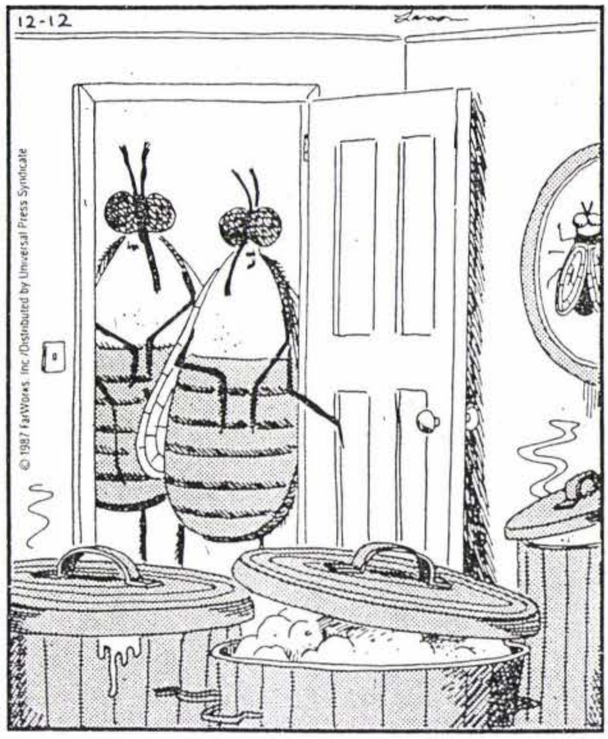

"And when the big moment comes,
here's the nursery Robert and I have fixed up."

FRONT PIECE.

HABITAT AND SEASONAL EFFECTS ON BLOWFLY ECOLOGY IN POSSUM CARCASES IN THE MANAWATU.

A thesis presented in partial fulfilment for the
requirements for the degree of Master of Science
in Ecology at Massey University.

Clive Appleton

1993.

ABSTRACT.

Flies were trapped on Keeble farm and in Keeble forest reserve between May 1992 to February 1993. Fewer Calliphoridae were trapped in pasture during summer than in autumn or winter and different fly species showed differing preferences for bush or pasture at different times of the year. More flies were trapped around the bush margin than in either bush or pasture during spring and summer. In pasture the most numerous calliphorid trapped was *Calliphora stygia* (Fabricius, 1781), whereas in bush during summer *Calliphora hilli* Patton, 1925 was the predominant species. *Lucilia sericata* (Meigen, 1826) was never trapped in bush.

Decaying possum carcases were examined in bush and pasture between February 1992 and February 1993. The number of maggots that left these carcases was affected by the time of the year and whether the carcases were in bush or pasture. More maggots left bush located possum carcases during spring and summer while more maggots left possum carcases in pasture during autumn and winter. Decay rates were most rapid during spring and summer. Temperatures were warm enough for adult fly activity during winter but the possum carcases decayed much slower, especially in bush.

C. stygia and *Calliphora vicina* Robineau-Desvoidy, 1830 were generally the first species of maggot to leave possum carcases and they were the only species present throughout the year in both habitats. *L. sericata* and *Chrysomya ruficacies* (Macquart, 1843) maggots were restricted to possum carcases in pasture during spring and summer while *Calliphoroides antennatis* (Hutton, 1881) was restricted to possum carcases in bush. *Hydrotaea rostrata* Robineau-Desvoidy, 1830 was the only species restricted to summer.

In spring 1992, 3400 flies emerged from a 2.5 kg possum carcase placed in pasture and 4200 flies emerged from a 3.1 kg possum carcase placed in bush. Estimated emergence success of adult flies was 22.0% in pasture and 20.2% in bush. This was 15% lower on average than the emergence level of comparable maggots raised in the laboratory. Flies began emerging in the bush 10 days after those in pasture. *L. sericata* was restricted to pasture and *C. antennatis* was restricted to bush. Overall the major flystrike species to emerge were *C. stygia* and *L. sericata*. *C. stygia* made

stygia made up 46% of the total number of flies that emerged in pasture and 78% of those in bush, while *L. sericata* comprised 15.5% of the total number of flies that emerged in pasture.

The emergence success of field-collected maggots in the laboratory was significantly correlated with the estimated average total number of maggots that left the carcases in the field. Maggots showed the highest emergence success in winter when larval competition in the carcase was lowest.

The temperature of a possum carcase containing fly maggots in bush reached 19.7°C during spring 1992 whereas the temperature exceeded 35°C on occasions in another carcase in pasture at the same time. Proportionally fewer maggots emerged from the possum carcase in pasture possibly because the high temperatures killed many maggots, especially those of *C. stygia.*

Maggots and bacterial decay both elevated carcase temperatures above ambient. Bacteria raised the temperature by about 2°C whereas maggots raised the temperature by 18.3°C to 26°C above ambient. The carcase temperature significantly affected the number of maggots that left the possum carcases, and the number of maggots that left was directly related to the total maggot biomass that left the carcase. A minimum of 24% to 26% of the fresh weight of the possum carcases was converted to maggot weight.

Acknowledgements.

I would like to firstly thank my supervisors Dr Ian Stringer and Dr Murray Potter (Ecology Dept Massey University) for their valuable contribution during research and writing of this thesis. Dr Allen Heath, David Cole and Dallas Bishop (AgResearch, Upper Hutt) for research advice and identification of specimens. Greg Arnold (Statistics Dept, Massey University) and Dr Ed Minot (Ecology Dept, Massey University) for statistical advice. Jens Jorgensen for helping with design suggestions and construction of carcase cages and emergence traps. Ellis Udy who supplied me with most of the possums for this study. Frank Arbon, for allowing me to shoot possums on his land. Keeble farm manager, Gerard Poff and Keeble Trust chairman, Mike Greenwood for permission to conduct this study on Keeble farm and in Keeble reserve. To my family for their support during this study. My wife Colleen, for her help in the field and encouragement during the writing of this thesis.

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Chapter one.

INTRODUCTION.

The major species responsible for flystrike on sheep in New Zealand between 1976 and 1984 were *Calliphora stygia* (Fabricius, 1781), which was found in 54.9% of cases and *Lucilia sericata* (Meigen, 1826) in 37.4% of cases. *Chrysomya rufifacies* (Maquart, 1843), and *Calliphora vicina* Robineau-Desvoidy, 1830 appeared in the remaining 6.6% of cases (Heath 1984). In the early 1980's *Lucilia cuprina* (Wiedemann, 1830) became established in New Zealand and has now become responsible for 62% of strikes (Dymock & Forgie 1993). For these five species, flystrike is an extension of the carrion feeding habit. Carrion may therefore be a major source of flystrike flies. Yet virtually nothing is known about blowfly association with carcases in New Zealand. The only research conducted has been on carcase colonization by blowflies in the Auckland region (Dymock & Forgie 1993). In rural areas where flystrike is a problem they discovered that *L. sericata* was more commonly reared from carcases than *C. vicina* overall, but *C. vicina* was the most common colonizer of carcases in April and May. Species such as *C. stygia*, *C. vicina* and *C. rufifacies* were most often found on large carcases such as possums and sheep, while *L. sericata* was collected more often from the carcases of small birds. There was a very low incidence of *L. cuprina*, despite carcases coming from areas where *L. cuprina* had caused flystrike on sheep.

Currently, possums are being poisoned throughout New Zealand to stem their spreading of Bovine Tuberculosis. Thus many thousands of possum carcases have become available for fly breeding. In light of this, along with the general lack of blowfly research, I was prompted to quantify the use of possum carcases by blowflies located in the agricultural region of Manawatu, New Zealand.

This thesis, beginning at chapter two, describes the study sites and how these were selected, along with data on the weather patterns at both sites during the study. Chapter three aims to analyze fly species presence and abundance in bush and pasture. Chapter four presents a study of maggot development, species succession and production from possum carcases. Chapter five compares blowfly emergence and blowfly species emergence succession between possum carcases located in bush and pasture. Chapter six investigates the influence temperature has on the number of maggots leaving decaying possum carcases. The percentage of carcase fresh weight converted into and removed by maggots is also investigated. In chapter seven, research findings are concluded and recommendations on the direction of future research are presented.

Chapter two.

STUDY SITE.

2.1 Location.

Keeble farm is a 228 ha beef and sheep farm owned and managed by Massey University. It is located 3 km from Palmerston North, along S.H. 57 heading south towards Shannon (NZMS 260, T24 Grid ref 305863). Keeble farm encompasses a 14.27 ha native bush reserve administered by the C.T. Keeble Memorial Trust Board. Thus both pasture and bush habitats adjacent to each other were available for this research (fig 2.1; plates 2.1 & 2.2).

2.2 Topography and vegetative cover.

The topography of the area consists of a flat low river terrace (46 m a.s.l.) along side the Manawatu River. Vehicle access is along grass or shingle roads. Shelter belts consist of pines, willows or flax. During 1992 approximately 300 friesian bulls and 2000 romney sheep were on the farm.

The vegetation of Keeble reserve is as described by Esler (1978). The reserve is the last remnant of podocarp-broadleaf forest in the Manawatu. The major tree species are tawa (*Beilschmiedia tawa*) and mahoe (*Melicytus ramiflorus*), with podocarps up to 30 m in height. Kawakawa (*Macropiper excelsum*) is the predominant understorey shrub. Along the south-west and north-west boundary are stands of mature *Cupressus macrocarpa*.

2.3 Climate.

Climatic conditions for the region are described by Owen (1954). The Manawatu area is characterised by warm summers, mild winters and a reliable rainfall well distributed throughout the year. The average number of rain days per annum ranges from 120 to 173. The driest month is March and the wettest month is June.

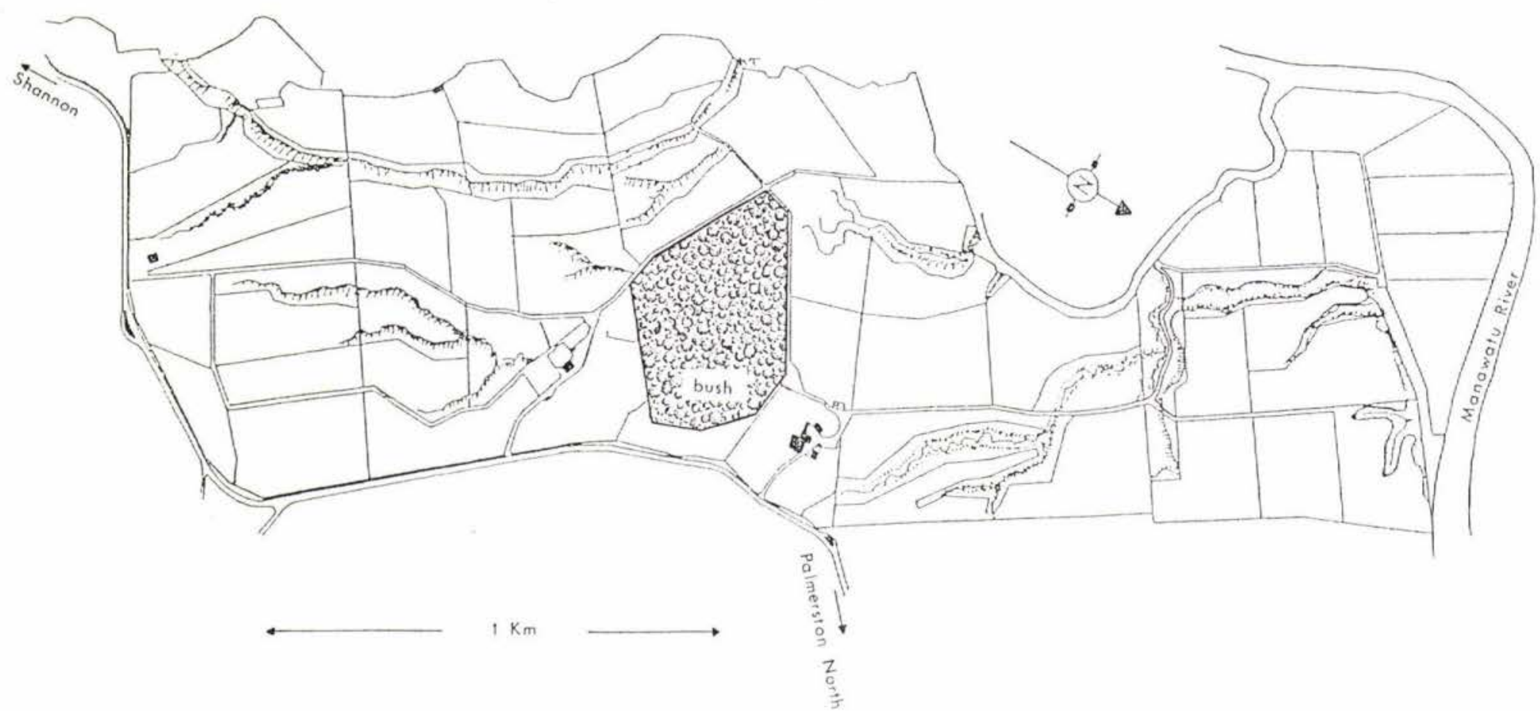


Fig 2.1 Map of Keeble farm and Keeble native bush reserve.

Plate 2.1 Keeble reserve.

Plate 2.2 Meterological station on the farm.

Mean monthly temperatures range from 8°C in July to 17.5°C in February and the mean annual temperature is 12.6°C. The number of days with ground frost recorded at the D.S.I.R. weather station averages 64.3 per year. Frosts are most common from April to October, with the greatest number occurring in June, July and August; the numbers average 1.5, 14.7 and 12 respectively and these include quite severe frosts. Prevailing winds are westerly to north-westerly with frequent gales.

2.4 Collection of meterological data.

Meterological data were collected to determine if climatic conditions were influencing fly use of possum carcases and habitat type. Meterological stations were erected in both pasture and bush. Stations consisted of a 46x19x23 cm wooden box, with slat sides, open bottom and metal roof. The station boxes holding meterological equipment stood 1.4 m above the ground on wooden legs (plate 2.2).

Temperature was recorded with a Brannan maximum and minimum thermometer (range -35°C to 50°C). Relative humidity measurements were taken using a Brannan Mansons wet dry bulb hygrometer (range -13°C to 50°C). Relative humidity was only recorded from August 1992 to February 1993. Apart from light and wind readings, meterological data were obtained during every visit into the field.

To gauge the amount of water reaching possum carcases, a rain gauge was made from a 0.5 m long, 15 cm diameter plastic pipe capped at the bottom. A plastic funnel was glued in the top to prevent evaporation. Water was tipped from the rain gauge into either a 500 or 25 cm^3 measuring flask and rainfall was determined after correcting for the cross-sectional area of the rain gauge.

Light intensity at carcase sites and trap sites were recorded in microeinsteins ($\mu Em^{-2}s^{-1}$) with a Li-Cor 188B photometer. Measurements were taken with the photo cell placed on the top centre of cages or traps. Readings were taken 20 seconds after the meter was turned on. Light readings were taken when it was overcast and clear, both in the morning and in the afternoon. Readings were completed within a period of an hour, and the order in which they were taken was reversed every recording session.

Dymock et al. (1991) found that blowfly trap catches were significantly greater at 0.65 m than at 1.5 m above ground, while Taylor (1974) found that the majority of insects flew within 0.3 m of the ground. In light of these findings, I decided to take wind readings at 1.5 m above the ground in both habitats and 0.3 m above the ground in pasture. Two AD AM500 airflow development limited meters were used. Readings were taken simultaneously in bush and pasture with the help of a partner and radio communication.

2.5 Climatic conditions during the research period.

During my research the wettest period was between August and October 1992 and the driest month was January 1993 (appendix 1). The warmest months were November 1992 to February 1993. The coldest period was between May and July 1992 (appendix 2). Over the entire research period ambient temperature and rainfall were not significantly different between bush and pasture (rainfall, df=128, t=1.075, $p>0.05$ (NS); mean ambient temperature, df=150, t=1.44, $P>0.05$ (NS)). There was, however, a significant difference in relative humidity. During August to October there was a higher humidity level in bush (df=28, t=3.27, $p<0.05$) though from November 1992 to February 1993 humidity was higher in pasture (df=68, t=2.77, $p<0.05$) (appendix 3).

Light intensity was significantly higher in the open pasture land, as expected (appendix 4 and 5). Wind velocity at 0.3 m above the ground in pasture was 4.3 times greater than in the bush (appendix 6).

Chapter three.

HABITAT AND SEASONAL INFLUENCES ON FLY NUMBERS IN THE MANAWATU REGION, NEW ZEALAND.

3.1 INTRODUCTION.

There are few published fly trapping surveys in New Zealand and most of these are concerned with the species involved in flystrike and the incidence of myiasis (Miller 1934, 1939; MacFarlane 1938, 1942; Miller 1939; Murray 1956). Studies at Upper Hutt, Auckland and northern Waikato, New Zealand have shown that habitat influences the number of flies and species attracted to carrion baited traps (Murray 1956; Dymock et al. 1991; Dymock & Forgie 1993). Murray (1956) reported that more flies were trapped in bush than in pasture. At Whatawhata reserve Dymock & Forgie (1993) found the dominant species in pasture was *Calliphora stygia* (Fabricius, 1781) while *Calliphora hilli* Patton, 1925 was most numerous in bush. Habitat use by *Lucilia sericata* (Meigen, 1826) is variable. At Whatawhata *L. sericata* was restricted to pasture, while at Waikowhai bush it was present in both bush and pasture (Dymock & Forgie 1993).

Vogt et al. (1985) and Vogt (1988) found that the trap catch rates for *L. sericata* and *Chrysomya rufifacies* (Macquart, 1843) were influenced by humidity, light intensity, ambient temperature and wind velocity. These climatic conditions vary between pasture and bush (see chapter 2) and it is possible that habitat could indirectly influence the number and species of flies trapped.

The general lack of trapping surveys in New Zealand prompted me to survey flies attracted to carrion to determine how trap catches varied during the year and which flies preferred bush or pasture. This was done to coincide with the study on maggot development, maggot production and fly species succession in possum carcases (chapter 4).

3.2 METHODS.

Six modified "Western Australian" fly traps (Dennison 1979), (plates 3.1 & 3.2) were positioned along a transect through bush and pasture on Keeble farm (fig 3.1).

Each trap was initially baited with 650 g of sheep's liver chopped into 1 cm cubes. This was placed in a small plastic dish and then submerged in water to prevent it from drying out. Sheep liver was used because it is a very effective blowfly attractant that is used almost universally as a bait (Waterhouse 1947; Murray 1956; Vogt & Havenstine 1974; Dennison 1979; Vogt et al. 1985; Dymock et al. 1991). The bait was then allowed to decay during each trapping sequence although it was stirred whenever traps were serviced to prevent mould from forming a layer on top and reducing its effectiveness.

None of the traps were moved during the first and second trapping runs but each was moved to the next position along the transect once a week during trapping runs three and four. This allowed individual trap effects to be determined.

Flies were collected from traps once every two to seven days depending on temperature. The collection chamber was first removed and domestic insecticide sprayed up the collection funnel. The collection chamber top was then removed to collect the flies once they were all dead.

3.3 Statistical analysis.

Analysis of variance (Proc GLM, SAS Institute Inc 1990) was applied to log transformed flytrap data (unamended data is given in appendix 7) to test whether trap location or season influenced the number of flies caught. As the individual flytraps were moved between sites during trap runs 3 and 4, for these runs it was also possible to analyze for individual trap effects. There was no significant species bias amongst the individual trap catches ($F(15,460)=1.38$, $P<0.1544$) but individual traps did have a significant effect on the total number of flies caught ($F(5,460)=18.73$, $P<0.0001$). This was therefore corrected for by dividing the number of flies caught in each trap by the estimated trapping effectiveness of that trap in relation to the other traps. Corrected data was then subjected to a Duncan's multiple range test to analyze for differences

Plate 3.1 **Western Australian fly trap fully assembled.**
Note opening on the side for allowing flies to enter the trap.

Plate 3.2 **Fly trap dismantled showing bait chamber top left, excluder bottom left, collection chamber top right (with funnel) and trap top, bottom right.**

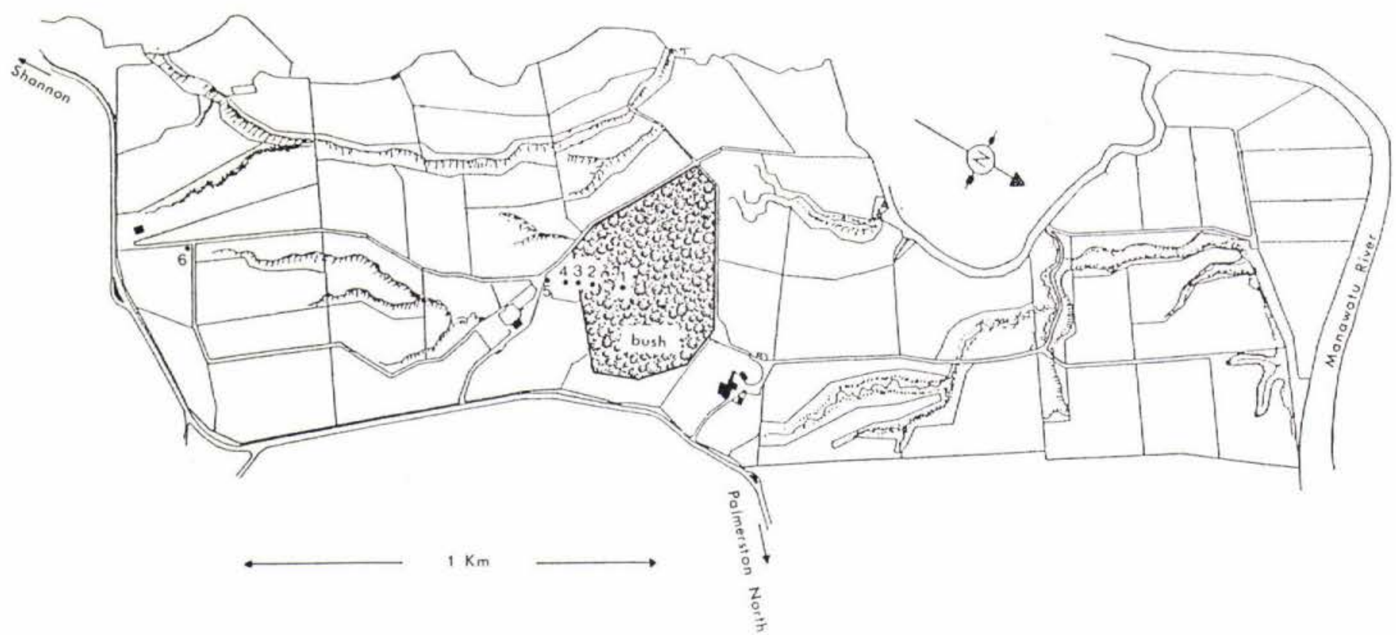


Fig 3.1 Map of Keeble farm and bush showing location of fly traps.

between the numbers of flies trapped in bush and pasture.

3.4 RESULTS.

At least 14 fly species from nine different families were attracted to decaying sheep liver during this survey (table 3.1 & 3.2). The most numerous flies caught were *Psychoda* species. These were trapped in their hundreds but they were not individually counted. The next most frequent flies trapped in order of abundance were *C. stygia, Calliphora vicina* Robineau-Desvoidy, 1830, *C. hilli, Calliphora quadrimaculata* (Swederus, 1787) and *L. sericata* (table 3.1). Other flies caught in low numbers ranging from 1 to 74 individuals included *Sciadocera rufomaculata* (White, 1916), *Calliphoroides antennatis* (Hutton, 1881), *Diplogeomyza sp., Sylvicola sp.* and *Dolichopodidae* (table 3.1 & 3.2). Minor catches of one to three flies included *Hybopygia varia* Walker, 1836, *Anthomyia sp.,* and *Ephydridae* (table 3.1).

The time of year and habitat influenced both the species of flies trapped and the numbers of flies trapped (table 3.1 & 3.2, fig 3.2). Trap catches for the four most common Calliphoridae caught, *C. vicina, C. stygia, C. hilli* and *C. quadrimaculata*, were significantly influenced by species ($F(3,460)=47.3$, $P<0.0001$), time of year ($F(1,460)=121.5$, $P<0.0001$) and habitat ($F(5,460)=58.2$, $P<0.0001$). Significantly more of these flies were trapped 10 m inside the bush than in any other trap location (fig 3.3) (Duncan's multiple range test, df=460, MSE= 22.8, LSD= 1.415). There was also a significant multiple interaction between the species caught, the time of year, and the habitat for these four species ($F(33,460)=7.03$, $P<0.0001$).

Average daily total trap catches (minus *Psychoda sp.*) were 1.2 flies from May to June, 2.8 flies during August to October, 59.4 flies in November to December and 32.6 flies during January and February.

In general, fewer Calliphoridae were caught in pasture during summer than in autumn or winter and these flies showed different preferences for bush or pasture at different times of the year (table 3.1 & 3.2, fig 3.2). More *C. vicina* and *C. stygia* were trapped in pasture than in bush during late autumn whereas in spring *C. stygia* became the most abundant species in pasture and *C. vicina* was the most abundant species in bush. Low numbers of *C. hilli* were caught in pasture throughout the year and in bush during autumn and winter. However, the numbers of *C. hilli* trapped in bush increased substantially in spring and it was the dominant species in bush during summer. The other blowfly species *L. sericata*, and *H. varia* were trapped only in pasture whereas *C. antennatis* was caught only in bush. All three species were present only during spring and summer and then only in low numbers. The non-blowfly species *S. rufomaculata* and *Diplogeomyza sp.* were trapped throughout the year in bush and were only caught in pasture during spring. The remaining flies were trapped in such small numbers that no preference for habitat could be ascertained.

Table 3.1 Number of flies trapped in pasture for each trapping occasion.

Season.	Autumn	Winter	Spring	Summer	Total
Trap run.	1	2	3	4	
Calliphoridae.					
Calliphora vicina	20	20	130		170
Calliphora stygia	6	34	392	6	438
Calliphora hilli	3	13	13	7	36
Calliphora quadrimaculata		16	18	1	35
Lucilia sericata		1	9	10	20
Sciadoceridae.					
Sciadocera rufomaculata			3		3
Sarchophagidae.					
Hybopygia varia				3	3
Heleomyzidae.					
Diplogeomyza sp.	1				1
Anisopodidae.					
Sylvicola sp.	6	3		3	12
Psychodidae.					
Psychoda sp.	>100	>100	>100	>100	
Ephydridae.	1				1
Dolichopodidae.	2				2
Anthomyiidae.					
Anthomyia sp.	1				1
Total.	**40**	**87**	**565**	**30**	**722**

Table 3.2 Number of flies trapped in bush for each trapping occasion.

Season.	Autumn	Winter	Spring	Summer	Total.
Trap run.	1	2	3	4	
Calliphoridae.					
Calliphora vicina	2	55	627	85	769
Calliphora stygia		29	542	294	865
Calliphora hilli	2	22	248	575	847
Calliphora quadrimaculata		14	65	37	116
Sciadoceridae.					
Sciadocera rufomaculata		18	74	4	96
Muscidae.					
Calliphoroides antennatis			18	20	38
Heleomyzidae.					
Diplogeomyza sp.	20	10	3	12	45
Anisopodidae.					
Sylvicola sp.	2	6		6	14
Psychodidae.					
Psychoda sp.	>100	>100	>100	>100	
Dolichopodidae.	18	1			19
Anthomyiidae.					
Anthomyia sp.			2		2
Total.	**44**	**155**	**1579**	**1034**	**2812**

Fig 3.2 **Numbers of flies caught for each species on each sample occasion in traps in bush and pasture.**

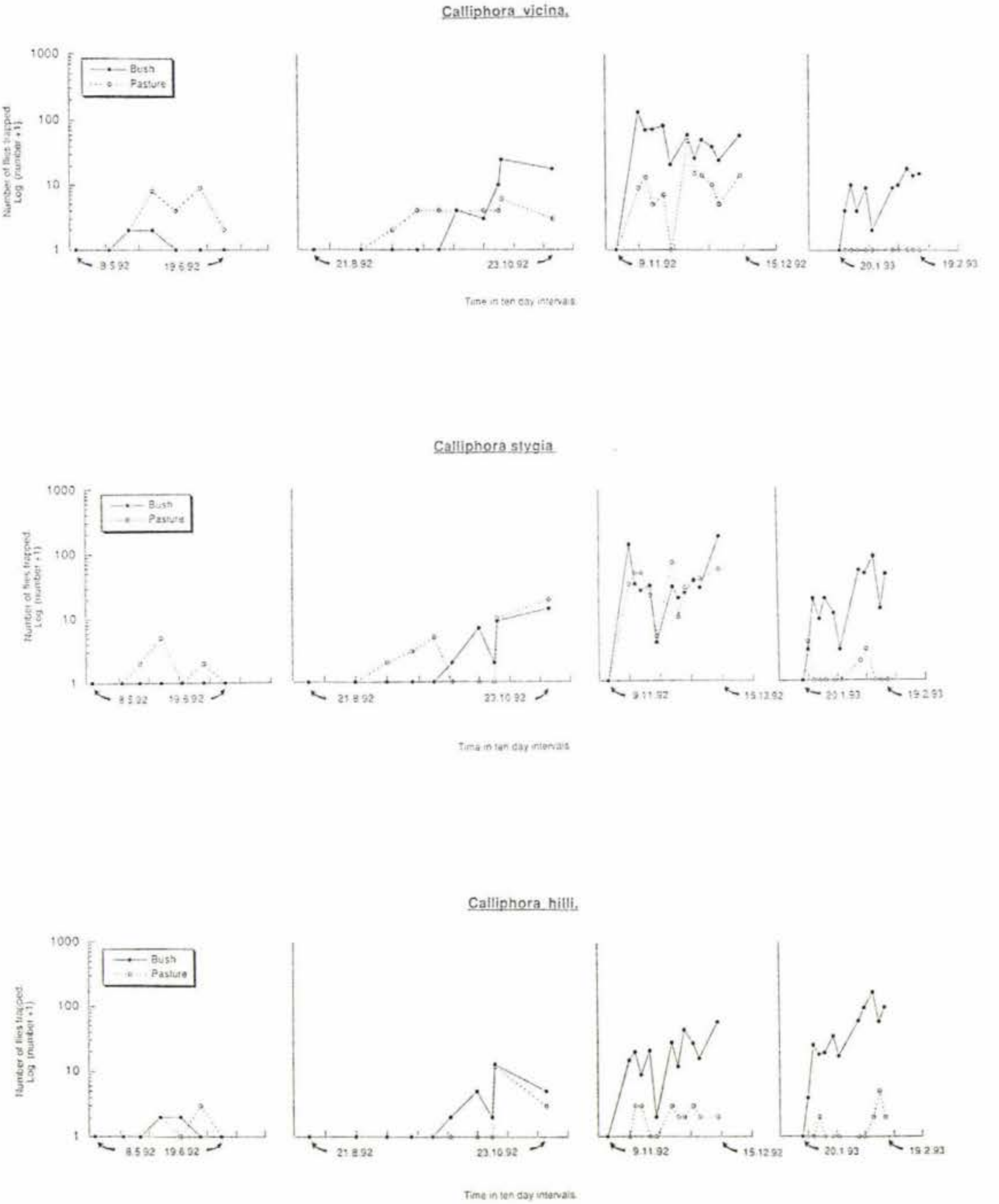
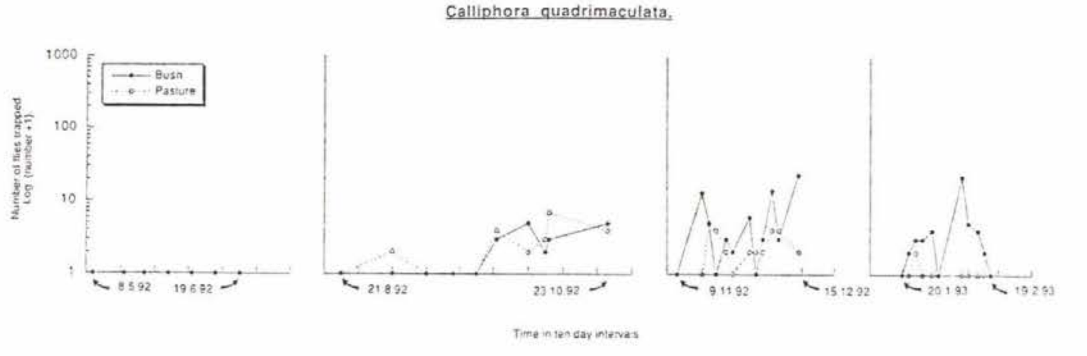


Fig 3.2 Continued.



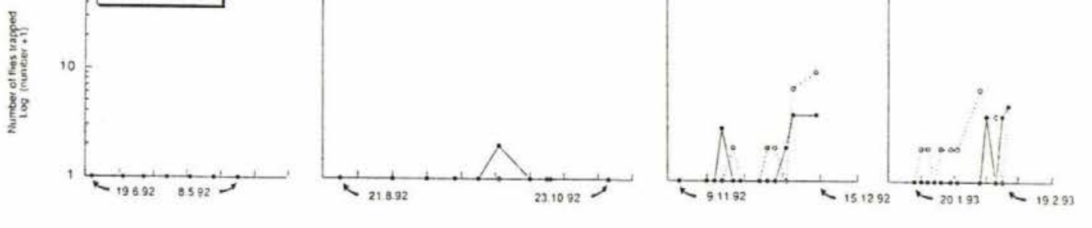
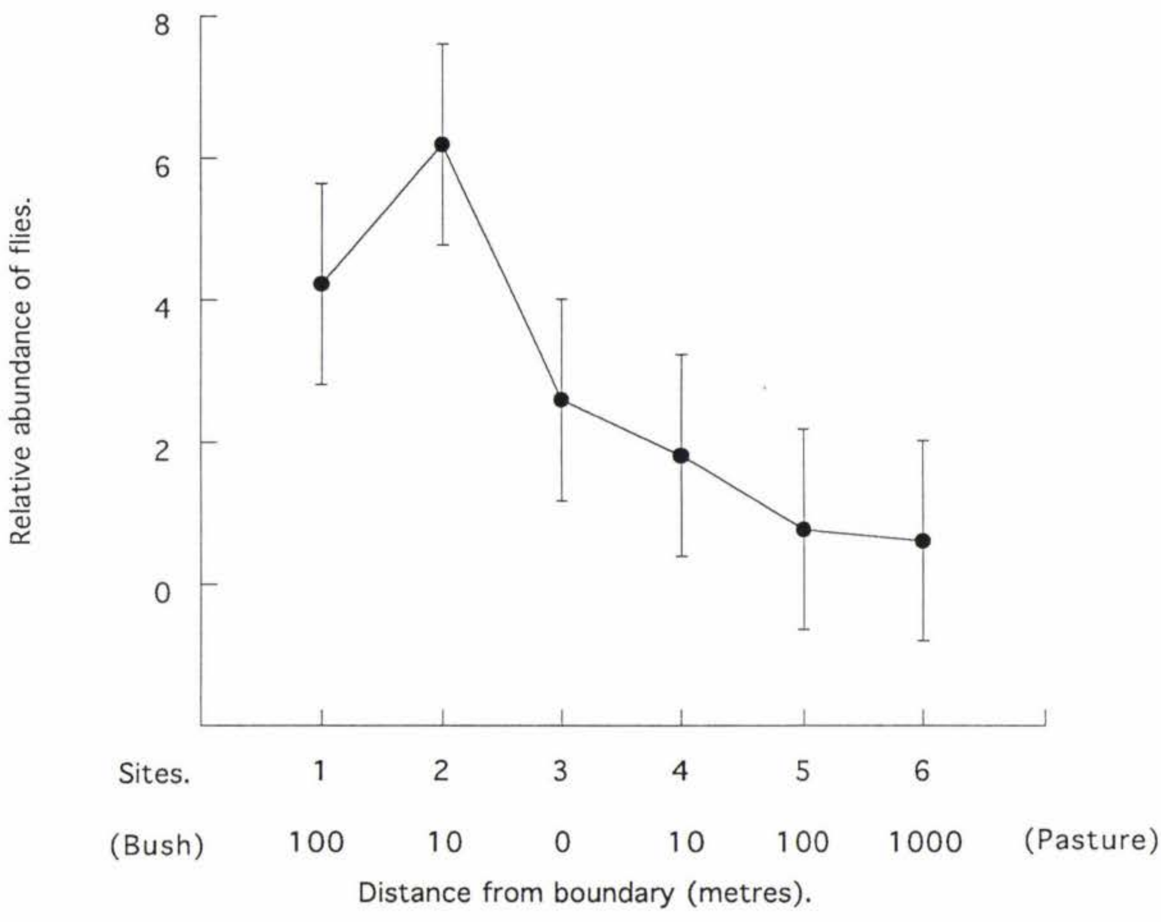


Fig 3.3 Relative abundance of flies at each trapping site during spring and summer.



3.5 DISCUSSION.

3.6 Habitat influence.

My research showed that more blowflies are attracted to carrion in bush than in pasture and this is supported by other studies in New Zealand (Murray 1956; Dymock & Forgie 1993). However, no other study has determined that the edge of the bush is even more important in this respect. A possible reason for more flies being trapped in bush than pasture may be related to the environmental factors that prevail in bush. The numbers of *Lucilia cuprina* (Wiedemann, 1830) trapped in Australia were shown to increase with increasing temperature and light intensity, and with decreasing wind velocity and decreasing humidity (Vogt et al. 1985). Trap catch rates for *C. rufifacies* were influenced in a similar way but only by ambient temperature and light intensity (Vogt 1988). The low light intensity levels in bush certainly do not seem to make this habitat favourable and I could not detect a significant difference between the mean ambient temperatures in bush and pasture at Keeble farm. These factors therefore were probably of little importance to the flies. I found, however, that during spring and summer there were lower relative humidity and wind velocity levels in bush than in pasture (appendix 3 and appendix 6). This was when the flies were most active so it appears that these factors have an overriding influence. But why are more flies trapped around the bush margin? Possible reasons could be that ambient temperature may be highest at the bush edge and that wind velocity may be locally reduced. The bush margin may also provide more suitable basking sites for the flies. Wratten et al. (1993) and Wratten unpublished data (1993) discovered that dispersal rates for syrphids and carabids were hindered by vegetative boundaries in pasture areas. Certainly greater numbers of these insects were found in and around such boundaries (Wratten et al. 1993; Butcher & Emberson 1981). If the bush-pasture boundary is influencing the rate of blowfly dispersal, then it may explain why more flies were trapped in this area.

Adults of *C. rufifacies* were never seen in bush, nor were their maggots found in possum carcases in Keeble reserve (chapter 4). However, *C. rufifacies* has been trapped in native bush at Whatawhata by Dymock & Forgie (1993), and this species made up 1.78% of the 14669 flies trapped in a Hong Kong forest where mean ambient temperature ranged between 13.5°C and 28.4°C over a six month period (So & Dudgeon 1990).

C. stygia was present in greater numbers in bush throughout the year, and because it is one of the major flystrike species, it may be responsible for a high percentage of the strikes on sheep grazing near bush.

Habitat use by *L. sericata* appears to vary from one location to another. It was trapped only in pasture at Keeble farm and Whatawhata Reserve in New Zealand (Dymock & Forgie 1993), and in Frankfurt, Germany (Kentner & Streit 1990) while at Waikowhai, New Zealand (Dymock & Forgie 1993) and at Berkshire, England (Lane 1975) it was trapped both in pasture and bush. In comparison, *C. antennatis* was found both here and in England (MacLeod & Donnelly 1960) to be a species predominantly restricted to bush. Dennison (1979) only trapped three *C. antennatis* out of 3308 flies in pasture in the Manawatu so it appears that this species is extremely rare in pasture.

It is also noteworthy that *H. varia* was the only species at Keeble farm which visited possum carcases exclusively to feed. All other species trapped were found breeding in possum carcases.

3.7 Seasonal influence.

There was a clear seasonal variation in the numbers of different calliphorid species attracted to carrion in bush and pasture but the pattern may vary from location to location. *C. stygia* for instance was the most numerous species in pasture both in the Manawatu and at Limestone Downs, Port Waikato (Dymock et al. 1991). At Keeble farm *C. stygia* was the dominant species in pasture during spring only but at Limestone Downs it continued to dominate right through to the end of summer.
C. hilli's preference for bush and overwhelming abundance during summer was also observed by Dymock & Forgie (1993) at Whatawhata research station and Waikowhai bush.

The genus *Chrysomya* is considered to be a tropical group known to be less cold-tolerant than temperate species (Zumpt 1965). The temperature threshold for *C. rufifacies* is 13°C-15°C (Nicholson 1934; Norris 1965; Dennison 1979; Vogt 1988) yet during spring and summer *C. rufifacies* was not trapped despite mean ambient temperatures being above 13-15°C. Possibly the severe frosts during May 1992 (the coldest being -3.5°C) killed the pupae of *C. rufifacies*. Certainly adult *C. rufifacies*, *C. antennatis*, *Hydrotaea rostrata* Robineau-Desvoidy, 1830 and *H. varia* were no longer observed in the field after these severe frosts. Fuller (1934) states that in Australia, a maximum soil temperature of 21°C is required in spring before *C. rufifacies* will appear. Soil temperatures exceeded 21°C on at least 9 separate days during spring 1992 on Keeble farm, but no adult *C. rufifacies* appeared. Hence neither a maximum ambient temperature above 15°C nor a maximum soil temperature reaching 21°C were factors governing the appearance of *C. rufifacies* in this study.

3.8 Further research.

It would be interesting to determine the relative abundance of flies at different heights throughout a forest ecotone and compare the results with trapping at different heights in mature forest and pasture. Would fly numbers be as abundant in the forest canopy as in the forest ecotone? Environmental factors influencing trap catch-rates for blowfly species, other than *L. cuprina* and *C. rufifacies*, could also be investigated to help explain why flies are found predominantly at the bush-pasture margin. There is also a need to investigate the critical soil temperature and ambient air temperature required for the appearance of adult *L. cuprina* and *C. rufifacies*.

Chapter four.

MAGGOT DEVELOPMENT, MAGGOT PRODUCTION AND FLY SPECIES SUCCESSION IN POSSUM CARCASES.

4.1 INTRODUCTION.

The species and numbers of maggots that emerge from decaying carcases is greatly influenced by environmental factors such as temperature (Fuller 1934; Nabaglo 1973; Johnson 1975) and habitat (Putman 1978; Reed 1958; Kentner & Streit 1990). Decay and species succession are most rapid during summer (Fuller 1934; Nabaglo 1973; Johnson 1975). During winter there are usually fewer Diptera species present but those species that are present are more numerous than in summer. This is particularly evident for *Calliphora stygia* (Fabricius, 1781) (Fuller 1934). Kentner & Streit (1990) concluded that habitat affects species succession because some Diptera are restricted to certain habitats. Reed (1958) found that, in general, species succession proceeds more rapidly in pasture than in wooded areas. He noticed that maggots frequently developed faster in carcases in pasture than in carcases of the same age in a wooded area.

Putman (1978) showed that both habitat and season influence the species of flies present at carcases. He recorded greater numbers of Diptera at carcases in grassland than at those in woodland areas. He concluded that carcases had a greater area of influence in the more open grassland habitat, and therefore attracted flies from a greater distance. More flies were found at carcases in both habitats during autumn than in summer months, suggesting that flies were generally more abundant during autumn.

The following experiment was designed to determine the combined effects of habitat and season on blowfly succession and on the number of maggots that leave possum (*Trichosaurus vulpecular* Kerr) carcases in the Manawatu.

4.2 METHODS.

4.3 Possum carcases.

Fifty possums were obtained from the Kimbolton and Pohangina districts. Possums in these districts are at present free from bovine tuberculosis. Ten were killed with cyanide poison, while the rest were shot with sub-sonic .22 cal ammunition. All were between 2.55 kg to 3.12 kg when killed. They were stored in individual bags at -11°C until required.

4.4 Field sites.

Possum carcases were placed at 10 sites on Keeble farm (labelled 1 to 10 in fig 4.1). Sites 1 to 5 were located in pasture as far away as possible from shelter belts that could influence the behaviour of adult flies (Wratten 1993). They were also situated more than 650 m from Keeble bush reserve (fig 4.1). Sites 6 to 10 were located 10 m within this bush or from a border of *Cupressus macrocarpa* along the south-west and north-west boundary of the bush. Access into the bush was considered when choosing these sites and this resulted in their uneven spacing (fig 4.1).

Ten possum carcases were placed into the field for each seasonal run: summer 1 run, 26th February to 15th April 1992; autumn run, 4th May to 9th July 1992; winter run, 6th August to 19th October 1992; spring run, 9th November to 9th December 1992; and summer 2 run, 18th January to 19th February 1993.

4.5 Possum carcase cages.

Each possum carcase was placed on a "carcase tray" measuring 50 cm square and 4.5 cm deep. This in turn was positioned above a maggot collection tray 50 cm square and over 12 cm deep. The frames for both trays were made from tannerlized pine and the bases were made respectively from plastic mesh (hole size 5 mm) and commercial "weed matting". The plastic mesh allowed maggots to drop into the collection tray beneath. Here they were retained by the weed matting which also

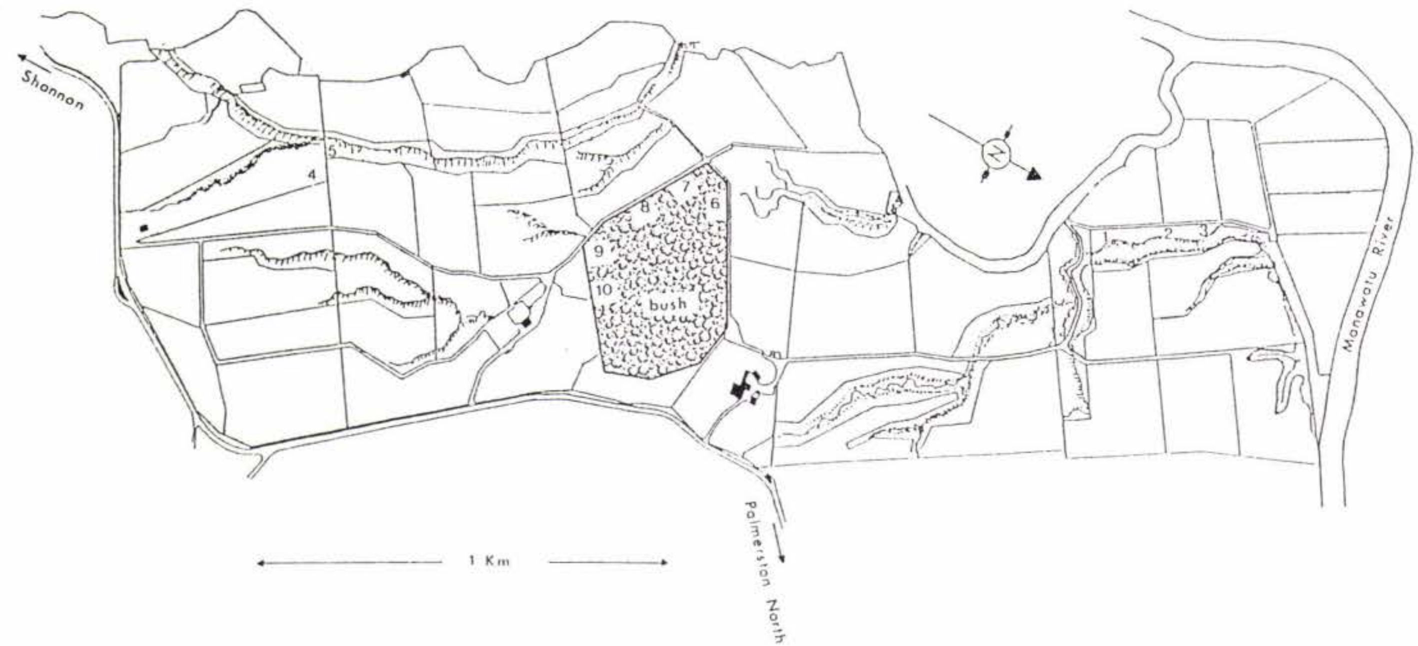


Fig 4.1 Map of Keeble farm and Keeble bush showing location of sites where possum carcases were placed. The sites are labelled 1 to 10. Sites 1-5 were located in pasture. Sites 6-10 were located in bush.

allowed any rain water to soak away. A 5 cm wide flashing of galvanized sheet metal was fitted around the top of the carcase tray preventing maggots from climbing out. Both carcase and collection trays were finally enclosed within a protective outer cage that excluded scavenging vertebrates (plate 2.2). This had a frame made from steel reinforcing rod covered with 1 cm diameter galvanized wire mesh.

4.6 Additional protection from attack by rats in the bush.

Eight rat bait stations were positioned around each site in the bush after the possum carcase at site 6 was attacked and destroyed during the autumn run. This possum carcase was excluded from the results. Each bait station consisted of a 50 cm long piece of 25 cm diameter black pvc drainage pipe that was staked to the ground with wire. Three cakes of talon bait were placed inside and replenished whenever necessary.

4.7 Sampling of maggots.

A measured amount (5.62 l) of dry untreated sawdust was placed in each collection tray for maggots to burrow into. Sawdust was light weight and inexpensive. The maggots burrowed quickly into it thereby escaping many surface active parasitoids and predators, and yet they were still easy to find and recover.

Once maggots began dropping from the possum carcases, samples were taken every second or third day during all seasonal runs, except during the winter run, when samples were taken whenever weather and farm conditions permitted vehicle access. Maggots were collected by tipping the sawdust from each collection tray into a 25 l bucket. The lid was then fastened on and the contents were shaken for approximately 30 seconds in such a way that the maggots were evenly distributed throughout the sample. A sub-sample of 1/8 of the volume of sawdust was taken by filling a 0.65 l food container. If the sawdust was wet a sub-sample of 0.79 l was taken with the aid of a second 0.65 l food container which took the additional 0.14 l of sawdust. This was approximately equivalent to 0.65 l of dry sawdust. Any maggots trapped between the weed mating and frame were squashed to prevent their appearance in later collections.

Finally the collection tray was replenished with fresh sawdust and the carcase cage was reassembled.

The recognition of the various stages of decay varies considerably between different observers (Schoenly & Reid 1987), and I therefore decided to stop sampling (except for summer 1 run) once 20 or fewer calliphorid maggots left the carcase on two consecutive sampling periods.

In the laboratory maggots were removed from sawdust samples and placed in plastic food containers 1/4 filled with vermiculite. No more than 100 maggots were placed in any one container. Due to their predatory nature *Chrysomya rufifacies* (Macquart, 1843) maggots were placed in their own containers. Larvae were not identified to species, except for *C. rufifacies*. To prevent the maggots becoming desiccated, water was sprayed into the containers before they were placed in constant temperature rooms at 21°C.

All adult flies and parasitoids that emerged were transferred to a sock net and then killed in a jar containing commercial insecticide. When dead they were identified to species. Flies and parasitoids were identified using keys from Dear (1985) and CSIRO (1970). Difficult species were identified by Dallas Bishop (AgResearch Centre, Wallaceville, Upper Hutt).

4.8 Estimating fly species succession in possum carcases.

If certain Diptera species are present in low numbers as maggots leave a possum carcase they may not be collected in individual sub-samples. If collected, they still have to emerge before being identified. Thus, each species was recorded as being present for a sampling occasion if it occurred in any one of the five sub-samples taken from the five possum carcases located in that habitat.

4.9 Estimating the number of maggots that escaped from the collection trays.

Estimates of the number of maggots that escaped from the collection trays were made during the spring run and the summer 2 run. Pairs of pitfall traps were positioned 20 cm from opposite sides of cages at sites 2 and 8. Each pitfall trap consisted of a 0.65 l plastic food container with a 15 cm diameter opening. This was buried with its opening flush with the ground. A 10 cm high sheet metal cover was placed over each pitfall trap to keep out rain and each trap was 1/4 filled with ethylene glycol to preserve any maggots that fell in. All pitfall traps were checked each time the farm was visited. After the summer 2 run, 0.01 m^3 soil was removed from site 2 and washed through a sieve to remove any pupae or pupal remains.

4.10 Statistical analyses.

Data for the estimated total number of maggots that left carcases in each seasonal run (appendix 8) were log transformed and analyzed using General Linear Model (GLM) (SAS Institute Inc 1990) to determine interactions between the number of maggots that left possum carcases and season, habitat and site position in pasture.

4.11 RESULTS.

4.12 Diptera.

Calliphora vicina Robineau-Desvoidy, (1830), *C. stygia*, *Calliphora hilli* Patton, 1925 and *C. rufifacies* were the first flies to arrive at fresh possum carcases between November and February. *Lucilia sericata* (Meigen, 1826) appeared 24 to 28 hours later, and *Calliphoroides antennatis* (Hutton, 1881) and *Hydrotaea rostrata* Robineau-Desvoidy, 1830 arriving two to eight days later depending on the state of carcase decay. The arrival times for *Calliphora quadrimaculata* (Swederus, 1787) and *Sciadocera rufomaculata* (White, 1916) were both highly variable though the latter species was generally the last to arrive. All flies deposited their eggs around the mouth, eyes and ears of possum carcases in both habitats.

The following order of events occurred throughout the year:- eggs appeared on possum carcases between 1 to 36? days after possum carcases were set out, first instar maggots appeared between 2 and 38? days and maggots started leaving the possum carcases after 4 to 42 days (table 4.1).

<u>Seasonal runs.</u>	Summer 1		Autumn		Winter		Spring		Summer 2	
P= Pasture. B= Bush.	P	B	P	B	P	B	P	B	P	B
Eggs.	1	1	3	?	25?	36?	1	1	2	2
1st instars.	3	2	8	8	27	38?	2	2	3	3
maggot drop.	5	5	10	10	31	42	5	5	4	4
Calliphoridae.										
Calliphora vicina	9	11	18	22	35	42	9	9	11	9
Calliphora stygia	9	9	29	32	48	75	9	9	9	6
Calliphora hilli	8	9	12	29	35	75		9		6
Calliphora quadrimaculata					66		11	13	16	18
Lucilia sericata			32				9		11	
Chrysomya rufifacies	9									
Muscidae.										
Calliphoroides antennatis		14						13	16	9
Hydrotaea rostrata	14	16							13	16
Sciadoceridae.										
Sciadocera rufomaculata	23	59	47		57		25		16	

Table 4.1 **Time taken for events to occur and species to leave possum carcases after they were placed in the field (in days).**

75% of the maggots that were found in the first two or three samples of maggots that left carcases during spring and summer were tiny while only 10% of maggots were tiny in samples of maggots that left possum carcases during autumn and winter runs. These tiny maggots did not pupate in the laboratory and were considered to be immature. During these first samples, maggots of the three major species *C. vicina*, *C. stygia* and *C. hilli* left carcases at varying times throughout the year. During summer 1 run through to the winter run they appeared 1, 8 and 18 days later respectively from possum carcases in bush than in pasture. During the spring run they appeared at the same time in samples from both habitats while during the summer 2 run they appeared 2.5 days earlier in bush samples (table 4.1).

The estimated mean number of maggots leaving possum carcases in spring and summer reaches a maximum within 4 days and then decreases to approximately 200 maggots per day, after 8 days (fig 4.2). During autumn and winter fewer maggots left possum carcases than in spring and summer. The estimated average total number of maggots produced by possum carcases during the year (fig 4.3 and appendix 9) exhibits a cyclic phase with a maximum in spring and a minimum in late winter. There was no significant difference between the estimated total number of maggots produced by possum carcases in the two different pasture locations. These locations included sites 1-3 and 4-5. However, the estimated total number of maggots that left possum carcases was found to be significantly influenced by season and habitat (Season $F(4,39)=30.84$, $P<0.0001$; Habitat $F(1,39)=5.84$, $P<0.02$), and the variation in estimated total number of maggots produced during the year was due to season and habitat interactions ($F(4,39)=6.57$, $P<0.0001$). This is clearly seen in fig 4.3. Here the estimated average total maggot production was greatest from possum carcases in bush during spring and summer whereas possum carcases in pasture were more productive than possum carcases in bush during autumn and winter. The estimated average total number of maggots produced was almost identical for both summers in both habitats (fig 4.3).

Decay rates were most rapid during spring and summer when carcases were completely decayed within 31 to 34 days. During autumn and winter, possum carcases (except for those at sites 6 and 7) took 66 and 75 days to decay completely. Photographs taken in May and November of possum carcases after 30 days in the field (plates 4.1 & 4.2) give some indication of the differences in the rates of decay at these

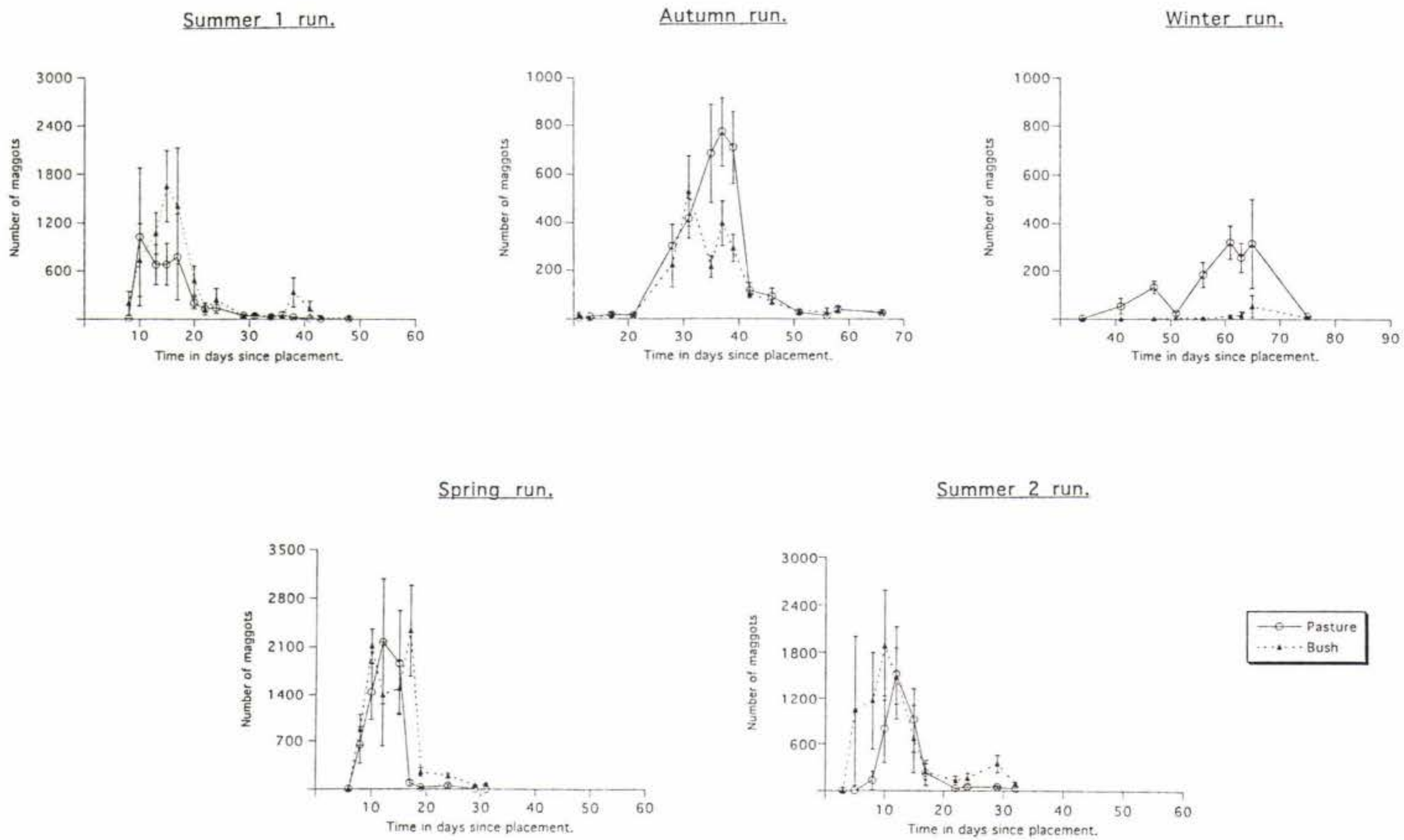
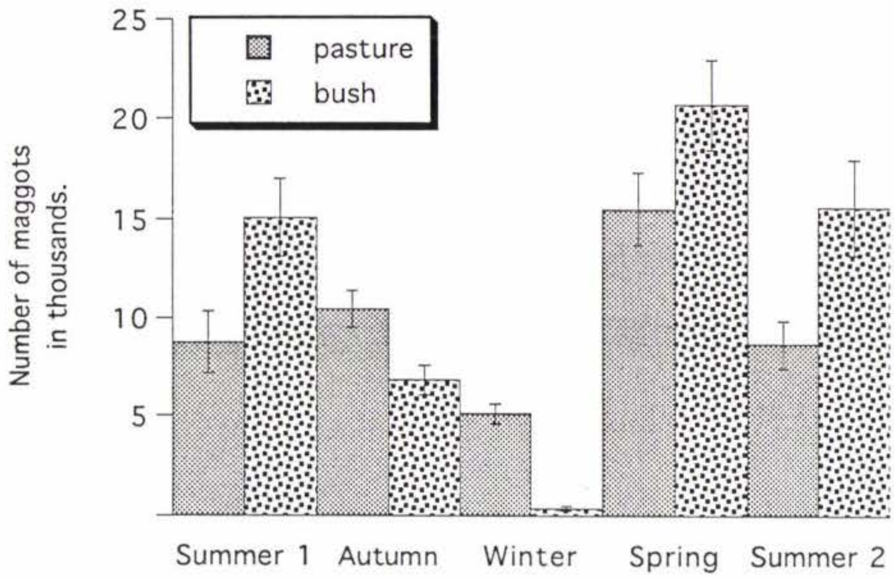


Fig 4.2 **The estimated mean number of maggots leaving possum carcases per day in bush and pasture, for each seasonal run.**

Fig 4.3 The estimated average total number of maggots that left possum carcases in bush and pasture for each seasonal run.



times.

Few maggots appeared to escape from collection trays. On two occasions during the winter run, seven maggots were found in the farm meterological station rain gauge, 2 m from site 2. During the spring run, 308 and 28 maggots were estimated to have escaped from the collection trays at sites 2 and 8 respectively, while during summer 2 run, 28 and 0 maggots were estimated to have escaped from sites 2 and 8 respectively. twelve puparium and three fragments of puparium were found in the soil sample taken from under site 2 at the end of summer 2 run. Puparia of *C. rufifacies* were present in carcase remains located in pasture at the end of summer 1 run, while *C. vicina* and *C. stygia* pupae were numerous in the remains of the possum carcase at site 7 at the end of the spring run, indicating that some maggots do not leave the carcase to pupate.

4.13 Predators and parasitoids of maggots.

The presence of numerous red ants and often up to 20 or 30 *Creophilus oculatus* Fabricius, 1775 (Coleoptera: Staphylinidae) in the sawdust gave clear indication that maggots had begun leaving the possum carcase. The ants and *C. oculatus* captured tiny immature maggots but neither were observed attacking large maggots.

Alysia manducator (Panzer, 1799) was the only species found throughout the year, while *Tachenophagus sp*, *Aphaereta aotea* Hughes & Woolcock, 1976 and *Alysia sp* were only present from spring to early autumn. Few *A. manducator* were found during winter though they were generally immobile and found on the possum carcase itself.

4.14 Species presence and succession.

C. vicina and *C. stygia* were the only calliphorid species present in both bush and pasture throughout the year whereas *L. sericata* and *C. rufifacies* were restricted to pasture and *C. antennatis* was restricted to bush (fig 4.4 & table 4.2). Other flies varied in their occurrence in bush and pasture during the year. *C. quadrimaculata* was present in pasture from winter through to summer and in bush from autumn through to

Plate 4.1 **Photograph showing the amount of material that had been removed from possum carcase at site 2 after 30 days during spring.**

Plate 4.2 **The amount of material removed from possum carcase at site 2 after 32 days during autumn. Compare this photo to the one above, note the difference in state of decay.**


Day 32 C2


Day 32 C2

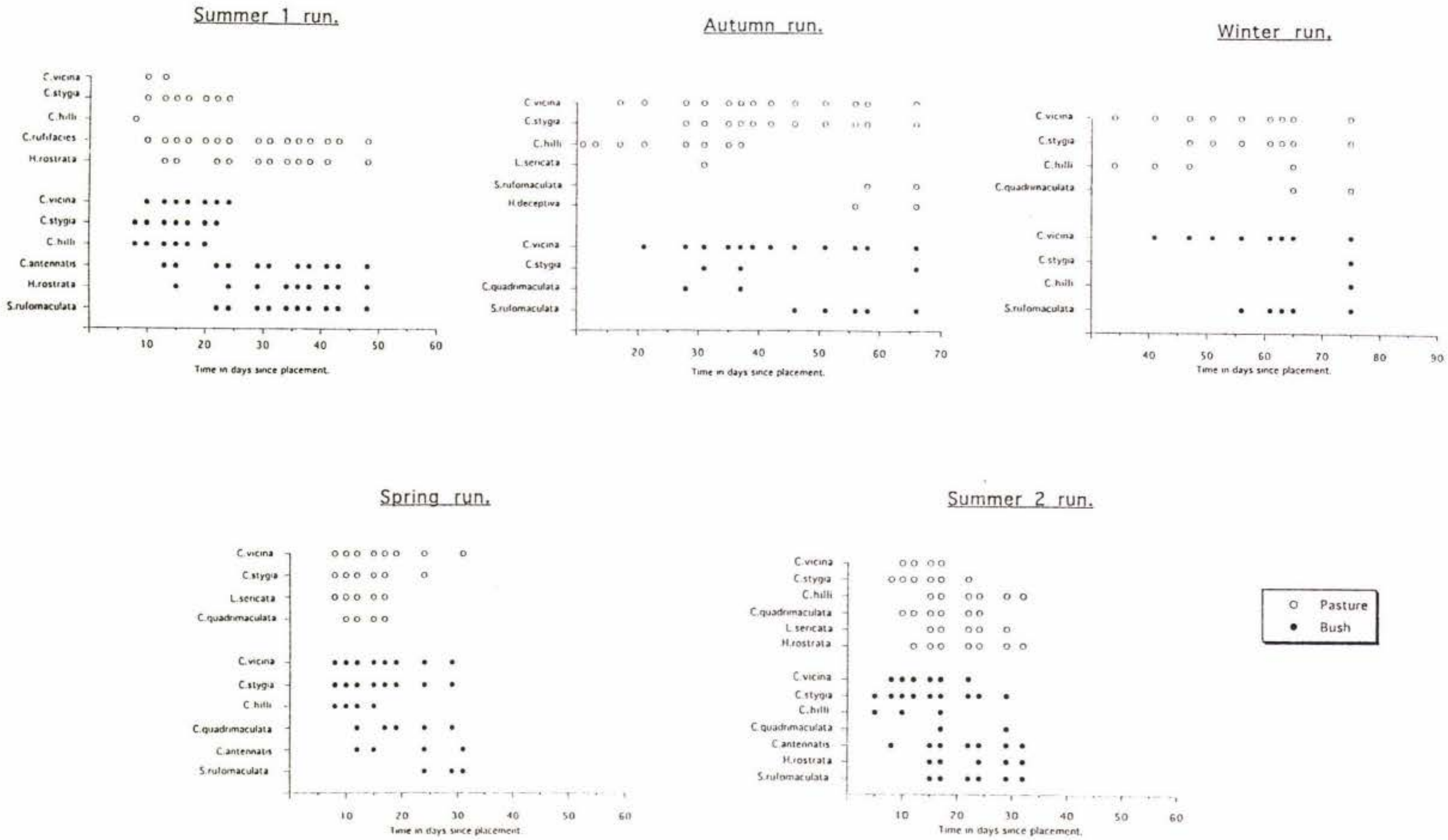


Fig 4.4 Diptera species succession in possum carcases located in bush and pasture during each seasonal run. Each dot signifies the presence of a species on a particular sampling occasion. Five possum carcases were sampled in each habitat at each sampling time.

Seasonal runs.	Summer 1		Autumn		Winter		Spring		Summer 2	
P= Pasture. B= Bush.	P	B	P	B	P	B	P	B	P	B
Calliphoridae.										
Calliphora vicina	1-2	1-2	1-2	1	1	1-2	1	1	2	1-2
Calliphora stygia	1-2	1-2	2-3	2	2	3	1-2	1	1	1-2
Calliphora hilli	1	1-3	1	1-2	1-3	3		1-2		1
Calliphora quadrimaculata				2-4		2-3	2	2-5	4	
Lucilia sericata			3				1-2		1-3	
Chrysomya rufifacies	1-2									
Muscidae.										
Calliphoroides antennatis		2-5						2-3	2-4	1-4
Hydrotaea rostrata	1-3	2-4							2-4	3-5
Sciadoceridae.										
Sciadocera rufomaculata		3-4	3-4	3		1-2		3-4		2-5

Table 4.2 **Range of appearance is taken over 5 possum carcases in pasture (P) and 5 in bush (B). For example, *C. quadrimaculata* was the second, third or fourth species to leave possum carcases in autumn in bush.**

summer *C. hilli* was absent from pasture only during spring and absent from bush during autumn. *H. rostrata, C. rufifacies* and *C. antennatis* were absent from pasture and bush during autumn and winter. *S. rufomaculata* occurred in bush throughout the year and was found in pasture only during autumn. The periods when different species of maggots were present in possum carcases and the order in which they emerged were variable (fig 4.4). Each species was found to be the first one present in a possum carcase on at least on one occasion except for *C. quadrimaculata* (table 4.2). *C. vicina, C. stygia, C. hilli, C. rufifacies* and *L. sericata* maggots were always the first maggots to leave possum carcases whenever they were present and *H. rostrata, C. antennatis, C. quadrimaculata* and *S. rufomaculata* were the next maggots to leave.

4.15 DISCUSSION.

4.16 Arrival of adult flies at possum carcases.

In this study, *L. sericata, C. rufifacies* and *C. vicina* were among the first species to arrive at possum carcases. These observations are consistent with those of O'Flynn & Moorhouse (1979) who recorded *C. rufifacies* as being the first species to colonise mammal carcases in Australia. In England, Lane (1975) discovered that *C. vicina* was the first species to arrive on mice carcases while *L. sericata* arrived 48 to 76 hours later. This difference was not observed here.

4.17 Succession.

The rate of carcase decay depends on the number of maggots present and on their rate of development. Since development is dependent on temperature, in a temperate climate such as New Zealand's, decay rates are most rapid in spring and summer. This finding is consistent with those of Fuller (1934) for carcase decay rates in Canberra, Australia and Johnson (1975) for carcase decays rates in the U.S.A. In a climate where the annual ambient temperature remains fairly constant as in Queensland, Australia, decay rates are similar throughout the year (Fuller 1934).

Reed (1958) found that maggot development was more advanced in carcases in pasture than in carcases in bush and stated that this was due to the higher temperature in the pasture areas. Even the normally greater insect activity at carcases in bush was not enough to hasten succession to levels of those found in carcases in pasture.

In my study there was no difference in maggot development rates between possum carcases in bush and those in pasture during spring through to autumn. Only during winter did maggot development occur more rapidly in possum carcases in pasture than in those in bush. In fact during autumn and winter more maggots left possum carcases in pasture, than carcases in bush whereas in spring and summer possum carcases in bush had more maggots leave them than did possum carcases in pasture. This variation in production is suspected to be directly related to solar heating of the possum carcases in pasture (see chapter 6, 6.10). Overall my findings agree with those of Putman (1978), where habitat and season were found to influence species presence and species succession.

Data for insect succession in animal carcases has been widely publicized Chapman & Sankey (1955); Bornemissza (1957); Reed (1958); Nabaglo (1973); Cornaby (1974); Johnson (1975); Jiron & Cartin (1981); O'Flynn (1983); Early & Goff (1986); and Tullis & Goff (1987) however I am unaware of any published succession data for most of the Dipteran species that I have presented here in my study.

4.18 Maggot dispersal.

Once completely developed, calliphorid maggots are capable of dispersing over great distances. Tullis & Goff (1987) found maggots 9 m away from carcases and observed them climbing tree trunks. Pupae were also recovered from litter accumulated in tree forks 1-2 m from the ground as well as from soil around the carcases. In my study, they appeared in the rain gauge located in pasture during the winter run and up to 308 maggots (2.7% of the estimated total number of maggots) were estimated to have escaped from the collection trays during spring and summer 2 runs. For the spring run, approximately 9.9 maggots were estimated to be escaping from the collection tray per day. This number would not have significantly affected my estimates for the mean number of maggots leaving possum carcases.

4.19 Habitat restriction.

L. sericata was never present in possum carcases in Keeble bush, however overseas it has been bred from carcases in bush in both the U.S.A (Johnson 1975) and Southern Ireland (Blackith & Blackith 1990). In addition, *C. rufifacies* was also absent from possum carcases in Keeble bush although it was found in cat and pig carcases in bush in Hawaii (Early & Goff 1986; Tullis & Goff 1987). I observed adults of both these species on surrounding pasture so why did they not take advantage of possum carcases in Keeble bush? Further research is clearly needed on the environmental conditions preferred by these two species. Certainly a study involving another bush site where the two species are present would be particularly useful as a comparison with my research at Keeble farm.

4.20 Species competition.

C. rufifacies was present in pasture only when *L. sericata* was absent and it was also absent during the spring and summer 2 run when *L. sericata* was present. A possible explanation is that *C. rufifacies* larvae readily prey upon other dipteran larvae, especially in instances when food is limited (Fuller 1934; Waterhouse 1947; Goodbrod & Goff 1990). Fuller (1934) and Ullyett (1950) stated that *L. sericata* is only found in carcases at the beginning of fly infestation because it can develop rapidly and leave the carcase before the arrival of *C. rufifacies*. However in this study both *L. sericata* and *C. rufifacies* were early colonists of possum carcases, and this may also explain why they never appeared in carcases together.

The high number of immature maggots present in the first samples taken during spring and summer runs probably indicates that there was severe competition between maggots for space in the carcase (see chapter 5). Certainly possum carcases quickly became a writhing mass of maggots at this time of the year. By contrast, only 10% of the first maggots that left the possum carcases were immature during autumn and winter and it can only be presumed that competition between maggots was not as intense during this period. Fewer maggots emerged in spring and summer than in autumn and winter (see chapter 5). This is further evidence that during warmer months severe maggot competition for space in the carcase has a direct influence on the number of immature maggots leaving the carcase.

Maggots of *S. rufomaculata* were reported to feed on the remains and fluids of carcases in Australia but its role in carcase decay was considered to be insignificant (Fuller 1934). This, however, is not always the case in New Zealand because I found large numbers of maggots of this species in possum carcases in bush well before calliphorid larvae were finished with the carcase. *S. rufomaculata* may therefore play an important role of the decay of possum carcases in bush.

4.21 Conclusion.

This study clearly shows that habitat and season significantly influence fly use of possum carcases in the Manawatu. Season influences possum carcase decay rates, species succession and the number of maggots that leave carcases, while habitat influences the number of maggots that leave carcases and species presence.

During spring and summer possum carcases in bush had more maggots leave them than did possum carcases in pasture and of these, a high percentage were major flystrike species. If the number of flystrike flies are to be kept to a minimum in pasture areas, then possum poisoning should be restricted to autumn and winter months.

Chapter five.

SPECIES EMERGENCE AND EMERGENCE TRENDS FROM POSSUM CARCASES LOCATED IN BUSH AND PASTURE.

5.1 INTRODUCTION.

The calliphorids *Calliphora vicina* Robineau-Desvoidy, 1830, *Calliphora stygia* (Fabricius, 1781), *Calliphora hilli* Patton, 1925, *Lucilia sericata* (Meigen, 1826), *Lucilia cuprina* (Wiedemann, 1830) and *Chrysomya rufifacies* (Macquart, 1843) are well known for their ability to colonize a wide range of carcases in New Zealand. These include sheep, possums, hares, small mammals and birds (Boswell 1967; Dymock & Forgie 1993). The emergence of flies that originate from such carcases has, however, only been reported from overseas. Blackith & Blackith (1990) discovered that *C. vicina* was the only colonizer of mice carcases in Ireland when Sarcophagidae were absent. In Australia, large numbers of *C. rufifacies* and *C. stygia* were reported to have emerged from sheep, hares, cats and guinea pig carcases (Fuller 1934; Waterhouse 1947). *L. sericata* was only abundant in these carcases when *C. rufifacies* was absent whilst only a few individuals of *C. stygia* and *C. rufifacies* emerged from small carcases such as lizards and birds (Fuller 1934; Waterhouse 1947). Habitat also influences which species of fly are present during the year and maggot development, but does it also influence pupal development and the number of flies that emerge?

Regular poisoning of possums to control the spread of bovine tuberculosis in New Zealand provides an abundance of possum carcases for flies to breed in. Of particular concern are the numbers of *C. stygia, L. sericata* and *L. cuprina* that emerge from such carcases because these are the major species responsible for cutaneous myiasis in sheep. This prompted me to investigate the species of flies that emerge from these carcases, the numbers of flies that emerge and whether bush and pasture influences which species are present. In addition, I compared emergence success in the field with that in the laboratory and this enabled me to estimate emergence success throughout the year.

5.2 METHODS.

An additional possum carcase was placed in bush and another in pasture during spring 1992 at the same time possum carcases were set out for the spring run to determine maggot development rates and fly species succession (chapter 4). The additional possum carcases were placed on carcase trays so that they were raised off the ground and they were then placed in mesh cages (as described in chapter 4). Each cage had a thick plastic base made of 5 mm diameter mesh. This allowed maggots to drop through onto the ground. A square sheet metal enclosure measuring 100x100 cm long by 30 cm high was partially embedded into the ground around each carcase to prevent maggots escaping (plate 5.1).

The cages were removed and the carcases were covered with emergence traps when the possum carcases became reduced to skin and bone (plate 5.2) and flies stopped visiting them (plate 5.3). Each emergence trap consisted of a pyramidal wooden frame covered with black weed matting. A removable collection chamber at the apex was attached by means of a metal base plate. The collection chamber was 10x10x20 cm high and was similar in design to that of the "Western Australian" fly-trap (chapter 3). A removable clear perspex top allowed light into the collection chamber so that flies moved upward into it after emerging. An upwardly tapering nylon mesh funnel at the bottom of the collection chamber enabled flies to enter but hindered their escape.

Flies were removed from the collection chamber every morning by first sliding the chamber off the base plate. A metal plate was simultaneously slid onto the base plate to prevent any flies still in the emergence trap from escaping. Flies in the collection chamber were then killed with domestic insecticide and recovered. The emergence traps and carcases were only removed from their field sites one week after the last fly emerged.

The estimation of emergence success in the field was based on the assumption that the number of maggots that left possum carcases in the emergence traps were equal to the estimated average total number that left the other possum carcases located in the same habitat during the spring run (appendix 9). The sampling of maggots is explained in chapter 4, 4.7. Emergence success was obtained from sub-samples of maggots which had been taken during the five seasonal runs (see chapter 4, 4.7).

Plate 5.1 **Cage set-up with metal maggot inclosure at the pasture site.**

Plate 5.2 **Pasture located carcase after 13 days, just before emergence trap was erected.**

Plate 5.3 Emergence trap in place over the possum carcase located in pasture.

5.3 Statistical analysis.

A regression analysis was used to determine the correlation between the percentage of flies that emerged in the laboratory and the estimated average total number of maggots that left carcases during each seasonal run.

5.4 RESULTS.

5.5 Emergence in the field.

Flies began emerging from the possum carcase in pasture eleven days before any emerged from the possum carcase in bush. Emergence from the pasture carcase also started five days before the last maggots had dropped from other possum carcases placed in pasture (chapter 4). 94% of the flies emerged from the two possum carcases during the first nine days of emergence in both habitats. Thereafter only a few flies emerged each day (fig 5.1). *C. vicina* and *C. stygia* together made up 80% and 96% of the total number of flies emerging in pasture and bush respectively (table 5.1). Both were present only during the initial nine day emergence period (fig 5.2). *L. sericata* and *Calliphora quadrimaculata* (Swederus, 1787) took longer to emerge in the pasture than in the bush. Adult *C. quadrimaculata*, *Calliphoroides antennatis* (Hutton, 1881), *Sciadocera rufomaculata* (White, 1916) and *Sylvicola sp.* also appeared after *C. vicina*, *C. stygia* and *C. hilli* (fig 5.3). *L. sericata* was restricted to pasture while *C. antennatis*, *S. rufomaculata*, *Sylvicola sp.* and *Therevidae* were restricted to bush. The maximum emergence of flies did not correspond with the period of highest mean ambient temperature in either habitat (fig 5.4).

In total 3398 flies emerged from the 2.5 kg possum carcase in pasture and 4163 flies emerged from the 3.1 kg possum carcase in bush. Possum carcases of these sizes were estimated to have 15,452 ± 1804.9 (S.E) and 20,641 ± 2268.9 (S.E) maggots leave them respectively (appendix 9). The emergence level was therefore estimated to be 20.2% ± 2.5% in the bush and 22.0% ± 2.9% in pasture. Their respective emergence levels in the laboratory were 11% and 17% higher than this (table 5.2).

5.6 Emergence in the laboratory.

Parasitoids were the major cause of mortality amongst blowfly pupae and maggots in both habitats. Often 50 or more parasitoids emerged in containers holding about 100 maggots and this reduced the emergence success of the flies. The dominant parasitoid was *Alysia manducator* (Panzer, 1799) (Braconidae). All parasitoids always emerged after flies, both in the laboratory and in emergence traps. Over the year emergence success and estimated average total maggot drop varied considerably (see table 5.2 & appendix 9). There was a significant inverse correlation between the percentage of flies emerging in the laboratory and the estimated average total number of maggots that left possum carcases in the field ($n=10$, $y=66.43+-0.0025x$, $R=0.63$, $P<0.05$) when data from both were combined (fig 5.5).

Table 5.1 Species percentage composition and the number of flies that emerged from possum carcases between the 4.12.92 and 22.2.93.

Species.	Pasture	(%)	Bush	(%)
Calliphoridae.				
Calliphora vicina	1190	(35.0)	718	(17.2)
Calliphora stygia	1556	(45.8)	3270	(78.5)
Calliphora hilli	1	(0.03)	41	(0.98)
Calliphora quadrimaculata	124	(3.70)	54	(1.30)
Lucilia sericata	527	(15.5)		
Muscidae.				
Calliphoroides antennatis			25	(0.60)
Sciadoceridae.				
Sciadocera rufomaculata			7	(0.17)
Anisopodidae.				
Sylvicola sp.			45	(1.10)
Therevidae			3	(0.07)
Total.	**3398**		**4163**	

Table 5.2 **The percentage of flies successfully emerging in the laboratory taken from each seasonal run.**

Seasonal run.	Pasture	n	Bush	n
Summer 1.	19.5	63	30.4	74
Autumn.	49.5	64	33.6	60
Winter.	74.9	41	84.4	25
Spring.	33.0	35	36.9	45
Summer 2.	24.4	40	7.6	47

Fig 5.1 **Total number of flies emerging per day.**

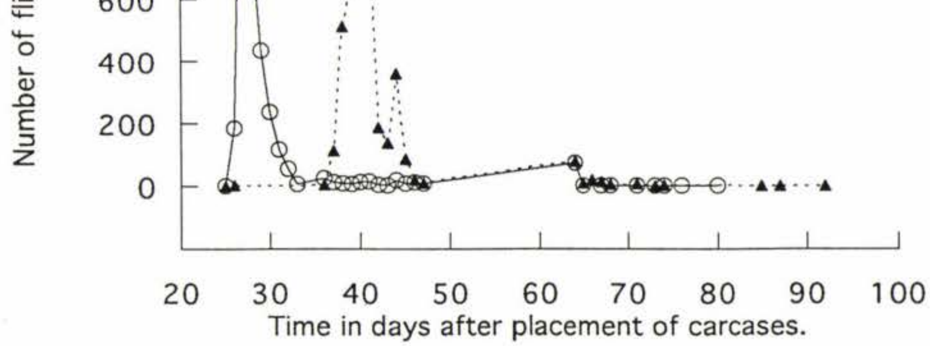
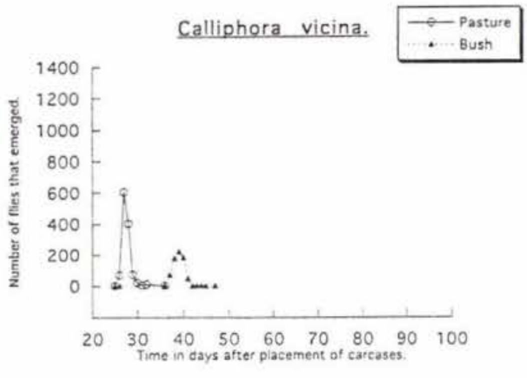
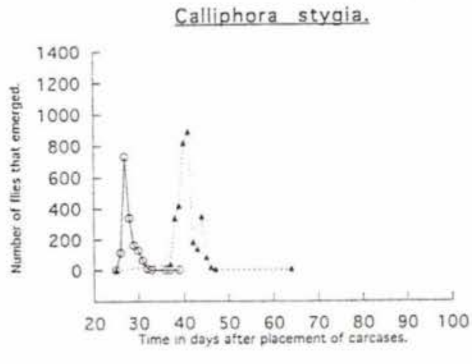


Fig 5.2 **The total number of flies emerging per day for each major species.**





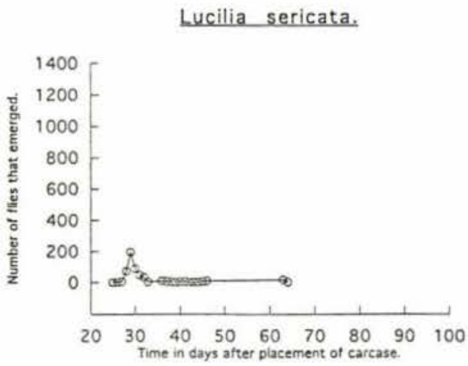


Fig 5.3 **Species emergence succession from possum carcases.**

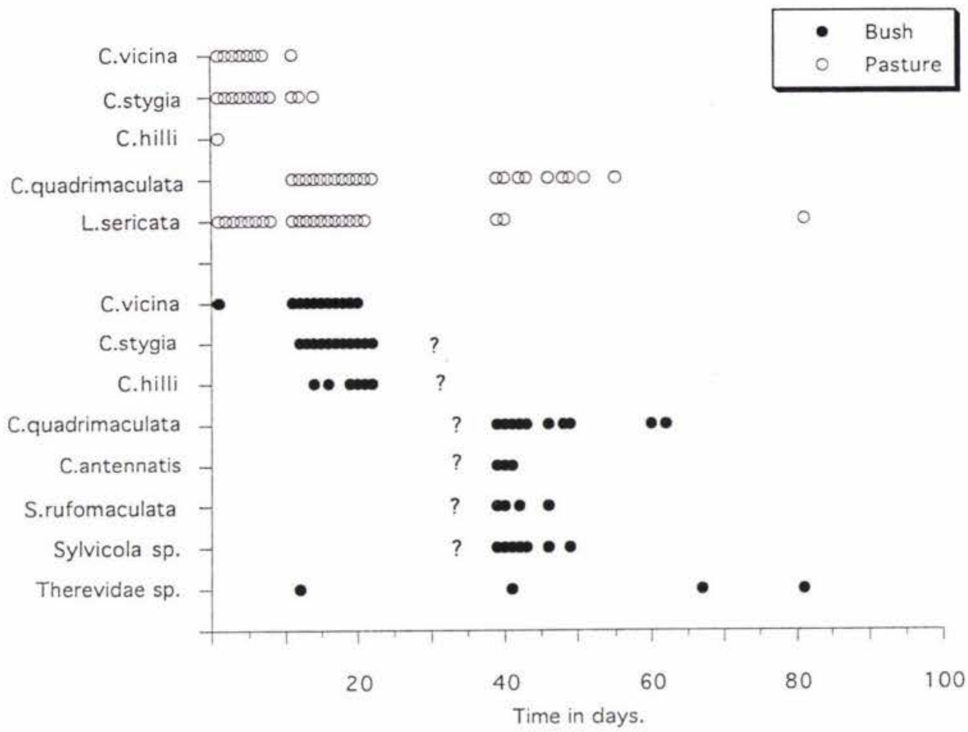


Fig 5.4 **Mean ambient temperature during fly emergence.**

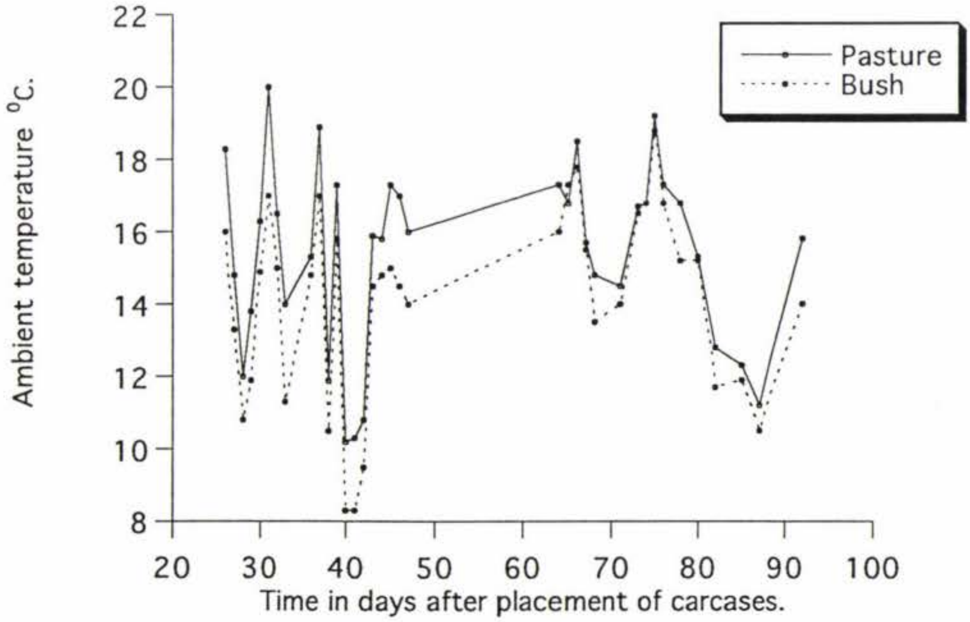
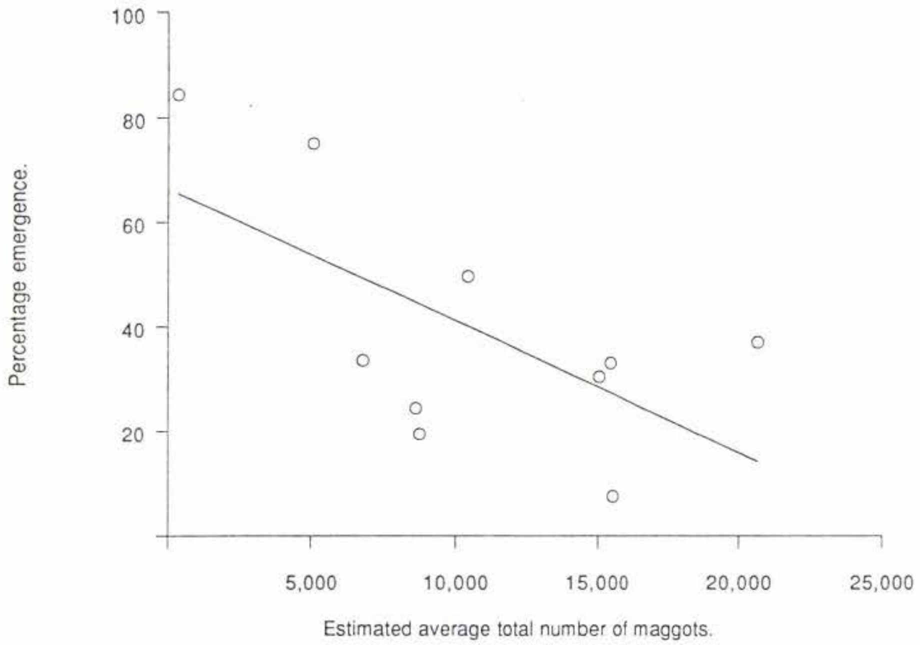


Fig 5.5 **Correlation between percentage of flies emerging in the laboratory and estimated average total number of maggots that left possum carcases during the seasonal runs.**



5.7 DISCUSSION.

5.8 Number of flies produced by possum carcases in the field.

Despite a relatively low successful emergence level in the field (average of 21%), a total of 3398 and 4163 flies emerged from the possum carcases in pasture and bush respectively. This represents a conversion value of 0.74 g of carcase per fly which is a similar value to that reported in Australia for lamb carcases weighing 3.63 kg to 4.99 kg (Waterhouse 1947). Lambs produced between 4,660 and 9,026 flies in spring which was equivalent to 0.4 to 1.1 g of carcase per fly.

The major flystrike species *C. stygia* and *L. sericata* comprised between 78.5% to 61.3% of the total number of flies that emerged in bush and pasture respectively. To reduce the number of flystrike flies breeding in possum carcases, possum poisoning should only be conducted in autumn and winter when these flies are least active.

5.9 Habitat influence on fly emergence.

Habitat had a major influence on the emergence rates of flies as evidenced by the earlier emergence of flies from the possum carcase in pasture compared to those from the possum carcase in bush. Solar heating of the soil in the pasture areas may have caused the maggots and pupae to develop more rapidly here than in the bush.

C. stygia was the most common fly to emerge from possum carcases in both pasture and bush, however its emergence success in the laboratory was lower than for other species such as *C. vicina*, this has also been observed by Heath (pers. comm. 1993). The next most common species to emerge, *C. vicina*, is also widely reported as colonizing carcases elsewhere in the world (Kneidel 1984; Davies 1990; Blackith & Blackith 1990). In my study *L. sericata* comprised 15.5% of the flies that emerged from the possum carcase in pasture. This is considerably higher than reported elsewhere. In Australia *L. sericata* made up between 0.8% and 8.2% of the total number of flies emerging from sheep heads (Fuller 1934) and 0.2% of the flies emerging from whole sheep carcases (Waterhouse 1947). In Britain this species rarely comprises more than 2% of the flies to emerge from sheep carcases (Cragg 1955). This led Cragg (1955) to believe that *L.*

sericata was a poor colonizer of this carcase type. *L. sericata* is also reported to occur in carcases at the start of fly infestation in Australia and before *C. rufifacies* becomes well established (Fuller 1934). When *C. rufifacies* is absent *L. sericata* is an excellent colonizer of medium sized carcases, as evidence in my study and in England where it was present throughout the entire two week decay period of rabbit carcases (Chapman & Sankey 1955).

5.10 Emergence success.

Emergence success of flies in the laboratory was lowered markedly by parasitism, especially by *A. manducator* which was not surprising since it will attack larvae at any stage of development (Reznik et al. 1992). The greater emergence success of maggots taken into the laboratory during winter is probably due to a reduction in competition for food and lower incidence of parasitism at this time. Certainly fewer maggots develop from possum carcases at this time of year (chapter 4). Severe competition is known to reduce the size of mature larvae and smaller pupae of *L. sericata* are known to have a low emergence success (Ulleytt 1950). Smaller larvae result in smaller adults (Ullyett 1950; Nicholson 1958; Putman 1977; Levot et al. 1979; Williams & Richardson 1983). For example, *C. rufifacies* and *C. stygia* adults can emerge from larvae that are only approximately 45.6% and 72.9% respectively of the normal mean weight (Levot et al. 1979). This in return results in a reduction in fecundity (Williams & Richardson 1983). This is not a disadvantage to the next generation because it results in no reduction in fitness or size for the following generation (Williams & Richardson 1983). In my study intense competition clearly results in a decrease in prepupal weight and this explains why the largest maggots and largest flies emerged in the laboratory during winter when competition was least intense. However, mortality of maggots that leave a carcase during winter is likely to be high because they are exposed to saturated soils, freezing temperatures and fungal infection. Thus emergence success of these maggots is likely to be similar to those maggots that survive to pupate in summer.

5.11 Further research.

It would be useful to expand this research to determine which species of blowfly and how many emerge from different carcase types at different times of the year. This should also include a study in the presence of *L. cuprina* and *C. rufifacies*.

Chapter six.

INFLUENCE OF TEMPERATURE ON THE NUMBER OF MAGGOTS LEAVING DECAYING POSSUM CARCASES.

6.1 INTRODUCTION.

Insect infested carcases can attain temperatures up to 18°C above ambient. Both the size of the carcase and the time of year influence the ability of insects to raise the carcase temperature (Deonier 1940; Waterhouse 1947; Payne 1965; Boswell 1967; Early & Goff 1986; Tullis & Goff 1987). Deonier (1940) concluded that the rise in temperature of a goat carcase during decay was entirely due to the insects within it. This conclusion was reached from a comparison of temperatures in a carcase before and after insects were allowed access to it. No attempt has been made to distinguish experimentally between the heating effects of insects and bacterial or other decay processes. The effects that solar heating has on the number of maggots leaving the carcase has also not been considered. Many investigations of carcase temperature have been accompanied by studies of the percentage loss in carcase weight during decay (Payne 1965; Boswell 1967; Early & Goff 1986; Tullis & Goff 1987). In all these cases carcases were left to decay until only dry skin, bones and fur weighing approximately 10% of the fresh carcase remained.

In chapter 4 I showed that during spring and summer at least 75% of maggots leaving possum carcases during the first week of decay are small. These samples also contained a greater total number of maggots than later samples where larger maggots predominated (chapter 4). In light of this I would predict that the number of maggots leaving possum carcases would not be significantly correlated with maggot sample weight.

This section of my study was carried out with the following intentions:- First, to determine how much maggot activity and bacterial action, together with other decay processes contribute to elevating the temperature of possum carcases. Second, to determine what effect solar heating has on the number of maggots produced by a possum carcase. Third, to determine how carcase temperature influences the number of maggots that leave the possum carcase each day. Fourth, to determine what percentage of fresh carcase weight is converted to total maggot weight. Fifth, to determine if the number and weight of maggots leaving a possum carcase are correlated. These questions were addressed by conducting two experiments during spring and summer. In the first experiment the temperatures of a possum carcase in pasture were compared with the temperatures of another possum carcase in bush. The second experiment compared the temperatures in two possum carcases exposed to insects with the temperatures in two possum carcases from which insects were excluded. These possum carcases were located in bush where they were shaded from direct sunlight.

6.2 METHODS.

The five possum carcases that were exposed to insects during experiments 1 and 2 were placed on collection trays in cages as described in chapter 4. The two possum carcases from which insects were excluded during experiment 2 were placed in separate cages measuring 90x90 by 80 cm high. These cages allowed the entry of rain and free movement of air around the possum carcases but prevented the entry of flies. Each cage consisted of a wooden frame with glass sides and an upper lid covered with fine aluminium mesh (plate 6.1). A floor of weed matting allowed free drainage of rain water while preventing insects from entering the cage. The inside of the cage was liberally sprayed with domestic insecticide every second day to ensure that it remained insect-free.

Averaged hourly temperatures were measured with thermistor probes attached to a data logger (Li-Cor 1000). Access to the cages in experiment 2 was through holes in the wooded frames (plate 6.2). One thermistor was inserted into the chest cavity of each carcase to measure internal temperature and another thermistor was placed in the collection tray underneath the possum carcase to record ambient temperature. Temperatures were recorded hourly, beginning 4 hours after the possum carcases were placed in the field. Recording was discontinued when the temperature in a possum carcase remained within 1°C of the ambient temperature over a period of 48 hours.

Sampling of maggots and estimation of the number leaving a possum carcase per day are detailed in chapter 4, 4.7. To determine the weight of maggots leaving

Plate 6.1 Two carcase cages in the bush site. One is insect-proof and the other on the left allows free access to flies.

Plate 6.2 Possum carcase 1 (table 6.1) showing the temperature probe in place.

possum carcases per day, maggots from sub-samples were washed, dried and weighed on a Mettler EA200 balance.

6.3 Statistical analyses.

Regression analyses were used for all correlation tests.

6.4 RESULTS.

6.5 The temperature of decaying possum carcases containing maggots in pasture and bush.

Possum carcase temperatures rose quickly above ambient over the first 2 days and then peaked approximately 8 days after carcase placement. The possum carcase in pasture attained a higher peak temperature than did the possum carcase in bush. Once insects had removed most of the possum carcase (approx. after 30 days) carcase temperature dropped to within 2°C of ambient. The maximum averaged hourly temperature in the pasture located carcase was 42°C on day 8 while the greatest temperature difference between the carcase and the ambient temperature was 26°C on day 9 (fig 6.1).

In contrast, the bush located possum carcase attained a maximum temperature of 19.7°C on day 7 while the greatest temperature difference between carcase and ambient temperature was 4.8°C on day 12 (fig 6.2).

6.6 Temperatures of possum carcases in bush with and without maggots present.

Temperatures in possum carcases infested with maggots exhibited trends similar to those described in the first experiment (fig 6.3). The maximum temperatures observed in possum carcases containing maggots were 32.4°C to 34.3°C and the greatest temperature differences between these carcases and the ambient temperature were 18.3°C to 19.4°C (fig 6.3). Temperature records for possum carcase 3 with maggots (fig 6.3)

Fig 6.1 **Daily mean temperatures during decay of a possum carcase in pasture.**

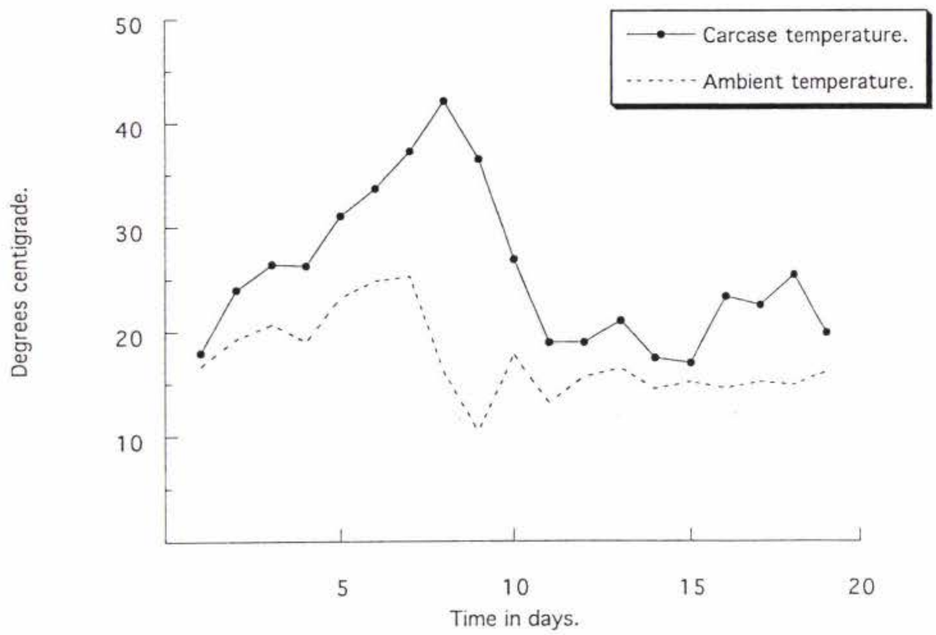


Fig 6.2 **Daily mean temperatures during decay of a possum carcase in bush.**

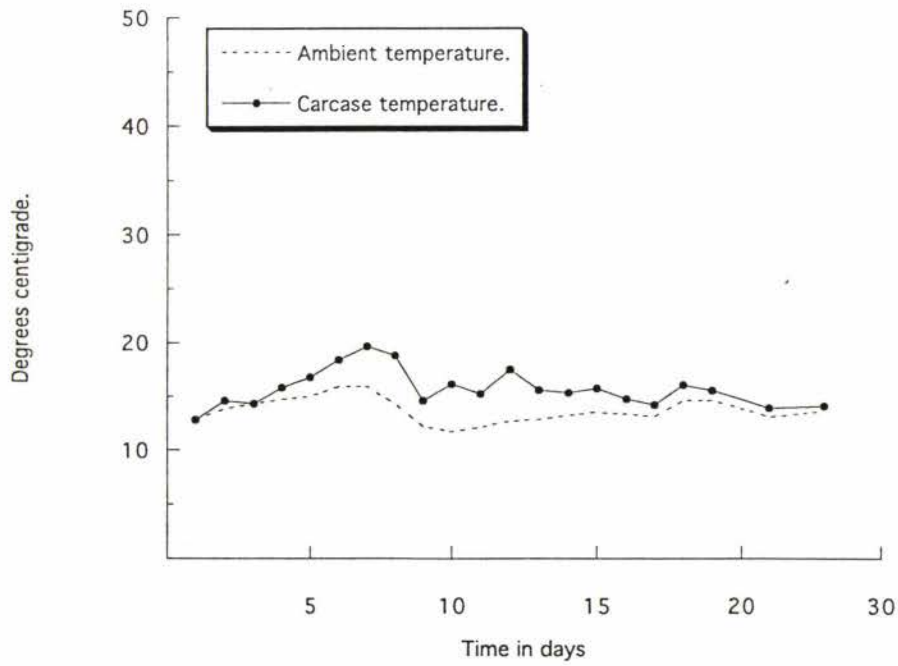


Fig 6.3 **Daily mean temperatures during decay of two possum carcases containing maggots in bush.**

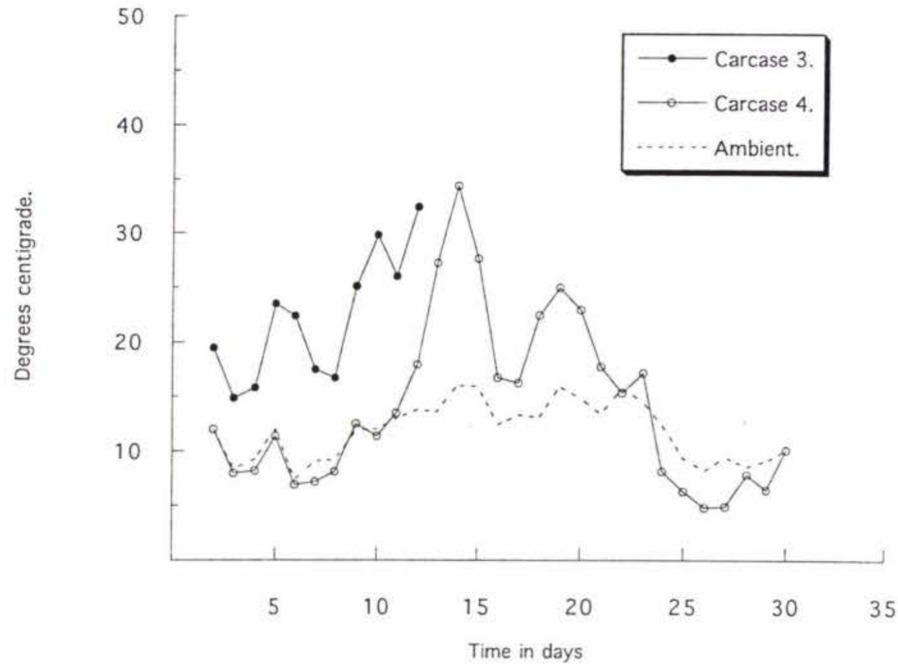
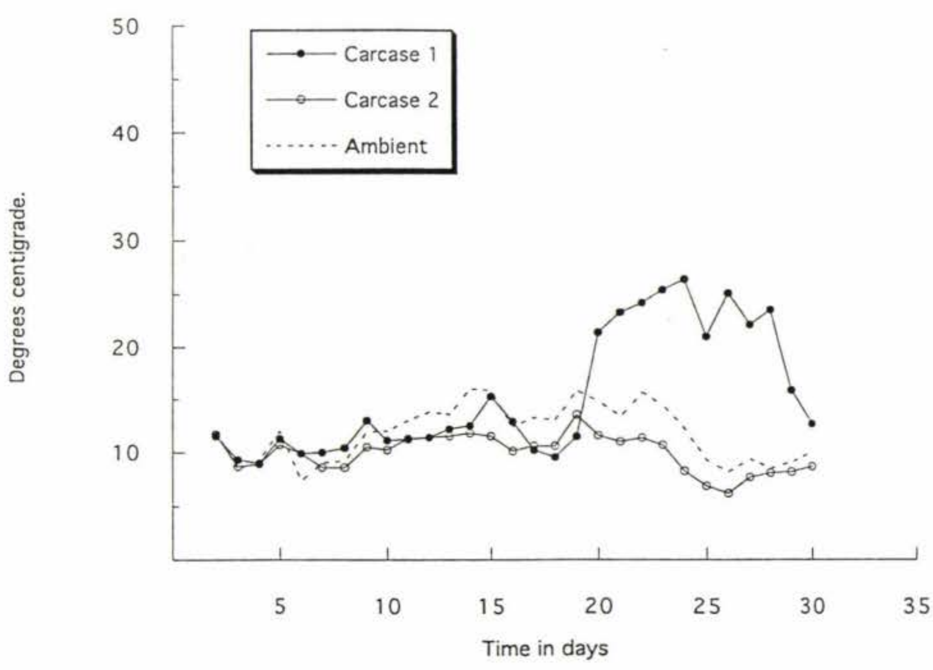


Fig 6.4 **Daily mean temperatures of two possum carcases without maggots in bush.**



were only available up to day 12 when the thermistor stopped functioning.

In contrast, the internal temperatures of possum carcases without maggots were within 2.0°C of the ambient temperature until day 19. Thereafter the temperature within possum carcase 2 continued to follow within 2°C of the ambient temperature but the other possum carcase 1 (fig 6.4) became bloated and its temperature increased to a maximum of 26.4°C on day 24 (fig 6.4). This was 16.9°C above the ambient temperature and was similar to the difference between the temperatures of carcases containing maggots and the ambient air temperature.

6.7 The relationship between the estimated number of maggots that left the possum carcase per day and the carcase temperature and ambient temperature.

Internal temperatures of possum carcases in bush were found to be significantly correlated with ambient temperature (fig 6.5; $n=63$, $y=-11.05+2.18x$, $R=0.72$, $P<0.001$). However internal temperatures of possum carcases in pasture were not correlated with ambient temperature. Further temperature analyses were restricted to possum carcases located in bush.

Throughout decay, possum carcase temperatures were found to be significantly correlated with the estimated number of maggots leaving the carcases per day (fig 6.6; $n=22$, $y=-857.57+135.41x$, $R=0.77$, $P<0.001$). It was not surprising ambient temperature and the estimated number of maggots leaving the possum carcase per day were also significantly correlated (fig 6.7; $n=22$, $y=-2712.1+322.85x$, $R=0.58$, $P<0.005$).

6.8 The amount of material remaining after decay of possum carcases.

Approximately 66% of the fresh carcase weight had been removed after maggots had left the possum carcase (table 6.1). Remains consisted of fur, bones and dried tissues (plate 6.3) which weighed 34% of the fresh carcase weight. 24.7% to 26.7% of the fresh weight was converted into maggots. At the end of the experiment, possum carcases not infested with maggots were found to have gained weight (table 6.1). This was probably due the carcases being rained on during the study. Possum carcases not

Fig 6.5 Relationship between the internal temperatures of possum carcases in pasture and bush and ambient temperature in these situations.

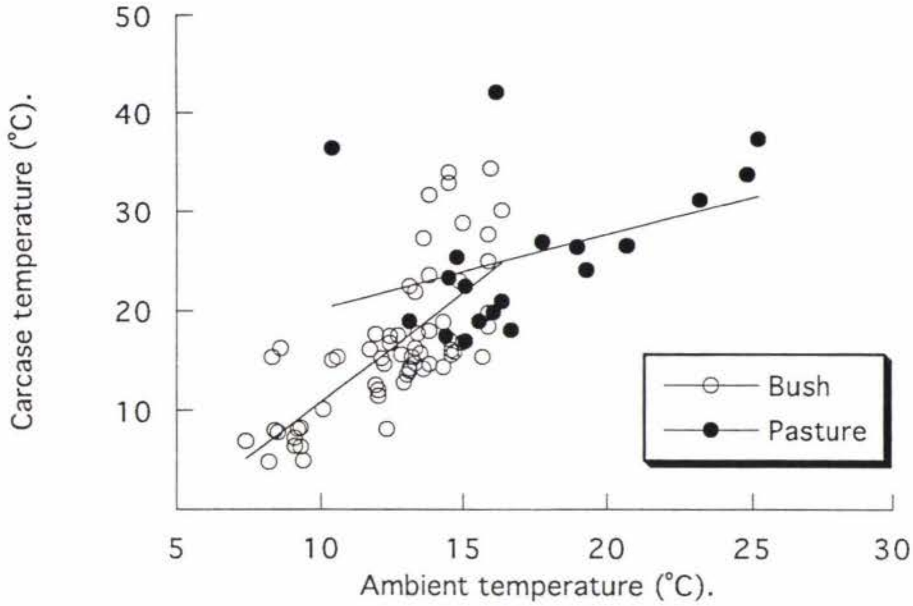


Fig 6.6 Relationship between the internal temperature of possum carcases and the estimated number of maggots that left these carcases per day.

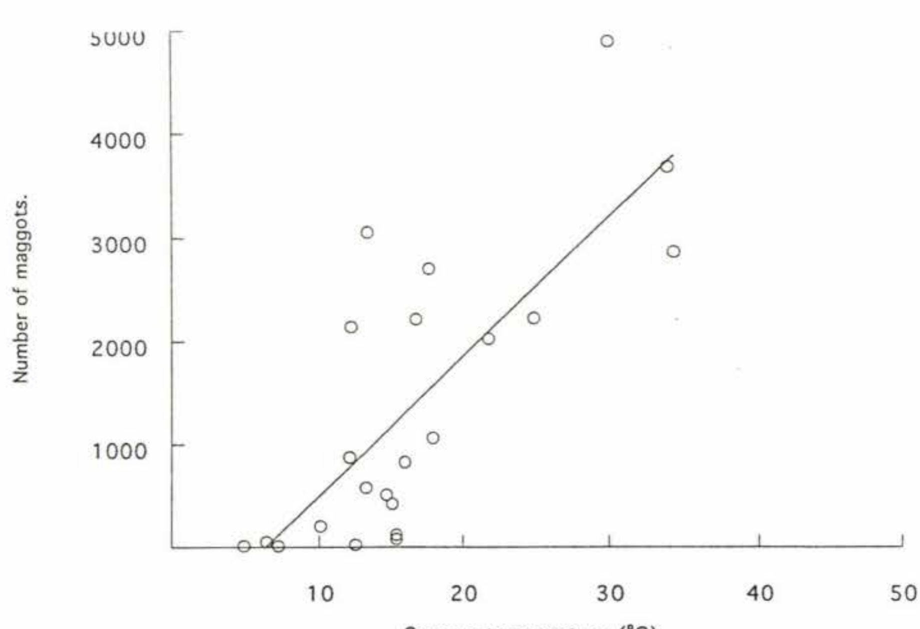


Fig 6.7 **Relationship between the ambient temperature and the estimated number of maggots that left the possum carcases per day.**

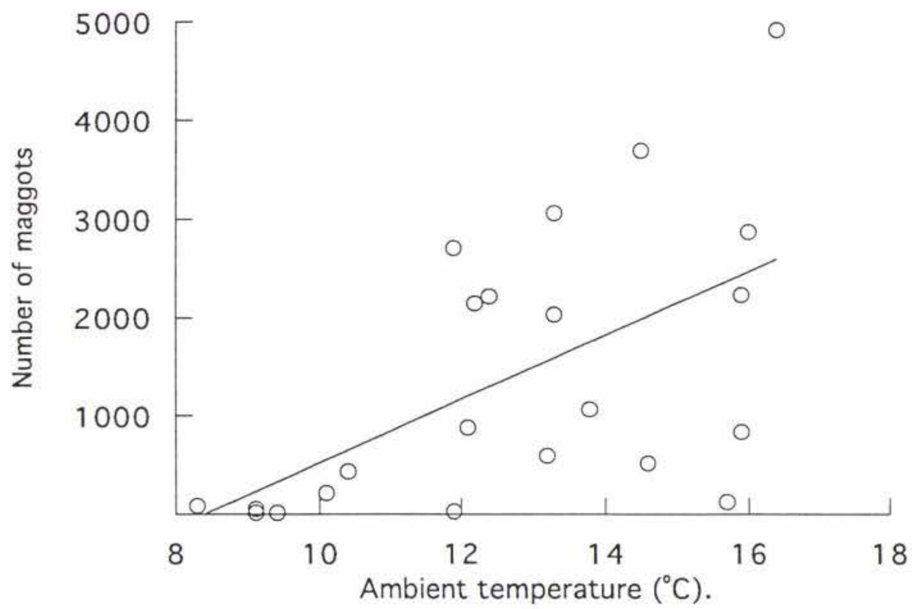


Table 6.1

The estimated number of maggots that left the possum carcases and weight differences of the carcases in bush between 24.3.93 and 16.4.93.

	Maggot-free		Maggots present.	
Possum carcases:	**1**	**2**	**3**	**4**
Fresh carcase weight (gm)	2488	2648	3143	2883
Final carcase weight (gm)	2535	2722	1083	998
Difference in weight (gm)	+47	+74	-2060	-1895
Total maggot weight (gm)			839	710
Total number of maggots			27,448	20,776

Fig 6.8 **The relationship between the estimated number of maggots that left the possum carcase and the total weight of these maggots.**

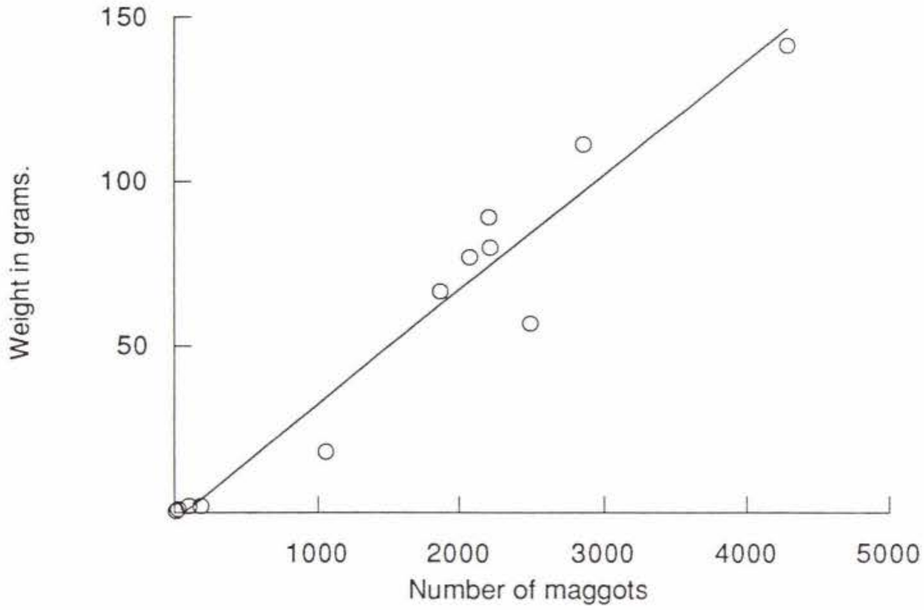


Plate 6.3 Possum carcase 3 (table 6.1) that had contained maggots at the end of the study.

Plate 6.4 Possum carcase 1 (table 6.1) that was not infested with maggots at the end of the study.

infested with maggots did not smell or show any sign of bacterial decay (plate 6.4). The estimated number of maggots leaving a possum carcase per day was found to be significantly correlated with maggot sample weight (fig 6.8; $n=20$, $y=-2.20+0.03x$, $R=0.97$, $P<0.001$).

6.9 DISCUSSION.

This study clearly shows that maggots elevate the internal temperature of possum carcases. This effect can be quite pronounced. In maggot infested possum carcases the temperature rose to 18.5°C above ambient over a period of 13.5 days. In comparison, the effects of bacteria and other decay processes on carcase temperature were small. In these carcases the temperatures usually fluctuated within approximately 2°C of ambient.

The temperatures observed in possum carcases containing maggots were similar to those found in other carcases of similar weight (between 2 kg and 4 kg) (Payne 1965; Early & Goff 1986; Boswell 1967). In all of these studies the maximum carcase temperatures recorded were between 37.7°C and 39.3°C, and the maximum differences between carcase temperature and ambient were between 13.3°C and 18.2°C.

Heavier carcases attain similar or higher temperatures during decay. Tullis & Goff (1987) recorded a maximum temperature of 37°C in 8.2-12.8 kg baby pigs that was 16°C above ambient. Sheep carcases reached temperatures of 40.6°C, approximately 22.3°C above ambient, during spring in Australia (Waterhouse 1947). Deonier (1940) recorded maximum temperatures of around 45°C in sheep and goat carcases during winter in Texas, USA. Such high temperatures at this time of the year were probably a product of solar heating as the temperature was taken directly underneath the skin of the carcase. Deonier (1940) makes no mention of this possibility. His reading of 21.8°C near the centre of the abdomen was probably a more accurate estimate of the temperature created by maggot activity. Using this value the carcase to ambient temperature difference is reduced to 4.6°C. Deonier (1940) also found that although small mammal carcases such as those of hares and possums were infested with maggots during winter they did not attain temperatures above ambient. I believe this to also be the case for possum carcases in bush during winter. Using the correlation equation for ambient temperature versus carcase temperature and the mean ambient temperature during winter, it was calculated that the carcase temperature would have been approximately 0.7°C below ambient. The rise in temperature above ambient for possum carcase 1 without maggots (fig 6.4) on day 20 suggests that during warmer weather bacterial decay or other decay processes can contribute substantially to heating of the carcase.

6.10 Solar heating effects.

Heating by the sun promotes maggot growth and activity in possum carcases in pasture during late autumn and winter (chapter 4). This was the only time when these possum carcases produced more maggots than carcases in the bush (fig 4.3).

During spring I frequently recorded temperatures above 35°C in the possum carcase in pasture. Such extreme temperatures are enough to prevent development of *Calliphora stygia* (Fabricius, 1781) but not high enough to adversely effect the development of *Chrysomya rufifacies* (Macquart, 1843) (O'Flynn 1983). The high temperatures during spring and summer probably killed a considerable percentage of the maggots that were present. There was certainly a lower estimated average total number of maggots produced from possum carcases in pasture than from possum carcases in bush during this time (fig 4.3).

6.11 Influence of temperature on the number of maggots leaving a possum carcase.

When possum carcase temperatures were at their highest in bush, 95% of the larvae dropping off the possum carcase were mature although many immature maggots were present on the carcase. This clearly indicates that immature maggots do not leave the carcase because of extreme temperatures. This suggests that the large number of immature maggots that left possum carcases during spring and summer (chapter 4) were doing so for some other reason. Fuller (1934) suggested that immature maggots are jostled off carcases by other maggots.

Overall possum carcase temperature was found to be significantly correlated to ambient temperature but this holds only when the carcase was shaded from the sun. Carcase temperature was also significantly correlated with the number of maggots leaving the carcase. The regression equation for this relationship could therefore be used to predict the number of maggots leaving a carcase at any given temperature.

6.12 Conversion of possum carcase weight to maggot weight.

The loss of weight during decay of possum carcases was less than reported for other carcases (Payne 1965; Boswell 1967; Early & Goff 1986, Tullis & Goff 1987). This is probably because I did not leave my possum carcases to decay past the stage where all non-calliphorid maggots had left the carcase. Here 38% to 41% of the possum carcase weight was converted into maggots or lost via other decay processes.

During possum carcase decay the number of maggots leaving carcases per day was significantly correlated with maggot sample weight. 90% of the maggots in the first 3 samples were mature, compared with 25% obtained during spring and summer runs, (chapter 4). This difference may not be significant since only two carcases were compared. Any further study should use more replicates.

Chapter seven.

CONCLUSIONS.

7.1 Habitat and seasonal effects on blowfly ecology.

1. Habitat influenced the relative abundance of flies. More flies were trapped around the bush margin and especially just inside the bush than in deeper bush or in open pasture.
2. *L. sericata* and *C. rufifacies* were restricted to pasture and *C. antennatis* was restricted to bush.
3. The greatest number of flies were trapped during spring. In pasture fewer were trapped during summer than in autumn or winter.
4. Habitat and season influenced fly numbers differently for different species. During spring *C. stygia* was the predominant species in pasture, while in bush *C. stygia* and *C. vicina* were equally common. The predominant species in bush during summer was *C. hilli*, and this species clearly favoured the bush habitat throughout the year.
5. Habitat and season influenced the number of maggots that left possum carcases. More maggots left possum carcases in bush during spring and summer, while during autumn and winter more maggots left possum carcases in pasture.
6. Decay rates and species succession were most rapid during spring and summer.
7. *C. vicina* and *C. stygia* were the only species present throughout the year in carcases in both habitats.

7.2 Temperatures of possum carcases containing maggots and those without maggots.

1. During spring and summer, possum carcase temperature was raised above 35°C by solar heating and this extreme temperature probably killed many maggots. Possum carcases in pasture certainly had fewer maggots leave them during spring and summer than during autumn and winter when maggot development probably benefited from solar heating.
2. Both insect infestation and bacterial decay were responsible for raising carcase temperature above ambient temperature.
3. In shade (bush) carcase temperature was significantly correlated with ambient temperature.
4. Carcase temperature was significantly correlated with the number of maggots leaving the carcase.
5. The weight of maggots leaving the possum carcase was significantly correlated with the number of maggots leaving the carcase.

7.3 Fly emergence in the field and laboratory.

1. 21% emergence success was obtained from the possum carcases located in both bush and pasture, but the total number emerging was greater in the possum carcase in bush than in the possum carcase in pasture.
2. Habitat influenced fly emergence. In pasture, flies emerged 10 days before those in bush. Higher soil temperatures in the pasture were probably responsible for the rapid development of flies in pasture compared to those in bush. This factor probably restricted *L. sericata* and *C. rufifacies* to breed in possum carcases in pasture.
3. *C. stygia* and *C. vicina* were the predominant species to emerge, making up 80% of the total number from bush and pasture.
4. The important flystrike species to emerge were *L. sericata* and *C. stygia*.
5. Emergence levels in the laboratory were 10% higher than in the field. Emergence success in the laboratory was significantly correlated with the

estimated average total number of maggots that left carcases throughout the year. Thus, emergence success appears to be directly related to competition pressures in the possum carcase.

7.4 FURTHER RESEARCH

Several areas in which the research presented here could be expanded are:

1. Determine whether there is a difference between the abundance of flies throughout the forest canopy and the forest ecotone.

2. Analyze the environmental factors influencing trap catch-rates for blowfly species, other than *L. cuprina* and *C. rufifacies*, to help explain why flies are found predominantly at the bush-pasture margin.

3. Investigate the critical soil temperature required for emergence of *L. sericata* and *C. rufifacies* to help ascertain why these species do not breed in possum carcases in Keeble bush.

4. Further Fuller's (1934) research into interspecific competition between *C. rufifacies, C. stygia* and *L. sericata* and expand this to include *C. vicina, C. quadrimaculata* and *H. rostrata.* This will help us understand the interactions between *C. rufifacies* and the other blowfly species in New Zealand.

5. Conduct research to determine which species of blowfly and how many emerge from different carcase types at different times of the year. This should also include a study in the presence of *L. cuprina* and *C. rufifacies*.

REFERENCES.

Blackith, R.E. & Blackith, R.M. (1990) Insect infestations of small corpses. *Journal of Natural History,* **24**, 699-709.

Bornemissza, G.F. (1957) An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. *Australian Journal of Zoology,* **5**, 1-12.

Boswell, C.C. (1967) An ecological study of the decomposition of the carrion of the European hare *Lepus europaus* Pallus with special reference to the insect fauna. M.Agr.Sc. Thesis, Lincoln.

Butcher, M.R. & Emberson, R.M. (1981) Aspects of the biology of carabid beetles of Ahuriri bush scenic reserve. *Mauri Ora*, **9**, 59-70.

Chapman, R.F. & Sankey, J.H.P. (1955) The larger invertebrate fauna of three rabbit carcases. *Journal of Animal Ecology,* **24,** 395-402.

Cornaby, B.W. (1974) Carrion reduction by animals in contrasting tropical habitats. *Biotropica,* **6**(1), 51-63.

Cragg, J.B. (1955) The natural history of sheep blowflies in Britain. *Annals of Applied Biology,* **42**, 197-207.

C.S.I.R.O. (1970) *The Insects of Australia.* Pub. Melbourne University Press.

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

Dear, J.P. (1985) Calliphoridae (Insecta: Diptera). *Fauna of New Zealand no.8.* 86pp.

Dennison, M.D. (1979) A trapping survey of flies in pasture habitat in autumn and winter. BSc. Hons thesis, Massey University.

Deonier, C.C. (1940) Carcase temperatures and their relation to winter blowfly populations and activity in the Southwest. *Journal of Economic Entomology,* **33**(1), 166-170.

Dymock, J.J. & 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**, 155-160.

Dymock, J.J., Peters, M.O.E., Herman, T.J.B. & Forgie, S.A. (1991) A study of sheepblowflies at Limestone Downs sheep station in the northern Waikato, New Zealand, over two summers. *New Zealand Journal of Agricultural Research,* **34**, 311-316.

Early, M. & Goff, L.M. (1986) Arthropod succession patterns in exposed carrion on the Island of O'ahu, Hawaiian Islands. *U.S.A. Journal of Medical Entomology,* **23**(5), 520-531.

Esler, A.E. (1978) **Botany of the Manawatu.** E.C.Keating, Government Printer, Wellington.

Fuller, M.E. (1934) The insect inhabitants of carrion: A study in animal ecology. C.S.I.R. Bulletin no.82.

Goodbrod, J.R. & Goff, L.M. (1990) Effects of larval population density on rates of development and interactions between two species of Chrysomya (Diptera: Calliphoridae) in lab culture. *Entomological Society of America,* **27**(3), 338-343.

Jiron, L.F. & Cartin, V.M. (1981) Insect succession in the decomposition of a mammal in Costa Rica. *New York Entomological Society,* **89**(3), 158-165.

Johnson, M.D. (1975) Seasonal and microseral variations in the insect populations on carrion. *The American Midland Naturalist,* **93**(1), 79-90.

Kentner, E. & Streit, B. (1990) Temporal distribution and habitat preference of congeneric insect species found at rat carrion. *Pedobiologica,* **34**(6), 347-359.

Kneidel, K.A. (1984) Competition and disturbance in communities of carrion-breeding diptera. *Journal of Animal Ecology,* **53**, 849-865.

Lane, R.P. (1975) An investigation into blowfly (Diptera: Calliphoridae) succession on corpses. *Journal of Natural History,* **9**, 581-588.

Levot, G.W., Brown, K.R. & Shipp, E. (1979) Larval growth of some calliphorid and sarcophagid diptera. *Bulletin of Entomological Research,* **69**, 469-475.

MacFarlane, W.V. (1938) Blowfly strike in Marlborough. Incidence and control discussed. *New Zealand Journal of Agriculture,* **57**, 388.

MacFarlane, W.V. (1942) Blowfly strike in Marlborough, New Zealand. *New Zealand Journal of Science and Technology,* (A)**23**, 205-213.

MacLeod, J. & Donnelly, J. (1960) Natural features and blowfly movement. *Journal of Animal Ecology,* **29**, 85-93.

Miller, D. (1934) Blowflies and the sheep maggot problem. Cawthron Institute Bulletin

No.9.

Miller, D. (1939) Blowflies (Calliphoridae) and their associates in N.Z. Cawthron Institute Monographs. No.2.

Murray, M.D. (1956) Observations on the biology of Calliphorids in New Zealand. *New Zealand Journal of Science and Technology,* **38**, 103-108.

Nabaglo, L. (1973) Participation of invertebrates in decomposition of rodent carcases in forest ecosystems. *Ekologia Polska,* **21**(18), 251-270.

Nicholson, A.J. (1934) The influence of temperature on sheep blowflies activity. *Bulletin of Entomological Research,* **25**, 85-99.

Nicholson, A.J. (1958) The self-adjustment of populations to change. *Population studies: Animal Ecology and Demography* (Ed. by K.B. Warren) *Cold Spring Harbor Symposium Quantitative Biology.* **22**, 153-173.

Norris, K.R. (1965) The bionomics of blowflies. Annual Review of Entomology, **10**, 47.

Nuorteva, P. (1970) Histerid beetles as predators of blowflies (Diptera, Calliphoridae) in Finland. *Annuals of the Zoological Fennici,* **7**, 195-198.

O'Flynn, M.A. (1983) The succession and rate of development of blowflies in carrion in Southern Queensland and the application of these data to forensic entomology. *Journal of the Australian Entomological Society,* **22**, 137-148.

O'Flynn, M.A. & Moorhouse, D.E. (1979) Species of *Chrysomya* as primary flies in carrion. *Journal of the Australian Entomological Society,* **18**, 31-32.

Owen, R.E. (1954) General survey of the soils of the North Island. *New Zealand. D.S.I.R. Soil Bureau,* Bulletin no.**33**. Government Printer, Wellington, New Zealand.

Payne, J.A. (1965) A summer carrion study of the baby pig *Sus scrofa. Ecology,* **46**(5), 592-602.

Putman, R.J. (1977) Dynamics of the blowfly *Calliphora erythrocephala*, within carrion. *Journal of Animal Ecology,* **46**, 853-866.

Putman, R.J. (1978) The role of carrion-frequenting arthropods in the decay process. *Journal of Ecological Entomology,* **3**, 133-139.

Reed, H.B. (1958) A study of dog carcass communities in Tennessee, with special reference to the insects. *The American Midland Naturalist,* **59**(1), 213-245.

Reznik, S.Y., Chernoguz, D.G & Zinovjeva, K.B. (1992) Host searching, oviposition preferences and optimal synchronization in *Alysia manducator* (Hymenoptera:Brachonidae), a parasitoid of the blowfly, *Calliphora vicina. Oikos,* **65**, 81-88.

SAS Institute Inc (1990) SAS/STAT User's Guide, Version 6, 4th Edition, volume **2** SAS Institute In, Cary, NC. USA.

Schoenly, K. & Reid, W. (1987) Dynamics of heterotrophic succession in carrion arthropod assemblages: discrete seres or a continuum of change? *Oecologia* **73**, 192-202.

So, P-M. & Dudgeon, D. (1990) Phenology and diversity of necrophagous diptera in a Hong Kong forest. *Journal of Tropical Ecology,* **6**, 91-101.

Taylor, L.R. (1974) Insect migration, flight periodicity and the boundary layer. *Journal of Animal Ecology,* **43**, 225-238.

Tullis, K. & Goff, L.M. (1987) Arthropod succession in exposed carrion in a tropical rainforest on O'ahu Island. Hawaii. *Journal of Medical Entomology,* **24**, 332-339.

Ullyett, G.C. (1950) Competition for food and allied phenomena in sheep-blowfly populations. *Phil. Transactions of the Royal Society London,* Ser.B. **234**, 77-174.

Vogt, W.G. (1988) Influence of weather on trap catches of *Chrysomya rufifacies* (Macquart)(Diptera:Calliphoridae). *Journal of Australian Entomology Society.* **n27**, 99-103.

Vogt, W.G. & Havenstine, D.E. (1974) A standardized bait trap for blowfly studies. *Journal Australian Entomology Society,* **13**, 249-253.

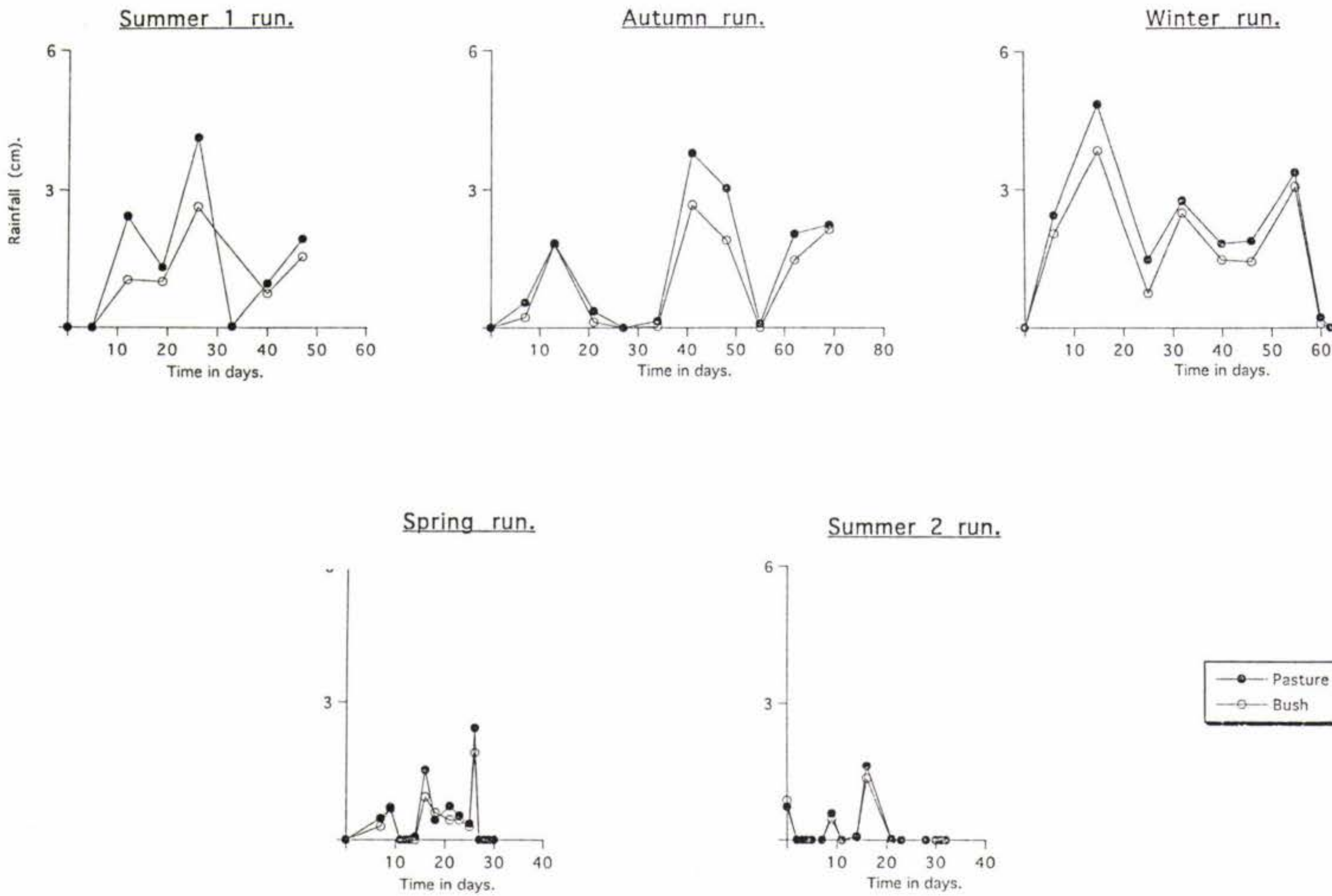
Vogt, W.G., Woodburn, T.L., Morton, R. & Ellem, B.A. (1985) The influence of weather and time of day on trap catches of males and females of *Lucilia cuprina* (Wiedemann) (Diptera:Calliphoridae). *Bulletin of Entomological Research,* **75**, 315-319.

Waterhouse, D.F. (1947) The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly *Lucilia cuprina.* C.S.I.R. Bulletin no.217.

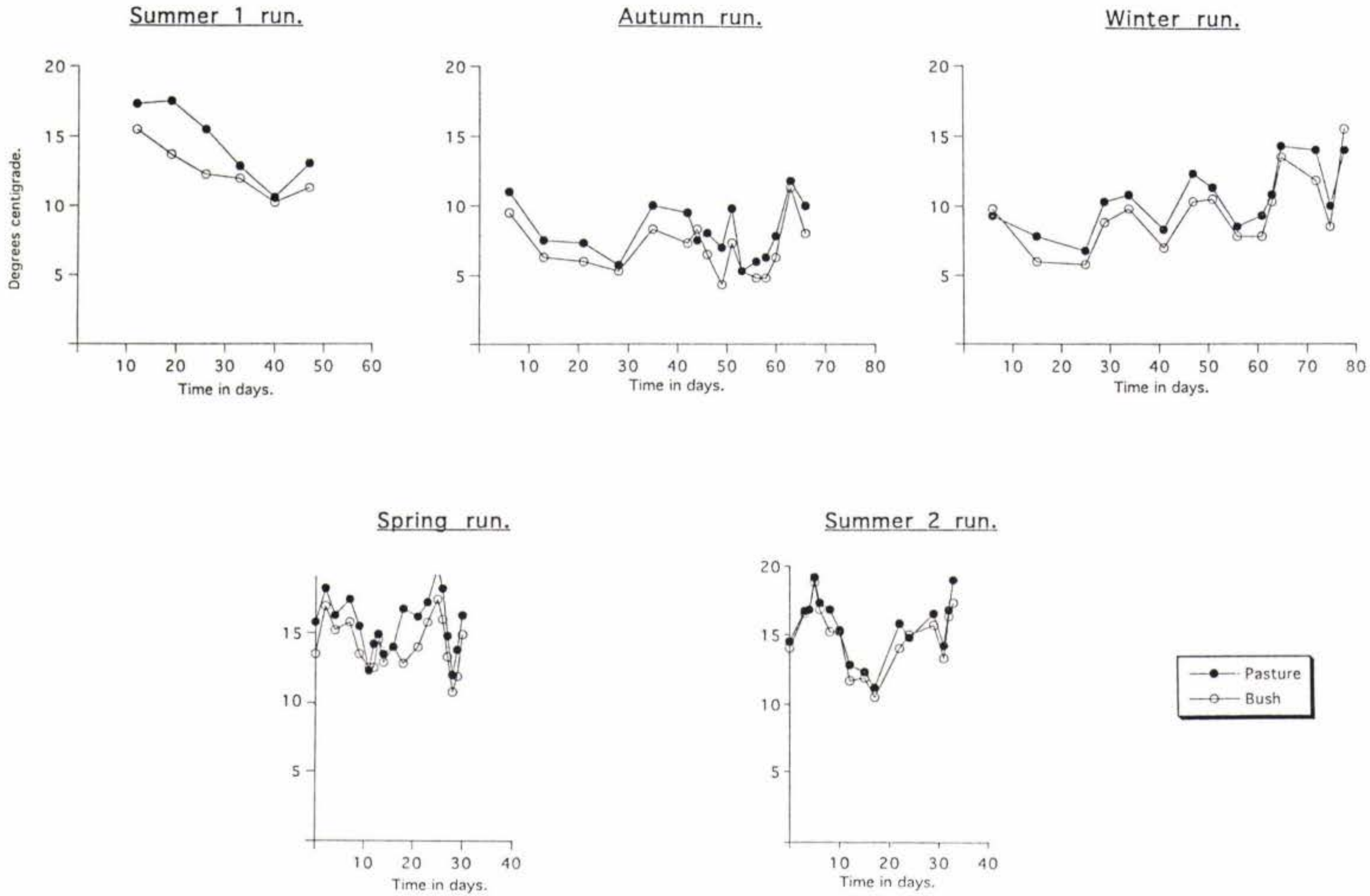
Williams, H. & Richardson, A.M.M. (1983) Life history responses to larval food shortages in four species of necrophagous flies (Diptera: Calliphoridae). *Australian Journal of Ecology,* **8**, 257-263.

Wratten, S.D., Bowie, M.H., Hickman, J.M. & Lovie, G.L. (1993) Movement and Phenology of hoverflies (Diptera: Syrphidae) in cultivated land. In prep.

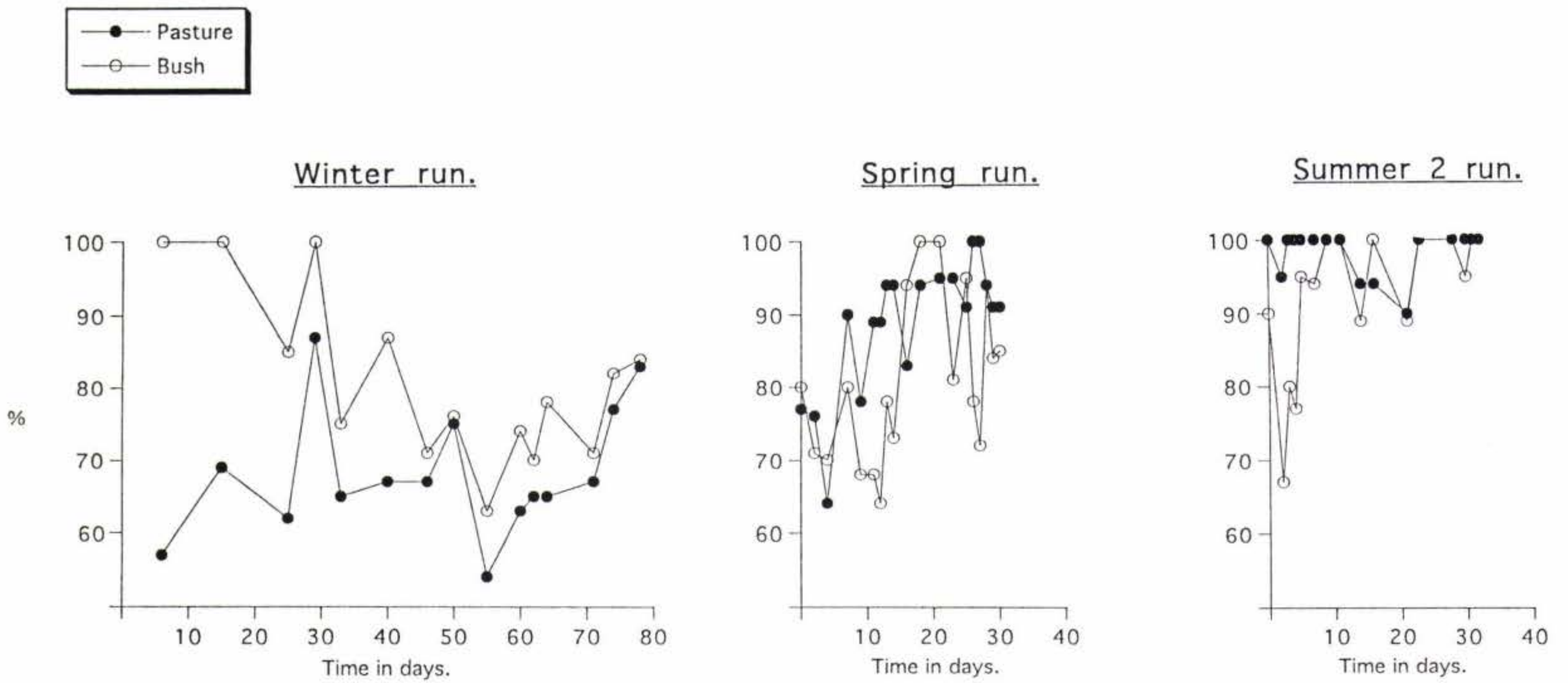
Zumpt, F. (1965) **Myiasis in man and animals in the old world.** Butterworths, London pp, 267.



1. **Rainfall recorded during the study period.**



2. Mean ambient temperature during the study period.



3. **Relative humidity for winter, spring and summer 2 runs.**

4. Light intensity (microeinsteins $\mu Em^{-2}s^{-1}$) at carcase sites.

Date.	Time.	Pasture.					Bush.				
Carcase sites.		1	2	3	4	5	6	7	8	9	10
21.8.92	10-12am	31700	28600	29000	28200	25000	846.0	329.0	412.0	1354.0	795.0
4.9.92	10-12am	662	664	630	590	508	13.9	5.8	23.3	29.3	9.4
21.10.92	10-11am	1200	1080	850	2000	2060	14.0	11.1	30.6	79.7	31.6
23.2.93	10-11am	906	820	845	982	794	6.9	4.2	12.9	17.0	36.9
25.2.93	11-12am	1500	1730	1790	1740	1610	5.2	3.3	6.5	20.6	9.5

5. Light intensity (microeinsteins $\mu Em^{-2}s^{-1}$) at flytraps.

Date.	Time.	Bush.			Pasture.		
Flytraps.		1	2	3	4	5	6
21.8.92	10-12am	617.0	780.0	5450.0	25900	16900	20000
4.9.92	10-11am	15.2	19.7	129.8	500	490	496
21.10.92	10-11am	20.9	22.0	220.0	1130	1150	850
23.2.93	10-11am	9.8	12.8	259.0	864	836	956
25.2.93	11-12am	5.7	10.9	128.0	1780	1590	1760

6. Wind readings (Km/hr) taken in bush and pasture.

Date	Bush (1.5m)	Pasture (1.5m)	Pasture (0.3m)
13.1.93	0.83	9.83	3.06
17.2.93	0.61	7.63	0.85
23.2.93	1.43	18.69	10.80
24.2.93	1.40	14.85	6.57

7. Number of flies trapped for each sample during each trapping run.

Species: 1= *C. vicina*; 2= *C. stygia*; 3= *C. hilli*; 4= *C. quadrimaculata*;
5= *L. sericata* (not used in ANOVA).

Habitat: 1= Pasture; 2= Bush.
Site: 1-3= Bush; 4-6= Pasture.

obs	run	sample	trap	site	sp.s	no.	habitat
1	1	2	5	5	1	1	1
2	1	2	5	5	2	1	1
3	1	2	2	2	1	1	2
4	1	3	5	5	1	7	1
5	1	3	5	5	2	4	1
6	1	3	5	5	3	1	1
7	1	3	1	1	3	1	2
8	1	3	3	3	1	1	2
9	1	4	5	5	1	3	1
10	1	4	2	2	3	1	2
11	1	5	5	5	1	8	1
12	1	5	5	5	2	1	1
13	1	5	5	5	3	2	1
14	1	6	5	5	1	1	1
15	2	1	5	5	4	1	1
16	2	2	5	5	2	1	1
17	2	3	5	5	1	1	1
18	2	3	5	5	2	2	1
19	2	4	5	5	1	3	1
20	2	4	5	5	2	4	1
21	2	5	5	5	1	3	1
22	2	5	5	5	4	3	1
23	2	5	5	5	5	1	1
24	2	5	2	2	1	3	2
25	2	5	2	2	2	1	2
26	2	5	2	2	3	1	2
27	2	5	2	2	4	2	2
28	2	6	5	5	1	3	1
29	2	6	5	5	4	1	1
30	2	6	2	2	1	2	2
31	2	6	2	2	2	6	2
32	2	6	2	2	3	3	2
33	2	6	2	2	4	4	2
34	2	6	3	3	3	1	2
35	2	7	4	4	1	2	1
36	2	7	5	5	1	1	1
37	2	7	5	5	4	2	1
38	2	7	2	2	1	9	2
39	2	7	2	2	2	1	2
40	2	7	2	2	3	1	2
41	2	7	2	2	4	1	2
42	2	8	4	4	2	7	1
43	2	8	4	4	3	2	1
44	2	8	4	4	4	1	1
45	2	8	5	5	1	5	1
46	2	8	5	5	2	2	1
47	2	8	5	5	3	9	1
48	2	8	5	5	4	5	1
49	2	8	1	1	3	1	2
50	2	8	2	2	1	24	2

obs	run	sample	trap	site	sp.s	no.	habitat
51	2	8	2	2	2	7	2
52	2	8	2	2	3	10	2
53	2	8	2	2	4	1	2
54	2	8	3	3	2	1	2
55	2	8	3	3	3	1	2
56	2	8	3	3	4	1	2
57	2	9	4	4	2	7	1
58	2	9	5	5	1	2	1
59	2	9	5	5	2	11	1
60	2	9	5	5	3	2	1
61	2	9	5	5	4	3	1
62	2	9	2	2	1	17	2
63	2	9	2	2	2	10	2
64	2	9	2	2	3	4	2
65	2	9	2	2	4	5	2
66	2	9	3	3	2	3	2
67	3	1	4	4	1	2	1
68	3	1	4	4	2	15	1
69	3	1	4	4	3	1	1
70	3	1	5	5	1	6	1
71	3	1	5	5	2	16	1
72	3	1	6	6	2	1	1
73	3	1	1	1	1	9	2
74	3	1	1	1	2	6	2
75	3	1	1	1	3	1	2
76	3	1	2	2	1	123	2
77	3	1	2	2	2	130	2
78	3	1	2	2	3	13	2
79	3	1	2	2	4	12	2
80	3	2	5	4	1	12	1
81	3	2	5	4	2	48	1
82	3	2	5	4	3	2	1
83	3	2	5	4	4	4	1
84	3	2	2	1	1	47	2
85	3	2	2	1	2	19	2
86	3	2	2	1	3	10	2
87	3	2	2	1	4	4	2
88	3	2	3	2	1	16	2
89	3	2	3	2	2	9	2
90	3	2	3	2	3	6	2
91	3	2	4	3	1	7	2
92	3	2	4	3	2	4	2
93	3	2	4	3	3	3	2
94	3	3	1	6	2	1	1
95	3	3	5	4	1	4	1
96	3	3	5	4	2	47	1
97	3	3	5	4	3	2	1
98	3	3	5	4	4	3	1
99	3	3	5	4	5	2	1
100	3	3	2	1	1	51	2
101	3	3	2	1	2	19	2
102	3	3	2	1	3	3	2
103	3	3	3	2	1	15	2
104	3	3	3	2	2	5	2
105	3	3	3	2	3	4	2
106	3	3	4	3	1	6	2
107	3	3	4	3	2	1	2
108	3	3	4	3	3	1	2
109	3	4	5	4	1	6	1
110	3	4	5	4	2	20	1
111	3	4	5	4	4	1	1
112	3	4	6	5	2	1	1
113	3	4	2	1	1	58	2
114	3	4	2	1	2	22	2
115	3	4	2	1	3	11	2
116	3	4	2	1	4	1	2
117	3	4	3	2	1	14	2
118	3	4	3	2	2	6	2
119	3	4	3	2	3	4	2
120	3	4	3	2	4	1	2
121	3	4	4	3	1	10	2
122	3	4	4	3	2	2	2
123	3	4	4	3	3	5	2

obs	run	sample	trap	site	sp.s	no.	habitat
124	3	5	6	4	2	4	1
125	3	5	3	1	1	5	2
126	3	5	3	1	2	1	2
127	3	5	4	2	1	10	2
128	3	5	4	2	2	2	2
129	3	5	5	3	1	5	2
130	3	5	5	3	3	1	2
131	3	5	5	3	4	1	2
132	3	6	1	5	1	8	1
133	3	6	1	5	2	16	1
134	3	6	1	5	3	2	1
135	3	6	2	6	1	39	1
136	3	6	2	6	2	40	1
137	3	6	2	6	4	1	1
138	3	6	6	4	2	15	1
139	3	6	3	1	1	20	2
140	3	6	3	1	2	6	2
141	3	6	3	1	3	9	2
142	3	6	3	1	4	4	2
143	3	6	4	2	1	29	2
144	3	6	4	2	2	14	2
145	3	6	4	2	3	14	2
146	3	6	5	3	1	10	2
147	3	6	5	3	2	9	2
148	3	6	5	3	3	4	2
149	3	6	5	3	4	1	2
150	3	7	1	4	1	2	1
151	3	7	1	4	2	7	1
152	3	7	2	5	1	12	1
153	3	7	2	5	2	1	1
154	3	7	2	5	3	1	1
155	3	7	2	5	4	1	1
156	3	7	3	6	2	1	1
157	3	7	4	1	1	10	2
158	3	7	4	1	2	3	2
159	3	7	4	1	3	6	2
160	3	7	5	2	1	5	2
161	3	7	5	2	3	2	2
162	3	7	6	3	1	10	2
163	3	7	6	3	2	16	2
164	3	7	6	3	3	3	2
165	3	8	1	4	1	2	1
166	3	8	1	4	2	9	1
167	3	8	1	4	4	1	1
168	3	8	2	5	1	10	1
169	3	8	2	5	2	11	1
170	3	8	2	5	3	1	1
171	3	8	3	6	1	1	1
172	3	8	3	6	2	8	1
173	3	8	4	1	1	6	2
174	3	8	4	1	2	16	2
175	3	8	4	1	3	13	2
176	3	8	4	1	4	1	2
177	3	8	5	2	1	40	2
178	3	8	5	2	2	7	2
179	3	8	5	2	3	27	2
180	3	8	5	2	4	1	2
181	3	8	6	3	1	3	2
182	3	8	6	3	3	3	2
183	3	9	1	4	1	1	1
184	3	9	1	4	2	31	1
185	3	9	1	4	3	2	1
186	3	9	1	4	4	3	1
187	3	9	2	5	1	6	1
188	3	9	2	5	2	5	1
189	3	9	3	6	1	2	1
190	3	9	3	6	2	1	1
191	3	9	3	6	5	1	1
192	3	9	4	1	1	12	2
193	3	9	4	1	2	24	2
194	3	9	4	1	3	11	2
195	3	9	4	1	4	10	2
196	3	9	5	2	1	22	2

obs	run	sample	trap	site	sp.s	no.	habitat
197	3	9	5	2	2	2	2
198	3	9	5	2	3	8	2
199	3	9	5	2	4	1	2
200	3	9	6	3	1	4	2
201	3	9	6	3	2	10	2
202	3	9	6	3	3	7	2
203	3	9	6	3	4	2	2
204	3	10	2	4	1	3	1
205	3	10	2	4	2	23	1
206	3	10	2	4	4	2	1
207	3	10	2	4	5	1	1
208	3	10	3	5	1	1	1
209	3	10	3	5	2	3	1
210	3	10	4	6	2	13	1
211	3	10	4	6	3	1	1
212	3	10	4	6	4	1	1
213	3	10	4	6	5	2	1
214	3	10	1	3	1	5	2
215	3	10	1	3	2	7	2
216	3	10	1	3	3	1	2
217	3	10	1	3	4	2	2
218	3	10	5	1	1	9	2
219	3	10	5	1	2	4	2
220	3	10	5	1	3	4	2
221	3	10	6	2	1	9	2
222	3	10	6	2	2	17	2
223	3	10	6	2	3	10	2
224	3	10	6	2	4	1	2
225	3	11	2	4	1	6	1
226	3	11	2	4	2	30	1
227	3	11	2	4	4	1	1
228	3	11	2	4	5	1	1
229	3	11	3	5	1	7	1
230	3	11	3	5	2	17	1
231	3	11	3	5	3	1	1
232	3	11	3	5	5	2	1
233	3	11	4	6	2	8	1
234	3	11	1	3	1	20	2
235	3	11	1	3	2	97	2
236	3	11	1	3	3	8	2
237	3	11	1	3	4	5	2
238	3	11	5	1	1	16	2
239	3	11	5	1	2	15	2
240	3	11	5	1	3	36	2
241	3	11	5	1	4	15	2
242	3	11	6	2	1	21	2
243	3	11	6	2	2	69	2
244	3	11	6	2	3	20	2
245	3	11	6	2	4	3	2
246	4	1	5	1	2	2	2
247	4	1	5	1	3	3	2
248	4	2	2	4	2	2	1
249	4	2	3	5	2	1	1
250	4	2	1	3	3	1	2
251	4	2	5	1	1	1	2
252	4	2	5	1	2	6	2
253	4	2	5	1	3	15	2
254	4	2	6	2	1	2	2
255	4	2	6	2	2	12	2
256	4	2	6	2	3	8	2
257	4	2	6	2	4	1	2
258	4	3	5	6	3	1	1
259	4	3	5	6	4	1	1
260	4	3	1	2	1	8	2
261	4	3	1	2	2	6	2
262	4	3	1	2	3	5	2
263	4	3	1	2	4	2	2
264	4	3	2	3	3	2	2
265	4	3	6	1	1	1	2
266	4	3	6	1	2	2	2
267	4	3	6	1	3	10	2
268	4	4	1	2	1	2	2
269	4	4	1	2	2	11	2

obs	run	sample	trap	site	sp.s	no.	habitat
270	4	4	1	2	3	9	2
271	4	4	1	2	4	2	2
272	4	4	2	3	1	1	2
273	4	4	2	3	2	6	2
274	4	4	2	3	3	4	2
275	4	4	6	1	2	1	2
276	4	4	6	1	3	5	2
277	4	5	1	2	2	1	2
278	4	5	1	2	3	7	2
279	4	5	1	2	4	3	2
280	4	5	2	3	1	7	2
281	4	5	2	3	2	7	2
282	4	5	2	3	3	18	2
283	4	5	6	1	1	1	2
284	4	5	6	1	2	2	2
285	4	5	6	1	3	8	2
286	4	6	1	1	3	6	2
287	4	6	2	2	1	1	2
288	4	6	2	2	2	2	2
289	4	6	2	2	3	10	2
290	4	7	5	5	2	1	1
291	4	7	1	1	2	3	2
292	4	7	1	1	3	20	2
293	4	7	2	2	1	6	2
294	4	7	2	2	2	46	2
295	4	7	2	2	3	33	2
296	4	7	2	2	4	21	2
297	4	7	3	3	1	2	2
298	4	7	3	3	2	2	2
299	4	7	3	3	3	5	2
300	4	8	5	5	5	1	1
301	4	8	6	6	2	2	1
302	4	8	6	6	5	2	1
303	4	8	1	1	2	5	2
304	4	8	1	1	3	15	2
305	4	8	2	2	1	9	2
306	4	8	2	2	2	40	2
307	4	8	2	2	3	76	2
308	4	8	2	2	4	4	2
309	4	8	3	3	3	2	2
310	4	9	5	5	3	1	1
311	4	9	1	1	2	5	2
312	4	9	1	1	3	24	2
313	4	9	2	2	1	14	2
314	4	9	2	2	2	78	2
315	4	9	2	2	3	129	2
316	4	9	2	2	4	3	2
317	4	9	3	3	1	3	2
318	4	9	3	3	2	1	2
319	4	9	3	3	3	9	2
320	4	10	1	6	3	4	1
321	4	10	1	6	5	3	1
322	4	10	2	1	1	8	2
323	4	10	2	1	2	12	2
324	4	10	2	1	3	43	2
325	4	10	2	1	4	1	2
326	4	10	3	2	1	5	2
327	4	10	3	2	3	13	2
328	4	11	1	6	3	1	1
329	4	11	5	4	5	1	1
330	4	11	6	5	5	3	1
331	4	11	2	1	1	13	2
332	4	11	2	1	2	44	2
333	4	11	2	1	3	75	2
334	4	11	3	2	1	1	2
335	4	11	3	2	3	20	2

8. The estimated total number of maggots produced by each possum carcase during each seasonal run.

Summer 1 run= 1; Autumn run= 2; Winter run= 3; Spring run= 4; Summer 2 run= 5.

Run.	Carcase.	Total.	Run.	Carcase.	Total.
1	1	9512	4	1	12096
1	2	4512	4	2	11256
1	3	13858	4	3	17688
1	4	6536	4	4	15183
1	5	9376	4	5	21039
1	6	8664	4	6	28928
1	7	12536	4	7	18816
1	8	17752	4	8	19600
1	9	17003	4	9	15176
1	10	19280	4	10	20688
2	1	11976	5	1	4664
2	2	13152	5	2	9984
2	3	8224	5	3	9752
2	4	9736	5	4	11534
2	5	9064	5	5	7212
2	7	8528	5	6	16608
2	8	7520	5	7	9308
2	9	5376	5	8	23468
2	10	5824	5	9	16026
3	1	3960	5	10	12234
3	2	5368			
3	3	5240			
3	4	4120			
3	5	6796			
3	6	520			
3	7	8			
3	8	608			
3	9	343			
3	10	316			

9. The estimated average total number of maggots that left possum carcases in bush and pasture for each seasonal run.

Seasonal run.	Pasture	± SE.	Bush	± SE.
Summer 1	8758.8	1579.9	15047.0	1950.8
Autumn	10430.4	922.3	6812.0	735.1
Winter	5096.8	511.3	359.0	103.3
Spring	15452.4	1804.9	20641.6	2268.9
Summer 2	8629.2	1209.7	15528.8	2387.4