that the larvae reared under the highest population density, on 4 g of diet, had the shortest development time. In the discussion I suggested that this reflected the ability of the larvae to respond to the food supply. Thus, after a few days the small blocks of diet dried up forcing the larvae to pupate. The larvae reared upon 4 g of cadmium diet did not survive to adulthood although some pupae were obtained. During the experiments carried out in this chapter the blocks of diet were replaced every two days and the pots containing the larvae were humidified. Under these conditions it would seem that the early pupation was not required for survival. The larvae could survive on the limited amounts of diet supplied to them and, with the reduced threat of desiccation, they could spend longer in the larval period. It is possible that low humidity in some way acts as a trigger for pupation.

It is therefore possible that reducing desiccation and providing a constant supply of fresh diet reduced the density-dependent mortality. In Chapter 5 the survival of the larvae reared on the cadmium diet was significantly lower than the control larvae. I have shown that cadmium reduces the metabolic rate, slows growth, and lengthens the feeding period and these factors would appear to be the main reason for the higher mortalities observed. If the larvae have longer to feed (by providing a continuous food source) and are kept in a humid environment the mortality of the larvae may be expected to be reduced. The experiments carried out in this chapter thus support the hypothesis that cadmium reduces the survival of larvae on limited, ephemeral patches of resource by reducing their ability to exploit it efficiently before it deteriorates.

6.4.2 The parameter estimates used in the model

In order to set up the population model a number of assumptions have been made regarding some of the parameters used. Before considering the performance of the model these assumptions must be considered. One of the first assumptions made is that the adults are subject to a constant mortality every day and that there is no difference between the longevity of the sexes. The three experiments used to estimate the daily mortality each have different longevities despite the fact that these flies all originated from the same population but at different times. Thus it would seem

reasonable to assume that there would be variation in the longevity and so variations in the daily mortality rate over time. Even if there was no difference between the different experiments, one may still expect the mortality to differ. Such slight variations over time may have long-term effects upon the dynamics.

The density-dependent mortality factor used in the model assumed that no larvae died during the feeding period allowing an average density to be calculated, and that all larvae present were equal competitors. During the four-day feeding period of the control larvae this assumption means that a four-day old larva and a one-day old larva would be equal competitors even though the four-day old larva may have a mass some fifty times greater than a one-day old larva. Thus it is possible that the survival in the model is slightly over estimated. Further experiments would be required to establish the degree of such asymmetric competition. Larvae do die during the feeding period and so to assume no deaths would have resulted in an overestimation of the larval density; this error may compensate to some extent for the asymmetry in competition.

The egg-to-adult development time was assumed to be constant throughout the time series of the model. The experiments carried out in this chapter, however, have shown clearly that the development time does vary with larval population density. Thus, when the adult populations are high, larval numbers would be high and development time would be at its maximum. When the adult populations are low, larval densities would be at their lowest and development time would be at its minimum. The overall mean development times used were the best approximation available. This fixed development time would also mean that all flies from a single egg batch would emerge as adults on the same day. Whilst the majority of flies did this, emergence was generally spread over a 2-3 day period.

Another assumption was that the production of eggs was constant, *i.e.* all flies laid the same number of eggs. The number of eggs laid was taken to be the mean batch size measured over the three experiments. When flies lay eggs they do not always lay the same number of eggs. Sometimes only one or two eggs were laid while on other occasions there may have been up to 300 eggs in a batch. Again such variability in egg laying may have consequences upon the dynamics. A final assumption regarding the eggs is that all of the eggs hatch and give rise to larvae. A value for the success of the eggs hatching has not been obtained and this omission may give rise to an over estimate of larval numbers. Overall the parameters used were considered to be the 'best fit'. Further experiments in the future may produce more refined variables, on the other hand such refinement may not be necessary.

6.4.3 The driving forces of the dynamics

i) The mean pupal mass cut-off

By running the model in a deterministic manner, with a constant daily egg production per breeding female, varying the different parameters allowed the behaviour of the dynamics to be studied. The first parameter to be varied was the mean pupal mass cut-off. Without a pupal mass cut-off, the control population model showed damped oscillations. The experiments in this chapter showed that the mean minimum mass of pupae obtained from the control experiments was 12.36 mg and from the cadmium experiment 11.01 mg. These were pupae obtained from a population density of 1000 larvae per 20 g diet. No pupae were obtained from higher densities and so a value of around 11 mg gives a good approximation of the mean minimum mass from which adults will emerge.

The mean pupal mass cut-off affected both the cycle length and the mean number of adults present. Increasing the cut-off reduced the mean number of adults present. Increasing the cut-off from 0 to 12.36 mg decreased the period of the cycles. Cut-off values above 12.36 mg become biologically unrealistic but the results are mathematically interesting. Increasing the cut-off further caused the cycle to lengthen (20 mg) and then to decrease as the cut-off value increased (30 mg). The reason for this trend is not clear. It cannot be related to larval density which decreases as the cut-off value increases such that a linear response of the cycle length would have been expected.

ii) The longevity of adults

The adult longevity varied with the type of dynamics shown, monotonic damping, damped oscillations, and stable limit cycles. Decreasing the adult longevity effectively reduces both generation time and the rate of population growth. This is reflected by the shortest longevity, which results in the population rapidly reaching a stable equilibrium at which the rate of births and deaths are equal. Increasing the longevity disrupts this equilibrium so that the number of births exceeds that of deaths. The consequence is that more adults are present and more eggs are produced. An increase in the larval numbers results in an increased larval mortality rate and a reduction in adult recruitment. The end result is a fall in adult population numbers and the stable limit cycles observed. Adult numbers fall until a density is reached such that the number of larvae produced is low enough to allow some to reach the adult stage. Increasing the longevity caused the length of the cycle to increase. As the flies

lived longer it would take longer for the numbers of adults to decline and so delay the time during which the next batch of larvae could mature.

iii) The mean egg production

Varying the number of eggs produced affected the type of dynamics, the mean number of adults present and the length of the cycle. With a low egg production the population soon reached a stable equilibrium. Increasing the number further caused the dynamics to enter stable limit cycles. The mean number of adults present decreased as egg production was increased due to the higher larval mortality. The length of the cycles appeared to increase over the range of 50 to 200 eggs. These figures represent biologically realistic mean egg batch sizes. The cycle length continued to increase up to a batch size of 1000 eggs but did not continue to increase indefinitely, because a batch size of 7000 eggs resulted in shorter cycles. This lack of a monotonic response cannot be explained in simple terms and it must be a product of the combined action of the density-dependent mortality, the pupal mass predictor and the mean pupal mass cut-off.

iv) The density-dependent mortality

Increasing the coefficient of density-dependent mortality affected the model in a predictable manner. With low values the mean number of adults was high because of high survival of larvae with the result of widely fluctuating numbers of adults. Increasing the density-dependent mortality reduced the mean number of adults present and caused progressively damped oscillations of the populations. The period of the cycles was not significantly affected, only their amplitude.

v) Egg-to-adult development time

Altering the egg-to-adult development time altered the delay between the cause and response of population fluctuations. If the development time had been 0 days then the response would have been instantaneous and the population would have gone straight to an equilibrium. My simulation results strongly support this with the population rapidly reaching equilibrium with the shortest development time. As the development time increased so did the amplitude of the fluctuations and the length of the cycles.

6.4.4 The performance of the stochastic models

With the stochastic element introduced into the control model, the regular cycles predicted by the deterministic model become greatly disrupted but not destroyed altogether. The resultant dynamics greatly resemble those of real fly populations.

The mean length of the cycles predicted by the model was 67 days. The mean generation time predicted by the life-table analysis was 36 days which is approximately half the length of the cycles. The fly populations studied by Daniels (1994) had a cycle length of 68-70 days with an estimated generation time of about half this (Appendix 5). Thus the control stochastic population model appears to predict values very close to those observed in real life.

The stochastic control model predicted that the mean number of adults would be 182 adults. The work of Daniels (1994) showed that the actual mean number observed was 139 adults. More recent observations of long term fly populations has shown a mean number of around 140 (Nick Downs pers. comm.). The reason for this difference may lie in the fecundity values used in the model. In Chapter 5, I commented on the fact that the observed mean number of eggs per batch was lower than I had expected. Had the mean number of eggs per batch been higher then the mean number of adults would have been considerably lower. For example when the mean number of eggs per batch was increased to 150 in the control stochastic population model then the mean number of adults was predicted to be around 130 adults.

The stochastic cadmium model predicted that the regular cycles were virtually destroyed and that the mean number of adults fluctuated around a lower mean of 94 adults. This result compared very well with the results of Daniels (1994) who observed the mean number of adults to be 97, again distinct cycles were absent from her polluted populations. She also made the interesting observation that the mean mass of individual pupae from the cadmium populations (20 mg) was significantly higher than in the control population (18 mg). The stochastic simulation models also predicted that the mean mass of the pupae from the cadmium treatment would be significantly higher than those from the control treatment. The values calculated by the control and cadmium models (15.7, 16.4 mg) were lower than those observed by Daniels (1994). However, the observed relationship between the two values does agree with Daniels' observations. This is an interesting result, however, since the presence of cadmium in the diet was shown significantly to reduce the mean mass of individual pupae (Section 6.3.5). Similarly the mean total biomass of a pupal cohort

calculated by my models shows the same relationship, with the cadmium model giving rise to a significantly heavier biomass, see Table 6.18. Daniels (1994) also showed this though she did find that the cadmium populations fluctuated around a heavier average pupal biomass, which was not predicted here, see Table 6.20. Averaged over time Daniels (1994) observed a daily biomass production of 184 mg/day for the control cages and 211 mg/day for the cadmium cages. The control value is higher than predicted by the model but it also includes the mass of pupae that may have not given rise to adults. The value predicted by the cadmium model is much lower than that observed by Daniels. This was due to the infrequency of egg laying events by the cadmium flies.

The differences between mean pupal biomass and individual mean individual pupal mass can be explained in terms of the reduced female fecundity in the cadmium population. Since there are fewer females producing eggs, and those eggs that are produced are produced less frequently, there will also be fewer larvae present at any given time. A reduced larval density will allow the larvae, and hence pupae in a cohort, to reach a greater mass. Thus the effects of the toxin interacted with the effects of density-dependence giving a result that contradicts, for mean individual mass and cohort biomass at least, the simple scope for growth prediction.

CHAPTER 7 DISCUSSION

7.1 THE LINK BETWEEN ECOTOXICOLOGY AND POPULATION DYNAMICS

Ecotoxicology is supposed to make predictions about the long-term effects of toxins on populations and communities. Much effort, however, has gone into studying the effects of the toxins upon the physiology of the individual without making the link with community or population dynamics. Calow (1989) reviewed physiological models that have the potential of making such links, and provides links between them and the demographic parameters of survival (S), fecundity (n) and the time between developmental events (t). The two models he discussed are the 'Scope For Activity' model (Fry (1947, 1971)) and the scope for growth model. Scope for activity represents the difference between the maximum sustainable metabolic rate and the standard basal metabolic rate. Basal metabolism includes all basic metabolic processes that are required for the maintenance of the animal and includes growth and reproduction as well as routine respiration. In-between the basal and maximum metabolism is the routine metabolism that animal may incur through its normal day-to-day existence (Figure 7.1).

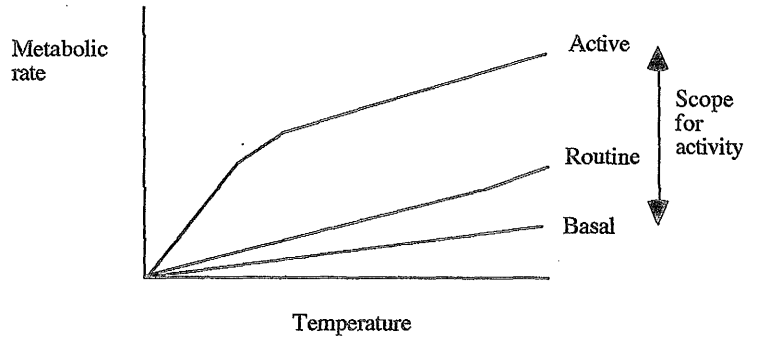


Figure 7.1) Scope for activity - the difference between the maximum sustainable metabolic rate and the basal metabolic rate represents the organism's scope for activity. The routine metabolic curve represents the metabolic rate that the organism may incur through its normal activities.

If an organism is exposed to a toxin its scope for activity may be reduced through one of two mechanisms. The basal metabolic rate may be increased in order to meet the metabolic demands of the detoxification mechanisms. Alternatively the maximum sustainable metabolic rate may be decreased through depression of metabolic activity

or through a reduced intake of contaminated food. In either case the organism's scope for activity may be reduced and this may result in the organism's chances of survival (S) being reduced. In Chapter 4 it was demonstrated how cadmium caused a reduction of the metabolic rate and ways were suggested in which this could reduce scope for growth. It is possible that this reduced metabolic rate also reflects a reduced scope for activity in the larval stage. It would be interesting to investigate the effects of cadmium on the adult metabolic rate to test the hypothesis that adults exposed to cadmium may also suffer a reduced scope for activity.

Scope for growth represents the difference between the energy content of food absorbed and the metabolic losses that occur over the same period. Thus scope for growth describes the amount of energy available for growth and reproduction. A reduced scope for growth may be expected to slow down the growth rate and hence to increase the time to the first breeding and between breeding seasons (t) and ultimately to reduce fecundity and so abundance of the animal. The results presented in Chapter 4 and Chapter 5 showed that the larvae suffered a reduced scope for growth and that the adult showed a reduced fecundity. That the adults showed a reduced fecundity may indicate that they also suffer a metabolic cost and a reduced scope for activity. The reduction in the scope for growth was much more severe in the experiments carried out in Chapter 5 than it was in Chapter 6. The reason for this was that in experiments described in Chapter 5 there was a time dependent factor, the larval food was only available for a limited time before it deteriorated. At the highest larval densities the diet was prone to desiccation after about four days. In the presence of a toxin which lengthens the feeding period, the animals ability to efficiently exploit the resource was reduced. Thus the reduction in the scope for growth was more marked than it was in the experiments described in Chapter 6 where the diet was replaced every two days.

These two models provide potential links between the physiological models and population dynamics but no formal links existed. Calow (1989) provided these links by reference to a simplified version of the Euler/Lotka equation, illustrated below. This equation includes the demographic parameters S, n and t and links them to the intrinsic rate of increase r, which can be calculated by solving the equation.

$$1 = \sum e^{-rt} S_m$$

Calculation of the intrinsic rate of increase, whilst providing a means of comparing the effects of a toxin, does not actually describe the type of dynamics one may expect

from a population if it is considered on its own. In order to do this the intrinsic rate of increase must be considered along with other parameters which affect population growth.

In Chapter 6, estimates of the intrinsic rate of increase per generation showed that there was a significant difference between the control and cadmium treatments but not how the population dynamics may differ. In order to gain an appreciation of how the population dynamics were affected by the toxins, the reproductive output of the females needed to be considered along with the density-dependent mortality of the larvae, the routine mortality of the adults and the temporal distribution of egg-laying episodes. The methods used to build the simulation models were simple and effective. The good agreement between the predictions of the models and the observations made by Daniels (1994) suggests that this population-simulation approach was valid for studying the effects of toxins upon population dynamics. Such simulation models could be applied to other species and may make a valuable contribution towards future ecotoxicological studies.

7.2 EXTRAPOLATING BETWEEN LABORATORY EXPERIMENTS AND NATURAL POPULATIONS

The experiments carried out in Chapter 5 gave rise to some interesting results. Clearly cadmium reduced the size of adult flies and their fecundity; and clearly larval survival at any given density was reduced when compared with the control experiments. Equally clear were the results describing the egg-to-adult development period. These showed how increasing the larval population density caused a decreased development time whilst the presence of a toxin increased the development time. Having obtained these results the processes in action in long-term population cages seemed much clearer and easier to understand. One would expect the populations of a polluted cage to contain fewer and smaller adult flies. These results would also be predicted from scope for growth theory.

It became clear through the experiments carried out in Chapter 6, however, that the processes that actually occurred in the long-term population cages were not as simple as suggested by the experiments in Chapter 5. The relationship between population density, survival and adult mass were very different in the experiments simulating the long-term population cages. Survival was not significantly reduced in the presence of cadmium, the density/development time relationship was reversed and, although the pupal mass was reduced at any given density in the presence of cadmium, the mean pupal mass and cohort biomass predicted by the population models were actually

higher in cadmium-polluted populations. The differences between the experiments of Chapters 5 and 6 were, in part, attributable to the experimental conditions and the time-dependent aspect of the scope for growth as discussed in section 7.1. The conflicting pupal mass results predicted by the population model were mainly due to the interaction of cadmium with population density and female fecundity.

These observations highlight some of the dangers in extrapolating from simple experiments to more complex situations. There may be subtle differences between laboratory and natural conditions that may have quite pronounced effects that have not been accounted for. With these limitations in mind I have made certain speculations about the way in which toxins may affect natural populations.

7.3 THE IMPACT OF TOXINS UPON NATURAL POPULATIONS

One of the aims of this study was to establish links between the effects of toxins on the individual and the dynamics of the whole population. This was accomplished through the construction of the population models. In this section I shall consider how natural populations may be affected by toxins. If the two extremes of the metapopulation continuum are considered, then the experiments carried out in Chapter 5 may be thought of as representing the effects of toxins in the ephemeral resource patches exploited by patchy populations. The experiments in Chapter 6 and the population model may be more representative of local populations in classical metapopulations (Harrison (1991)).

7.3.1 Patchy populations

Blowflies naturally exist as patchy populations which are stable neither in time or space. This was demonstrated in Chapter 3 where the best that could be said of the populations was that they showed an aggregated distribution. The importance of the resource patch, however, as the fundamental unit of such populations was demonstrated. The presence of toxins in a patch was investigated in Chapter 5 and has shown clearly that there may be severe consequences to the local population. These consequences may be immediate by reducing survival of larval stages to the adult stage. Such a reduction in survival would be more pronounced in small resource patches, which are more likely to deteriorate before the larvae can make full use of them. Even in cases where adults do survive they are likely to be of a reduced size. With a reduction in size a reduction in fecundity will follow. Overall the consequences of this may be a reduction in the local abundance of species using such resources.

To say that the abundance of an organism will be reduced in the presence of a toxin may be a rather simplistic prediction for at least two reasons. First, the toxins need to be present in sufficient concentration to bring about an effect and second, a reduction in fecundity may not result in a reduction in abundance.

Are toxins such as cadmium likely to occur in high enough concentrations to cause reductions in survival, size and fecundity in natural populations? In the general introduction some examples of research were described in which cadmium was shown to be concentrated along the food chain. Martin and Coughtrey (1975) showed how, in a polluted woodland ecosystem, cadmium at a soil concentration of 42 ppm was concentrated to a level of 387 ppm (dry weight) in the kidney of the thrush (*Turdus philomelos*). Shore (1995) described levels in the common shrew (*Sorex araneus*) of 578 mg/kg and 253 mg/kg (dry weight) in the liver and kidney respectively. These results are, however, atypical and such high levels of cadmium are rare in nature.

In my experiments cadmium was used at a concentration of 50 mg/kg (50 ppm wet weight). This concentration on a dry weight basis would be higher than those given for the thrush and shrew and so perhaps represent a more severe level of pollution. It does seem feasible, however, to assume that the sub-lethal effects described in Chapters 4 and 5 would occur even if at a reduced level. Such effects also depend upon the animals not becoming adapted to the toxin. Daniels (1994) carried out experiments testing for adaptation to cadmium in *L. sericata*. Over the two years of her experiments she found no evidence of adaptation or increased tolerance to cadmium. If the long-term dynamics of other species were to be considered, evolution might need to be taken into account as short term experiments may not give an accurate prediction of the effects of toxins in the long term.

The second point raised above was that a reduction in fecundity may not bring about a reduction in abundance; in the population models a reduction in the fecundity resulted, paradoxically, in more adults being present. A reduction in fecundity may actually result in lower larval densities being present on a patch, which in turn may actually increase larval survival. This phenomenon only applies, however, to larger patches of resource that persisted long enough to allow population development. A reduction in the larval density on a small patch, a 4 g block of diet for example, would not enhance survival of larvae exposed to cadmium as it appears that the patch deteriorates before the larvae reach the end of their feeding phase. In future experiments, long-term population cages could be set up in which the flies are provided with resource patches rather than a continually renewed source of food.

Observations could then be made of the dynamics under control and polluted conditions. This would make an interesting area of study, the dynamics observed being more representative of a natural population.

The nature of a patchy population, its lack of any permanent or stable features, makes it difficult to say what the consequences of a toxin would be on a scale larger than the immediate local population. It is perhaps more useful to consider the effects of toxins in the context of a classical metapopulation.

7.3.2 Classical metapopulations

Using Harrison's (1991) definitions a classical metapopulations consists of discrete local populations, with limited movement between them, that are subject to extinctions but the regional population persists due to colonisation and re-colonisation of local patches. Each of these local populations is capable of existing at a stable equilibrium, unlike the resource patches of patchy populations. A classical metapopulation is illustrated in figure 7.1.

Each of the local populations would be subject to the same governing rules. The growth of the local populations would be density regulated and movement between local populations limited by the distance (x) between them. Any one of the local populations might be represented by a population of blowflies maintained in a population cage. In each local population, the presence of a toxin may have predictable effects upon the dynamics of a local population. In Chapter 6 I described how the presence of a toxin dampened the population fluctuations mainly through reduction in the fecundity. Reductions in fecundity may be so severe that the population becomes extinct.

Different local populations may be affected to different degrees and a smaller population will be more likely to become extinct than a larger one. The effect of a toxin may be such that it reduces the persistence of the smaller populations and shifts the metapopulation dynamics towards the mainland-island scenario described by Harrison (1991), in which the smaller local populations (islands) may be prone to extinction but are re-colonised by colonists from a larger, more persistent 'mainland' population. Similarly if pollution was severe then the larger 'mainland' itself may become extinct and consequently all of the local populations may be subject to a gradual decline in numbers.

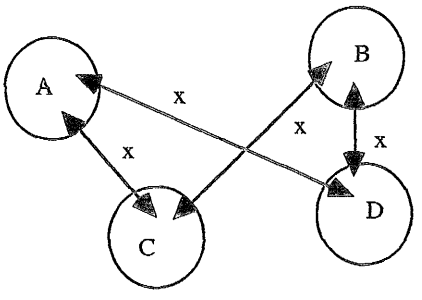


Figure 7.1) Diagrammatic representation of a classical metapopulation consisting of four local populations (A, B, C, D) separated by distance *x*. Each population can exist at equilibrium and may be subject to limited movement of individuals between patches, indicated by the arrows.

One of the key features of the different metapopulation scenarios is the movement of individuals between local populations. Does a toxin only affect the fecundity or is there also a reduction in the animal's ability to disperse? The question of dispersal does raise some interesting questions and may provide the basis for future research. If the movement between local populations could be described, then the model presented in Chapter 6 could be expanded to describe simple metapopulation dynamics. The question of dispersal is also of relevance to patchy populations. In these populations dispersion and movement between patches may be so frequent that local populations if they actually exist are blurred. Reducing the level of dispersion in such populations may have some interesting consequences.

Harrison, Murphy, and Ehrlich (1988) studied the metapopulation structure of the Bay checkerspot butterfly (*Euphydryas editha bayensis* Boisuval). The metapopulation fitted the mainland-island scenario. This population consisted of a 2000 ha habitat patch that served as a 'mainland' with a population of about one million butterflies. Surrounding this 'mainland' were smaller resource patches. They demonstrated that patch occupancy decreased with distance from the 'mainland' which served as a source of colonists for the smaller patches. The importance of dispersal to metapopulation structure was therefore demonstrated.

There appear to be two ways in which dispersal could be affected by the presence of a toxin. The first of these relates to the scope for activity model. If less energy is available for activity then it is possible that this in turn may reduce the movement of individuals between local populations. The experiments in Chapter 5 have shown that, under limited resource conditions, the size of the resultant adults was reduced. This

reduction was greater in the presence of cadmium. If size is related to flight activity then this reduction is size could also have an effect upon dispersal. Berrigan (1991) demonstrated that lift production in the flesh fly *Neobellieria bullata* (Parker) increased with the mass of the fly. He suggests that overall flight performance may be proportional to lift production, thus larger flies may be better fliers. In contrast to this Wickman and Karlsson (1989) showed that body mass and wing surface area increased at different rates in a range of insects. The consequence of this was a greater wing loading and hence higher energy requirement during flight for larger insects.

Such studies make it difficult to predict what effect body mass may have on the insects' ability to disperse. In the case of the limited resource patches the flies fed upon the control diet were larger than the ones reared upon the cadmium diet. These flies may have had a greater ability to disperse than the smaller flies. The flies modelled by the cadmium simulation were larger than the flies modelled by the control simulation. In this situation, would the cadmium flies have a greater ability to disperse or might their larger size, with higher energy demands, combined with a reduced scope for activity hinder them? The ability to disperse, and the effect of the interaction between body mass and the toxins on this ability, may form the basis of some interesting research in the future.

7.4 CONCLUSION

The experiments carried out in this thesis have demonstrated how the presence of a toxin in the diet of *L. sericata* may have an effect upon metabolism and how this may manifest itself, in conjunction with a reduced food intake, as a reduction in the scope for growth of these insects. The reduction in the scope for growth was demonstrated in terms of slowed development time, reduced adult mass, and reduced fecundity. Incorporating these effects into the population model allowed the effects of reduced scope for growth on the long term population dynamics to be investigated. Overall this thesis achieves the aims of ecotoxicology by demonstrating the link between the effects of toxins upon the individual and the long-term population dynamics.

I have suggested some of the ways in which the metapopulation dynamics may be affected, but this has largely been speculation, and much research is needed in this area. The way forward from this work must be to investigate the effects of toxins at the next level, *i.e.* at the level of the metapopulation, and ultimately at the level of the community.

APPENDIX 1: The raw species data collected during the field work

The tables presented on the following pages give the numbers of each fly species reared from the individual chick carcasses during the field work. The fly species are represented in some table by abbreviations a key to these is given below.

Species	Abbreviation used
Calliphora vicina (Robineau-Desvoidy)	*C. vic*
Muscina prolapsa (Harris)	*M. pro*
Muscina assimilis (Fallén)	*M. ass*
Nemapoda nitudula (Fallén)	*N. nit*
Fannia sp (Desvoidy)	*F. sp*
F. coracina (Loew)	*F. cor*
F. scalaris (Fabricus)	*F. scal*
F. manicata (Meigen)	*F. man*
Lucilia sericata (Meigen)	*L. ser*
L. illustris (Meigen)	*L. ill*
L. caesar (Linnaeus)	*L. cae*
Ophyra leucostoma (Weidemann)	*O. leu*
Spinophora bergenstammi (Malloch)	*S. ber*
Sarcophaga carnaria (Linnaeus)	*S. car*
Cynomya mortuorum (Linnaeus)	*C. mor*

Appendix 1 - Table 1. The species found on Transect 1 during the first sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	*L. sericata*	Trap	*C. vicina*	*L. sericata*
1	100	0	36	56	0
2	0	0	37	124	1
3	59	0	38	0	0
4	0	0	39	0	0
5	188	0	40	78	0
6	66	0	41	0	0
7	80	0	42	0	0
8	163	0	43	0	0
9	0	0	44	0	0
10	0	0	45	0	0
11	70	0	46	0	0
12	8	0	47	0	0
13	0	0	48	0	0
14	62	0	49	120	0
15	63	0	50	0	0
16	63	0	51	76	0
17	0	0	52	0	0
18	0	0	53	0	0
19	0	0	54	42	0
20	0	0	55	60	0
21	0	0	56	0	0
22	143	0	57	6	0
23	3	0	58	0	0
24	0	0	59	0	0
25	63	0	60	0	0
26	0	0	61	145	0
27	0	0	62	0	0
28	0	0	63	0	0
29	0	0	64	0	0
30	0	0			
31	80	0			
32	0	0			
33	0	0			
34	0	0			
35	0	0			

Appendix 1 - Table 2. The species found on Transect 1 during the second sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	*M. prolapsa*	*M. assimilis*	*N. nitidula*	*F. coracina*
1	2	100	0	0	0
2	0	0	0	295	0
3	0	127	0	0	12
4	84	58	0	0	0
5	0	0	0	0	450
6	0	30	0	0	0
7	0	310	0	0	0
8	167	0	0	0	0
9	0	124	0	0	0
10	0	71	0	0	0
11	0	75	0	0	0
12	137	0	0	0	0
13	0	105	0	0	0
14	57	0	0	0	0
15	1	0	0	0	0
16	63	0	0	0	0
17	0	0	0	0	0
18	0	133	0	0	0
19	0	88	0	0	0
20	17	0	0	0	0
21	0	107	0	0	2
22	0	0	0	0	0
23	0	0	0	0	0
24	0	101	0	0	0
25	0	8	0	1	1
26	0	0	0	0	0
27	14	63	0	0	0
28	0	0	0	0	0
29	25	39	0	10	0
30	0	142	0	0	0
31	0	229	0	0	0
32	9	68	0	0	0
33	0	33	0	0	0
34	34	5	0	0	0
35	0	0	0	0	0

Trap	*C. vicina*	*M. prolapsa*	*M. assimilis*	*N. nitidula*	*F. coracina*
36	0	115	0	0	0
37	0	187	0	0	0
38	0	177	0	0	0
39	0	58	0	0	0
40	3	0	0	107	0
41	272	53	0	0	0
42	0	0	0	0	0
43	19	0	0	60	0
44	0	0	0	0	0
45	0	0	0	0	0
46	0	0	0	0	0
47	0	1	0	0	0
48	0	0	0	0	0
49	104	0	0	0	0
50	0	0	0	667	21
51	0	89	0	0	0
52	0	0	24	0	0
53	0	0	0	33	0
54	1	6	0	0	89
55	0	0	0	0	0
56	0	18	0	0	17
57	0	121	0	0	0
58	0	0	0	0	17
59	0	0	0	0	0
60	0	0	0	0	0
61	0	0	0	0	0
62	0	13	0	2	5
63	0	0	0	0	0
64	0	0	0	0	2

Appendix 1 - Table 3. The species found on Transect 1 during the third sampling session and the numbers reared from each chick carcass

Trap	C. vic	F. cor	F. scal	F. sp.	M. ass	M. pro	N. nit
1	0	0	0	0	0	0	0
2	0	0	0	0	0	31	0
3	0	0	0	0	0	0	0
4	0	0	0	0	0	89	0
5	0	0	0	0	0	93	0
6	0	0	0	0	0	0	0
7	0	0	0	0	0	184	0
8	0	0	0	0	0	208	0
9	0	0	0	0	0	144	0
10	0	0	0	0	0	69	0
11	79	0	0	0	0	79	0
12	0	0	0	0	0	65	0
13	0	0	0	0	0	157	0
14	0	0	0	0	0	0	0
15	0	0	0	0	0	123	0
16	0	0	0	2	0	60	0
17	0	0	0	0	0	109	0
18	0	0	0	0	0	0	0
19	0	0	0	0	11	0	4
20	0	0	0	0	0	119	119
21	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0
23	0	0	0	0	10	84	0
24	0	0	0	0	0	0	0
25	0	0	0	0	0	0	28
26	12	0	0	2	0	0	0
27	0	0	0	0	0	127	0
28	0	0	0	0	0	0	0
29	0	0	0	2	0	110	0
30	0	0	0	0	0	125	0
31	0	0	0	0	0	116	0
32	0	0	0	0	0	85	0
33	0	0	0	0	0	256	0
34	0	0	0	0	0	316	0
35	0	0	0	0	0	0	0

Trap	*C. vic*	*F. cor*	*F. scal*	*F. sp.*	*M. ass*	*M. pro*	*N. nit*
36	0	1	0	0	0	149	0
37	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0
39	0	0	0	0	0	103	0
40	0	0	0	0	0	30	0
41	70	0	0	0	0	70	0
42	0	0	0	0	0	0	0
43	0	0	0	0	2	0	116
44	0	0	0	0	0	20	0
45	0	0	0	0	0	147	0
46	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0
48	0	0	0	0	1	117	6
49	0	0	0	0	0	0	0
50	0	0	0	0	0	171	0
51	0	0	0	2	0	0	48
52	0	0	0	0	0	127	0
53	0	0	0	0	2	21	0
54	0	0	0	0	0	98	0
55	0	0	0	0	0	87	2
56	0	0	0	0	0	80	0
57	0	0	0	0	0	187	0
58	0	0	0	0	0	0	0
59	0	0	9	0	0	18	9
60	0	0	0	0	0	183	0
61	0	0	0	0	6	23	4
62	0	0	0	0	0	15	0
63	0	0	0	0	0	74	0
64	0	15	0	0	0	58	8

Appendix 1 - Table 4. The species found on Transect 1 during the fourth sampling session and the numbers reared from each chick carcass

Trap	*F. man*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*L. ser*	*S. car*	*S. ber*
1	0	0	0	1	0	0	0	0
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	0	3	0	0	0
5	0	0	0	121	0	0	0	0
6	0	0	0	71	0	0	0	0
7	0	0	0	0	0	0	0	0
8	0	0	0	11	0	0	0	0
9	0	0	0	90	0	0	0	0
10	0	0	0	20	1	0	0	0
11	0	0	0	0	0	5	0	0
12	0	0	0	90	0	0	0	0
13	0	0	0	0	0	0	0	19
14	0	0	0	0	0	0	0	54
15	0	3	0	128	0	0	0	0
16	0	0	0	57	0	0	0	0
17	0	0	0	0	0	0	0	0
18	0	0	0	39	0	0	0	0
19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0
22	0	0	0	0	9	0	0	0
23	0	0	0	158	0	0	0	0
24	0	0	0	0	0	0	0	0
25	0	0	0	4	0	0	0	0
26	0	0	0	0	0	0	0	0
27	0	0	0	43	0	0	0	0
28	0	0	0	88	0	0	0	0
29	0	0	0	62	0	0	0	0
30	0	0	0	0	0	0	0	0
31	0	0	0	4	5	0	0	1
32	0	0	0	121	0	0	0	0
33	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0

Trap	*F. man*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*L. ser*	*S. car*	*S. ber*
36	0	0	0	24	9	0	1	0
37	0	0	0	106	0	0	0	0
38	0	0	0	0	0	0	0	0
39	0	0	0	90	0	0	0	0
40	0	0	0	3	0	0	0	0
41	0	7	0	0	0	0	0	0
42	0	0	0	51	0	0	0	0
43	0	0	0	22	0	0	0	0
44	0	0	0	0	0	0	0	0
45	5	0	0	0	11	0	0	7
46	0	0	9	0	9	0	0	0
47	0	0	0	1	0	0	0	0
48	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0
50	0	0	0	70	0	0	0	0
51	0	0	0	37	0	0	0	0
52	0	0	0	0	0	0	0	0
53	0	0	0	18	0	0	0	0
54	0	0	0	40	0	0	0	0
55	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0
57	0	0	0	21	0	0	0	0
58	0	0	0	0	0	0	0	0
59	0	0	0	1	0	0	0	0
60	0	0	0	30	0	0	0	0
61	0	0	0	18	0	0	0	0
62	0	1	0	5	61	0	0	0
63	0	0	0	0	0	0	0	0
64	0	0	0	0	38	0	0	0

Appendix 1 - Table 4. The species found on Transect 1 during the fifth sampling session and the numbers reared from each chick carcass

Trap	*F. man*	*M. ass*	*M. pro*	*N. nit*	*L. ill*	*S. car*	*O. leu*
1	3	0	30	0	0	0	0
2	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0
4	0	0	1	0	0	5	0
5	0	0	14	0	0	0	0
6	0	0	0	0	0	0	0
7	0	0	17	0	0	0	0
8	0	0	58	0	0	0	0
9	0	0	4	0	0	0	9
10	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0
13	0	0	0	0	16	0	0
14	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0
25	0	0	166	0	0	0	0
26	0	0	0	0	0	0	0
27	0	0	21	0	0	0	0
28	0	0	14	0	0	0	0
29	0	0	0	0	0	0	0
30	0	0	73	0	0	0	0
31	0	0	0	9	0	0	0
32	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0
34	0	0	2	0	0	0	0
35	0	0	0	0	0	0	0

Trap	*F. man*	*M. ass*	*M. pro*	*N. nit*	*L. ill*	*S. car*	*O. leu*
36	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0
39	0	0	21	0	0	0	0
40	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0
45	0	0	26	0	0	0	0
46	0	7	6	0	0	0	0
47	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0
49	0	0	0	3	0	1	0
50	0	0	3	1	0	0	0
51	0	7	2	0	0	0	0
52	0	0	23	0	0	0	0
53	0	0	0	0	0	0	0
54	0	1	16	1	0	0	0
55	0	0	6	0	0	0	0
56	0	0	0	0	0	0	0
57	0	0	0	1	0	0	0
58	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0
60	0	24	1	0	0	0	0
61	0	0	9	0	0	0	0
62	0	0	0	0	0	0	0
63	0	0	1	0	0	0	0
64	0	0	0	0	0	0	0

Appendix 1 - Table 6. The species found on Transect 1 during the sixth sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*M. ass*	*M. pro*	*N. nit*	*O. leu*
1	0	0	0	0	0
2	0	0	0	0	0
3	0	0	0	0	0
4	0	0	18	0	0
5	0	0	50	0	0
6	0	0	0	0	0
7	0	0	2	0	0
8	0	0	0	0	0
9	0	0	0	0	0
10	0	1	0	39	0
11	0	0	0	0	0
12	0	0	0	0	0
13	0	0	42	0	0
14	0	0	0	0	0
15	0	0	7	0	0
16	0	0	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	40	18	0
20	0	0	0	0	0
21	0	0	0	0	0
22	0	0	0	0	0
23	0	0	0	0	0
24	0	0	0	0	0
25	0	0	0	0	0
26	0	5	0	0	0
27	0	0	0	0	0
28	0	0	0	0	0
29	0	0	0	0	0
30	0	0	0	0	0
31	0	0	0	0	0
32	0	0	0	0	0
33	0	0	0	0	0
34	0	0	0	0	0
35	0	0	10	0	0

Trap	*C. vic*	*M. ass*	*M. pro*	*N. nit*	*O. leu*
36	0	0	0	1	0
37	0	2	11	10	0
38	0	0	0	0	0
39	0	0	74	0	0
40	0	0	0	0	0
41	0	1	0	6	0
42	0	0	0	0	0
43	0	0	0	0	2
44	0	0	0	0	0
45	0	0	0	0	0
46	0	0	0	0	0
47	0	0	0	0	0
48	0	0	0	0	0
49	0	0	0	1	0
50	0	0	0	1	0
51	0	0	0	0	0
52	0	1	0	0	0
53	0	0	0	9	0
54	0	0	1	0	0
55	0	2	0	0	0
56	1	0	0	0	0
57	0	0	0	0	0
58	0	0	0	0	0
59	0	0	0	0	0
60	0	0	0	13	0
61	0	0	0	0	0
62	0	0	0	0	0
63	0	0	0	1	0
64	0	0	0	0	0

Appendix 1 - Table 7. The species found on Transect 1 during the seventh sampling session and the numbers reared from each chick carcass

Trap	*F. cor*	*F. scal*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*L. ill*	*L. ser*	*L. cae*
1	0	28	0	0	5	1	0	0	0
2	0	0	0	0	0	0	5	0	0
3	0	0	0	0	95	0	0	0	0
4	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	0	0	11	0	0	0	0
8	0	0	0	1	63	0	0	0	0
9	0	0	0	0	27	1	0	0	0
10	0	0	0	0	0	0	66	9	6
11	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0
13	0	0	0	0	14	0	0	0	0
14	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0
18	0	0	0	0	10	0	0	0	0
19	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	5	0	0
21	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0
23	0	0	0	0	2	0	0	0	0
24	1	0	0	0	10	0	0	0	0
25	0	0	0	0	0	0	0	0	0
26	0	0	0	0	4	0	0	0	0
27	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0
29	0	0	0	0	14	0	0	0	0
30	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	1	0	0	0
32	0	0	0	0	68	0	0	0	0
33	0	0	0	0	83	0	0	0	0
34	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0

Trap	*F. cor*	*F. scal*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*L. ill*	*L. ser*	*L. cae*
36	0	0	0	18	18	1	0	0	0
37	0	0	0	0	6	0	0	0	0
38	0	0	0	0	8	0	0	0	0
39	0	0	0	0	27	0	0	0	0
40	0	0	0	5	1	1	0	0	0
41	0	0	0	0	27	0	0	0	0
42	0	0	3	4	8	14	0	0	0
43	0	0	0	0	38	12	0	0	0
44	0	0	0	0	36	0	0	0	0
45	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0
49	0	0	0	0	69	0	0	0	0
50	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0
52	0	0	0	1	4	23	0	0	0
53	0	0	0	0	39	0	0	0	0
54	0	0	0	0	4	0	0	0	0
55	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0
57	0	0	0	0	3	7	0	0	0
58	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	3	0	0	0
60	0	0	0	0	0	0	0	0	0
61	0	0	0	0	5	0	0	0	0
62	0	0	0	2	117	0	0	0	0
63	0	0	0	0	32	1	0	0	0
64	0	0	0	0	0	0	0	0	0

Appendix 1 - Table 8. The species found on Transect 1 during the eighth sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	*M. prolapsa*	*N. nitidula*	*M. assimilis*
1	0	1	0	0
2	0	0	0	0
3	0	0	0	0
4	0	4	0	0
5	0	0	0	0
6	0	0	0	0
7	0	0	0	0
8	0	0	0	0
9	0	49	0	0
10	0	0	0	0
11	0	0	0	0
12	0	0	0	0
13	0	0	0	0
14	0	0	0	0
15	0	3	0	0
16	0	0	0	0
17	0	0	0	0
18	0	0	0	0
19	0	2	0	0
20	0	0	0	0
21	0	0	0	0
22	0	1	0	0
23	0	0	0	0
24	0	0	0	0
25	0	0	0	0
26	0	0	0	0
27	0	0	0	0
28	17	3	0	0
29	0	1	0	0
30	0	0	0	0
31	0	13	0	0
32	0	123	0	0
33	0	11	0	0
34	0	1	0	0
35	0	0	0	0

Trap	*C. vicina*	*M. prolapsa*	*N. nitidula*	*M. assimilis*
36	0	2	0	0
37	0	18	0	0
38	0	14	0	3
39	0	36	0	0
40	0	3	0	0
41	0	10	4	0
42	0	38	0	0
43	0	0	0	0
44	0	0	0	0
45	0	0	0	0
46	0	0	0	0
47	0	0	0	0
48	0	0	0	0
49	0	0	0	0
50	0	0	0	0
51	0	0	0	0
52	0	0	0	0
53	0	0	0	0
54	0	0	0	0
55	0	0	1	0
56	0	0	0	0
57	0	0	0	0
58	0	0	0	0
59	0	0	0	0
60	0	0	18	0
61	0	0	0	0
62	0	2	1	0
63	0	0	0	0
64	0	0	0	0

Appendix 1 - Table 9. The species found on Transect 1 during the ninth sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	*F. scalaris*	*F. sp*	*M. prolapsa*	*N. nitidula*
1	3	0	0	0	0
2	0	0	0	0	0
3	5	0	0	0	0
4	5	0	0	0	0
5	0	0	0	0	0
6	0	0	0	0	0
7	0	0	0	0	0
8	0	0	0	0	0
9	0	0	0	0	0
10	7	0	0	0	0
11	11	0	0	0	0
12	0	0	0	0	0
13	0	0	0	0	0
14	0	0	0	0	0
15	0	0	0	0	0
16	0	0	0	0	0
17	0	0	0	3	0
18	7	0	0	0	0
19	0	0	0	0	0
20	6	0	0	0	0
21	0	0	0	2	0
22	12	0	0	0	0
23	0	0	0	0	0
24	0	0	0	0	0
25	0	0	0	0	0
26	0	0	0	0	0
27	0	0	0	0	0
28	0	0	0	0	0
29	0	0	0	0	0
30	0	0	0	0	0
31	0	0	0	0	0
32	0	2	0	0	0
33	0	0	0	0	2
34	0	0	0	6	0
35	0	0	0	0	0

Trap	*C. vicina*	*F. scalaris*	*F. sp*	*M. prolapsa*	*N. nitidula*
36	0	0	0	0	0
37	0	0	0	0	0
38	0	0	0	0	0
39	0	0	0	0	0
40	0	0	0	0	0
41	0	0	0	0	0
42	0	0	0	0	0
43	54	0	0	0	0
44	0	0	0	0	0
45	0	0	0	0	0
46	0	0	0	0	0
47	2	0	0	0	0
48	0	0	0	0	0
49	1	0	0	0	0
50	0	0	0	0	0
51	0	0	1	0	0
52	0	0	0	0	0
53	0	0	0	19	0
54	0	0	0	0	0
55	0	0	0	0	0
56	0	0	0	0	0
57	0	0	0	0	0
58	0	0	0	0	0
59	0	0	0	2	0
60	0	0	0	0	0
61	0	0	0	0	0
62	0	0	0	0	0
63	0	0	0	11	0
64	0	0	0	0	0

Appendix 1 - Table 10. The species found on Transect 1 during the tenth sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	Trap	*C. vicina*
1	0	36	0
2	0	37	0
3	0	38	18
4	0	39	0
5	0	40	0
6	0	41	0
7	0	42	0
8	0	43	0
9	0	44	2
10	0	45	61
11	51	46	0
12	0	47	0
13	0	48	0
14	0	49	40
15	0	50	0
16	0	51	0
17	0	52	0
18	89	53	0
19	0	54	0
20	0	55	0
21	0	56	0
22	0	57	0
23	0	58	0
24	0	59	0
25	0	60	0
26	0	61	0
27	0	62	0
28	0	63	0
29	0	64	0
30	0		
31	1		
32	0		
33	6		
34	0		
35	0		

Appendix 1 - Table 11. The species found on Transect 1 during the eleventh sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	*L. caesar*	Trap	*C. vicina*	*L. caesar*
1	123	0	36	0	0
2	6	0	37	0	0
3	0	0	38	49	0
4	97	0	39	128	0
5	0	0	40	0	0
6	0	0	41	178	0
7	0	0	42	82	0
8	0	0	43	61	0
9	127	0	44	45	0
10	127	0	45	38	0
11	154	0	46	0	0
12	76	0	47	0	0
13	0	0	48	0	0
14	99	0	49	39	0
15	0	0	50	0	0
16	4	0	51	145	0
17	0	0	52	38	0
18	177	0	53	57	0
19	0	0	54	2	0
20	54	0	55	5	0
21	0	0	56	120	30
22	61	0	57	0	0
23	0	0	58	0	0
24	0	0	59	0	0
25	123	0	60	0	0
26	54	0	61	2	0
27	0	0	62	70	0
28	4	0	63	0	0
29	72	0	64	20	0
30	0	0			
31	0	0			
32	0	0			
33	0	0			
34	90	0			
35	0	0			

Appendix 1 - Table 12 . The numbers of *C. vicina* found on Transect 1 during the Twelfth to fifteenth sampling sessions and the numbers reared from each chick carcass

Trap	12th	13th	14th	15th	Trap	12th	13th	14th	15th
1	85	120	0	0	36	217	30	125	1
2	3	0	240	0	37	0	143	0	0
3	87	0	127	0	38	2	68	0	0
4	3	83	266	0	39	3	0	67	0
5	154	66	260	0	40	23	117	205	7
6	65	115	67	8	41	72	80	0	0
7	10	100	0	4	42	191	84	98	0
8	68	0	173	0	43	165	30	142	0
9	3	100	270	0	44	20	0	0	0
10	58	16	366	0	45	14	24	155	0
11	36	143	360	13	46	280	143	0	0
12	6	11	209	159	47	0	0	38	0
13	147	0	123	0	48	138	18	0	23
14	91	34	149	0	49	162	0	0	0
15	143	0	95	0	50	13	69	430	0
16	7	56	277	65	51	0	0	0	0
17	0	0	166	0	52	0	0	3	3
18	320	132	177	0	53	182	7	182	51
19	134	0	152	0	54	28	101	263	0
20	3	39	88	0	55	229	8	292	0
21	15	0	0	0	56	68	0	0	0
22	5	1	22	0	57	0	17	208	0
23	70	54	165	14	58	5	0	253	0
24	0	0	0	0	59	1	45	80	0
25	110	0	0	0	60	19	0	120	0
26	118	0	145	64	61	29	93	221	31
27	158	0	161	0	62	161	0	302	0
28	0	0	0	0	63	0	0	0	7
29	39	41	61	0	64	192	11	179	237
30	0	0	0	0					
31	0	0	224	0					
32	0	145	106	0					
33	0	107	159	0					
34	50	0	139	0					
35	0	0	0	0					

Appendix 1 - Table 13. The species found on Transect 2 during the first sampling session and the numbers reared from each chick carcass

Trap	*C. vicina*	*L. sericata*	Trap	*C. vicina*	*L. sericata*
1	0	0	36	0	0
2	0	0	37	111	0
3	0	0	38	0	0
4	60	0	39	0	0
5	0	0	40	2	0
6	0	0	41	56	0
7	0	0	42	0	0
8	0	0	43	97	0
9	17	0	44	0	0
10	140	0	45	0	0
11	0	0	46	0	0
12	0	0	47	7	1
13	0	0	48	184	0
14	73	0	49	0	0
15	0	0	50	64	0
16	0	30	51	35	0
17	0	0	52	0	0
18	0	0	53	100	0
19	125	0	54	110	0
20	0	0	55	158	0
21	0	0	56	0	0
22	0	0	57	0	0
23	0	0	58	0	0
24	0	0	59	197	0
25	0	0	60	270	0
26	0	0	61	54	0
27	0	0	62	1	0
28	0	0	63	0	0
29	173	0	64	10	0
30	0	0	65	0	0
31	20	0	66	0	0
32	88	0	67	0	0
33	0	0	68	0	0
34	0	0			
35	0	0			

Appendix 1 - Table 14. The species found on Transect 2 during the second sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*M. pro*	*F. cor*	*N. nit*	*L. cae*	*L. ill*	*L. ser*
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0
8	1	0	1	0	0	0	0
9	3	82	4	5	0	0	0
10	0	0	0	0	0	0	0
11	59	1	0	0	0	0	0
12	3	8	0	0	0	0	0
13	0	105	0	0	0	0	0
14	13	0	0	0	0	0	0
15	137	0	0	0	0	0	0
16	128	0	0	0	0	0	0
17	0	0	12	20	0	0	0
18	36	0	0	0	0	0	0
19	286	0	0	0	0	0	0
20	0	0	0	0	0	2	0
21	0	0	0	0	0	0	0
22	283	0	0	0	0	0	0
23	148	0	0	0	3	14	0
24	0	0	0	0	0	25	0
25	0	0	1	0	0	0	0
26	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0
28	2	0	0	0	0	0	0
29	175	0	0	0	0	0	0
30	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0
33	2	20	0	1	0	0	0
34	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0

Appendix 1 - Table 14 continued

Trap	*C. vic*	*M. pro*	*F. cor*	*N. nit*	*L. cae*	*L. ill*	*L. ser*
36	0	0	0	0	0	0	0
37	3	0	0	0	0	0	0
38	0	0	0	0	0	0	0
39	2	0	0	0	0	0	0
40	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0
44	70	0	0	112	0	0	0
45	0	0	0	0	0	0	0
46	210	2	0	0	0	0	0
47	16	0	4	9	0	0	0
48	146	0	0	0	0	0	0
49	48	1	0	18	0	0	0
50	146	0	21	0	0	0	0
51	0	0	0	0	0	0	0
52	107	0	0	0	0	0	0
53	32	0	0	0	0	0	3
54	0	0	0	0	0	0	2
55	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0
57	259	0	0	0	0	0	0
58	0	0	0	0	0	0	0
59	0	0	0	0	0	0	15
60	0	0	0	0	0	0	0
61	0	0	1	0	0	0	0
62	0	25	2	0	0	0	0
63	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0
67	357	0	0	0	0	0	0
68	0	0	0	0	0	0	0

Appendix 1 - Table 15. The species found on Transect 2 during the third sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. cor*	*F. man*	*F. sca*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*S. ber*	*L. ll*	*C. mor*
1	4	0	0	0	3	0	25	3	0	0	0
2	0	0	0	0	0	0	128	0	0	0	0
3	0	0	0	0	0	0	178	0	0	0	0
4	56	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	190	0	0	0	0	0	0	0	0	0	0
7	326	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	191	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	1	96	64	0	0	0	0
11	0	0	0	0	1	2	0	7	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0
13	0	8	0	0	0	0	98	0	0	30	0
14	330	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	6	0	0	0
16	0	0	0	0	0	0	159	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	2	0	0	61	0	0	0	0
20	0	92	0	0	0	0	0	161	0	0	0
21	72	0	0	0	0	0	0	0	0	6	0
22	0	0	0	0	0	66	0	0	0	0	0
23	0	0	0	0	0	0	11	0	0	0	0
24	0	7	0	0	0	42	3	0	1	0	0
25	99	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0
27	84	0	0	0	0	1	0	0	0	0	0
28	0	7	0	0	0	0	51	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0
31	39	0	0	0	0	120	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0
33	0	1	0	0	0	0	2	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 - Table 15 continued

Trap	*C. vic*	*F. cor*	*F. man*	*F. sca*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*S. ber*	*L. ill*	*C. mor*
35	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	82	0	0	0	0
37	0	0	0	0	0	0	158	0	0	0	0
38	0	0	0	0	0	46	0	0	0	0	16
39	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	135	0	0	0	0
41	0	0	0	0	0	0	55	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0
43	2	0	0	0	0	0	0	0	0	0	0
44	168	0	0	0	0	0	168	0	0	0	0
45	0	33	2	0	0	1	0	92	0	0	0
46	0	0	0	0	0	0	82	0	0	0	0
47	0	0	0	0	2	12	0	13	0	0	0
48	0	11	0	0	0	0	11	6	0	0	0
49	116	0	0	0	0	0	13	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	103	0	0	0	0
52	2	0	0	0	0	0	30	0	0	0	0
53	115	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0
55	208	0	0	0	0	0	0	0	0	0	0
56	98	0	0	0	0	0	0	0	0	0	0
57	17	0	0	0	0	0	17	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0
61	77	0	0	0	0	0	2	0	0	0	0
62	0	0	0	0	0	0	13	3	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0
64	16	0	0	0	1	0	34	0	0	0	0
65	3	0	0	0	0	0	5	7	0	0	0
66	0	0	0	0	0	0	25	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 - Table 16. The species found on Transect 2 during the fourth sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. cor*	*F. man*	*F. scal*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*O. leu*	*S. ber*
1	0	0	0	0	0	0	0	0	10	0
2	0	0	0	0	0	1	18	0	0	0
3	0	0	0	0	0	0	1	0	0	0
4	0	0	0	4	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	1	0	0	0	0	0
7	0	6	0	0	0	0	0	72	0	0
8	0	0	0	0	0	0	34	1	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	17	0	0
11	0	0	0	0	2	0	0	0	0	0
12	0	0	0	0	1	0	6	0	0	0
13	0	0	0	0	0	0	39	0	0	0
14	0	0	0	0	0	0	0	11	0	0
15	0	0	0	0	0	20	12	0	0	0
16	0	0	0	0	0	0	11	0	0	0
17	0	0	0	0	0	0	0	1	0	0
18	0	0	0	0	2	0	4	1	0	0
19	0	0	0	0	0	0	31	4	0	0
20	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	16	0	0
22	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	60	0	0	0
24	0	0	0	0	0	0	12	0	0	0
25	0	1	0	0	0	34	0	0	0	0
26	0	0	0	0	0	0	8	1	0	0
27	0	0	0	0	0	0	67	0	0	0
28	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	6	60	0	0	0
31	0	0	0	0	0	20	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	1	0	0	0
34	0	0	0	0	0	0	0	0	0	0

Appendix 1 - Table 16 continued

Trap	*C. vic*	*F. cor*	*F. man*	*F. scal*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*O. leu*	*S. ber*
35	2	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0
37	0	1	0	0	0	0	45	0	0	0
38	0	0	0	0	0	0	1	2	0	0
39	0	0	0	0	0	0	71	0	0	0
40	0	0	0	0	0	0	34	81	0	0
41	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	7	0	0	0
43	0	0	0	0	1	0	0	37	0	0
44	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	18	0	0	0
46	0	0	0	0	0	0	50	0	0	0
47	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0
49	0	0	2	0	0	0	27	10	0	0
50	0	0	0	0	9	0	6	1	0	0
51	0	0	0	0	18	30	0	0	0	0
52	0	0	0	0	0	0	167	0	0	0
53	0	0	0	0	0	0	5	0	0	0
54	0	0	0	0	0	2	69	1	0	0
55	0	0	0	0	0	0	9	2	0	0
56	0	0	0	0	0	0	16	0	0	2
57	14	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0
59	0	0	3	0	0	0	46	0	0	0
60	0	0	0	0	0	0	0	0	0	0
61	1	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	32	0	0	0
63	0	0	0	0	0	0	0	0	4	0
64	22	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	1	0	54
66	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0

Appendix 1 - Table 17. The species found on Transect 2 during the fifth sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. cor*	*F. man*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*O. leu*
1	0	0	0	0	0	42	22	0
2	0	0	0	0	0	52	0	0
3	0	0	0	0	2	30	0	0
4	0	0	0	0	0	8	3	0
5	0	0	0	0	0	0	0	17
6	0	0	0	0	1	0	32	0
7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	65	1	0
9	0	0	0	0	0	29	0	0
10	0	1	0	0	0	8	0	0
11	0	4	0	0	0	38	4	0
12	0	1	0	0	34	6	37	0
13	0	0	0	0	0	0	0	0
14	0	3	4	0	0	0	0	0
15	0	0	0	0	0	0	0	0
16	0	5	0	0	0	40	0	0
17	0	10	0	0	4	41	0	0
18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0
20	0	0	0	35	0	3	104	0
21	0	0	0	0	0	49	0	0
22	0	0	0	0	0	158	0	0
23	0	0	0	0	0	40	0	0
24	0	21	0	0	2	39	0	0
25	0	0	0	0	0	11	0	0
26	0	0	0	0	0	24	0	0
27	0	0	0	0	28	0	4	0
28	0	0	0	0	0	83	0	0
29	0	0	0	0	0	0	11	0
30	0	0	0	0	0	83	0	0
31	0	0	0	0	0	13	8	0
32	0	0	0	0	0	0	0	0
33	0	0	0	0	0	71	0	0
34	0	0	0	0	0	0	0	0

Appendix 1 - Table 17 continued

Trap	*C. vic*	*F. cor*	*F. man*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*O. leu*
35	0	0	0	0	0	7	0	0
36	0	0	0	0	0	1	49	0
37	0	0	0	0	0	2	0	0
38	0	0	0	0	0	13	0	0
39	0	0	0	0	0	0	0	0
40	0	0	0	0	0	2	0	0
41	0	0	0	0	0	10	0	0
42	0	0	0	0	0	2	0	0
43	0	0	0	0	0	1	0	0
44	0	0	0	0	0	0	0	0
45	0	0	0	0	0	2	0	0
46	0	0	0	1	0	0	0	0
47	0	0	0	0	0	139	0	0
48	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0
50	6	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0
52	0	0	0	0	0	109	0	0
53	0	0	0	0	3	0	0	0
54	0	0	0	0	0	0	0	0
55	0	0	0	2	0	0	0	0
56	0	0	0	0	26	1	2	0
57	0	0	0	0	0	0	0	0
58	0	0	0	0	0	3	0	0
59	0	0	0	0	2	26	0	0
60	0	2	0	0	1	0	0	1
61	0	0	0	0	0	0	0	0
62	0	0	0	0	0	3	0	2
63	0	0	0	0	0	0	0	0
64	0	0	0	0	0	145	0	0
65	0	0	0	0	0	0	0	0
66	0	0	0	3	0	0	0	0
67	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0

Appendix 1 - Table 18. The species found on Transect 2 during the sixth sampling session and the numbers reared from each chick carcass

Trap	*F. cor*	*F. man*	*F. scal*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*L. ill*	*L. ser*	*L. cae*	*O. leu*
1	0	0	0	0	0	0	8	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0
7	0	5	0	0	0	0	1	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	4	0	0	0	0	0	1	0	0	0	0
11	0	0	0	32	0	0	32	2	0	0	0
12	0	0	0	0	0	0	4	0	0	0	0
13	0	0	0	0	0	19	1	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	3	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	5	0	0	0	0
20	0	0	0	0	0	14	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	3	0	0	0	0	0	0
23	0	0	0	0	0	0	8	0	0	0	0
24	0	0	0	0	0	10	0	0	0	0	0
25	0	0	6	0	0	0	0	0	0	0	0
26	0	0	0	1	1	2	24	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	26	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	5	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0
32	0	1	0	0	0	0	20	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0
34	6	0	0	0	0	2	9	0	0	0	0

Appendix 1 - Table 18 continued

Trap	*F. cor*	*F. mann*	*F. scal*	*F. sp*	*M. ass*	*M. pro*	*N. nit*	*L. ill*	*L. ser*	*L. cae*	*O. leu*
35	6	0	0	0	0	0	11	0	0	0	0
36	0	0	0	0	0	0	7	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	6	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	1	0	1	0	0	0	0
42	0	0	0	0	0	0	3	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0
46	0	8	0	0	0	0	6	0	0	0	0
47	0	0	0	0	0	11	8	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	9	0	0	0	0
50	0	0	0	0	0	4	58	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	2	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	29
56	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	91
58	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	11	0	0	0	0
63	0	0	0	4	0	0	0	0	0	0	4
64	0	0	0	0	0	4	0	0	0	0	0
65	0	0	0	0	0	0	0	27	2	43	0
66	0	0	0	0	0	1	0	0	0	0	0
67	0	0	0	2	0	5	9	0	0	0	0
68	0	0	0	0	0	19	0	0	0	0	0

Appendix 1 - Table 19. The species found on Transect 2 during the seventh sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. cor*	*F. man*	*F. scal*	*M. ass*	*M. pro*	*N. nit*
1	0	0	0	0	0	0	0
2	0	0	0	0	0	37	0
3	0	0	0	0	0	17	0
4	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0
6	0	0	0	0	0	5	0
7	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0
9	0	0	0	0	0	9	0
10	0	0	0	0	48	48	0
11	0	0	0	0	0	46	0
12	0	0	1	0	0	21	0
13	0	0	0	0	0	4	8
14	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0
16	4	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	2	0
19	0	0	0	0	0	17	0
20	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0
22	0	0	0	0	0	4	0
23	0	0	0	0	0	0	0
24	0	0	0	0	0	1	0
25	0	0	0	0	0	14	0
26	0	0	0	0	0	2	0
27	0	0	0	0	0	28	0
28	0	0	0	0	0	0	0
29	0	0	0	0	0	64	0
30	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0
32	0	0	0	0	0	0	5
33	0	0	0	0	0	0	0
34	0	4	0	0	0	13	1
35	0	0	0	0	0	0	0

Appendix 1 - Table 19 continued

Trap	*C. vic*	*F. cor*	*F. man*	*F. scal*	*M. ass*	*M. pro*	*N. nit*
36	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0
38	0	0	0	0	0	12	12
39	0	1	0	0	0	2	0
40	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0
42	0	1	0	0	0	0	5
43	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0
48	27	0	0	0	0	0	0
49	0	0	0	0	0	26	0
50	0	0	0	0	0	19	0
51	0	0	0	1	0	12	0
52	0	0	0	0	0	2	0
53	6	0	0	0	0	0	0
54	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0
59	0	0	0	0	0	1	0
60	0	0	0	0	0	57	0
61	0	0	0	0	0	0	0
62	0	0	0	0	0	42	0
63	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0
66	0	3	0	0	0	17	0
67	0	0	0	0	0	85	1
68	0	0	0	0	1	0	0

Appendix 1 - Table 20. The species found on Transect 2 during the eighth sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. scal*	*F. sp*	*M. pro*	*N. nit*
1	0	0	0	2	0
2	0	0	0	0	0
3	0	0	0	0	0
4	0	0	0	0	0
5	0	0	0	0	0
6	0	0	0	0	0
7	0	0	0	0	0
8	0	2	0	0	0
9	0	0	0	0	0
10	0	0	0	0	0
11	0	0	0	0	2
12	0	0	0	0	0
13	0	0	0	1	0
14	0	0	0	0	0
15	0	0	0	0	0
16	0	0	0	0	0
17	0	0	0	5	0
18	0	0	0	0	0
19	0	0	0	1	0
20	0	0	0	0	0
21	0	0	0	0	0
22	0	0	0	22	0
23	0	0	0	9	0
24	0	0	0	0	0
25	0	0	0	4	0
26	0	0	0	0	0
27	0	0	0	5	0
28	0	0	0	10	0
29	0	0	0	0	0
30	0	0	0	0	0
31	0	0	0	1	0
32	0	0	0	37	1
33	0	0	0	1	0
34	0	0	0	0	0
35	0	0	0	0	0

Appendix 1 - Table 20 continued

Trap	*C. vic*	*F. scal*	*F. sp*	*M. pro*	*N. nit*
36	0	0	0	0	0
37	0	0	0	0	0
38	0	0	0	5	0
39	9	0	0	0	0
40	0	0	0	0	0
41	0	0	0	1	0
42	0	0	0	0	0
43	0	0	0	0	0
44	0	0	0	0	0
45	0	0	0	0	0
46	0	0	0	9	0
47	0	0	0	0	0
48	0	0	0	0	0
49	0	0	0	0	0
50	0	0	2	0	0
51	0	0	0	0	0
52	0	0	0	0	0
53	0	0	0	0	0
54	0	0	0	0	0
55	1	0	0	0	0
56	0	0	0	0	0
57	0	0	0	0	0
58	0	0	0	0	0
59	0	0	0	0	0
60	0	0	0	0	0
61	0	0	0	0	0
62	0	0	0	0	0
63	0	0	0	0	0
64	0	0	0	0	0
65	0	0	0	0	0
66	0	0	0	0	0
67	0	0	0	0	0
68	0	0	0	0	0

Appendix 1 - Table 21. The species found on Transect 2 during the ninth sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. cor*	*F. sp*	*S. ber*	Trap	*C. vic*	*F. cor*	*F. sp*	*S. ber*
1	0	0	0	0	36	0	0	0	0
2	0	0	0	0	37	0	0	0	0
3	0	0	0	0	38	0	0	0	0
4	0	0	0	0	39	50	0	0	0
5	0	0	0	0	40	0	0	0	0
6	0	0	0	0	41	0	0	0	0
7	0	0	0	0	42	0	0	0	0
8	0	0	0	0	43	0	0	0	0
9	8	0	0	0	44	0	0	0	0
10	0	0	0	0	45	0	0	0	0
11	0	0	0	0	46	0	0	0	0
12	0	0	0	0	47	0	0	0	0
13	0	0	0	2	48	1	0	0	0
14	0	0	0	0	49	0	0	0	0
15	0	0	0	0	50	0	0	0	0
16	0	0	0	0	51	0	0	0	0
17	0	0	0	0	52	13	0	0	0
18	0	0	0	0	53	0	0	2	0
19	0	0	0	0	54	0	0	0	0
20	0	0	0	0	55	0	0	0	0
21	0	0	0	0	56	0	0	0	0
22	0	0	0	0	57	0	0	0	0
23	0	0	0	0	58	0	0	0	0
24	0	0	0	0	59	0	0	0	0
25	0	0	0	0	60	0	0	0	0
26	0	0	0	0	61	1	0	0	0
27	0	0	0	0	62	0	0	0	0
28	0	0	0	0	63	0	0	0	0
29	0	1	0	0	64	0	0	0	0
30	17	0	0	0	65	0	0	0	0
31	0	0	0	0	66	0	0	0	0
32	0	0	0	0	67	0	0	0	0
33	0	0	0	0	68	0	0	0	0
34	0	0	0	0					
35	0	0	0	0					

Appendix 1 - Table 22. The species found on Transect 2 during the tenth sampling session and the numbers reared from each chick carcass

Trap	*C. vic*	*F. scal*	Trap	*C. vic*	*F. scal*
1	0	0	36	0	0
2	0	0	37	0	0
3	0	0	38	145	0
4	0	0	39	0	0
5	0	0	40	0	0
6	0	0	41	0	0
7	0	3	42	0	0
8	0	0	43	0	0
9	0	0	44	0	0
10	0	0	45	0	0
11	0	0	46	0	0
12	0	0	47	0	0
13	0	0	48	0	0
14	0	0	49	0	0
15	0	0	50	0	0
16	0	0	51	0	0
17	0	0	52	59	0
18	0	0	53	0	0
19	0	0	54	16	0
20	0	0	55	0	0
21	0	0	56	0	0
22	12	0	57	0	0
23	0	0	58	0	0
24	26	0	59	0	0
25	21	0	60	0	0
26	0	0	61	0	0
27	0	0	62	0	0
28	0	0	63	0	0
29	0	0	64	0	0
30	0	0	65	0	0
31	0	0	66	0	0
32	0	0	67	0	0
33	0	0	68	0	0
34	116	0			
35	0	0			

Appendix 1 - Table 23. The numbers of *C. vicina* found on Transect 2 during the eleventh to fifteenth sampling sessions and the numbers reared from each chick carcass

Trap	11th	12th	13th	14th	15th	Trap	11th	12th	13th	14th	15th
1	0	15	0	59	0	36	0	0	0	0	0
2	0	0	0	0	0	37	95	129	0	0	0
3	190	0	0	8	1	38	0	47	0	0	0
4	105	80	35	209	101	39	54	0	0	0	0
5	0	98	0	0	0	40	0	95	0	53	0
6	0	0	0	0	0	41	0	200	53	158	0
7	0	121	89	0	0	42	0	0	0	0	0
8	0	0	0	0	0	43	58	33	0	210	0
9	0	14	0	0	0	44	0	0	0	104	0
10	0	57	0	0	0	45	168	0	0	61	0
11	47	28	0	0	0	46	8	0	0	0	0
12	0	72	0	0	0	47	0	114	0	0	0
13	0	0	0	0	0	48	0	93	0	0	0
14	0	0	0	60	0	49	63	0	190	0	0
15	0	111	93	0	0	50	0	0	0	0	0
16	0	133	0	160	0	51	0	73	80	272	0
17	0	68	0	0	0	52	201	45	77	59	0
18	0	350	0	0	0	53	0	76	103	163	0
19	0	208	139	319	0	54	0	45	0	123	0
20	0	96	0	0	0	55	0	45	0	0	0
21	140	174	103	0	0	56	31	132	0	0	0
22	0	46	0	0	0	57	4	21	0	138	0
23	0	146	0	0	0	58	120	25	147	77	0
24	0	0	0	0	0	59	92	1	169	174	0
25	150	33	28	0	0	60	0	0	23	109	0
26	0	0	145	0	0	61	0	3	0	87	0
27	0	50	0	108	0	62	0	61	0	97	0
28	0	85	0	0	0	63	0	112	0	107	0
29	51	26	212	0	0	64	0	92	0	167	0
30	206	47	81	209	0	65	0	6	0	74	0
31	0	106	0	126	0	66	180	80	0	0	0
32	155	0	0	0	0	67	0	0	0	291	0
33	0	0	0	210	0	68	0	0	11	234	0
34	0	125	86	0	0						
35	0	90	0	136	0						

APPENDIX 2: The raw respirometry data used for the comparisons of respirometry rate of *L.sericata* larvae.

Where;

Log_{10} mass = log_{10} (mass in mg)
Log_{10} rate = log_{10} (µl oxygen/larva/hour)
Δ methrin = Deltamethrin

Control (log_{10} mass)	Control (log_{10} rate)	Cadmium (log_{10} mass)	Cadmium (log_{10} rate)	Δ methrin (log_{10} mass)	Δ methrin (log_{10} rate)
1.20	1.69	0.40	0.63	0.51	1.00
1.22	1.66	0.46	0.66	0.57	0.86
1.22	1.59	0.60	1.08	0.64	0.93
1.27	1.70	0.70	0.98	0.68	1.01
1.29	1.57	0.93	1.39	0.76	1.19
1.31	1.61	0.96	1.25	0.81	1.04
1.31	1.67	0.96	1.08	0.83	1.13
1.34	1.17	0.97	1.28	0.83	1.12
1.34	1.73	0.99	1.38	0.83	1.19
1.35	1.70	1.00	1.40	0.84	1.00
1.37	1.70	1.06	1.47	0.84	1.32
1.39	1.62	1.08	1.52	0.85	1.32
1.40	1.67	1.11	1.52	0.88	1.20
1.40	1.79	1.13	1.47	0.91	1.17
1.40	1.64	1.13	1.43	0.95	1.15
1.40	1.39	1.13	1.47	1.01	1.18
1.41	1.59	1.16	1.47	1.03	1.25
1.43	1.68	1.18	1.48	1.03	1.27
1.47	1.68	1.21	1.40	1.04	1.39
1.48	1.79	1.21	1.60	1.05	1.36
1.52	1.67	1.23	1.49	1.08	1.34
1.52	1.72	1.25	1.55	1.10	1.25
1.54	1.68	1.26	1.52	1.11	1.39
1.54	1.69	1.28	1.51	1.12	1.48

APPENDIX 2 continued

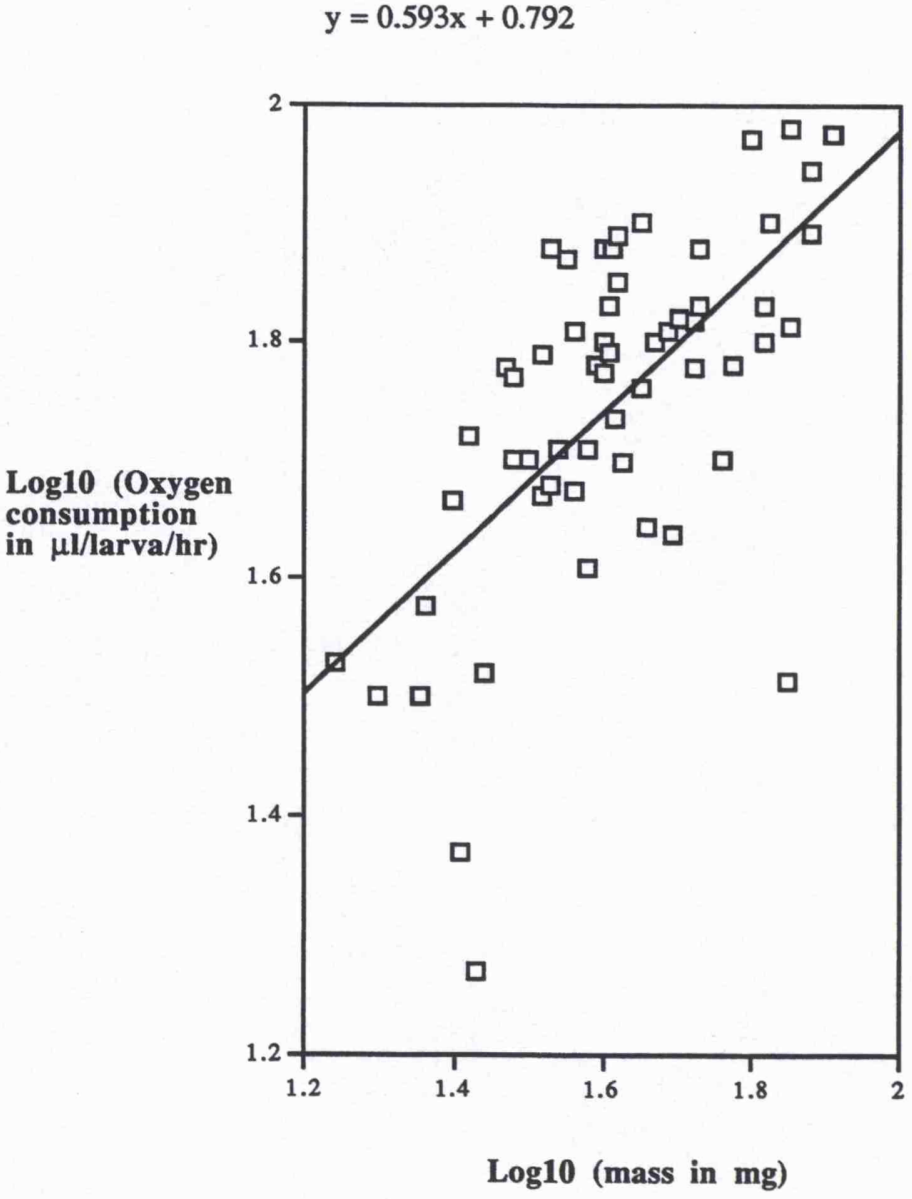
Control (log10 mass)	Control (log10 rate)	Cadmium (log10 mass)	Cadmium (log10 rate)	Δ methrin (log10 mass)	Δ methrin (log10 rate)
1.55	1.78	1.29	1.61	1.12	1.49
1.56	1.66	1.29	1.01	1.14	1.45
1.57	1.68	1.29	1.39	1.15	1.47
1.57	1.73	1.30	1.67	1.16	1.57
1.58	1.80	1.31	1.60	1.16	1.57
1.60	1.76	1.32	1.41	1.21	1.61
1.62	1.77	1.35	1.61	1.21	1.58
1.62	1.81	1.37	1.58	1.22	1.39
1.63	1.80	1.40	1.66	1.23	1.63
1.70	1.64	1.42	1.43	1.23	1.65
1.71	1.84	1.44	1.46	1.23	1.49
1.71	1.93	1.49	1.71	1.26	1.57
1.73	1.82	1.49	1.63	1.26	1.65
1.74	1.86	1.49	1.71	1.29	1.78
1.74	1.91	1.51	1.64	1.31	1.68
1.74	1.97	1.58	1.75	1.31	1.61
1.74	1.96	1.58	1.68	1.32	1.77
1.75	1.94	1.62	1.71	1.33	1.70
1.75	1.88	1.64	1.67	1.33	1.67
1.75	1.84	1.67	1.75	1.34	1.43
1.76	1.92	1.70	1.79	1.34	1.69
1.76	1.88			1.35	1.50
1.76	1.86			1.37	1.68
1.76	1.87			1.38	1.70
1.77	1.75			1.39	1.66
1.77	1.89			1.39	1.70
1.77	1.87			1.39	1.68
1.77	1.88			1.39	1.77
1.78	1.85			1.41	1.64
1.78	2.00			1.42	1.73
1.78	1.97			1.42	1.71
1.79	1.95			1.43	1.75

APPENDIX 2 continued

Control (log_{10} mass)	Control (log_{10} rate)	Cadmium (log_{10} mass)	Cadmium (log_{10} rate)	Δ methrin (log_{10} mass)	Δ methrin (log_{10} rate)
1.79	1.90			1.44	1.65
1.80	1.99			1.44	1.78
1.80	1.96			1.45	1.56
1.80	1.96			1.45	1.72
1.83	1.98			1.46	1.70
				1.47	1.80
				1.48	1.80
				1.48	1.76
				1.49	1.76
				1.50	1.66

APPENDIX 3: The raw respirometry data collected for *C. vicina* during preliminary experiments

Log_{10} mass (mg)	Log_{10} oxygen consumption (µl oxygen/larva)	Log_{10} mass (mg)	Log_{10} oxygen consumption (µl oxygen/larva)
1.35	1.50	1.62	1.85
1.82	1.80	1.65	1.9
1.91	1.97	1.58	1.61
1.82	1.83	1.43	1.27
1.66	1.65	1.61	1.88
1.40	1.67	1.52	1.67
1.36	1.58	1.55	1.87
1.85	1.98	1.7	1.82
1.76	1.70	1.67	1.8
1.80	1.97	1.73	1.88
1.62	1.73	1.72	1.78
1.69	1.64	1.5	1.7
1.82	1.90	1.6	1.8
1.60	1.78	1.6	1.88
1.85	1.51	1.44	1.52
1.65	1.76	1.54	1.71
1.73	1.83	1.24	1.53
1.72	1.82	1.3	1.5
1.59	1.78	1.56	1.81
1.88	1.89	1.47	1.78
1.85	1.81	1.62	1.89
1.62	1.70	1.58	1.71
1.88	1.94	1.41	1.37
1.69	1.81	1.48	1.7
1.78	1.78	1.53	1.88
1.61	1.79	1.53	1.68
1.56	1.67	1.42	1.72
1.61	1.83	1.48	1.77
1.52	1.79		



Appendix 3 - Figure 1) The allometric relationship between mass and respiration rate in *C.Vicina*

APPENDIX 4: Life-table analysis

Table 1. Life-table analysis of the control experiment 1

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
0	96	0	1	0	0	0	0
1	96	0	1	0	0	1	0
2	96	0	1	0	0	2	0
3	91	0	0.948	0	0	2.84	0
4	86	0	0.896	0	0	3.58	0
5	82	0	0.854	0	0	4.27	0
6	81	0	0.844	0	0	5.06	0
7	79	0	0.823	0	0	5.76	0
8	79	0	0.823	0	0	6.58	0
9	77	0	0.802	0	0	7.22	0
10	76	0	0.792	0	0	7.92	0
11	75	0	0.781	0	0	8.59	0
12	74	0	0.771	0	0	9.25	0
13	74	0	0.771	0	0	10	0
14	74	0	0.771	0	0	10.8	0
15	72	0	0.75	0	0	11.3	0
16	71	0	0.74	0	0	11.8	0
17	68	0	0.708	0	0	12	0
18	67	0	0.698	0	0	12.6	0
19	66	0	0.688	0	0	13.1	0
20	66	0	0.688	0	0	13.8	0
21	66	73	0.688	1.106	15.969	14.4	0.76041667
22	65	0	0.677	0	0	14.9	0
23	64	0	0.667	0	0	15.3	0
24	62	119	0.646	2.081	32.25	15.5	1.34375
25	61	0	0.635	0	0	15.9	0
26	60	12	0.625	0.2	3.25	16.3	0.125
27	57	0	0.594	0	0	16	0
28	57	0	0.594	0	0	16.6	0
29	57	0	0.594	0	0	17.2	0
30	55	0	0.573	0	0	17.2	0
31	54	16	0.563	0.296	5.1667	17.4	0.16666667
32	54	0	0.563	0	0	18	0
33	53	0	0.552	0	0	18.2	0

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
34	52	216	0.542	4.154	76.5	18.4	2.25
35	51	0	0.531	0	0	18.6	0
36	48	17	0.5	0.354	6.375	18	0.17708333
37	48	266	0.5	5.542	102.52	18.5	2.77083333
38	44	0	0.458	0	0	17.4	0
39	43	106	0.448	2.465	43.063	17.5	1.10416667
40	41	94	0.427	2.293	39.167	17.1	0.97916667
41	39	224	0.406	5.744	95.667	16.7	2.33333333
42	35	92	0.365	2.629	40.25	15.3	0.95833333
43	33	0	0.344	0	0	14.8	0
44	31	196	0.323	6.323	89.833	14.2	2.04166667
45	28	0	0.292	0	0	13.1	0
46	25	22	0.26	0.88	10.542	12	0.22916667
47	24	0	0.25	0	0	11.8	0
48	20	85	0.208	4.25	42.5	10	0.88541667
49	18	237	0.188	13.17	120.97	9.19	2.46875
50	17	7	0.177	0.412	3.6458	8.85	0.07291667
51	15	0	0.156	0	0	7.97	0
52	13	36	0.135	2.769	19.5	7.04	0.375
53	12	0	0.125	0	0	6.63	0
54	11	0	0.115	0	0	6.19	0
55	11	0	0.115	0	0	6.3	0
56	8	0	0.083	0	0	4.67	0
57	8	0	0.083	0	0	4.75	0
58	7	0	0.073	0	0	4.23	0
59	7	0	0.073	0	0	4.3	0
60	7	0	0.073	0	0	4.38	0
61	6	0	0.063	0	0	3.81	0
62	6	0	0.063	0	0	3.88	0
63	4	34	0.042	8.5	22.313	2.63	0.35416667
64	2	0	0.021	0	0	1.33	0
65	1	0	0.01	0	0	0.68	0
66	0	0	0	0	0	0	0
		Generation time (T)			39.7570194		
		Net repro rate (R0)			19.2196667		
		intrinsic rate/day			0.07444404		
		r/generation			2.95967322		

APPENDIX 4 - Table 2. Life-table analysis of the control experiment 2

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
0	96	0	1	0	0	0	0
1	96	0	1	0	0	1	0
2	96	0	1	0	0	2	0
3	88	0	0.917	0	0	2.75	0
4	87	0	0.906	0	0	3.63	0
5	83	0	0.865	0	0	4.32	0
6	83	0	0.865	0	0	5.19	0
7	78	0	0.813	0	0	5.69	0
8	77	0	0.802	0	0	6.42	0
9	74	0	0.771	0	0	6.94	0
10	73	0	0.76	0	0	7.6	0
11	73	0	0.76	0	0	8.36	0
12	72	0	0.75	0	0	9	0
13	68	0	0.708	0	0	9.21	0
14	68	0	0.708	0	0	9.92	0
15	60	0	0.625	0	0	9.38	0
16	58	0	0.604	0	0	9.67	0
17	57	0	0.594	0	0	10.1	0
18	56	0	0.583	0	0	10.5	0
19	52	0	0.542	0	0	10.3	0
20	52	178	0.542	3.423	37.0833	10.8	1.85416667
21	51	416	0.531	8.157	91	11.2	4.33333333
22	50	296	0.521	5.92	67.8333	11.5	3.08333333
23	49	0	0.51	0	0	11.7	0
24	47	0	0.49	0	0	11.8	0
25	46	48	0.479	1.043	12.5	12	0.5
26	46	305	0.479	6.63	82.6042	12.5	3.17708333
27	45	0	0.469	0	0	12.7	0
28	43	152	0.448	3.535	44.3333	12.5	1.58333333
29	41	0	0.427	0	0	12.4	0
30	40	0	0.417	0	0	12.5	0
31	39	161	0.406	4.128	51.9896	12.6	1.67708333
32	38	86	0.396	2.263	28.6667	12.7	0.89583333
33	37	0	0.385	0	0	12.7	0
34	36	389	0.375	10.81	137.771	12.8	4.05208333
35	30	0	0.313	0	0	10.9	0

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
36	27	102	0.281	3.778	38.25	10.1	1.0625
37	26	98	0.271	3.769	37.7708	10	1.02083333
38	24	0	0.25	0	0	9.5	0
39	22	302	0.229	13.73	122.688	8.94	3.14583333
40	19	0	0.198	0	0	7.92	0
41	17	119	0.177	7	50.8229	7.26	1.23958333
42	13	108	0.135	8.308	47.25	5.69	1.125
43	12	0	0.125	0	0	5.38	0
44	11	0	0.115	0	0	5.04	0
45	11	0	0.115	0	0	5.16	0
46	11	0	0.115	0	0	5.27	0
47	11	95	0.115	8.636	46.5104	5.39	0.98958333
48	11	0	0.115	0	0	5.5	0
49	11	94	0.115	8.545	47.9792	5.61	0.97916667
50	11	96	0.115	8.727	50	5.73	1
51	8	85	0.083	10.63	45.1563	4.25	0.88541667
52	7	0	0.073	0	0	3.79	0
53	5	0	0.052	0	0	2.76	0
54	3	1	0.031	0.333	0.5625	1.69	0.01041667
55	3	31	0.031	10.33	17.7604	1.72	0.32291667
56	2	0	0.021	0	0	1.17	0
57	2	0	0.021	0	0	1.19	0
58	2	40	0.021	20	24.1667	1.21	0.41666667
59	2	0	0.021	0	0	1.23	0
60	1	0	0.01	0	0	0.63	0
61	1	0	0.01	0	0	0.64	0
62	1	0	0.01	0	0	0.65	0
63	1	0	0.01	0	0	0.66	0
64	1	0	0.01	0	0	0.67	0
65	1	0	0.01	0	0	0.68	0
66	1	0	0.01	0	0	0.69	0
67	1	0	0.01	0	0	0.7	0
68	1	0	0.01	0	0	0.71	0
69	1	0	0.01	0	0	0.72	0
70	0	0	0	0	0	0	0
	Generation time (T)		2.4606496		intrinsic rate/day		0.10804413
	Net repro rate (R0)		33.3541667		r/generation		3.5071827

APPENDIX 4 - Table 3. Life-table analysis of the control experiment 3

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
0	96	0	1	0	0	0	0
1	96	0	1	0	0	1	0
2	96	0	1	0	0	2	0
3	95	0	0.99	0	0	2.97	0
4	93	0	0.969	0	0	3.88	0
5	92	0	0.958	0	0	4.79	0
6	92	0	0.958	0	0	5.75	0
7	90	0	0.938	0	0	6.56	0
8	88	0	0.917	0	0	7.33	0
9	87	0	0.906	0	0	8.16	0
10	87	0	0.906	0	0	9.06	0
11	87	0	0.906	0	0	9.97	0
12	87	0	0.906	0	0	10.9	0
13	87	0	0.906	0	0	11.8	0
14	84	0	0.875	0	0	12.3	0
15	78	0	0.813	0	0	12.2	0
16	70	0	0.729	0	0	11.7	0
17	65	0	0.677	0	0	11.5	0
18	63	0	0.656	0	0	11.8	0
19	62	0	0.646	0	0	12.3	0
20	61	0	0.635	0	0	12.7	0
21	59	0	0.615	0	0	12.9	0
22	57	0	0.594	0	0	13.1	0
23	57	104	0.594	1.825	24.9167	13.7	1.08333333
24	57	604	0.594	10.6	151	14.3	6.29166667
25	56	65	0.583	1.161	16.9271	14.6	0.67708333
26	56	193	0.583	3.446	52.2708	15.2	2.01041667
27	56	0	0.583	0	0	15.8	0
28	56	0	0.583	0	0	16.3	0
29	56	92	0.583	1.643	27.7917	16.9	0.95833333
30	56	426	0.583	7.607	133.125	17.5	4.4375
31	55	1	0.573	0.018	0.32292	17.8	0.01041667
32	54	273	0.563	5.056	91	18	2.84375
33	54	660	0.563	12.22	226.875	18.6	6.875
34	54	195	0.563	3.611	69.0625	19.1	2.03125
35	50	8	0.521	0.16	2.91667	18.2	0.08333333

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
36	48	297	0.5	6.188	111.375	18	3.09375
37	46	88	0.479	1.913	33.9167	17.7	0.91666667
38	45	85	0.469	1.889	33.6458	17.8	0.88541667
39	42	533	0.438	12.69	216.531	17.1	5.55208333
40	41	59	0.427	1.439	24.5833	17.1	0.61458333
41	38	136	0.396	3.579	58.0833	16.2	1.41666667
42	37	263	0.385	7.108	115.063	16.2	2.73958333
43	31	54	0.323	1.742	24.1875	13.9	0.5625
44	28	0	0.292	0	0	12.8	0
45	28	0	0.292	0	0	13.1	0
46	20	72	0.208	3.6	34.5	9.58	0.75
47	20	35	0.208	1.75	17.1354	9.79	0.36458333
48	14	384	0.146	27.43	192	7	4
49	11	3	0.115	0.273	1.53125	5.61	0.03125
50	11	0	0.115	0	0	5.73	0
51	11	70	0.115	6.364	37.1875	5.84	0.72916667
52	11	0	0.115	0	0	5.96	0
53	11	0	0.115	0	0	6.07	0
54	8	0	0.083	0	0	4.5	0
55	8	116	0.083	14.5	66.4583	4.58	1.20833333
56	8	174	0.083	21.75	101.5	4.67	1.8125
57	8	0	0.083	0	0	4.75	0
58	7	0	0.073	0	0	4.23	0
59	6	0	0.063	0	0	3.69	0
60	5	0	0.052	0	0	3.13	0
61	5	0	0.052	0	0	3.18	0
62	5	0	0.052	0	0	3.23	0
63	4	0	0.042	0	0	2.63	0
64	2	0	0.021	0	0	1.33	0
65	2	0	0.021	0	0	1.35	0
66	2	0	0.021	0	0	1.38	0
67	2	0	0.021	0	0	1.4	0
68	1	0	0.01	0	0	0.71	0
69	0	0	0	0	0	0	0

Generation time (T)	35.8587174	intrinsic rate/day	0.11017803
Net repro rate (R0)	51.9791667	r/generation	3.950843

APPENDIX 4 - Table 4. Life-table analysis of the cadmium experiment 1

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
0	96	0	1	0	0	0	0
1	96	0	1	0	0	1	0
2	96	0	1	0	0	2	0
3	94	0	0.979	0	0	2.94	0
4	91	0	0.948	0	0	3.79	0
5	86	0	0.896	0	0	4.48	0
6	83	0	0.865	0	0	5.19	0
7	78	0	0.813	0	0	5.69	0
8	73	0	0.76	0	0	6.08	0
9	71	0	0.74	0	0	6.66	0
10	63	0	0.656	0	0	6.56	0
11	59	0	0.615	0	0	6.76	0
12	57	0	0.594	0	0	7.13	0
13	56	0	0.583	0	0	7.58	0
14	54	0	0.563	0	0	7.88	0
15	54	0	0.563	0	0	8.44	0
16	48	0	0.5	0	0	8	0
17	43	0	0.448	0	0	7.61	0
18	43	0	0.448	0	0	8.06	0
19	41	0	0.427	0	0	8.11	0
20	40	0	0.417	0	0	8.33	0
21	40	0	0.417	0	0	8.75	0
22	39	152	0.406	3.897	34.8333	8.94	1.58333333
23	39	0	0.406	0	0	9.34	0
24	38	0	0.396	0	0	9.5	0
25	38	9	0.396	0.237	2.34375	9.9	0.09375
26	38	112	0.396	2.947	30.3333	10.3	1.16666667
27	37	55	0.385	1.486	15.4688	10.4	0.57291667
28	36	0	0.375	0	0	10.5	0
29	34	219	0.354	6.441	66.1563	10.3	2.28125
30	33	0	0.344	0	0	10.3	0
31	32	0	0.333	0	0	10.3	0
32	32	0	0.333	0	0	10.7	0
33	32	0	0.333	0	0	11	0
34	31	107	0.323	3.452	37.8958	11	1.11458333
35	30	0	0.313	0	0	10.9	0

Day (x)	Total larvae	Eggs	lx	mx	x*lx*mx	x*lx	lx*mx
36	28	0	0.292	0	0	10.5	0
37	28	21	0.292	0.75	8.09375	10.8	0.21875
38	26	147	0.271	5.654	58.1875	10.3	1.53125
39	24	0	0.25	0	0	9.75	0
40	24	35	0.25	1.458	14.5833	10	0.36458333
41	23	0	0.24	0	0	9.82	0
42	22	0	0.229	0	0	9.63	0
43	19	43	0.198	2.263	19.2604	8.51	0.44791667
44	16	91	0.167	5.688	41.7083	7.33	0.94791667
45	15	0	0.156	0	0	7.03	0
46	15	0	0.156	0	0	7.19	0
47	14	81	0.146	5.786	39.6563	6.85	0.84375
48	13	42	0.135	3.231	21	6.5	0.4375
49	13	0	0.135	0	0	6.64	0
50	10	0	0.104	0	0	5.21	0
51	10	0	0.104	0	0	5.31	0
52	8	0	0.083	0	0	4.33	0
53	8	0	0.083	0	0	4.42	0
54	8	0	0.083	0	0	4.5	0
55	7	0	0.073	0	0	4.01	0
56	7	0	0.073	0	0	4.08	0
57	7	0	0.073	0	0	4.16	0
58	6	0	0.063	0	0	3.63	0
59	4	0	0.042	0	0	2.46	0
60	2	0	0.021	0	0	1.25	0
61	2	0	0.021	0	0	1.27	0
62	1	0	0.01	0	0	0.65	0
63	1	0	0.01	0	0	0.66	0
64	1	0	0.01	0	0	0.67	0
65	1	0	0.01	0	0	0.68	0
66	1	0	0.01	0	0	0.69	0
67	0	0	0	0	0	0	0

Generation time (T)	33.567325
Net repro rate (R0)	11.6041667
intrinsic rate/day	0.07302829
r/generation	2.45136423

APPENDIX 4 - Table 5. Life-table analysis of the cadmium experiment 2.

Day (x)	total larvae	eggs	lx	mx	x*lx*mx	x*lx	lx*mx
0	96	0	1	0	0	0	0
1	96	0	1	0	0	1	0
2	96	0	1	0	0	2	0
3	84	0	0.875	0	0	2.63	0
4	78	0	0.813	0	0	3.25	0
5	72	0	0.75	0	0	3.75	0
6	72	0	0.75	0	0	4.5	0
7	69	0	0.719	0	0	5.03	0
8	66	0	0.688	0	0	5.5	0
9	61	0	0.635	0	0	5.72	0
10	55	0	0.573	0	0	5.73	0
11	51	0	0.531	0	0	5.84	0
12	48	0	0.5	0	0	6	0
13	45	0	0.469	0	0	6.09	0
14	44	0	0.458	0	0	6.42	0
15	42	0	0.438	0	0	6.56	0
16	30	0	0.313	0	0	5	0
17	30	0	0.313	0	0	5.31	0
18	30	0	0.313	0	0	5.63	0
19	26	0	0.271	0	0	5.15	0
20	26	0	0.271	0	0	5.42	0
21	26	0	0.271	0	0	5.69	0
22	23	0	0.24	0	0	5.27	0
23	23	174	0.24	7.565	41.6875	5.51	1.8125
24	23	0	0.24	0	0	5.75	0
25	23	0	0.24	0	0	5.99	0
26	23	0	0.24	0	0	6.23	0
27	22	0	0.229	0	0	6.19	0
28	21	0	0.219	0	0	6.13	0
29	21	0	0.219	0	0	6.34	0
30	21	0	0.219	0	0	6.56	0
31	19	0	0.198	0	0	6.14	0
32	17	0	0.177	0	0	5.67	0
33	17	0	0.177	0	0	5.84	0
34	17	0	0.177	0	0	6.02	0
35	14	0	0.146	0	0	5.1	0

Day (x)	total larvae	eggs	lx	mx	x*lx*mx	x*lx	lx*mx
36	14	0	0.146	0	0	5.25	0
37	11	62	0.115	5.636	23.8958	4.24	0.64583333
38	10	60	0.104	6	23.75	3.96	0.625
39	10	65	0.104	6.5	26.4063	4.06	0.67708333
40	10	0	0.104	0	0	4.17	0
41	10	0	0.104	0	0	4.27	0
42	9	0	0.094	0	0	3.94	0
43	6	0	0.063	0	0	2.69	0
44	6	0	0.063	0	0	2.75	0
45	4	0	0.042	0	0	1.88	0
46	3	0	0.031	0	0	1.44	0
47	3	0	0.031	0	0	1.47	0
48	3	0	0.031	0	0	1.5	0
49	3	0	0.031	0	0	1.53	0
50	3	0	0.031	0	0	1.56	0
51	3	0	0.031	0	0	1.59	0
52	1	0	0.01	0	0	0.54	0
53	1	0	0.01	0	0	0.55	0
54	1	0	0.01	0	0	0.56	0
55	0	0	0	0	0	0	0

Generation time (T)	30.7783934
Net repro rate (R0)	3.76041667
intrinsic rate/day	0.0430344
r/generation	1.32452977

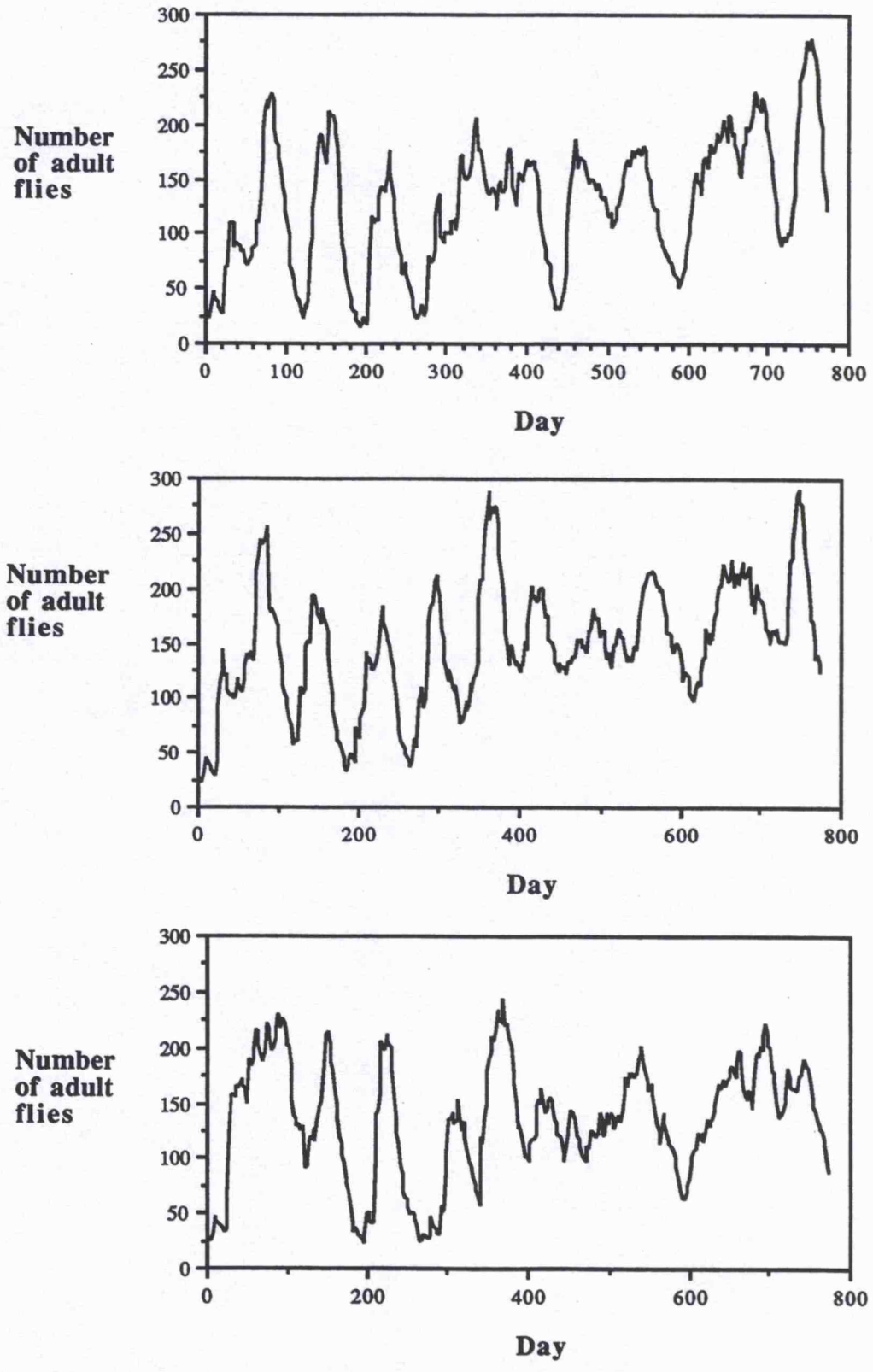
APPENDIX 4 - Table 6. Life-table analysis of the cadmium experiment 3.

Day (x)	total larvae	eggs	lx	mx	x*lx*mx	x*lx	lx*mx
0	96	0	1	0	0	0	0
1	96	0	1	0	0	1	0
2	96	0	1	0	0	2	0
3	95	0	0.99	0	0	2.97	0
4	95	0	0.99	0	0	3.96	0
5	94	0	0.979	0	0	4.9	0
6	93	0	0.969	0	0	5.81	0
7	88	0	0.917	0	0	6.42	0
8	81	0	0.844	0	0	6.75	0
9	76	0	0.792	0	0	7.13	0
10	69	0	0.719	0	0	7.19	0
11	64	0	0.667	0	0	7.33	0
12	60	0	0.625	0	0	7.5	0
13	56	0	0.583	0	0	7.58	0
14	55	0	0.573	0	0	8.02	0
15	53	0	0.552	0	0	8.28	0
16	43	0	0.448	0	0	7.17	0
17	34	0	0.354	0	0	6.02	0
18	30	0	0.313	0	0	5.63	0
19	18	0	0.188	0	0	3.56	0
20	16	0	0.167	0	0	3.33	0
21	10	0	0.104	0	0	2.19	0
22	9	0	0.094	0	0	2.06	0
23	9	0	0.094	0	0	2.16	0
24	9	0	0.094	0	0	2.25	0
25	9	0	0.094	0	0	2.34	0
26	9	0	0.094	0	0	2.44	0
27	9	0	0.094	0	0	2.53	0
28	9	0	0.094	0	0	2.63	0
29	9	0	0.094	0	0	2.72	0
30	8	0	0.083	0	0	2.5	0
31	8	0	0.083	0	0	2.58	0
32	8	0	0.083	0	0	2.67	0
33	8	0	0.083	0	0	2.75	0
34	7	0	0.073	0	0	2.48	0
35	7	23	0.073	3.2857	8.38542	2.55	0.23958333

Day (x)	total larvae	eggs	lx	mx	x*lx*mx	x*lx	lx*mx
36	6	0	0.063	0	0	2.25	0
37	6	0	0.063	0	0	2.31	0
38	6	0	0.063	0	0	2.38	0
39	4	0	0.042	0	0	1.63	0
40	4	0	0.042	0	0	1.67	0
41	4	0	0.042	0	0	1.71	0
42	4	47	0.042	11.75	20.5625	1.75	0.48958333
43	4	0	0.042	0	0	1.79	0
44	3	0	0.031	0	0	1.38	0
45	3	0	0.031	0	0	1.41	0
46	2	0	0.021	0	0	0.96	0
47	2	0	0.021	0	0	0.98	0
48	1	0	0.01	0	0	0.5	0
49	0	0	0	0	0	0	0

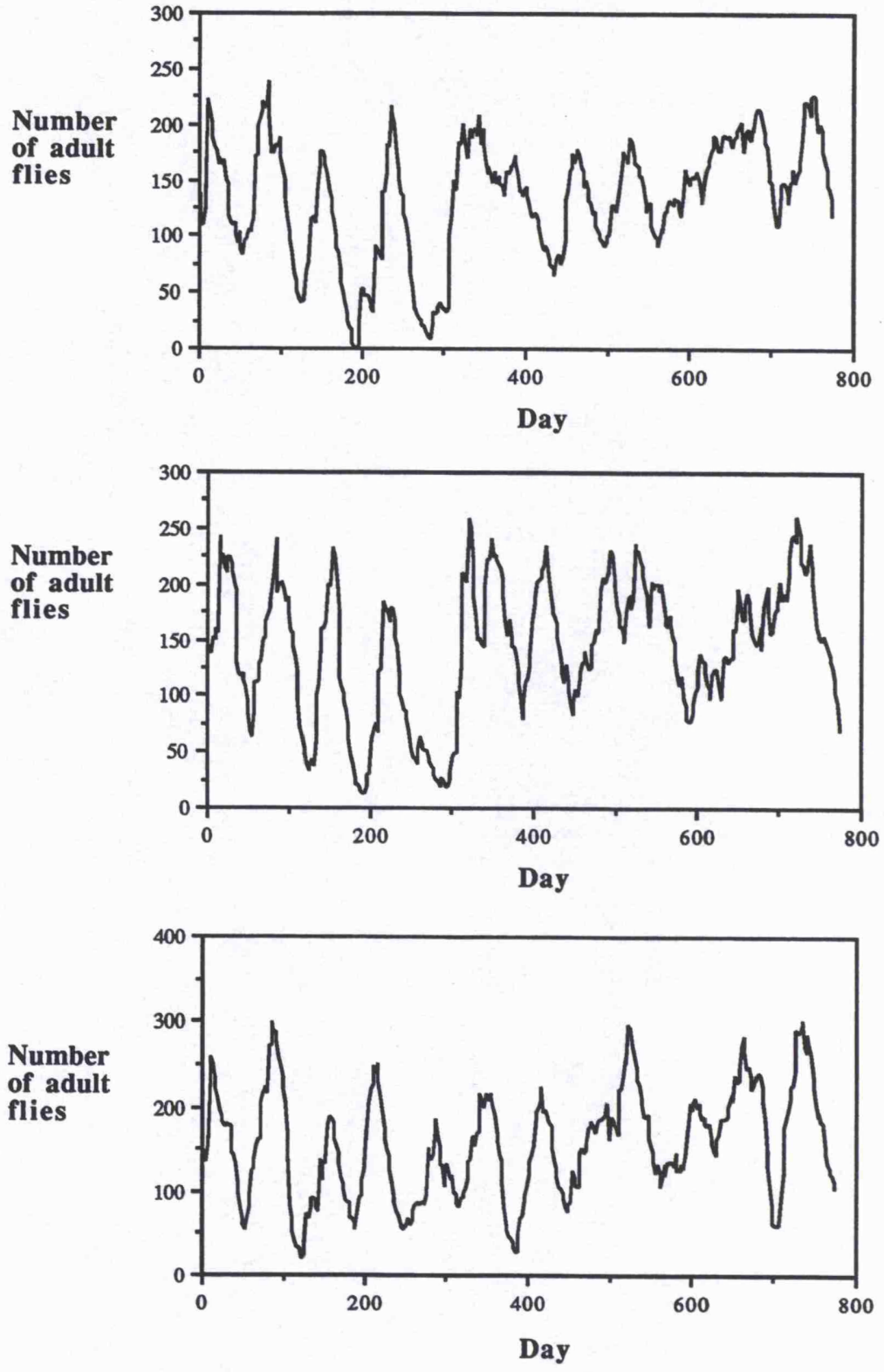
Generation time (T)	39.7
Net repro rate (R0)	0.72916667
intrinsic rate/day	-0.007956
r/generation	-0.3158529

APPENDIX 5: The time series data collected by Susan Daniels (1994)



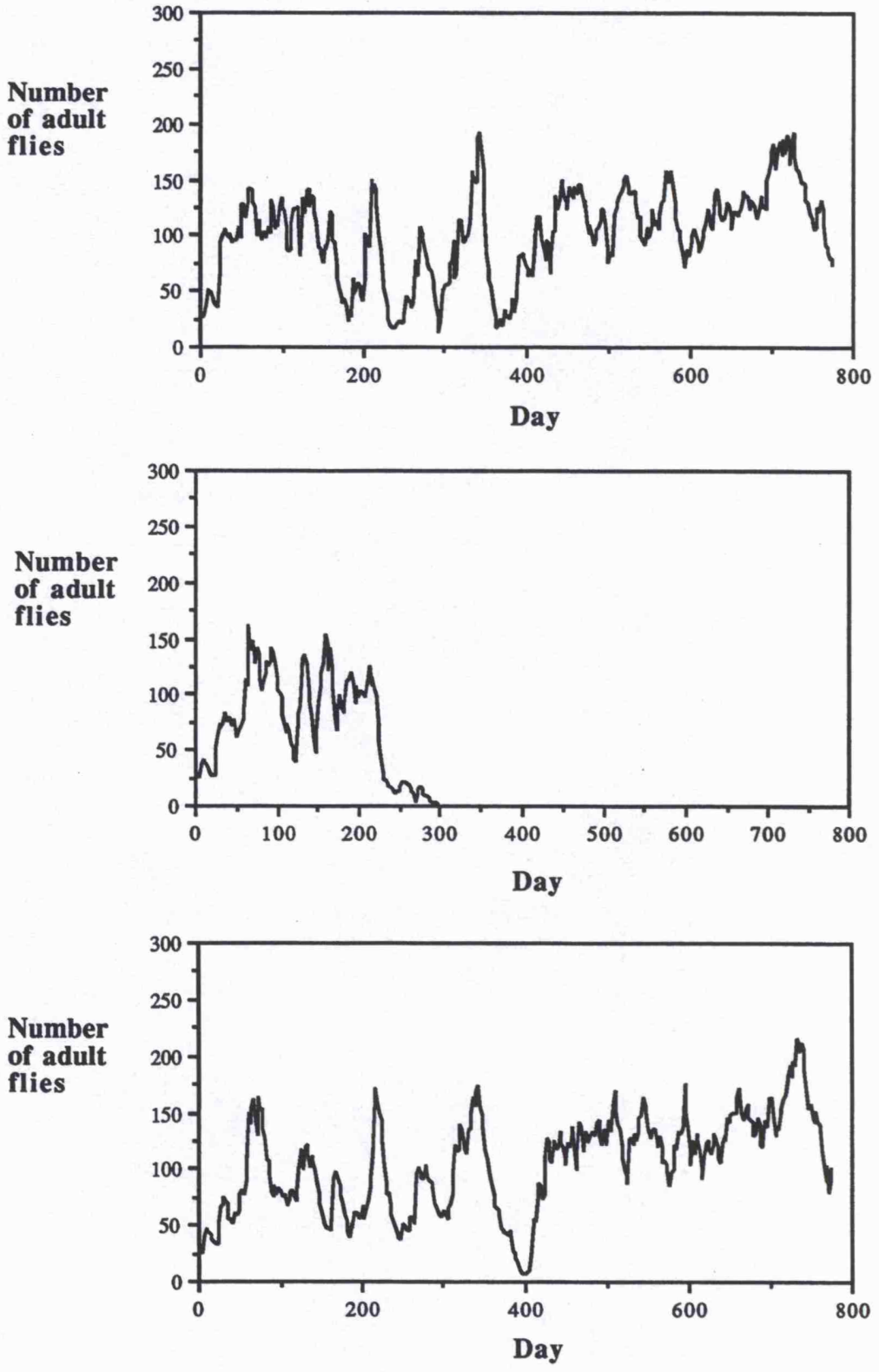
Appendix 5 - Figure 1a-c) The time series data showing the numbers of adult flies in the control population cages 1a-1c of Daniels (1994)

Appendix 5 continued



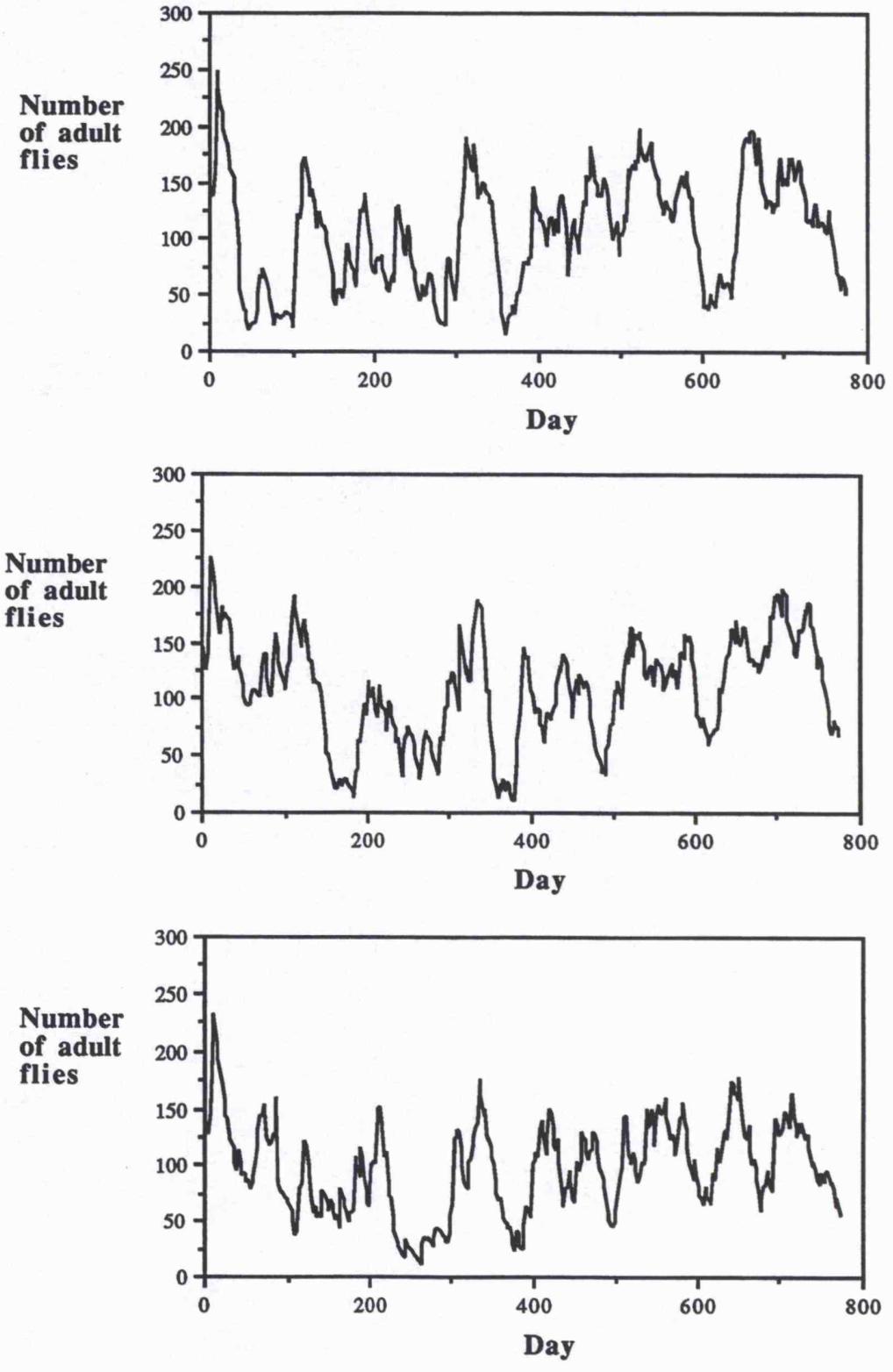
Appendix 5 - Figure 2a-c) The time series data showing the numbers of adult flies in the control population cages 2a-2c of Daniels (1994)

Appendix 5 continued



Appendix 5 - Figure 3a-c) The time series data showing the numbers of adult flies in the cadmium population cages 3a-3c of Daniels (1994)

Appendix 5 continued



Appendix 5 - Figure 3a-c) The time series data showing the numbers of adult flies in the cadmium population cages 3a-3c of Daniels (1994)

REFERENCES

Aldrige, W. N. (1990). An assesment of the toxicological of pyrethroids and their neurotoxicity. *Critical Reviews in Toxicology,* 21, 2, PP 89-104.

Anderlini, V. C. (1992). The effect of sewage on trace metal concentrations and scope for growth in *Mytilus edulis aoteanus* and *Perna canaliculus* from Wellington Harbour, New Zealand. *The Science of the Total Environment,* 125, PP 263-288.

Andrewartha H. G. and Birch, L. C. (1954). The distribution and abundance of animals. Cambridge University Press, London.

Banno, H. (1990). Plasticity of size and relative fecundity in the aphidophagous lycaenid butterfly, *Taraka hamada. Ecological Entomology,* 15, PP 111-113.

Barnes, R. S. K., Calow, P. and Olive, P. J. W. (1989). The Invertebrates: a new synthesis: Blackwell Scientific Publications.

Barber, I, Baird, D. J, Calow, P. (1990). General respones of *Daphnia magna* Straus to toxic stress-II: physiological effects. *Functional Ecology*, 4, PP409-414.

Beaver, R. A. (1977). Non-equilibrium 'island' communities: Diptera breeding in dead snails. *Journal of Animal Ecology,* 46, PP 783-798.

Berrigan, D. (1991). Lift production in the flesh fly, *Neobellieria* (= *Sarcophaga*) *bullata* Parker. *Functional Ecology,* 5, PP 448-456.

Block, W., Erzingclioglu, Y. Z. and Worland, M. R. (1990). Cold resistance in all life stages of two blowfly species (Diptera, Calliphoridae). *Medical and Veterinary Entomology,* 4, PP 213-219.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. and Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia,* 37, PP 257-272.

Braack, L. and Retif, P. F. (1986). Dispersal, density and habitat prefernce of the blowflies *Chrysomya albiceps* (WD) and *Chrysomya marginalis* (WD). *Onderstepoort Journal of Veterinary Research,* 53, 1, PP 13-18.

Braack, L. E. O. and De Vos, V. (1990). Feeding Habits and flight range of blow-flies (*Chysomya* Spp.) in relation to Anthrax transmission in the Kruger National Park, South Africa. *Onderstepoort Journal of Veterinary Research.*, **57**, PP 141-142.

Brallier, S., Harrison, R. B., Henry, C. L. and Dongsen, X. (1996). Liming effects on availability of Cd, Cu, Ni, and Zn in a soil amended with sewage sludge 16 years previously. *Water Air and Soil Pollution*, **86**, PP 195-206.

Calow, P. (1989). Physiological ecotoxicology: Theory, practice, and application. *Proceedings of the First European Conference on Ecotoxicology*, PP 23-35, Conference Organising Committee, Lyngby, Denmark.

Calow, P. (1991). Physiological costs of combating chemical toxicants: ecological implications. *Comparative Biochemistry and Physiology.* **100C**, PP 3-6.

Chinery, M. (1993). Insects of Britain and Northern Europe. 3rd Edition: Collins Field Guide, Harper Collins.

Chua, T. H. (1992). Relationship between female body size and demographic parameters in *Bactrocera* Malaysian A (Diptera: Tephritidae). *Researches on Population Ecology*, **34**, No. 2, PP 285-292.

Colegrave, N. (1993). Does larval competition affect fecundity independently of its effect on adult weight. *Ecological Entomology*, **18**, PP 275-277.

Cousin, G. (1932). Étude expérimentale de la diapause des insects. *Bulletin of Biology* , Supplement 15, PP 1-341.

Cragg, J. B. and Cole, P. (1952). Diapause in *Lucilia sericata*. *Journal of Experimental bBology*, **29**, PP 600-604.

Cragg, J. B. and Hobart, J. (1955). A study of a field population of the blowflies *Lucilia caesar* (L.) *and L. sericata* (MG.). *Annals of Applied Biology,* **43**, 4, PP 645-663.

Daniels, S. (1994). Effects of cadmium toxicity on population dynamics of the blowfly *Lucilia sericata.* Ph.D Thesis. Reading University.

Daniels, S., Simkiss, K. and Smith, R. H. (1991). A simple diet for population studies on the blowfly *Lucilia sericata* (Diptera: Calliphoridae). *Medical and Veterinary Entomology,* 5, PP 283-292.

D'Assis Fonseca, E. C. M. (1968). Diptera Cyclorrhapha Calyptrata, Section (b) Muscidae. *Handbooks for the Identification of British Insects,* 10, Part 4. Royal Entomological Society of London.

Davies, M. D. (1934). The sheep blowfly problem in north Wales. *Annals of Applied Biology,* 21, PP 267-282.

Davies, L. (1990). Species composition and larval habitats of blowfly (Calliphoridae) populations in upland areas in England and Wales. *Medical and Veterinary Entomology,* 4, PP 61-68.

Davies, L. and Ratcliffe, G. G. (1994). Development rates of some pre-adult stages in blowflies with reference to low temperatures. *Medical and Veterinary Entomology,* 8, PP 245-254.

Delinger, L. D. and Zdarek, J. (1994). The metamorphosis behavior of flies. *Annual Review of Entomology,* 39, PP 243-266.

Disney, R. H. L. (1983). Scuttle flies. Diptera Phoridae (except *megaselia*): *Handbooks for Identification of British Insects,* Vol. 10 Part 6. Royal Entomological Society of London.

Doube, B. M. (1986). Spatial and Temporal organisation in communities associated with dung pads and carcasses. *27th Symposium of the British Ecological Society,* Gee, J. H. R. and Giller, P. S. (Eds) Blackwell Scientific Publications.

Dymock, J. J., Peters, M. O. E., Herman, T. J. B. and Forgie, S. A. (1991). A study of sheep blowflies at limestone downs in the northern Waikata. *New Zealand Journal of Agricultural research,* 34, 3, PP 311-316.

Dymock, J. J. and Forgie, S. A. (1993). Habitat preferences and carcase colonization by sheep blowflies in the northern North Island of New Zealand. *Medical and Veterinary Entomology,* 7, PP 155-160.

Erzincliogiu, Y. Z. (1985). The immature stages of British *Calliphora* and *Cynomya* with a re-evaluation of the taxonomic characters of larval Calliphoridae (Diptera). *Journal of Natural History,* **19**, PP 69-96.

French, N. P., Wall, R., Cripps, P. J. and Morgan, K. L. (1992). Prevalence, regional distribution and control of blowfly strike in England and Wales. *Veterinary Record,* **131**, PP 337-342.

French, N., Wall, R., Cripps, P. J. and Morgan, K. L. (1994). Blowfly strike in England and Wales: the relationship between farm management factors. *Medical and Veterinary Entomology,* **8**, PP 51-56.

French, N., Wall, R., and Morgan, K. L. (1995). The seasonal pattern of sheep blowfly strike in England and Wales. *Medical and Veterinary Entomology*, **9**, PP 1-8.

Fry, F. E. J. (1947). The effect of the environment on animal activity. *University of Toronto Studies in Biology Series,* **55**, PP 1-62.

Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. *Physiology of Fishes*, 1, PP 1-98.

Gammon, W. D., Brown, M. A., Casida, J. E. (1981). Two classes of pyrethroid activity in the cockroach. *Pesticides Biochemistry and Physiology,* **15**, PP 181-191.

Gilbert, M. D. and Wilkinson, C. F. (1974). Microsomal oxidases in the honey bee, *Apis mellifera* (L.). *Peticides Biochemistry and Physiology,* 4, PP 56-66.

Goyer, R. A. (1986). Toxic effects of metals*: Toxicology*, 3rd edition, Coolier Macmillans.

Greenberg, B. (1990). Nocturnal ovipsition behaviour of blowflies (Diptera; Calliphoridae). *Journal of Medical Entomology,* **27**, 5, PP 807-810.

Greenberg, B. (1991). Flies as forensic indicators. *Journal of Medical Entomology,* **28**, 5, PP 565-577.

Greenberg, B. and Tantawi, T. I. (1993). Different developmental strategies in two boreal blow flies (Diptera: Calliphoridae). *Journal of Medical Entomology,* **30**, 2, PP 485-488.

Greig-Smith, P. (1964). Quantitative plant ecology (2nd edition). Butterworths, London.

Gunjima, K. and Sato, K. (1992). Oral toxicities of some pyrethroids to the housefly, *Musca domestica* L. (Diptera: Muscidae). *Applied Entomol.ogy and Zool.ogy,* 27, 3, PP 319-324.

Gurney, W. S. C., Blythe, S. P. and Nisbet, R. M. (1980). Nicholson's blowflies revisited. *Nature,* 287, PP 17-21.

Hanski, I. (1987). Carrion fly community dynamics; patchiness, seasonality and coexistence. *Ecological Entomology,* 12, PP 257-266.

Hanski, I. and Gilpin, M. (1991). Metapopulation Dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society.,* 42, 1&2, PP 3-16.

Harrison, S., Murphy, D. D. and Ehrlich, P. R. (1988). Distribution of the Bay Checkerspot butterfly, *Editha bayensis* : evidence for a metapopulation model. *The American Naturalist,* 132, 3, PP 360-382.

Harrison, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society,* 42, 1&2, PP 73-88.

Hassell, M. P. (1975). Density-dependence in single species populations. *Journal of Animal Ecology*, 44, no. 1, PP 283-295.

Hassell, M. P., Lawton, J. H. and May, R. M. (1976). Patterns of dynamical behaviour in single-species populations. *Animal Ecology*, 45, no. 2, PP 471-486.

Hopkin, S,. P. (1989). Ecophysiology of metals in terrestrial invertebrates. Elsevier Applied Science, London.

Ishaaya, I. and Casida, J. E. (1980). Properties and toxicological significance of esterases hydrolysing permethrin and cypermethrin in *Trichoplusia ni* larval gut and integument. *Pesticide Biochemistry and Physiology,* 14, PP 178-184.

Isiche, J. (1990). A study of the decomposition of small mammal carcasses in two habitats. M.Sc Thesis, University of Reading.

Joa, L. T. and Casida, J. E. (1974). Insect pyrethroid-hydrolyzing esterases. *Pesticide Biochemistry and Physiology*, 4, PP 465-472.

Khalil, M. A., Donker, M. H., Van Straalen, N. M. (1995). Long-term and short-term changes in the energy budget of *Porcellio scaber* Latreille (Crustacea) exposed to cadmium polluted food. *European Journal of Soil Biology*, 31, no. 3, PP 163-172.

Kneidel, K. A. (1984). Competition and disturbance in communities of carrion breeding Diptera. *Journal of Animal Ecology*, 53, PP 849-865.

Kneidel, K. A. (1984 (a)). Influence of carcass taxon and size on species composition of carrion breeding Diptera. *The American Midland Naturalist*, 111, 1, PP 57-63.

Kneidel, K. A. (1985). Patchiness, aggregation, and the coexistence of competitors for ephemeral resources. *Ecological Entomology*, 10, PP 441-448.

Kuusela, S. and Hanski, I. (1982). The structure of carrion fly communities: the size and type of carrion. *Holarctic Ecology*, 5, PP 337-348.

Laskowski, R. and Hopkin, S. P. (1996). Accumulation of Zn, Cu, Pb, and Cd in the garden snail (*Helix aspersa*): implications for predators. *Environmental Pollution*, 91, no. 3, PP 280-297.

Le Bras, S. (1987). Influence du lindane sur le metabolisme respiratoire d'*Asellus aquaticus* L. Relation concentration - perturbation. *Hydrobiologia*, 148, PP 115-122.

Lund, L. J., Betty, E. E., Page, A. L., Elliot, R. A. (1981). Occurrence of naturally high cadmium levels in soils and its accumulation by vegetation. *Journal of Environmental Quality*, 10, no. 4, PP 551-556.

Mackerras, M. J. (1933). Observations on the life-histories, nutritional requirements and fecundity of blowflies. *Bulletin of Entomological Research*, 24, PP 353-362.

MacLeod, J. (1937). The species of Diptera concerned in cutaneous myiasis of sheep in Britain. *Proceedings of the Royal Entomological Socoiety of London (A)*, 12, PP 127-133.

Maltby, L. and Naylor, C. (1990). Preliminary observations of the ecological relevance of the *Gammarus* scope for growth assay: effect of zinc on reproduction. *Functional Ecology,* 4, PP 393-397.

Martin, M. H., Coughtrey, P. J. (1975). Preliminary observations on the levels of cadmium in a polluted environment. *Chemosphere*, 4, no. 3, PP 155-160.

Martin, M. H., Coughtrey, P. J. (1976). Comparisons between the levels of lead, zinc and cadmium within a contaminated environment. *Chemosphere,* 5, no. 1, PP 15-20.

Martin, M. H., Coughtrey, P. J. and Young, E. W. (1976). Observations on the availability of lead, zinc, cadmium and copper in woodland litter and the uptake of lead, zinc and cadmium by the woodlouse, *Oniscus asellus*. *Chemosphere*, 5, no 5, PP 313-318.

May, R. M. (1975). Biological populations obeying difference equations: stable points, stable cycles and chaos. *Journal of Theoretical Biology*, 49, 511-524.

Mellanby, K. (1938). Diapause and metamorhposis of the blowfly *Lucilia sericata* Mg. *Parasitology*, 30, PP 392-402.

Mestres, R. and Mestres, M. (1992). Deltamethrin: uses and environmental safety. *Reviews of Environmental Contamination and Toxicology,* 124, PP 1-18.

Nicholson, A. J. (1945a). Compensatory reactions of populations to stresses and their evolutionary significance. *Australian Journal of Zoology*, 2, PP 1-8.

Nicholson, A. J. (1945b). An outline of the dynamics of animal populations. *Australian Journal of Zoology*, 2, PP 0-65.

Oldroyd, H. (1970). Diptera introduction and key to families: *Handbooks for the Identification of British Insects*, 9, Part 1. Royal Entomological Society of London.

Partridge, L. and Farquhar, M. (1981). Sexual activity reduces lifspan of male fruitflies. *Nature*, 294, PP 580-582.

Philipson, J. , Watson, J. (1965). Respiratory metabolism of the terrestrial isopod *Oniscus asellus* L. *Oikos*, 16, PP 78-87.

Pitcairn, M. J. and Gutierrez, A. P. (1992). Influence of adult size and age on the fecundity and longevity of *Tetrastichus inceratus* (Hymenoptera, Eulophidae). *Annals of the Entomological Society of America.* **85**, No. 1, PP 53-57.

Plant, R. E. and Cunningham, R. T. (1991). Analysis of the dispersal of sterile mediterranean friut flies (Diptera: Tephritisae) released from a point source. *Environmental Entomology*, **20**, No. 6, PP 1493-1503.

Posthuma, L., and Van Straalen N. M. (1993). Heavy-metal adaptation in terrestrial invertebrates: a review of occurrence, genetics physiology and ecological consequences. *Comparative Biochemistry and Physiology*, **106**C, PP 11-38.

Pont, A. C. (1979). Sepsidae. Diptera Cyclorrhapha, Acalyptrata.: *Handbooks for Identification of British Insects*, Vol. 10 Part 5c. Royal Entomological Society.

Pough, F. H., Heiser, J. B. and McFarland, W. N. (1989). Vertebrate life (3rd edition), Collier Macmillan Publishers , London.

Prinkkilä, M. and Hanski, I. (1995). Complex interactions in four species of *Lucilia* blowflies. *Ecological Entomology*, **20**, PP 261-272.

Putman, R. J. (1978). The role of carrion-frequenting arthropods in the decay process. *Ecological Entomology*, **3**, PP 133-139.

Putman, R. J. (1983). Carrion and Dung: *Studies in Biology no. 156*, Edward Arnold.

Quimby, P. C., Frick, K. E., Wauchope, R. D., and Kay, S. H. (1979). Effects of cadmium on two biocontrol insects and their host weeds. *Bulletin of Environmental Contamination and Toxicology*, **22**, PP 371-378.

Ramade, F. (1979). Ecotoxicology. John Wiley and Sons.

Reddy, P. S. and Bhagyalakshmi, A. (1994). Changes in oxidative metabolism in selected tissues of the crab (*Scylla serrata*) in response to cadmium toxicity. *Ecotoxicology and Environmental Saftey*, **29**, PP 255-264.

Reiss, J. M. (1989). The allometry of growth and reproduction. Cambridge University Press.

Riskallah, M. R. (1983). Esterases and resistance to synthetic pyrethroids in the egyptian cotton leafworm. *Peticide Biochemistry and Physiology,* **19**, PP 184-189.

Roberts, R. D., and Johnson, M. S. (1978). Dispersal of heavy metals from abandoned mine workings and their transference through terrestrial food chains. *Environmental Pollution,* **16**, PP 293-310.

Rognes, K. (1991). Blowflies (Diptera, Calliphoridae) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica,* **24**.

Ruzo, L. O., Unai, T. and Casida, J. E. (1978). Decamethrin metabolism in rats. *Journal of Agriculture Food and Chemistry*, **26**, PP 918-925.

Sahgal, A., Kumar, S. and Pillai, M. K. K. (1994). Microplate assay of elevated eaterase activity in individual pyrethroid-resistant mosquitoes. *Journal of Bioscience,* **19**, 2, PP 193-199.

Shore, R. F. (1995). Predicting cadmium, lead and flouride levels in small mammals from soil residues and by species-species extrapolation. *Environmental Pollution,* **88**, PP 333-340.

Shorrocks, B. and Rosewell, J. (1986). Spatial patchiness and community structure: coexistence and guild size. In Organisation of communities past and present Gee, J. H. R. and Giller, P. S. (Eds). Blackwell Scientific publications.

Shorrocks, B. (1990). Coexistence in a patchy environment: In Living in a patchy environment. (Shorrocks, B. and Swingland, I. R. (Eds)) PP 91-106. Oxford University Press

Simkiss, K., Daniels, S. and Smith, R. H. (1993). Effects of population density and cadmium toxicity on growth and survival of blowflies. *Environmental Pollution,* **81**, PP 41-45.

Simkiss, K. and Taylor, M. G. (1989). Metal fluxes across the membranes of aquatic organisms. *Critical Reviews in Aquatic Science*, **1**, PP 173-188.

Smith, K. G. V. (1986). A Manual of Forensic Entomology: The Trustees of the British Museum.

Smith, K. G. V. (1989). An introduction to the immature stages of British flies: *Handbooks for the Identification of British Insects*, Vol. 10 Part 14. Royal Entomological Society of London.

Tasei, J. N., Carre, S., Moscatelli, B. and Grondeau, C. (1988). Recherche de la D.L 50 de la deltaméthrine (Decis) chez *Megachile rotudata* F. abeille pollinsatrice de la luzerne (*Medicago sativa* L.) et des effets de doses infraléthales sur les adults et les larves. *Apidologie*, **19**, 3, PP 291-306.

Tasei, J. N., Sabik, H., Pirastru, L., Langiu, E., Blanche, J. M., Fournier, J. and Taglioni, J. P. (1994). Effects of sublethal doses of deltamethrin (Decis Ce) on *Bombus terrestris*. *Journal of Apicultural Research*, **33**, 3, PP 129-135.

Taylor, I. R. (1927). Oxygen consumption of individual pupae during metamorhosis. *Journal of Morphology*, **44**, PP 313-339.

Van Emden, F. I. (1954). Diptera Cyclorrhapha Calyptrata (1) Section a Tachinidae and Calliphoridae. *Handbooks for Identification of British Insects*, **10**. Part 4a. Royal Entomological Society.

Vogt, W. G., Woodburn, T. L., Morton, R., and Ellem, B. A. (1983). The analysis and standardisation of trap catches of *L. cuprina* (Wiedemann) (Diptera: Calliphoridae). *Bulletin of Entomological Research*. **73**, PP 609-617.

Wall, R., Green, C. H., French, N. and Morgan, K. L. (1992). Development of an attractive target for the sheep blowfly *Lucilia sericata*. *Medical and Veterinary Entomology*, **6**, PP 67-74.

Wall, R. (1993). The reproductive output of the blowfly *Lucilia sericata*. *Journal of Insect Physiology*, **39**, 9, PP 743-750.

Warren, C. E. and Davies, G. L (1967). Laboratory studies on the feeding of fishes. The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Webb, N. R. (1975). Respiratory metabolism of *Steganacarus magnus* (Acari). *Oikos*, **26**, PP 43-46.

Weismann, L. and Reháková, M. (1994). Toxic influence of cadmium on insects. *Ekológia,* 13, 1, PP 3-13.

Wickman, P. O. and Karlsson, B. (1989). Abdomen size, body size and the reproductive efforts of insects. *Oikos*, 56, PP209-214.

Widdows, J. and Donkin, P. (1991). Role of physiological energetics in ecotoxicology. *Comparative Pharmacology and Toxicology-c,* 100, 1-2, PP 69-75.

Wigglesworth, V. B. (1972). Principles of Insect Physiology: Chapman and Hall.

Wiles, A. J. and Jepson, P. C. (1993). The dietary toxicity of deltamethrin to the Carabid, *Nebria brevicollis* (F.). *Pesticide Science,* 38, PP 329-334.

Xue, R. D. and Ali, A. (1994). Oviposition, fecundity, and body size of a pestiferous midge *Chironomus crassicaudatus*. *Environmental Entomology*, 23, No. 6, PP1480-1484.

Yamamoto, I., Kimmel, E. C and Casida, J. E. (1969). Oxidative metabolism of pyrethroids. *Journal of Agriculture Food and Chemistry*, 17, No. 6, PP 1227-1236.

Yu, S. J., Robinson, F. A. and Nation, J. L. (1984). Detoxification capacity in the honey bee, *Apis mellifera* L. *Pesticide Biochemistry and Physiology,* 22, PP 360-368.