PESTICIDES AND NATURAL ENEMIES

(PARTICULARLY GROUND BEETLES)

OF APHIDS ON POTATO

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PhD

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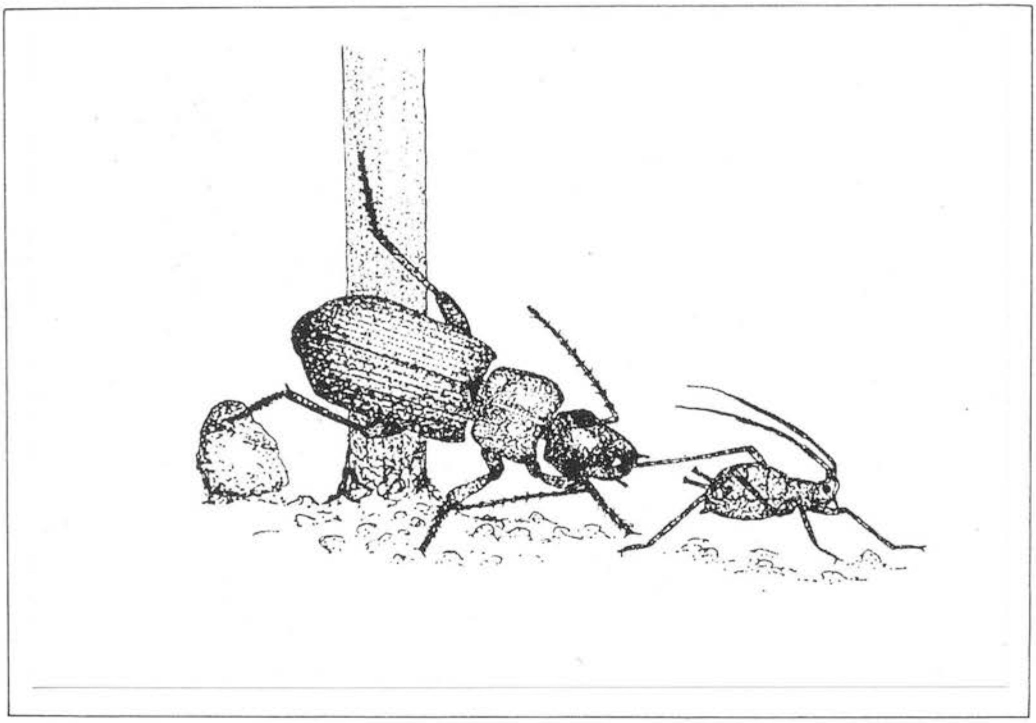
For

Mom, Dad and Bob



Declaration

I declare that this thesis has been composed by me and is a record of my own work.

ABSTRACT

The arthropod fauna of fields of ware potatoes in eastern Scotland was assessed to determine the species composition and relative abundance of the natural enemies of aphids on potato. Aphids and aphid-specific predators and parasitoids were surveyed by visual searches of foliage; epigeal arthropods were assessed by pitfall trapping.

Aphid-specific natural enemies were generally uncommon but may have been underestimated. Approximately 11,000 animals were caught in pitfall traps and most were of the ground beetle genus Pterostichus (Coleoptera : Carabidae). Gut dissections showed that 14.4 and 30.5 per cent of Pterostichus melanarius and Pterostichus madidus respectively, contained aphid remnants. In the laboratory, demeton-S-methyl applied directly to these beetles had little apparent effect but 19.1 per cent died after consumption of treated aphids. Field experiments indicated that demeton-S-methyl influenced the trap catch of Pterostichus spp by altering their predatory activity. Caution should thus be exercised when interpreting such data.

It is suggested that certain species of Carabidae may be important in the control of aphids on potato. Their potential is discussed and suggestions given for further research.

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LIST OF ABBREVIATIONS

cv	cultivar (cultivated variety)
ha	hectare
N	north
S	south
E	east
W	west
UK	United Kingdom
kph	kilometres per hour
kPa	kilo Pascals
pers comm	personal communication
spp	species
°	degrees
°C	degrees Cent igrade
VTSC	virus-tested stem cuttings
n	number
ie	example
eg	example
c	approximately
ANOVA	analysis of variance
F	variance ratio
p	probability
df	degrees of freedom
X^2	Chi-square
♀ (♀)	female(s)
♂ (♂)	male(s)
>	greater than
<	less than
mm	millimetre
cm	centimetre
m	metre
m^2	metre-squared
km	kilometre
t	tonne
mg	milligram
kg	kilogram
ul	microlitre
ml	millilitre
l	litre
T	treatment

CHAPTER 1

GENERAL INTRODUCTION

1-1 INTRODUCTION : POTATOES

1-1-1 HISTORICAL ASPECTS

The potato of commerce belongs to a single species, Solanum tuberosum L, of the family Solanaceae; 7 other cultivated and 150 wild species are recognized (Harris, 1978). The potato originated in antiquity in the Peru-Bolivian region of South America (Hawkes, 1978). It appeared in Europe during the last part of the sixteenth century but in Great Britain was simply a botanical curiosity for nearly 200 years (Harris, 1978). Potato was first grown as a field crop in Scotland in the eighteenth century (Todd, 1961).

1-1-2 CURRENT PRODUCTION

Worldwide, potato ranks fourth in terms of production, following wheat, rice and maize (Anon, 1984b). Total production in 1984 was estimated at 312,209,000 tonnes, of which the USSR was the largest single contributor (Anon, 1984b).

The potato industry is very important to Great Britain. In 1983, the total value of the crop was approximately £600,000,000 (Anon, 1984a). Tables 1 and 2 present some statistics on potato production in Great Britain and Scotland over the period of the current study.

1-1-3 PESTS AND INSECTICIDES

Potatoes are attacked by a variety of pests and disease (Eddowes, 1976), of which aphids are among the most damaging. Granular and foliar insecticides may be applied to potatoes for aphid control (Anon, 1983; McKinlay and Franklin, 1984) and since the mid-1970s the use of insecticides on potato has increased (Anon, 1975-6; Aveyard, 1981). In 1984, nearly half the British potato crop was treated with insecticides (Anon, 1985-6).

Table 1

Potato production in Great Britain 1983-1985

statistic \ year	1983	1984	1985
area planted ('000 ha)	183	185	179
average yield (t/ha)	30.3	37.8	36.9
production ('000 t)	5525	6985	6596

(Anon, 1986a)

Table 2

Potato production in Scotland 1983-1985

statistic \ year		1983	1984	1985
area planted ('000 ha)	seed	20	21	20
	ware	14	14	13
production ('000 t)		999	1305	1167

(Anon, 1985; Anon, 1986b)

This increase in insecticide use and the prevalence of insurance spraying has contributed to the development of resistance in aphid populations (Anon, 1983; Furk et al, 1983). Over half the world's pests show tolerance to at least one major group of insecticides (van Emden, 1980), and the cost of developing new pesticides has risen dramatically in the last decade (Kinoshita, 1985). These problems of resistance and cost of development, together with increasing public interest in health and the environment, has meant that total reliance on insecticides for crop protection is not feasible (McEwen, 1985). It is essential that alternative methods of controlling insects are found which are both effective and acceptable to the public. One such method is "biological control", the use of natural enemies either exotic (classical biological control) or resident (manipulative biological control) to aid regulation of pest populations.

1-1-4 TYPES OF NATURAL ENEMIES

Natural enemies of aphids may conveniently be divided into 2 main groups. Those which feed exclusively, or nearly so, on aphids are variously termed specific, aphidophagous or obligatory. Natural enemies which are opportunistic feeders, with aphids comprising only a part of their diet, are generalist, polyphagous or facultative. The latter are also called epigeal because many live primarily on or in the soil. The terms specific or aphidophagous, and epigeal or generalist are used in this thesis. It is recognized that some "specific" predators will take prey other than aphids and some "epigeal" species may climb plants or have the capacity for flight.

1-1-5 NATURAL ENEMIES OF APHIDS ON POTATO

Many arthropods and fungi attack aphids (Figure 1). Specific natural enemies include fungi, parasitoids, hoverfly larvae and adult and larval ladybirds and lacewings (Rotheray, 1986). Polyphagous predators include ground and rove beetles, earwigs, harvestmen, spiders and ants (Rotheray, 1986). Knowledge of the ecology of aphidophagous insects, their response to pesticides and the subsequent response of aphid populations is indispensable if natural enemies are to be used to the best advantage in aphid control. The specific natural enemy complex of aphids on potato has been rather well studied (eg Dunn, 1949; Shands et al, 1965, 1972, 1975; Agyen-Sampong, 1972; Foster, 1972).

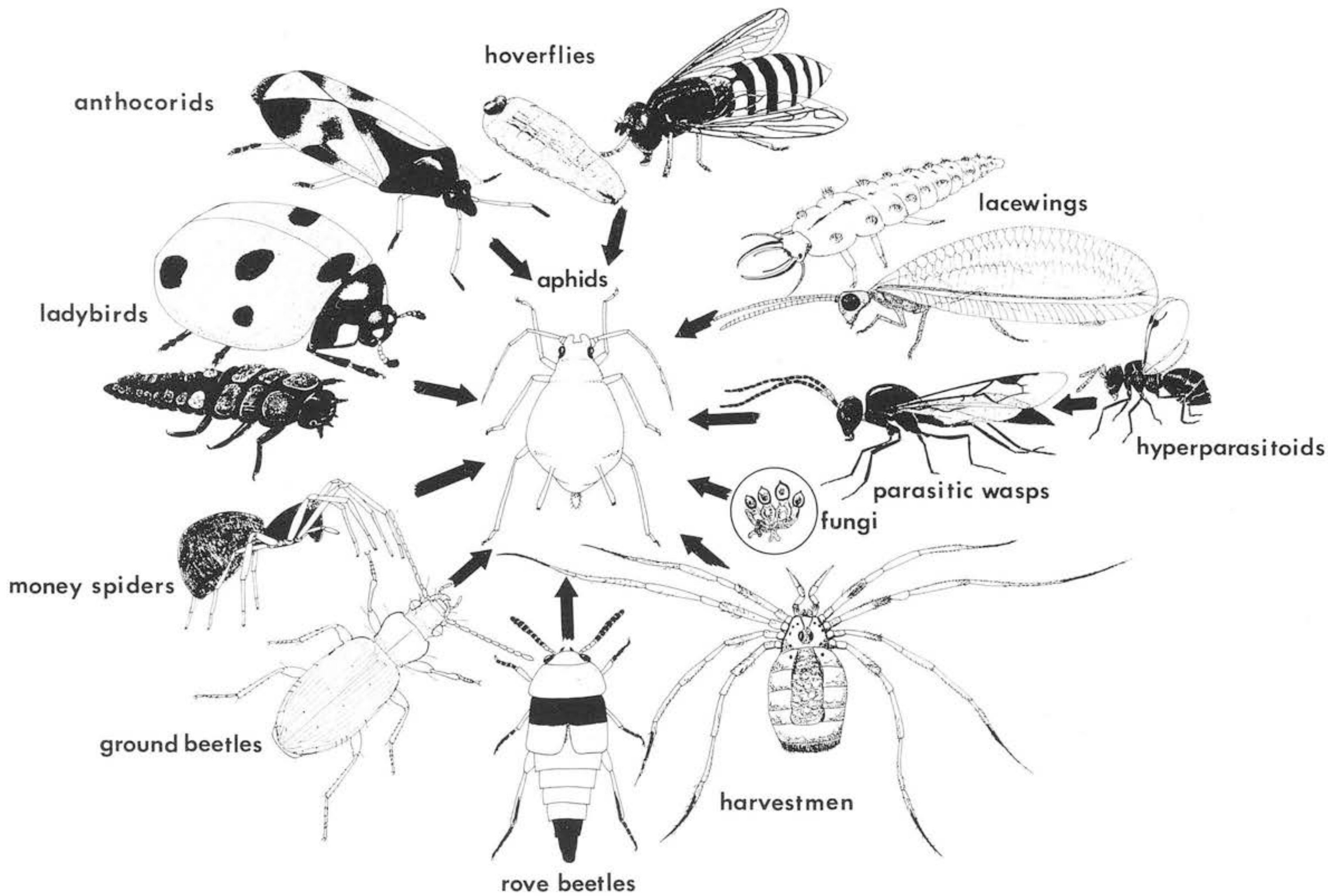


Figure 1: Natural enemies of aphids (after Foster, 1976).

Epigeal predators have received less attention, and the few studies incorporating them have been mainly descriptive. For Scotland not even descriptive data exist.

1-1-6 AIMS OF PRESENT STUDY

The present study was undertaken to obtain data particularly on epigeal predators of aphids on potato and its aims were:

(a) to determine the species composition and relative abundance of the natural enemies of aphids on potato, with particular emphasis on polyphagous predators;

(b) to manipulate the natural enemy fauna in the field by applying combinations of pesticides which suppress different components of the fauna, and thus subject aphid populations to predation by either polyphagous or aphid-specific natural enemies alone or by both together;

(c) through (b), to determine whether suppression of polyphagous predators results in increased aphid numbers;

(d) to assess, in the field, the effects of the insecticide most commonly used in potatoes on aphids, aphid-specific natural enemies and polyphagous predators;

(e) to assess, in the laboratory, the effects of this insecticide on the most abundant polyphagous predators and

(f) to assess, if possible, the degree of aphid predation by the most abundant polyphagous predators.

1-2 MATERIALS AND METHODS

1-2-1 SITE DESCRIPTIONS

Experiments were done in the spring and summer of 1983, 1984 and 1985 in sections of fields of maincrop potatoes, cv Maris Piper, on commercial farms near Edinburgh. Background information on each field is given in Table 3. Although herbicides and fungicides were applied routinely, no insecticides were used except as experimental treatments.

The 1983 trial site covered approximately 1.3 ha of a field bordered by an alder hedge (Alnus spp), a grass strip and a hayfield (Figure 2). Ridges ran N-S. In 1984 and 1985, each trial site covered 2 ha. The Sheriffhall (1984) field was bordered on 3 sides by a hawthorn hedge (Crataegus spp), and was beside a mixed deciduous wood (Figure 3a). Ridges ran NE-SW. A hawthorn hedge bordered 2 sides of the Turnhouse (1985) site; early potatoes (cv Wilja) and spring barley the other 2 (Figure 3b). Ridges ran NE-SW.

1-2-2 EXPERIMENTAL DESIGN AND INSECTICIDE APPLICATION

Three components of the potato aphid-natural enemy system were manipulated in 1983: aphids, epigeal predators and aerial predators. An experiment was done using the systemic organophosphate insecticide thiometon (Ekatin^R, Sandoz Products Ltd), to remove aerial predators. Thiometon was chosen on the advice of Dr G Foster (1983, pers comm), who in 1976 found that, although ineffective against many aphids, the material was toxic to other insects. Thus in theory aphids would survive, the specific natural enemies would be killed and the epigeal predators would perhaps survive due to poor insecticide penetration of the potato canopy. Information on the effects of ground predators alone on aphid numbers could then be obtained.

To remove the epigeal fauna, pellets of methiocarb (Draza^R, Bayer UK Ltd), a carbamate pesticide with contact action were used, although whether these would be eaten was speculative. Some plots received both thiometon and methiocarb- to permit study of aphid population changes in the "absence" of natural enemies. Demeton-S-methyl (Metasystox 55^R, Bayer UK Ltd), a systemic organophosphate with some contact action, was tested as it is currently the insecticide most commonly used on commercial seed potatoes in Scotland (Table 4; McKinlay and Kerr, 1985).

A randomized design with 4 replicates of each treatment was used in all 3 years except during the first 2 weeks of sampling in 1984 (see below).

Table 3

Details of potato fields used for field experiments

Year / Category	1983	1984	1985
Farm	Crookston	Sheriffhall Mains	Turnhouse
Grid Reference	NT 365714	NT 323686	NT 164749
Height above sea level (m)	36	59	46
Total field size (ha)	18	8	22
Soil type	Sandy loam	Sandy loam	Sandy loam
Soil pH (average)	6.4	6.1	5.9
Field History	barley (1982) barley (1981) barley (1980)	barley (1983) barley (1982) hay (1981)	barley (1984) barley (1983) wheat (1982)
Planting Details:			
Date	13-23 April	25 April - 4 May	27-29 April
Drill width (cm)	76	76	86
Intertuber spacing (cm)	30	25	25
Crop History:			
Herbicide	25 May - 1 June: (Gramoxone^R -100 at 3l/ha a.i. in 2001 water)	8/9 June: (Gramonol^R (linuron) at 5l/ha a.i. in 2001 water)	30 May: (Gramoxone and Bronox (linuron))
Ridging	20 June	2/3 July	30 May
Fungicide	4-13, 25-28 July; 16, 25-30 August: (Fubol^R 58 at 1.5 kg/ha a.i. in 2001 water)	NONE	17, 31 July; 10 August: (Dithane at 1.7 kg a.i. in 2001 water) 19 August: (Brestan 60 (mancozeb) at 0.5 kg a.i. in 2001 water)
Harvest	10-28 October	7 October - 15 November	1-10 October

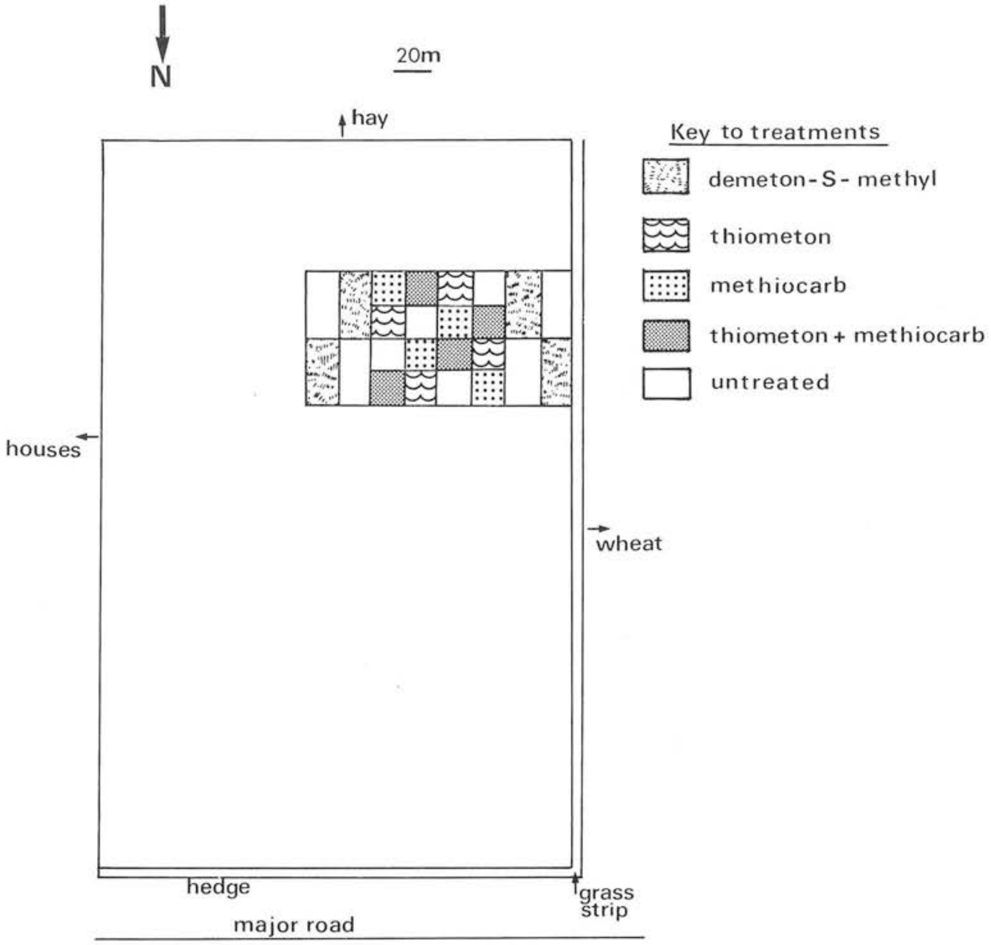


Figure 2: Layout of trial site in 1983. See text for details of plot treatments.

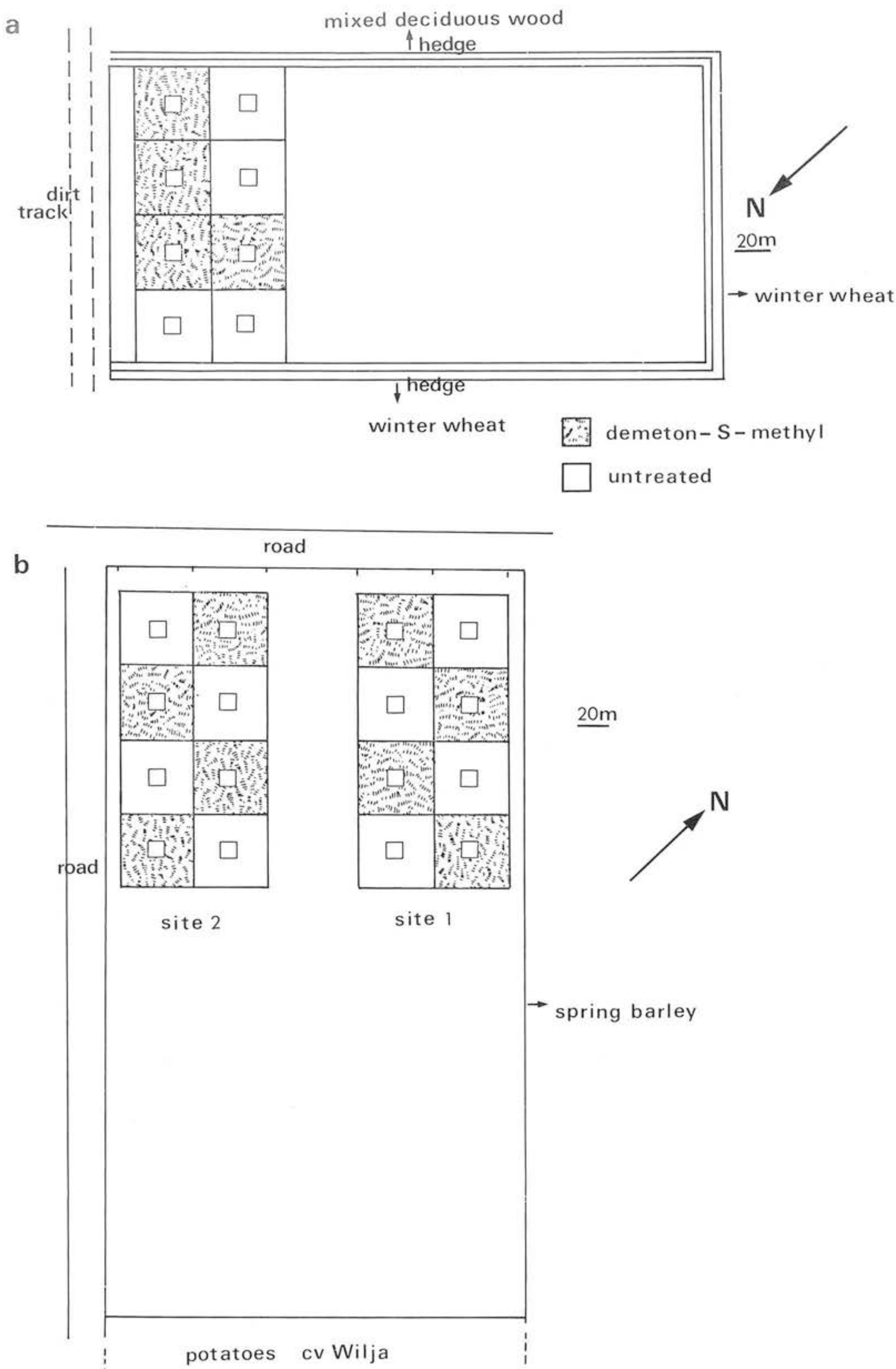


Figure 3: Layout of trial sites in 1984 (a) and 1985 (b). See text for details.

Table 4

Insecticides commonly used in Scotland for control of aphids on potato
(After McKinlay and Kerr, 1985)

Aphicidal sprays used in Scotland
(1977 - 1981)

Insecticide	% growers using
demeton-S-methyl	42
pirimicarb	16
dimethoate	11
oxydemeton-methyl	11
thiometon	9

Originally the 1983 trial was to be observational only but due to forecasts for early and heavy aphid migrations to potato fields, the trial was replicated.

The 1983 "manipulative" trial was done on 16 20 m x 20 m plots, 4 of which were untreated, arranged in a square (Figure 2). The demeton-S-methyl experiment was considered to be separate from the manipulative trial and was arranged such that assessment of edge effects was possible: 4 20 m x 40 m plots adjoined the small-plot area at east and west sides. Demeton-S-methyl plots were larger than the others. It was thought desirable to have the outlines of the trials contiguous but sampling of 8 replicates of demeton-S-methyl treatments was considered too time-consuming. Larger plots were therefore used in the demeton-S-methyl trial.

Methiocarb pellets were shaken from bait tins on to soil underneath plants in ridges and on soil in furrows, at 36 pellets/m^2 (equivalent to 5.5 kg/ha). Thiometon was applied at 1104 ml/ha in 333 l water, demeton-S-methyl at 420 ml/ha in 200 l water. Thiometon and demeton-S-methyl were applied using ICI mark-3 handpumped back-pack sprayers of 18 or 22 l capacity, with single cone-jet nozzles of 1 mm aperture. In 1983 all treatments were applied on 21 July.

In 1984 the experimental area was divided into 10 40 m x 40 m plots, on 13 May. This plot size was originally considered adequate as the most numerous ground beetle in 1983 was known to travel a mean of 3 m in oats and maize over 24 hours (Rivard, 1966). Subsequent to 13 May, it was learned that recent work indicated an average dispersal of 10 m and a maximum measurable in the experiment of 41 m in 24 hours in winter wheat (J Cory, pers comm). On 29 May therefore, the plot size was increased to 50 m x 50 m and the number of plots reduced to 8 (Figure 3a). A similar layout was used in 1985 (Figure 3b). In a treated plot, the entire 50 m x 50 m area was sprayed. Arthropods were sampled in 6 m x 6 m centrally-positioned subplots within these larger areas. There were 4 replicates each of demeton-S-methyl treated, and untreated plots in 1984 and 1985. Replicates were assigned randomly (blocked in 1985 only); application rate was 420 ml/ha in 200 l water.

In 1984 an Allmet sprayer moving at 6.4 kph applied the insecticide. The

12 m boom carried 24 hydraulic, flat-fan drop nozzles each with a spray angle of 110°. The boom was carried at approximately 0.5 m above the crop canopy. Plots were treated on 12 July and 7 August in 1984 with a pump pressure of 241.3 kPa. A Technoma sprayer moving at 4.8 kph was used in 1985. Twenty-four hydraulic Technoma yellow fan-jet nozzles applied pesticide at a spray angle of 110° and a pump pressure of 344.7 kPa. The 12 m boom was carried about 0.5 m above the crop canopy. There were 2 sites in the same field in 1985; one was sprayed on 25 July (site 1), the other on 14 August (site 2) (Figure 3b). One field was used for both sites due to a scarcity of aphids in other potential trial areas. Wind speeds on each spray date are given in Appendix 2.

1-3 LAYOUT OF THESIS

Each chapter or section within a chapter contains its own literature review, results and discussion. Chapter 2 refers to the aphids present on potato and Chapter 3 to specific natural enemies. Chapter 4 gives results of field trapping for epigeal predators. Chapters 5 and 6 describe various laboratory and field experiments using polyphagous predators. Chapter 7 is a general discussion and includes suggestions for future research.

Nomenclature follows Kloet and Hincks (1977) and authors of generic and specific names are given in the faunal list in Appendix 1 only. Where publications used names of animals which are not currently recognized, current names only are given. Specimens of some insect species collected are deposited in the Royal Museum of Scotland, Chambers Street, Edinburgh (see Appendix 1).

CHAPTER 2

APHIDS

2-1 INTRODUCTION

The Aphididae is one of the largest and most successful of all insect families (Harries, 1966), with over 4000 species worldwide (Mackauer and Way, 1976). Damage to plants by aphids is of 3 kinds: (a) direct tissue injury due to sap removal or injection of saliva, (b) transmission of viruses (Jones and Jones, 1984) and (c) moulds growing on honeydew may reduce aesthetic quality and decrease the area of leaf available for photosynthesis (Beirne, 1972).

2-1-1 LIFE-CYCLES

The following generalized account is largely after Dixon (1973), Blackman (1974) and Jones and Jones (1984).

Aphids may reproduce parthenogenetically throughout the year (anholocycly) or incorporate a sexual phase (holocycly). In the holocyclic life-cycle, aphids pass the unfavourable season as diapausing eggs, usually on perennial woody hosts. In temperate climates egg hatch in spring produces wingless females, the "fundatrices". After a number of generations on the woody host, alatae are produced which migrate to the annual, herbaceous secondary hosts.

Aphids moving from overwintering to summer hosts can migrate up to 1300 km but are weak fliers and are likely to be carried passively by air currents. After settling on a suitable host an alata will usually feed and deposit nymphs prior to a series of short flights from plant to plant, nymphs being produced on each.

The wingless females which develop from these nymphs are the familiar summer forms, and several generations may develop on summer hosts. If conditions become unfavourable, winged females are produced which may fly to new plants. In autumn, environmental factors such as lengthening dark period (Lees, 1966), and low temperatures induce the production of sexual forms. Alate female aphids (gynoparae) fly to overwintering hosts and parthenogenetically produce wingless female "oviparae". Synchronous with the appearance of oviparae, alate males are produced on secondary hosts, and these fly to primary hosts. Males and oviparae mate and eggs are laid.

In the anholocyclic life-cycle parthenogenesis is continuous throughout the year. Species which overwinter holocyclically in cold areas may also reproduce anholocyclically in sheltered environments such as glasshouses (Beirne, 1972).

Parthenogenetic reproduction enables aphids to expend with mate-searching. More significantly, embryos can begin development before birth; a female may contain developing young which carry partially developed embryos. Viviparity, the avoidance of an egg stage, and parthenogenesis effectively shorten generation time and provide aphids in summer with the means of enormous rates of multiplication (Harries, 1966).

2-1-2 APHIDS ON POTATO

Four species of aphid commonly infest potatoes in Scotland: Macrosiphum euphorbiae, Myzus persicae, Aphis nasturtii and Aulacorthum solani. Rhopalosiphonius latysiphon, which occasionally infests stolons, Myzus ascalonicus and Myzus ornatus also occur (Anon, 1983).

(a) Macrosiphum euphorbiae

The "potato aphid" is cosmopolitan and polyphagous and is usually more numerous in Scotland than other species. It occurs mainly on upper leaves (Bradley, 1952; Gordon and McEwen, 1984) and unlike other aphids on potato tends to multiply on flowers and at shoot tips (Aveyard, 1981). M euphorbiae overwinters holocyclically on rose (DeLong, 1952; Shaw, 1976) but is largely anholocyclic in Scotland, overwintering successfully outside on weeds (Turl, 1983) and strawberries and in glasshouses on lettuce and flowers (Fisken, 1959a).

(b) Myzus persicae

The "peach-potato aphid" is a widespread and polyphagous species (Sylvester, 1954), and is a known vector of over 100 virus diseases of plants

(Jones and Jones, 1984). M persicae is able to overwinter outside in Scotland on brassicas (Fisken, 1959a), and weeds, particularly Urtica urens (Turl, 1983); in glasshouses on lettuce and flowering plants (Fisken, 1959a); and on potatoes in storage (R McKinlay, pers comm). Hundreds of summer host plants have been recorded for this species, many of them agricultural crops (Taylor, 1908; Essig, 1938; Beirne, 1972; Anon, 1983). On potatoes it occurs mainly on lower leaves (Bradley, 1952; Drübbisch, 1985). For a review of this aphid see van Emden et al (1969).

(c) Aphis nasturtii

The "buckthorn-potato aphid" overwinters as eggs on buckthorn and migrates to potatoes in late June. Numbers can be large but vary considerably from year to year (Anon, 1983). An aggregative species, A nasturtii is a vector of potato virus diseases but is considered unimportant (Jones and Jones, 1984).

(d) Aulacorthum solani

The "glasshouse-potato aphid" is more common in northern areas than elsewhere in Scotland and, although rarely numerous, dense colonies occasionally cause leaf distortion of apical shoots of potatoes (Shaw, 1976). It occurs on a wide variety of hosts in glasshouses (Fisken, 1959a) and can pass the winter on chitting potatoes (Anon, 1983).

2-1-3 DAMAGE CAUSED BY APHIDS

Aphids on potato are most serious as virus vectors but M euphorbiae can cause false toproll if present in sufficient numbers (Sparrow, 1976; Anon, 1983). Potato virus Y (PVY) and potato leafroll virus (PLRV) are the most damaging viral diseases of potato in Scotland (Anon, 1983). PLRV is circulative, PVY stylet-borne (Anon, 1983).

M persicae, M euphorbiae and A solani have been recorded as vectors of both diseases (Howell, 1974; Sparrow, 1976). M persicae is, however, considered the principal vector (Shaw, 1976); although rarely numerous (Dixon, 1973), it is more restless and active than the other species (Woodford, 1976). In Scotland most spread of virus is probably from infective sources within the potato crop (Sparrow, 1976).

A large proportion of the potatoes grown in Scotland are destined for seed. This is because in Scotland aphid-borne virus is not usually a serious problem: few aphids survive the cold winters, those that do are less active (Anon, 1983) and migration from overwintering hosts occurs relatively late (Fisken, 1959b). Infector plants usually express disease symptoms before aphid migration (Turl, 1983) and are rogued. Where aphid numbers and activity are high, ware crops are mostly grown.

2-1-4 CONTROL OF APHID-TRANSMITTED VIRUSES

The primary method of control is the use of basic and classified seed for the production of seed and ware crops respectively. The seed potato classification scheme established by the Board of Agriculture for Scotland in 1918 was originally concerned with management of potato wart diseases (Todd, 1961). In 1932, health gradings were introduced to effect control of potato virus diseases and the initial tolerance level of 5 per cent has been progressively lowered since then (Howell, 1973).

In the mid-1970s in Scotland there was a substantial increase in the proportion of the potato crops rejected due to PLRV (Aveyard, 1981). A series of mild winters allowed greater aphid survival and an earlier migration to crops than usual; sufficiently early that virus symptoms had not been expressed and potatoes had not been rogued (Sparrow, 1976). Additional aphid control was required and by 1975 insecticides were recommended for use on seed crops in most areas (Aveyard, 1981). Insecticide use on ware crops increased also: in 1973 only 2 per cent of ware potatoes were treated, by 1975 41 per cent were sprayed (Anon, 1975-76).

Currently, seed crops are usually protected until about the end of June by granular insecticides applied at planting (McKinlay and Franklin, 1984). Thereafter foliar sprays are used at regular intervals until haulm destruction (Anon, 1983). Granules are unnecessary in ware crops, although foliar treatments may be recommended by the Scottish Agricultural Colleges if aphid populations exceed 3-5 aphids per true leaf (R McKinlay, pers comm).

2-1-5 RESISTANCE TO INSECTICIDES

Concurrent with increased insecticide use has been an increase in problems of aphid resistance. Although insecticide resistance in M euphorbiae is not established (Aveyard, 1981; Furk and Roberts, 1985), M persicae highly resistant to organophosphate and moderately resistant to carbamate insecticides now occur in several parts of the United Kingdom (Anon, 1983).

The multiplicative potential of insecticide-resistant M persicae, as measured by potential fecundity, development time and reproductive rate, has been shown to be significantly higher than that of susceptible clones (Eggers-Schumacher, 1983). Esterases conferring resistance pass from mothers to offspring, and thus resistance is perpetuated (Bunting, 1981). The existence of insecticide-resistant aphids with an increased potential for population growth makes research on alternative methods of aphid control imperative.

2-2 MATERIALS AND METHODS

Aphid sampling began in 1983 and 1984 at approximately 50 per cent crop emergence (8 June, 12 June respectively) and in 1985 a few hours before the first treatment application (25 July). In 1985, sampling for aphids and natural enemies was not begun until July so that certain laboratory studies could be completed. Until late June, 20 hills per plot were randomly chosen and examined. Aphids present were transferred to 70 per cent alcohol and species, life-stage (nymph and adult only) and alary-state determined.

From 4 July in 1983 and 1984, and 25 July in 1985, aphid numbers were counted on 60 randomly chosen potato hills per plot, using the 3-leaf method (Anscombe, 1948). At each hill, one leaf from either upper (U), middle (M) or lower (L) (Taylor, 1953) areas of the plant, was examined. Upper leaf samples included flowers if present. Axillary shoots were ignored.

In 1983, leaves with aphids were cut and returned to the laboratory for analysis. In 1984 and 1985, most identification was done in the field with the aid of a hand-lens.

2-3 RESULTS AND DISCUSSION

Of the aphids commonly infesting potato in Scotland, Macrosiphum euphorbiae, Myzus persicae and Aulacorthum solani were found in all three years; Myzus ascalonicus in 1984 only. Two alate adult Brachycaudus helichrysi were seen on 4 July 1984.

A three-season total exceeding 52,000 individuals was comprised primarily of M euphorbiae: 96, 99 and 93 per cent in 1983, 1984 and 1985 respectively. M persicae and A solani ranged from 0.5 to 4 per cent of the aphid total.

Data refer to all aphids of a particular species regardless of alary state or life-stage. There was no significant difference ($p > 0.05$) between numbers of M euphorbiae on upper, middle or lower leaves on most sampling occasions. Unless stated otherwise, data represent mean numbers of aphids from 12 leaf-groups per treatment (3 leaf positions x 4 replicates). As each of the 12 counts represents total numbers on 20 leaves per replicate per date, presented means are the numbers of aphids on 20 leaves.

Numbers of aphids other than M euphorbiae were so few that statistical analyses were not performed on data relating to them.

2-3-1 Macrosiphum euphorbiae

(a) Statistical analysis

Data followed the Poisson distribution and were transformed to square roots before analysis (see Sokal and Rohlf, 1969). Data are presented as back-transformed means with comparable confidence limits. Analyses of variance were performed on data from selected sampling occasions using the Genstat statistical package on the VAX-11/750 computer at the Edinburgh School of Agriculture.

(b) Population trends

Peak populations in untreated plots were recorded on 25 July in both 1983 and 1984 and on 14 August in 1985. Numbers in 1983 were lower than in other years, with a peak population of 55 aphids (on 20 leaves). Peak numbers were 595 and 219 in 1984 and 1985 respectively. The 1983 site was more exposed than the others, and this may have contributed to smaller populations in that year. Note that peak population levels in 1984 and 1985, but not in 1983, exceeded the economic threshold.

Aphid numbers in all plots in 1983 increased slowly through June to peak in mid to late July. After the peak, populations declined and by mid-August few aphids were recorded. Pre-treatment populations in both trials were not significantly different ($p > 0.05$) but post-treatment numbers were significantly different in plots treated with demeton-S-methyl ($F = 26.84$; df = 1, 15; $p \leq 0.05$) (Figure 4) or thiometon alone or together with methiocarb ($F = 34.67$; df = 3, 33; $p \leq 0.05$) (Figure 5), from numbers in untreated plots. Methiocarb apparently had little effect on aphid populations (Figure 5).

The magnitude of the aphid population peak was much greater in 1984 than 1983 (Figures 4-6). Aphid numbers often fluctuate dramatically year to year due in part to fluctuations in the effectiveness of summer predation and to the winter weather. These factors probably influence the number of aphids surviving to the spring and available to colonize crops.

Demeton-S-methyl was an effective aphicide in 1984 also: intensive sampling showed that aphid numbers, although similar before treatment, were reduced significantly ($p \leq 0.001$) in sprayed areas within 2 hours of the first (on 12 July) pesticide application (Figure 6). M persicae leaves demeton-S-methyl-treated foliage within 30 minutes (Rice et al, 1983); M euphorbiae appears to behave similarly.

Aphid numbers were significantly different between treatments ($p \leq 0.05$) immediately before the second spray in 1984. This was probably because populations did not recover in treated areas after the first spray. After mid-August aphids were not recorded from any plots (Figure 6).

Population trends around time of treatment were similar in 1985 to those of other years (Table 5) but aphids were very late arriving at the site and populations slow to increase.

Numbers before the first spray on 25 July were low (Table 5). Samples were

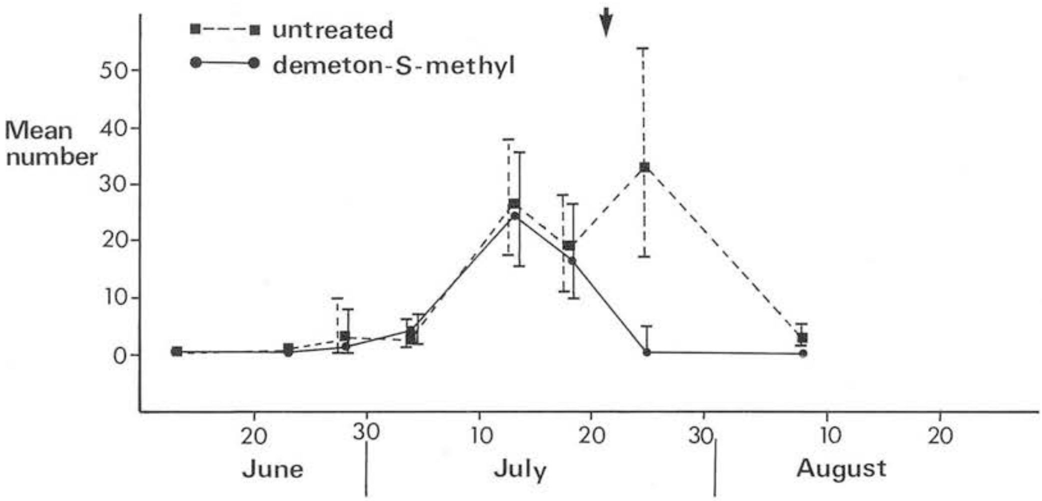


Figure 4: Back-transformed means and 95 per cent confidence intervals of Macrosiphum euphorbiae in 1983. Arrow indicates treatment application.

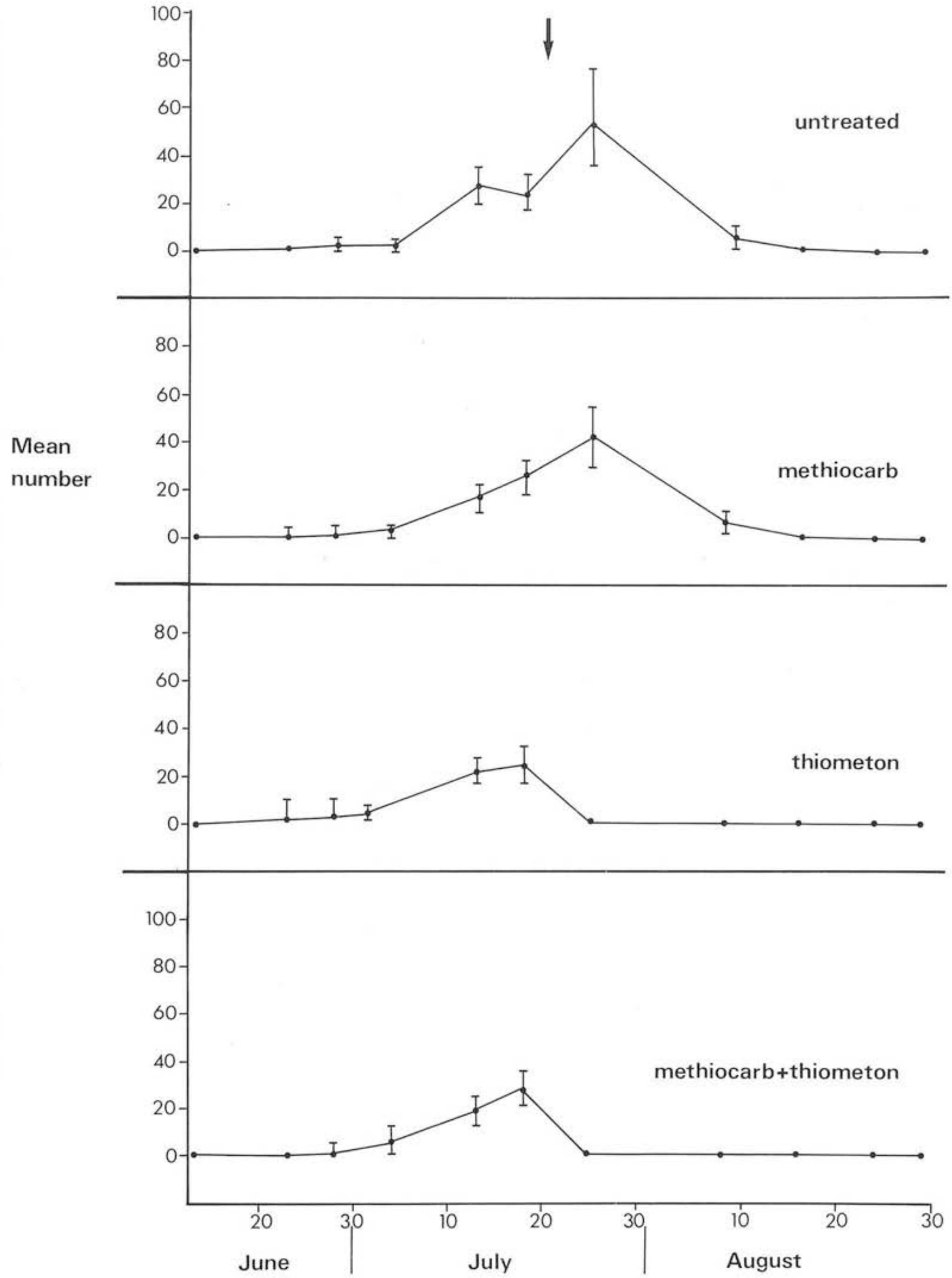


Figure 5: Back-transformed means and 95 per cent confidence intervals of Macrosiphum euphorbiae in 1983. Arrow indicates treatment application.

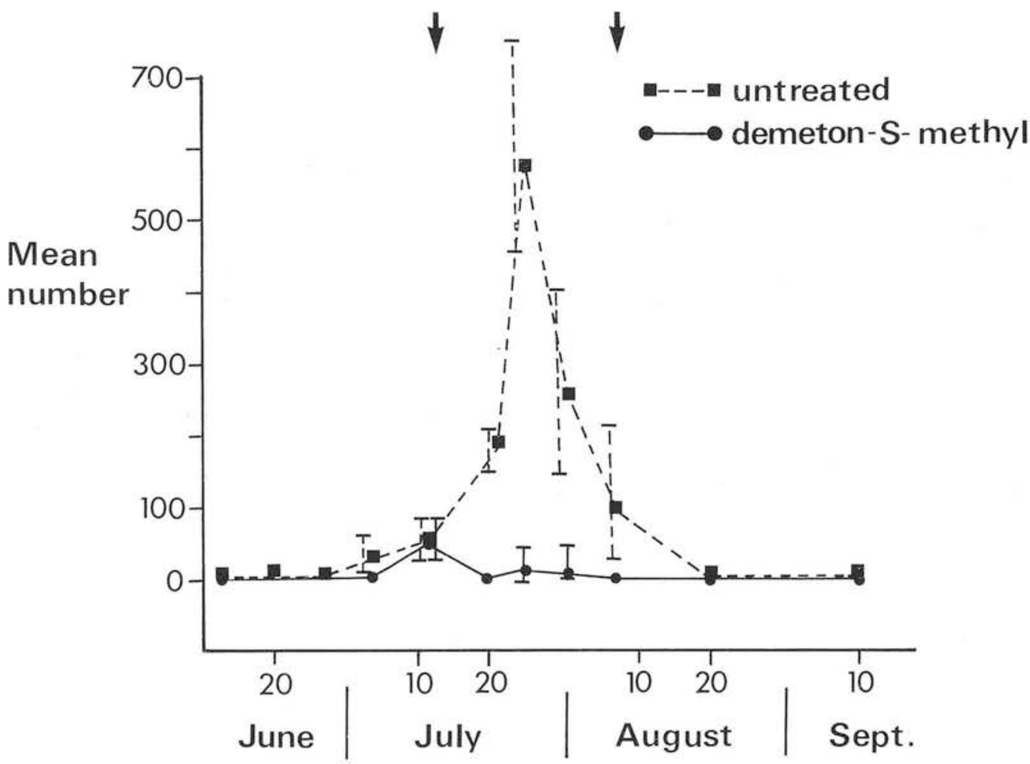


Figure 6: Back-transformed means and 95 per cent confidence intervals of Macrosiphum euphorbiae in 1984. Arrows indicate dates of pesticide application.

Table 5

Back-transformed means and 95% confidence limits of *M euphorbiae* at various post-treatment intervals in plots treated with demeton-S-methyl or untreated; (a) spray 1, 1984; (b) spray 1, 1985; (c) spray 2, 1985

Post-treatment Interval

(a)		2hr pre-treatment	2h	4h	7h	24h	48h	72h
Untreated	$\bar{x}$	51.8	47.6	46.2	50.4	96.0	68.9	106.1
	CL_{95}	(71,36)	(66,32)	(67,29)	(74,31)	(123,72)	(94,48)	(135,81)
Metasystox	$\bar{x}$	54.8	5.8	1.4	0.4	0.5	0.0	0.2
	CL_{95}	(76,37)	(11,2)	(4,0)	(1,0)	(2,0)	-	(1,0)
Level of significance		NS	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$

(b)		2hr pre-treatment	24h	48h	72h	1 week	2 weeks
Untreated	$\bar{x}$	19.4	-	-	4.8	25.6	23.0
	CL_{95}	(27,13)	-	-	(9,2)	(40,14)	(36,13)
Metasystox	$\bar{x}$	19.4	-	-	0	0	0.01
	CL_{95}	(27.13)	-	-	-	-	(0,0)
Level of significance		NS			$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$

(c)		2hr pre-treatment	24h	48h	72h	1 week	2 weeks
Untreated	$\bar{x}$	219.0	136.9	132.2	110.2	116.6	20.2
	CL_{95}	(289,158)	(177,102)	(166,102)	(144,81)	(151,86)	(34,10)
Metasystox	$\bar{x}$	216.1	3.6	2.0	1.4	1.4	0.2
	CL_{95}	(266,172)	(7,1)	(3,0)	(4,0)	(4,0)	(1,0)
Level of significance		NS	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$	$p \leq 0.001$

not taken at 24 or 48 hours after spray due to heavy rainfall (Appendix 2). The observed reduction of aphid numbers in untreated plots at the first sample after treatment (at 72 hours), was probably caused by rain: apterae are known to be dislodged from plants during heavy rain (Edwards and Wratten, 1980; Jones and Jones, 1984).

Populations were greater at the second treatment on 14 August and, although at both sites numbers of aphids in treated and untreated areas were not significantly different ($p > 0.05$) immediately before spray (on 25 July in site 1, 14 August in site 2), numbers in treated plots were significantly lower ($p \leq 0.001$) than in untreated plots on all sampling occasions after spray (Table 5b,c).

(c) Alary state/life-stage

Nymphs were the predominant life-stage on every sampling occasion. In the first year and on every date in 1984 except 25 July, the majority of nymphs was apterous. On 25 July 1984, 96 per cent of potato aphids were nymphs, of which 80 per cent were alatae. This situation coincided with the aphid population peak, and alate production may have been stimulated by overcrowding. On 1 August, the next sampling date, numbers of alate and apterous nymphs were similar, suggesting maturation and departure of many alate nymphs in the intervening days.

At the first spray in 1985 there were more apterous than alate nymphs; at the second spray alate nymphs outnumbered apterae on nearly every occasion, again due perhaps to overcrowding or to a deteriorating food source. Overall in 1985, 94 per cent of aphids were nymphs, 6 per cent adults; 65 per cent alatae, 35 per cent apterae.

(d) Leaf position

In 1983 and 1985, aphid numbers were often greatest on upper leaves, but variation was high with populations often evenly spread throughout the leaf strata. This is surprising as the potato aphid is considered to occur mainly on upper leaves (Bradley, 1952). Leaf position was not significant except on 2 dates in 1983 and one date in 1985. There were significantly more aphids on upper leaves in all manipulative trial plots on 13 July ($p \leq 0.05$) and 18 July

($p \leq 0.001$), and in all demeton-S-methyl plots on 18 July ($p \leq 0.05$), in 1983.

Twenty-four hours after the second spray in 1985, there were more aphids on upper leaves in untreated plots ($p \leq 0.05$) and more on lower leaves in treated plots ($p \leq 0.05$). The latter is probably due to less pesticide exposure of aphids on lower leaves; leaf x spray interaction was significant on that date ($p \leq 0.05$).

The 1984 situation was somewhat different. Analyses of variance were performed on all aphid data from the pre-spray sample on 12 July to the count on 8 August. Up to and including 25 July in untreated plots, significantly more aphids were present on upper leaves ($p \leq 0.05$) but on 1 August more were found on lower leaves ($p \leq 0.01$). On that date the mean number on 20 lower leaves in untreated plots exceeded 860, on upper leaves was just 100. Ladybirds were abundant in 1984 and may have eaten proportionately more aphids on upper than lower leaves. The interaction between leaf position and treatment was significant ($p \leq 0.05$) from 2 hours after the first treatment on 12 July, to 25 July in 1984. Aphid numbers in treated plots were likely to be lowest on upper leaves.

2-3-2 OTHER APHIDS

(a) *Myzus persicae*

Numbers of this aphid were low in all three years with totals in all plots of 195, 141 and 611 in 1983, 1984 and 1985 respectively. In all years the majority was apterous nymphs, mostly on lower leaves (eg 82 per cent on lower leaves in 1984).

In 1983, the first peach-potato aphid was observed on 13 June, populations peaked (with a total of 45 individuals in 24 plots) on 18 July and the last individual was seen on 16 August. The first in 1984 was seen on 26 June, the peak occurred on 1 August and the last specimen was seen on 7 August. Very few *M persicae* were observed in 1985 until late August, with numbers reaching their maximum (148 individuals) on 21 August.

(b) *Myzus ascalonicus*

This species was seen on 4 July 1984 only: one apterous adult and 2 apterous nymphs were present on upper leaves.

(c) Aulacorthum solani

A solani was most abundant in 1985 when a total in all plots of 648 was observed. Sixty-three individuals were seen in 1983, 20 in 1984. In all years most were apterous nymphs occurring on lower leaves. In 1983, the first was seen on 13 June, the last on 16 August; in 1984 corresponding dates were 26 June and 1 August respectively.

2-4 ADDITIONAL EXPERIMENTAL WORK

2-4-1 PETRI PLATES UNDER POTATO PLANTS

Materials and Methods

A field experiment was done in 1984 to test whether aphids in plots sprayed with demeton-S-methyl fell from plants.

The day before the first treatment, 18 randomly chosen plants in each 6 m x 6 m sub-plot were tagged, 144 in total. In the laboratory a layer of "sticktite" (Bol-tac Grease, Pan Brittania Industries), was applied to the insides of the bottom halves of 144, 9 cm plastic petri dishes. Two hours before treatment, 18 petri dishes per plot were placed under tagged plants. Dishes were placed on ridges under foliage, usually at the centres of hills. Three plates per plot were collected at various intervals after spraying (2, 4, 7, 24, 48 and 72 hours). Covers were replaced and plates transferred to the laboratory where numbers of aphids trapped were counted.

Results and Discussion

Data followed a Poisson distribution and were transformed to square roots before analysis using t-tests. Counts are presented as back-transformed means with comparable confidence limits. Significantly more aphids were collected on petri plates from sprayed than unsprayed plots at 2, 4, 7, 24 and 48 hours after treatment ($p \leq 0.001$) (Figure 7). A pre-treatment petri plate sample was not taken but as visual counts showed aphid numbers to be similar before

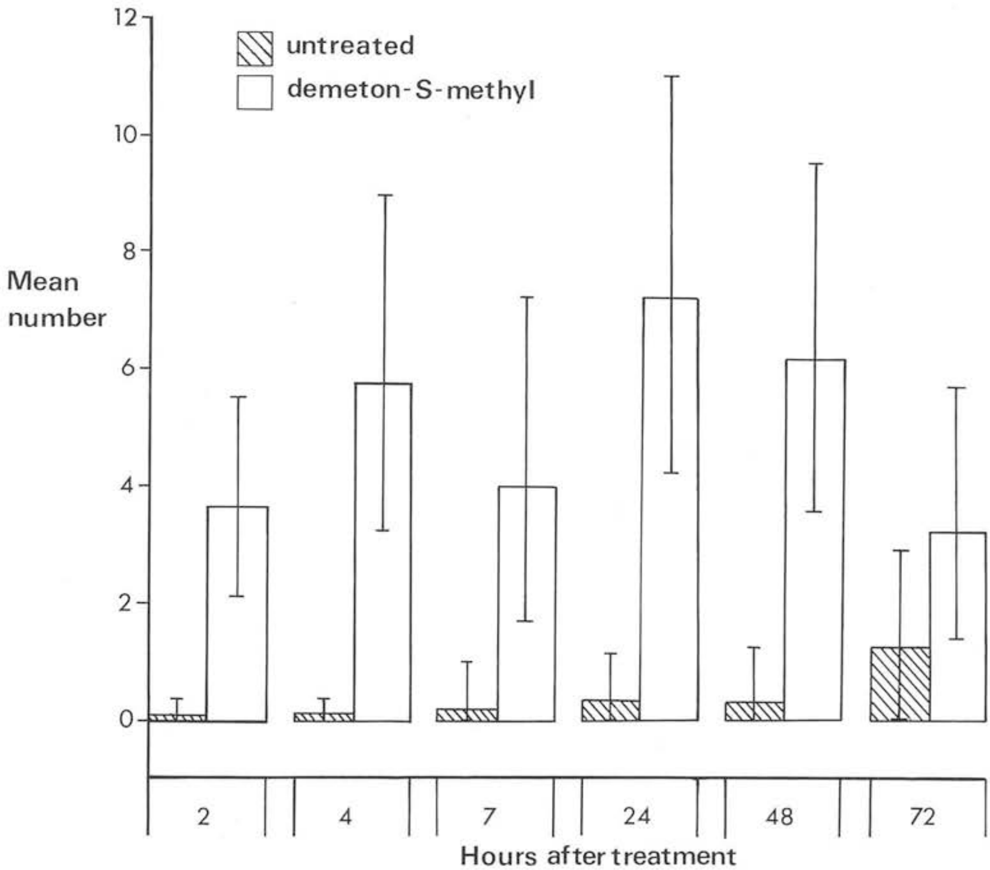


Figure 7: Back-transformed means and 95 per cent confidence intervals of Macrosiphum euphorbiae on petri plates under potato foliage after the first (12 July) demeton-S-methyl treatment in 1984. Counts are cumulative (see text).

treatment, plate results may probably be taken to represent differences due to demeton-S-methyl application.

The majority of aphids on petri plates was M euphorbiae apterous nymphs. At 48 and 72 hours many had deteriorated and identification was difficult. Dew and rain collecting in plates contributed to the deterioration.

Aphids on plates in untreated areas may have fallen from plants either naturally or due to foliage disturbance during plate collection. All plates were placed in the field at the same time and results are thus cumulative. A continual increase or a levelling off of numbers of aphids on plates in treated areas would thus be expected. Although variation is great, a peak at 24 hours is followed by a decline until by 72 hours there is no significant difference between numbers collected in different areas (Figure 7). Reasons for this are unknown. It is extremely unlikely that aphids were able to leave the sticktite after falling on to the plates, even if they survived exposure to the demeton-S-methyl. Trapped aphids were generally engulfed in sticktite as were other small arthropods. Stealing of aphids by predators seems unlikely. Perhaps on occasion there was sufficient dew or rain that aphids were washed out. This was, however, never observed.

2-4-2 FATE OF DEMETON-S-METHYL TREATED APHIDS

Materials and Methods

An experiment to determine whether aphids falling from plants sprayed with water alone, or with water and demeton-S-methyl, died was done in August 1984. Aphid numbers at the time of this trial were low, so leaves with a combined total of 160 aphids were removed from plants. Four 25.5 cm x 35.5 cm white enamel trays were placed on the soil at the ends of 4 potato rows, each tray separated by 2 rows. Leaves were placed, undersides down and supported by their stalks only, on trays such that each tray held 20 aphids. Ten metres of each row were sprayed with water only using an ICI mark-3 18 l capacity backpack sprayer incorporating a single cone-jet nozzle with a 1 mm aperture. Spraying was begun 10 m from row-ends and continued until leaves in trays were treated.

The above was repeated with 4 trays each with 20 aphids using demeton-S-methyl at 420 ml/ha in 200 l water. After 30 and 120 minutes, aphids in all trays were examined and deaths recorded. After 120 minutes surviving aphids were brought to the laboratory and kept on potato leaves for 3 days, after which further mortality was recorded.

Results and Discussion

Examinations were made at a maximum of 2 hours post-spray as field trials had shown a significant number of aphids to fall from plants within this period. Due to low numbers data were not transformed.

Mean numbers of aphids falling into each tray were 1.2 ($\pm$0.8) and 14.0 ($\pm$1.7) for those sprayed with water and demeton-S-methyl respectively. In the latter case, approximately 25 per cent of aphids remained on leaves (mean/tray = 5.8 $\pm$ 1.9). If this value is applicable to the field situation, it should be considered a minimum proportion not falling to the ground: on a whole plant with more foliage between aphid and soil, the likelihood of reaching ground level would be less.

All aphids treated with demeton-S-methyl, whether on leaves or in trays, were dead within the 2 hours whereas none sprayed with water only died within that time. No deaths were recorded over the 3-day period aphids were kept in the laboratory.

2-4-3 FATE OF APHIDS SPRAYED WITH WATER

Materials and Methods

Whether aphids from insecticide-treated plants were being "washed off" by the water, rather than being killed by the active ingredient in the pesticide, was tested using an ICI back-pack sprayer (as above). Water was sprayed onto 10 plants known to contain aphids. Enamel trays placed under plants before treatment were examined at 10 minute intervals for 1 hour following spraying. Numbers of aphids in the trays at each examination were recorded.

Results and Discussion

Aphids were not observed in any tray at any time after plants were sprayed with water. It thus seems likely that aphids from plants treated with demeton-S-methyl were responding to the active ingredient and not the water.

2-5 MISCELLANEOUS

2-5-1 APHIDS

(a) Following the first demeton-S-methyl application in 1984, many M euphorbiae were observed walking on the ground in furrows in sprayed plots only, within 2 hours of treatment.

(b) In 1985, pitfall traps emptied at 72 hours after the second spray contained many aphids. Traps from treated plots contained 38.9 (±7.7) aphids (combined species and stages), those from untreated plots 1.5 (±1.0). This difference was significant ($p \leq 0.001$).

2-5-2 FOLIAGE COUNTS

Materials and Methods

An attempt was made to quantify crop growth so that aphid data could be converted to numbers per hectare.

In 1983, the numbers of hills per row and haulms per hill were calculated by counting, on 25 July, numbers of hills in 5 x 20 m lengths of row and numbers of haulms in 5 hills per plot (each chosen randomly). Estimates of leaf area were made on 18 July when 2 haulms per plot were brought to the laboratory. Leaves were removed from each and those from upper, middle and lower regions were kept separate. Eight leaves from each region were selected at random. One disc was cut from each leaf using a metal corer (area: 2.5 cm^2). Each disc, and the remaining leaves from each region, were weighed. As the disc area was known, the area of leaf per haulm could be calculated.

In 1984, various counts were made: numbers of ridges per plot, hills per row, haulms per hill and leaves per stratum were counted on 12 July. Numbers of haulms per hill and leaves per stratum were also counted on 6 August, and the latter only on 14 and 20 August and 10 September.

Results and Discussion

Data were so variable that aphid numbers per hectare could not be calculated. Leaf-area analysis, as well as being very variable, proved extremely time-consuming and was not continued. Selected results are presented for interest only.

Numbers of haulms per hill were similar in both years: 6.2 (n=120) on 25 July 1983, 6.3 (n=50) and 5.5 (n=50) on 12 July and 6 August 1984 respectively.

Mean leaf areas (cm^2) in 1983 were as follows (n=24):

Upper stratum - 233.2 (±63.0)
Middle stratum - 300.1 (±23.4)
Lower stratum - 613.0 (±43.5)

Leaf number per haulm (1984) varied from an average of 12 on 12 July to 17 on 10 September. On nearly every occasion, upper leaves were most numerous, lower leaves fewest. Leaf area and number at each position in 1983 were inversely related, indicating larger bottom leaves and smaller upper ones.

CHAPTER 3

SPECIFIC NATURAL ENEMIES

3-1 INTRODUCTION

3-1-1 FUNGI

Entomogenous fungi occur in all the major fungal divisions (Wilding, 1983), particularly the Deuteromycetes and Zygomycetes (Burnett, 1970). The Zygomycetes include the order Entomophthorales which contains most of the aphid-infecting species (Hagen and van den Bosch, 1968).

Conidial spores of *Entomophthora* spp are self-propelled (Hussey and Bravenboer, 1969), and if carried to a susceptible insect will, under favourable conditions, germinate and penetrate the body via the cuticle (Milner, 1985). Victims become brown and inflated with liquid (Blackman, 1974). Host death may be due to toxin production or to growth of fungal hyphae into tissues (Milner *et al*, 1984).

Sporulation and spread are restricted by environmental conditions, high humidity in particular being essential (van Emden, 1980). Epizootics usually occur after heavy rainfall or periods of high humidity only (Shands *et al*, 1962).

Many species of parasitic fungi have been recorded from aphid populations in the field: *Erynia neoaphidis*, *Conidiobolus obscurus* and *Entomophthora planchoniana* on cereal aphids in Belgium (Coremans-Pelseneer *et al*, 1983); various *Entomophthora* species on pea aphids (*Acyrthosiphon pisum*) in Britain (Wilding, 1975) and on *Macrosiphum euphorbiae* in eastern North America (Remaudierè *et al*, 1978); and *Entomophthora ignobilis* on *M euphorbiae* and *Myzus persicae* on potatoes in Maine (Shands *et al*, 1962). A heavy toll of aphids is sometimes taken, but generally only when the aphid population has already reached its peak (Blackman, 1974). High levels of infection are occasionally recorded (see Milner, 1985) but low levels seem more common (eg Shands *et al*, 1962; Mackauer and Way, 1976).

The use of parasitic fungi in aphid control is not without problems. A form of pea aphid resistant to *Erynia neoaphidis* occurs in Australia (Milner, 1985). Also, insect parasitic fungi may be affected by pesticides. Most fungicides inhibit their growth (Tedders, 1981; Wilding, 1983; Saito, 1984; Carruthers *et al*, 1985) and insecticides detrimental to entomogenous fungi have been recorded: azinphos-methyl and carbofuran decreased mycelial growth of *Beauveria bassiana* by nearly 50 per cent (Clark *et al*, 1982). Malathion altered the behaviour of the onion fly (*Delia antigua*) such that dispersal of *Entomophthora muscae* spores was reduced (Carruthers *et al*, 1985). Untreated flies sporulated at the tops of barley plants, while treated individuals remained on the soil surface where wind-assisted conidial dispersal was less effective.

An advantage of entomogenous fungi from the point of view of integrated control is their narrow spectrum of activity. Although predators and insect parasitoids are susceptible to infection, a fungal strain applied to control a particular pest is unlikely to affect natural enemies in the same environment due to a high degree of pathogenic specificity (Wilding, 1983). The effectiveness of fungi in pest control may be increased by manipulation of humidity in crops and glasshouses via irrigation or increasing the degree of weed cover (Hall, 1984).

3-1-2 PARASITOIDS (Hymenoptera)

Parasitic wasps are not true parasites as host death invariably occurs; the term parasitoid is more accurate (Blackman, 1974) and is used in this thesis. A dead parasitised aphid assumes a characteristic appearance and is called a "mummy". The aphid integument after death appears opaque and papery and may change colour and shape (Hughes *et al*, 1981; Starý, 1983).

The majority of insect parasitoids of aphids occur in 2 families in the order Hymenoptera, the Aphidiidae and Aphelinidae (Mackauer, 1968). Reviews of the Aphidiidae are given by Starý (1966, 1970) and of the Aphelinidae by Viggiani (1984).

(a) Aphidiidae

Super and multiparasitism are not uncommon in this family, particularly when hosts are scarce (Mackauer, 1983), but in general aphidiids are solitary endoparasitoids (Hagen and van den Bosch, 1968). All stages of aphids except eggs may be attacked but apterous nymphs are the usual targets (Mackauer, 1968). Aphid nymphs parasitised before the 3rd instar do not reproduce (Dunn, 1949).

Parasitoid fecundity varies tremendously, from about 50 to nearly 100 eggs per female in some species (Hagen and van den Bosch, 1968; Mackauer, 1982). There are 4 larval instars (Spencer, 1926; Pare et al, 1979). Host vital organs are consumed last so the aphid is alive until just before parasitoid pupation (Blackman, 1974).

The commonest method of pupation among the aphidiid wasps (eg Aphidius, Diaeretiella) is the spinning of a cocoon within the mummified aphid (Starý, 1983). Other methods occur: a full-grown larva of Praon spp pupates within a cocoon it has spun beneath the aphid body (Shands et al, 1965). All aphidiids are arrhenotokous, ie unfertilised eggs produce only males (Starý, 1966). Adult wasps feed mainly on honeydew (Spencer, 1926).

Overwintering occurs as pupae within mummified aphids in the field (Hagen and van den Bosch, 1968), and possibly in mummies in glasshouses (Spencer, 1926). Many are likely destroyed during the harvesting of agricultural crops. Chambers et al (1982) postulate that adults may disperse from one crop to another, and that parasitoids may enter a crop as eggs or larvae within alate aphids.

(b) Aphelinidae

The majority of Aphelinidae are parasitic on scale insects (Mackauer, 1968). Of the 600 described species, 50 are solitary endoparasitoids of nymphal and adult aphids (Mackauer, 1968). Oviposition generally occurs in first or second instar nymphs (Hagen and van den Bosch, 1968), and the adults sometimes feed on aphid haemolymph at host oviposition punctures (Schlinger and Hall, 1959).

(c) Hyperparasitoids

Natural enemies of aphid parasitoids include larvae of Chrysopa spp

(Starý, 1966), entomogenous fungi (Keller, 1975) and other hymenopterous wasps - "hyperparasitoids". Hyperparasitoids occur in several families, including the Cynipidae, the Pteromalidae and the Megaspilidae. Pteromalids and megaspilids are external, solitary parasitoids of Aphidiidae and Aphelinus (Dunn, 1949). The Cynipidae are solitary endoparasitoids and oviposition is always in living aphids containing Aphidiidae or Aphelinus (Dunn, 1949).

(d) Pesticides

Parasitoids may be affected by pesticides. Toxicity of contact materials is predominantly expressed against adults, with immature stages somewhat protected within their cocoons (Bartlett, 1963; Godfrey and Root, 1968). However, laboratory mortality of Aphidius ervi (within Sitobion avenae) was very high when mummies were treated with field-rate doses of mevinphos, dimethoate and pirimicarb (Süss, 1983). Numbers of adult wasps in winter wheat fields in Britain were also reduced by pirimicarb and dimethoate, although benomyl had little effect (Powell et al, 1985). Demeton had a high contact toxicity, in the laboratory, to adults of several species of parasitic wasps (Bartlett, 1963).

Many species of parasitoids have been recorded from potato-infesting aphids (see Table 6 - (M euphorbiae)). A review of species attacking M persicae was given by Mackauer (1968).

3-1-3 LACEWINGS (Neuroptera)

Sixty species of lacewings occur in Britain (Chinery, 1984). They are mainly crepuscular or nocturnal insects and aphid predators occur in 2 families, the Chrysopidae, the green lacewings, and the Hemerobiidae, the brown lacewings (Killington, 1936).

Eggs are generally laid singly either on stalks (Chrysopidae) or directly on foliage (Hemerobiidae). The 3 larval instars are entirely carnivorous, and use their mandibles as tubes through which the juices of their prey are sucked (Chinery, 1984). Adults, which have biting mouthparts (Chinery, 1984), may

Table 6

Some primary parasitoids recorded from Macrosiphum euphorbiae on potato

Species	Country	Reference
Aphidiidae		
Aphidius ervi Haliday	England USSR	Dunn (1949) Starý (1973)
Aphidius matricariae Haliday	England USA	Dunn (1949) Shands et al (1972)
Aphidius nigripes Ashmead	Canada USA Canada	MacGillivray & Spicer (1953) Shands et al (1972) Gordon - unpublished (1980)
Aphidius obscuripes Ashmead	USA	Shands et al (1972)
Aphidius picipes Nees	England	Dunn (1949)
Aphidius rosae Haliday	Canada	MacGillivray & Spicer (1953)
Diaeretiella rapae (McIntosh)	USA	Shands et al (1972)
Ephedrus incompletus (Provancher)	USA	Shands et al (1972)
Praon aguti Smith	Canada	MacGillivray & Spicer (1953)
Praon occidentalis Baker	Canada	MacGillivray & Spicer (1953)
Praon simulans Provancher	Canada	MacGillivray & Spicer (1953)
Praon volucre Haliday	England	Dunn (1949)

take aphids but usually feed on honeydew and pollen (Rotheray, 1986).

In a laboratory study larvae and adults of Chrysoperla carnea were killed by most of the tested organophosphates and chlorinated hydrocarbons (Bartlett, 1964). C carnea was susceptible to several materials including dimethoate, chlorpyrifos and diflubenzuron when exposed to pesticide films on glass plates (Hassan et al, 1985). Laboratory exposure to dry films of demeton-S-methyl killed over 99 per cent of C carnea (Hassan et al, 1983) but the stage tested was not stated.

3-1-4 LADYBIRDS (Coleoptera : Coccinellidae)

Over 3000 species of ladybirds occur world-wide (Pope, 1953) but 42 only are known from Britain (Rotheray, 1986). Many species eat aphids but some aphidophagous ladybirds will take other prey and others feed primarily on scale insects or mites (Rotheray, 1986). Adults and larvae are predatory (Gurney and Hussey, 1970).

Ladybird eggs are laid singly, in clusters or in rows (Pope, 1953). On emergence, larvae may eat their own egg-shell, unhatched eggs and even smaller larvae (Banks, 1956). There are 4 larval instars (Rotheray, 1986) and pupation takes place on the plant where the larva has been feeding (Pope, 1953). Most British coccinellids are univoltine (Mills, 1981) although some adults live for more than one season. Ladybirds overwinter as adults under loose bark, in crevices and hollow plant stems and even in houses, often in large aggregations (Moreton, 1969).

The number of aphids eaten by a coccinellid varies with the species and life-stage of both predator and prey. Coccinella septempunctata and Adalia bipunctata during their life-times ate an average of 173 and 206 Myzus persicae respectively (Gurney and Hussey, 1970), and C septempunctata larvae ate approximately 100 Macrosiphum euphorbiae (Dunn, 1949). Weather and level of hunger may also affect consumption. In the field, adult C septempunctata may eat more than 40 aphids per day (Honěk, 1985) but in the laboratory after a period of starvation adults ate up to 54 aphids in 3 hours (Nakamuta, 1983). When prey is abundant larvae destroy more aphids than they require for their development (Hodek, 1970) but on plants with few aphids many larvae die of starvation because of their inefficient searching patterns (Moreton, 1969).

Ladybirds vary in response to pesticides depending on species and life-stage, with larvae in general more susceptible than adults (Bartlett, 1963). Adults may be killed by pesticides: cypermethrin and methyl-parathion were toxic to adult C septempunctata, although pirimicarb was harmless (Brown et al, 1983).

Reviews of literature on coccinellids are given by Hagen (1962) and Hodek (1967).

3-1-5 HOVERFLIES (Diptera : Syrphidae)

About 250 species of hoverfly occur in Britain (Chinery, 1984). Of these, approximately 100 species in 2 sub-families, have aphidophagous larvae: the Pipizini which are specialized predators of wax-secreting aphids, and the Syrphini. The larvae, despite being legless, are active and mobile (Stubbs and Falk, 1983). There are 3 larval instars each of which is a fluid-feeder (Rotheray, 1984). Larvae of many species feed at night (Rotheray, 1986) and spend the day in leaf curls and folds or near leaf veins (Rotheray, 1984).

Adults are diurnally active, feed on pollen, nectar and honeydew (Rotheray, 1986) and may be important in pollination (Coe, 1953). Some species appear to be univoltine while others have several generations per year (Moreton, 1969). They overwinter usually as larvae or pupae (Moreton, 1969) but in some species as adults (Pollard, 1971).

A number of hoverfly species is migratory. Episyrphus balteatus migrates from continental Europe to Britain in late summer and is generally uncommon in spring and early summer (Rotheray, 1984). Migrations of some species, eg Metasyrphus corollae, do not occur every year (Svensson and Janzen, 1984) but in seasons when they are plentiful hoverflies can considerably reduce aphid infestations (Moreton, 1969).

Susceptibility to pesticides varies with species, life-stage and chemical (see Moreton, 1969). In the laboratory, 70-100 per cent of syrphid larvae died after eating aphids treated with "Systox" (Ahmed et al, 1954). Hassan et al (1983) tested 40 pesticides against Syrphus vitripennis but did not specify the stage used. Susceptibility varied but demeton-S-methyl was highly toxic.

A review of the bionomics and physiology of aphidophagous hoverflies is given by Schneider (1969).

3-2 MATERIALS AND METHODS

3-2-1 FUNGI

Aphids infected with fungi present on potato leaves examined during routine aphid sampling were counted in each year. Species or life-stage of infected aphids was not determined. Diseased aphids were not removed from plants after counting. In 1985, several diseased individuals were sent for identification to S Mardell at Rothamsted Experimental Station.

3-2-2 PARASITOIDS

(a) Field

Mummified aphids present on leaves examined during routine aphid sampling were placed in plastic test-tubes and stoppered with cotton wool in the laboratory. A piece of potato leaf was placed in each tube to reduce dessication. Tubes were kept at about 20°C under a natural light regime. Emerged insects were identified and a selection mounted. Empty mummies observed in the field were not counted.

(b) Laboratory

The percentage of aphid parasitism is likely to be underestimated when assessed by mummy counts in the field. Aphid mummies may occur off the plant (Powell, 1980; Carter et al, 1982) and thus be unrecorded. Percentage parasitism may also be assessed by collecting apparently healthy aphids from the field for dissection or rearing (see Hughes et al, 1982). Experiments to determine the degree of underestimation of parasitism by mummy counts were done in 1983.

On 18 and 25 July up to 40 aphids per treatment were reared under parasitoid-free conditions in the laboratory. Samples of aphids were taken from all treatments on 18 July and from untreated and methiocarb-treated plots only on 25 July due to low numbers in other plots.

Aphids were placed on potato leaves collected from untreated field plots. Leaves were inserted into petri dishes containing water and were placed in plastic, ventilated 1 litre growth chambers and kept at approximately 20°C with natural light. Fresh leaves were supplied as required. Mummy counts were made after one week.

On 18 July only, apparently unparasitised adult M euphorbiae apterae (n=292) and alatae (n=57) were placed in 70 per cent alcohol. Aphids selected randomly from all plots were later dissected to determine whether any contained parasitoid larvae.

3-2-3 LACEWINGS, LADYBIRDS AND HOVERFLIES

From about mid-June in 1983 and 1984, and during the entire field experiment in 1985, all potato plants in 5 randomly-chosen, 5 m lengths of row were visually searched in each plot. All stages of lacewings, ladybirds and hoverflies present were recorded. Larvae were collected and reared to adult in the laboratory.

3-3 RESULTS AND DISCUSSION

3-3-1 FUNGI

Aphids infected with entomogenous fungi were seen in each year but numbers were generally low. The overall percentage infection was 6-7 per cent. In 1983, percentages of diseased aphids were similar on upper, middle and lower leaves and aphid numbers were combined across leaf positions. The numbers of infected individuals were directly proportional to total aphid numbers. Data from plots sprayed with demeton-S-methyl or thiometon, where aphid numbers were significantly reduced after treatment, were combined for presentation. Similarly, data from untreated plots and those treated with methiocarb alone, were combined. In 1983, therefore, presented means represent per cent infection in 12 plots per date. Data for 1984 and 1985 are given as means of percentage infected aphids at each leaf position per treatment. Numbers of apparently healthy aphids in each year are also given.

Overall infection was 3.5 per cent in 1983 (n=232), 2.3 per cent in 1984 (n=667) and 12.1 per cent in 1985 (n=2469). Considering only occasions when diseased individuals were observed, percentage infection was 3.8, 16.7 and 13.1 in 1983, 1984 and 1985 respectively.

In 1983 and 1984, parasitic fungi did not appear to contribute substantially to aphid control. Infected aphids were first seen on 13 July in 1983 and were present in low numbers until 16 August (Table 7). In 1984, diseased aphids were observed on 2 dates only, 7 and 8 August (Table 8). The reason for infected aphids being seen on 2 days only is unknown.

Fungal infection was, however, important in reducing aphid populations in 1985. Diseased aphids were present in low numbers (4.2 per cent of total) on 8 August in untreated plots only. At the second spray in 1985, per cent infection increased steadily until nearly 40 per cent of aphids in untreated plots were infected on the last sampling occasion, 28 August (Table 9). The unusually wet weather probably contributed to this epizootic (Appendix 2).

Percentage infection was often higher in treated than untreated plots (Tables 7-9). This was probably because uninfected aphids in treated areas fell from foliage after spray application, but infected individuals remained on the plants.

Generally in each year, proportions of diseased aphids were highest on lower leaves (Tables 7-9), possibly due to humidity levels being higher in this region. Also, percentages of infected aphids were related in a density-dependent manner to the proportion of the aphid population present at each leaf position: eg in 1984 85, 7 and 8 per cent of diseased aphids were present on lower, middle and upper leaves respectively. Corresponding percentages of total aphids were 86, 7 and 6 respectively.

All the aphids sent to Rothamsted were infected with Entomophthora planchoniana Cornu. It is not known if this species was present in 1983 or

Table 7

Mean ± SE_{95} per cent aphids infected with fungi on all leaves, 1983
*(n = mean number healthy and diseased aphids per plot)

Treatment / Date	Untreated and methiocarb	demeton-S-methyl and thiometon
13 July	2.5±2.2 *(n=79.2±12.9)	2.1±1.7 (n=69.7±11.6)
18 July	3.1±2.0 (n=82.4±15.1)	4.5±2.5 (n=79.7±13.3)
25 July	7.7±6.2 (n=167.9±52.6)	12.3±10.1 (n=3.5±2.8)
8 August	12.4±6.3 (n=28.8±12.9)	0 (n=0)
16 August	14.6±15.5 (n=1.7±0.9)	6.1±10.1 (n=1.0±0.5)

Table 8

Mean ± SE_{95} per cent aphids infected with fungi on upper, middle and lower leaves, 1984

*(n= mean number healthy and diseased aphids per plot)

	Untreated		demeton-S-methyl	
Date / Leaf Position	7 August	8 August	7 August	8 August
Upper	11.3±6.2 *(n=37.5±5.5)	12.4±9.4 (n=24.5±21.3)	0 (n=0.5±0.5)	25.0±25.0 (n=0.7±0.7)
Middle	15.9±10.1 (n=36.7±8.1)	13.6±7.8 (n=18.2±13.7)	0 (n=0.5±0.5)	0 (n=O)
Lower	18.9±4.1 (n=651.0±459.7)	48.9±18.1 (n=204.5±96.7)	12.0±4.9 (n=12.2±3.7)	18.7±18.7 (n=1.0±1.0)

Table 9

Mean ± SE_{95} per cent aphids infected with fungi on upper, middle and lower leaves, 1985

*(n= mean number healthy and diseased aphids per plot)

	Untreated			demeton-S-methyl		
Leaf Position / Date	Upper	Middle	Lower	Upper	Middle	Lower
14 August (pre-spray sample)	15.5±7.4 *(n=827.0±514.2)	12.2±1.5 (n=174.7±55.6)	22.9±10.5 (n=168.0±95.5)	9.3±2.2 (n=338.7±108.6)	10.0±4.1 (n=318.7±115.8)	27.9±11.0 (n=186.2±45.1)
15 August	13.9±7.1 (n=321.7±116.3)	5.8±2.4 (n=221.2±77.7)	25.6±5.6 (n=63.5±12.0)	40.1±19.1 (n=7.7±2.2)	55.6±13.9 (n=21.5±8.8)	32.0±13.6 (n=31.2±16.3)
16 August	16.1±5.3 (n=252.7±98.3)	8.3±4.4 (n=191.7±46.8)	31.0±6.2 (n=99.5±5.6)	20.0±20.0 (n=2.5±1.4)	40.0±24.5 (n=11.0±8.0)	20.0±20.0 (n=11.0±2.8)
17 August	13.9±3.9 (n=251.5±91.0)	12.1±4.8 (n=171.2±62.0)	22.4±8.8 (n=69.7±14.9)	14.3±14.3 (n=2.2±1.6)	0.6±0.6 (n=10.5±9.8)	0 (n=5.5±3.6)
21 August	16.7±4.8 (n=262.0±145.4)	24.3±4.7 (n=195.5±69.6)	20.0±2.5 (n=137.5±27.3)	25.0±25.0 (n=2.0±1.3)	10.4±10.4 (n=3.5±2.9)	13.2±13.2 (n=9.0±8.3)
28 August	30.5±8.4 (n=96.2±32.5)	17.4±5.9 (n=53.5±22.4)	46.0±15.9 (n=108.5±28.5)	25.0±25.0 (n=2.7±1.8)	15.0±15.0 (n=2.2±1.0)	63.4±23.8 (n=18.0±12.9)

1984. E planchoniana has been recorded from potato aphids in Maine (Shands et al, 1962), where epizootics generally followed periods of heavy rainfall or high humidity. Wilding (1975) reported peak levels of infection of pea aphid on lucerne by E planchoniana in Britain, during warm periods. This species has also been observed attacking aphids in eastern North America (Remaudière et al, 1978), and cereal aphids in Belgium (Coremans-Pelseneer et al, 1983).

Entomogenous fungi apparently did not play a significant role in reducing aphid numbers, apart from during the unusually wet summer of 1985. Parasitic fungi are generally considered not to contribute substantially to aphid control in Britain (Dunn, 1949; Foster, 1972; Heathcote, 1972; Mackauer and Way, 1976).

The effectiveness of entomopthorous fungi may be improved by increasing humidity levels in crops or by application of spore preparations (Hall, 1984). Increasing humidity levels may, however, also improve conditions for sporulation and spread of crop fungal diseases. Entomogenous fungi in the current study were most common at about the same time of year that late blight (Phytopthora infestans (Montagné) De Bary) was prevalent. Farmers usually apply fungicides for late blight control, and these may be detrimental to entomogenous as well as to plant pathogenic fungi (see Saito, 1984; Carruthers et al, 1985).

3-3-2 PARASITOIDS

(a) Field

Table 10 lists the primary parasitoids and hyperparasitoids reared from mummies of potato-infesting aphids during the 3 years. Overall, primary parasitoids comprised nearly 78 per cent of the total: the majority was Aphidius picipes. Secondary parasitoids (approximately 22 per cent of total) were mainly Dendrocerus aphidum and a small number of tertiary Alloxystinae emerged from Praon spp mummies.

Percentage parasitism (calculated as:

$$\frac{\text{No aphids parasitised (mummies)}}{\text{No aphids apparently unparasitised + mummies}} \times 100)$$

, was low, ranging from 0.01 per cent (1985) to 6.09 per cent (1983). These percentages

Table 10

Parasitoids reared from mummified potato-infesting aphids, 1983-1985
Numbers are totals collected in each year

Species \ Year	1983	1984	1985	Total
Aphidiidae				
Aphidius picipes*	327	16	2	345
Praon spp*	0	9	0	11
Pteromalidae				
Asaphes vulgaris ǂ	33	9	0	42
Megaspilidae				
Dendrocerus aphidum ǂ	48	5	0	53
Dendrocerus carpenteri ǂ	4	0	0	4
Cynipidae				
Alloxystinae ǂ	0	2	0	2
Total	412	43	2	457
Overall parasitism %	6.09	0.27	0.01	1.12
(n = total number aphid mummies + healthy aphids)	(n=6764)	(n=16,114)	(n=17,878)	(n=40,756)

NB * : primary parasitoid
ǂ : hyperparasitoid

are probably underestimates as some parasitised aphids leave the plant prior to death and mummy formation (Powell, 1980; Walker et al, 1984), and are not recorded.

Ninety per cent of all parasitoids were collected in 1983, and data from that year only are presented in detail. Data for 1984 are given in Appendix 3. Two mummies only were collected in 1985. Dates reflect time of mummy collection in the field rather than of parasitoid emergence. The species of aphid from which parasitoids emerged was not determined but as the majority of aphids present were the potato aphid, it is likely that the majority of mummified aphids was M euphorbiae.

(i) Primary parasitoids

Primary parasitoids constituted 80 per cent of all parasitoids in 1983, 63 per cent in 1984. The 2 mummies collected in 1985, both on 1 August, contained Aphidius picipes. All primary parasitoids in 1983 (n=327) and 60 per cent in 1984 (n=16) were A picipes. In 1984, Praon spp emerged from 9 mummies.

A picipes was first collected on 13 July in 1983 and was last seen on 30 August. Percentage parasitism was variable with respect to leaf position (Table 11), although unlike aphid populations was highest, before treatment, on middle leaves. Proportions of parasitised aphids increased in treated plots after spraying (Table 12) in a manner similiar to per cent aphids infected with fungi. As with fungi, percentages are probably artificially high in plots where demeton-S-methyl or thiometon were applied, arising from unparasitised aphids falling off plants after treatment.

The overall sex ratio of A picipes in 1983 was 0.7 (♂:♀). The proportion of males varied through the summer, but was always lower than that of females except on 30 August when one parasitoid only was collected (Table 13).

In 1984, the first A picipes and Praon spp were collected on 25 July. The last A picipes was sampled on 14 August, the last Praon mummy on 8 August.

Wasp cocoons were present underneath 11 mummies collected in 1984,

Table 11

Per cent parasitism of aphids by *Aphidius picipes* on upper, middle and lower leaves in all plots, 1983

*(n=number parasitised and unparasitised aphids)

Leaf Position / Date	Upper	Middle	Lower
13 July	4.4 *(n=795)	4.3 (n=557)	2.1 (n=468)
18 July	6.7 (n=1083)	12.1 (n=454)	5.6 (n=485)
25 July	4.6 (n=818)	9.9 (n=362)	1.3 (n=898)
8 August	3.8 (n=104)	2.8 (n=107)	1.2 (n=86)
16 August	46.1 (n=13)	37.5 (n=8)	11.8 (n=17)
25 August	75.0 (n=4)	16.7 (n=6)	0 (n=3)
30 August	100 (n=1)	0 (n=0)	0 (n=0)

Table 12

Per cent parasitism by <u>Aphidius picipes</u> on all leaves immediately before, and at the first sample after treatment, 1983
*(n=number healthy and number parasitised aphids)

Treatment \ Date	18 July (pre-spray)	25 July (post-spray)
demeton-S-methyl trial untreated	9.8 * (n=296)	3.0 (n=566)
demeton-S-methyl	10.4 (n=259)	58.3 (n=24)
manipulative trial untreated	5.6 (n=356)	2.0 (n=848)
methiocarb	9.2 (n=389)	2.4 (n=588)
thiometon	4.4 (n=343)	33.3 (n=39)
methiocarb + thiometon	7.1 (n=378)	84.6 (n=13)

Table 13

Sex ratio of <u>Aphidius picipes</u> in 1983 (♂ : ♀)
(n=total number of <u>Aphidius picipes</u>)

Date	13 July	18 July	25 July	8 August	16 August	25 August	30 August
Ratio ♂/♀	0.8 (n=79)	0.8 (n=155)	0.5 (n=86)	0 (n=8)	0.8 (n=11)	0.3 (n=4)	1.0 (n=1)

indicating Praon spp. Of these, adults emerged from only 2, and as each was damaged, species identifications were not made. The 9 intact cocoons were dissected and 7 contained Praon spp adults. Dunn (1949) notes that Praon mummies are very susceptible to drying out and if kept too dry many wasps dessicate and fail to emerge. This was probably the case in the present study.

In 1984, 23/27 primary parasitoids were found in untreated plots and overall 12, 8 and 7 on upper, middle and lower leaves respectively.

Primary parasitism of 0.01-6.09 per cent in this study was lower than that reported by Dunn (1949) for potato-infesting aphids in England: 9.4-15.7 per cent. Mann (1976) recorded 5.2-12.6 per cent parasitism of Myzus persicae on Brussels sprouts in south-east Scotland. Great variation has, however, been recorded in per cent parasitism of aphids on potato in the United States of America (Shands et al, 1972).

Aphidius picipes has been recorded attacking M euphorbiae, M persicae and Aulacorthum solani on potatoes (Dunn, 1949). Dunn (1949) regarded it as the only parasitoid to exert a controlling influence on potato aphid populations in northern England, and noted that a generation takes approximately 3 weeks during the summer.

Starý (1973) states that the main hosts of A picipes are Sitobion spp and Acyrthosiphum spp, and to a lesser extent, Myzus and Macrosiphum spp. The position of A picipes in the European parasitoid spectrum is occupied in North America by Aphidius nigripes Ashmead; the two are considered to be closely related (Mackauer, 1968). A nigripes has been collected from the potato aphid, the peach-potato aphid and the buckthorn aphid in Canada (MacGillivray and Spicer, 1953), and a long-term survey of aphids infesting potato in Maine showed A nigripes to be the single most important parasitoid of M euphorbiae and M persicae (Shands et al, 1955).

Praon spp was the dominant primary parasitoid on M persicae and M euphorbiae on Brussels sprouts in the Edinburgh area (Agyen-Sampong, 1972) but appears generally to occur in low numbers on aphids on potato (eg Dunn, 1949), as in the current study.

(ii) Hyperparasitoids

Overall per cent hyperparasitism was 20.6 in 1983 (see Table 14) and 27.1 in 1984. Asaphes vulgaris (Pteromalidae) and Dendrocerus aphidum (Megaspilidae) were the most common species in both years. In 1983, 4 D carpenteri (3♂♂, 1♀) emerged from mummies collected on 25 July. D aphidum was first collected on 13 July and last observed on 8 August in 1983: corresponding dates for 1984 are 1 and 14 August. Asaphes vulgaris emerged from mummies collected between 13 July and 8 August in 1983, and 1 and 8 August in 1984. An alloxystine (Cynipidae) adult was present in each of the 2 Praon cocoons dissected in 1984 and lacking Praon adults. One of these mummies was collected on 7 August, the other on 8 August. Sex ratios of hyperparasitoids (♂:♀) in 1983 were: D aphidum - 1.0 (n=48), A vulgaris - 2.0 (n=33), D carpenteri - 3.0 (n=4).

Hyperparasitism decreases the impact of parasitoids on aphid populations, although hyperparasitoids are beneficial if they attack secondary parasitoids. Hyperparasitism of the potato aphid was very high on tomatoes in Ohio (Walker et al, 1984), and in Maine hyperparasitism of aphids on potato ranged from 2.8-46.3 per cent over 9 years (Shands et al, 1955).

A vulgaris was the dominant hyperparasitoid (20 per cent) of M euphorbiae and M persicae on Brussels sprouts near Edinburgh (Agyen-Sampong, 1972), and Asaphes spp have been reported from potato aphids in the USA (Shands et al, 1955), Canada (MacGillivray and Spicer, 1953) and England (Dunn, 1949). Alloxystinae and Dendrocerus spp have also been recorded from aphids on potato (Dunn, 1949; MacGillivray and Spicer, 1953; Shands et al, 1955, 1965).

(b) Laboratory

Percentage parasitism of Macrosiphum euphorbiae differed with the method of assessment used. Of 57 alate adults dissected in 1983, none contained parasitoid larvae; of 290 apterae dissected, parasitoid larvae were present in 14 (about 5 per cent); and of living aphids reared in the laboratory, approximately 27 per cent of those collected on 18 July and 19 per cent of those sampled on 25 July were parasitised (Tables 15 and 16).

On 18 July mummy counts in the field indicated about 8 per cent of aphids

Table 14

Total number hyperparasitoids in 1983

Species \ Date	13 July	18 July	25 July	8 August	16 August	25 August	30 August	Total
Asaphes vulgaris	0	0	12	14	4	2	0	32
Dendrocerus aphidum	2	6	34	3	0	0	0	45

Table 15

Per cent parasitism of the potato aphid estimated by field mummy counts (*Aphidius picipes* only) or by the number of apparently healthy aphids collected on 18 July 1983 and mummifying within 7 days
*(n=number parasitised and number unparasitised aphids)

Treatment / Method of estimation	demeton-S -methyl trial untreated	demeton-S methyl	Manipulative trial untreated	methiocarb	thiometon	methiocarb + thiometon	Overall mean
Live aphids reared in laboratory	21.7 *(n=23)	22.2 (n=18)	29.4 (n=17)	37.5 (n=8)	28.6 (n=14)	20.0 (n=20)	26.6±2.7
Mummy counts in field	9.8 (n=296)	10.4 (n=259)	5.6 (n=356)	9.2 (n=389)	4.4 (n=343)	7.1 (n=378)	7.7±1.0

Table 16

Per cent parasitism aphids estimated as for Table 15 but counts and collections made on 25 July 1983
*(n=number parasitised and number unparasitised aphids)

Treatment / Method of estimation	demeton-S-methyl trial untreated	Manipulative trial untreated	methiocarb	Overall mean
Live aphids reared in laboratory	20.8 (n=25)	21.2 (n=33)	15.4 (n=26)	19.1±2.0
Mummy counts in field	3.0 * (n=566)	2.0 (n=848)	2.4 (n=588)	2.5±0.3

were parasitised. Corresponding figures for dissection and live aphid rearing were 8 and 27 per cent respectively. Many published data of per cent parasitism may therefore be underestimates if mummy counts only were used.

Assessment of primary parasitism based on mummification of laboratory reared aphids may, however, be artificially high in the present study. Wasps were not reared from mummies and some may have been hyperparasitoids. In the field, more parasitoids die before host mummification than die in the laboratory (Carter et al, 1982), perhaps due to improved environmental conditions in the laboratory. Also, adult parasitoids may have been inadvertently confined with the live aphid sample. As Agyen-Sampong (1972) noted that A picipes induced host mummification after 9.5 days at 20-23°C, it seems unlikely that mummies would have formed within 7 days of oviposition.

The main reason for observed differences in per cent parasitism may be that many aphids leave the plant prior to mummification, and are never recorded during mummy counts (see Powell, 1980). If a substantial proportion leave plants before death, assessment of parasitoid impact may be grossly underestimated by mummy counts in the field.

3-3-3 LACEWINGS

Few lacewings were seen in this study, none in 1985. Eight stalked eggs, indicating Chrysopidae, were found on potato foliage, 2 in 1983 and 6 in 1984, all in July and August. No adults or larvae were seen on plants but a total of 19 larvae were caught in pitfall traps, 18 in 1983 and one in 1984. In both years larvae were trapped in late summer/early autumn, and may have been actively searching for food. Larvae were not identified further.

One adult Chrysopa phyllochroma was caught in a pitfall trap in 1984. This species is uncommon in Scotland (I Baldwin, pers comm).

3-3-4 LADYBIRDS

A total of over 600 ladybirds was counted in 3 years, 500 by visual searching and 130 by pitfall trapping. Of the larvae and pupae reared to adults all were

Coccinella septempunctata, the commonest of the British ladybirds (Blackman, 1965). It was found on potatoes in northern England but was not common except sporadically when it appeared in large numbers in swarms (Dunn, 1949). Only 10 of 274 adults in the current study were of species other than C septempunctata: one Adalia decempunctata and 9 Coccinella undecimpunctata were present on foliage in 1983 and 1984.

In 1983, numbers of coccinellid adults, larvae and pupae on foliage were low until August, although the first adult had been seen on 20 June (Figure 8). Few were present at time of treatment and data were combined such that means represent total numbers in 24 plots. After treatment numbers were low in plots sprayed with demeton-S-methyl or thiometon, probably due to lack of aphid prey. Numbers peaked on 8 August when there was a mean of 6.2 ladybirds (adults, larvae and pupae) in untreated or methiocarb plots, and 0.7 in plots sprayed with demeton-S-methyl or thiometon. On 8 August most were adults and pupae and few larvae were seen at any time. Between 29 June and 7 September, 16 coccinellid larvae and 13 C septempunctata adults were found in pitfall traps.

Few ladybirds were present at the first treatment date in 1984. Peak numbers occurred in early August (Figure 9), and few were seen at any time in plots sprayed with demeton-S-methyl, again likely due to a scarcity of aphids. Individuals were first seen on 19 June and were present until the last sample in August. The decline after 20 August is likely due to adults leaving the crop and to starvation of some larvae as aphid numbers declined. Larvae were seen cannibalising pupae and other coccinellid larvae in August. Nearly 80 larvae were caught in pitfall traps in untreated plots on 10 and 15 August 1984, and may have been searching for food before capture. Few larvae were trapped in treated plots.

In 1985, 75 adults, but no larvae or pupae, were seen on foliage. Three adults and one larva were trapped in pitfall traps. Most ladybirds in 1985 were from untreated plots (Table 17), even at the sample before the second spray, although numbers were low. Thirty-eight coccinellid eggs were seen in 1985, in 3 batches of 12, 16 and 10. Eggs were not seen in 1983 or 1984.

Overall in the 3 years, there were 274 adults, 261 larvae and 70 pupae. Adults

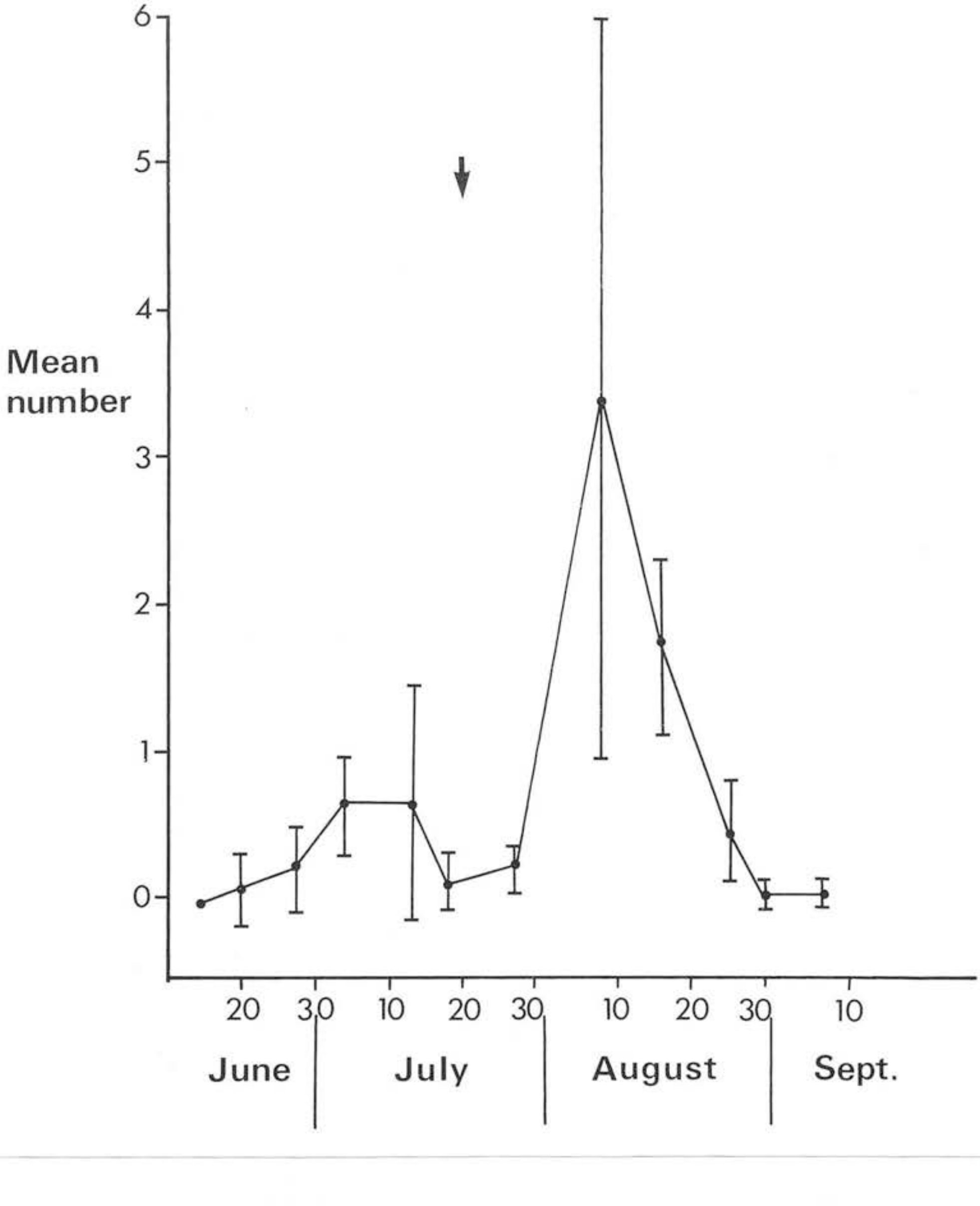


Figure 8. Means and 95 per cent confidence intervals of ladybird adults, larvae and pupae per plot, sampled visually, 1983. Data from all treatments are combined. Arrow indicates treatment.

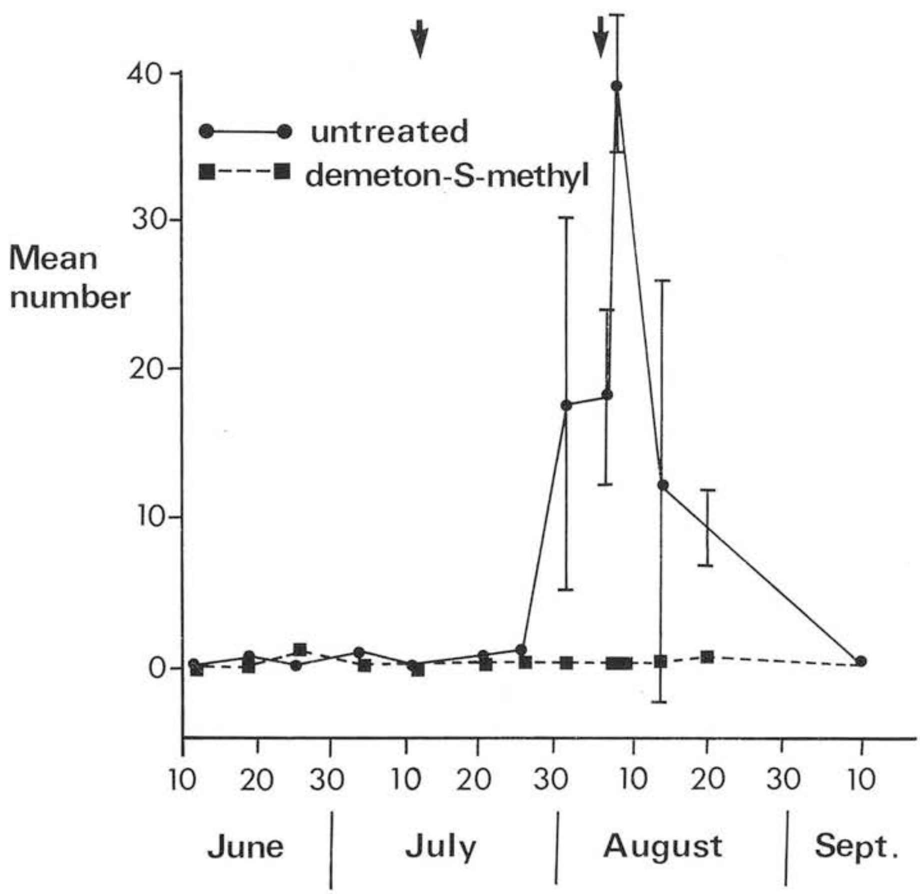


Figure 9: Means and 95 per cent confidence intervals of ladybird adults, larvae and pupae per plot, sampled visually, 1984. Arrows indicate treatment.

Table 17

Total number <u>Coccinella septempunctata</u> adults in all plots per treatment sampled visually in 1985
Arrows indicate treatment

		Treatment	
	Date	Untreated	demeton-S-methyl
→	25 July	15	9
	26 "	-*	-
	27 "	-	-
	28 "	0	0
	1 August	3	0
	8 "	3	1
→	14 "	13	3
	15 "	9	1
	16 "	10	1
	17 "	6	0
	21 "	1	0
	28 "	0	0

* - : no samples taken due to heavy rainfall

were the commonest stage in 1983 and 1985, and larvae were commonest in 1984. Numbers were low at times of treatment so any direct effects of the pesticides used could not be determined.

3-3-5 HOVERFLIES

Few hoverflies were seen in any year. Overall, 6 adults, all from pitfall traps, and 18 larvae, of which 14 were found in pitfall traps, were sampled. Most were present in August and September in 1983 and 1984. In 1985, 2 larvae and 5 eggs were observed on foliage in untreated plots only.

Four species of adult hoverfly were trapped: *Syrphus vitripennis*, *Metasyrphus corollae* and *Episyrphus balteatus* are common and generally distributed species with aphidophagous larvae (Coe, 1953); *Eumerus strigatus* larvae are pests of bulbs (Coe, 1953). Although uncommon in the fields studied, hoverflies, particularly *E balteatus*, were one of the most abundant groups of predators of potato-infesting aphids in a study in Essex (Foster, 1972).

CHAPTER 4

POLYPHAGOUS PREDATORS

FAUNAL ASSESSMENT

4-1 INTRODUCTION

Thiele (1977) stated that the epigeal fauna of agricultural crops was not well studied and certainly until that time few such studies were reported in the literature: for example, Coaker and Williams, 1963; Mitchell, 1963b; Rivard, 1966; Kirk, 1971. Over the past 10 years interest has expanded considerably and information now exists on the fauna of many different crops. Epigeal arthropods in cereals have received most attention (eg Speight, 1976; Ericson, 1978; Sunderland and Vickerman, 1980; Sotherton, 1982; Pietraszko and de Clercq, 1983a,b; Scheller, 1984; Powell et al, 1985). Less well studied crops include apples (Holliday and Hagley, 1978; Hagley et al, 1982), brassicas (Coaker and Williams, 1963; Mitchell, 1963b), carrots (Andersen, 1985), lucerne (Lyngby and Nielsen, 1981; Leathwick and Winterbourn, 1984), maize (Tyler and Ellis, 1979), sugar beet (Baker and Dunning, 1975; Wratten and Pearson, 1982), and swedes (Andersen, 1985).

Ground beetles (Coleoptera : Carabidae) appear to be the numerically dominant epigeal arthropods in many arable situations (eg Jones, 1976; Purvis and Curry, 1984; Andersen, 1985) with rove beetles (Coleoptera : Staphylinidae) and arachnids often common (eg Foster, 1972; Wratten and Pearson, 1982). Other arthropods, including predaceous bugs (Hemiptera : Anthocoridae) and earwigs (Dermaptera) occur less consistently (eg Vickerman and Sunderland, 1975; Root and Gowan, 1978). Root crops including potatoes are considered to differ from other crops particularly in their ground beetle fauna (Thiele, 1977). Results obtained from one crop cannot therefore confidently be extrapolated to another. The potato fauna must be determined separately and results for parts of eastern Scotland are given in this chapter.

Populations of epigeal arthropods are commonly assessed by pitfall trapping, a sampling method discussed in the following section.

4-1-1 METHODOLOGICAL PITFALLS

Populations of epigeal arthropods may be assessed using a range of sampling methods, each of which is biased towards particular components of the fauna (Sunderland and Chambers, 1983). Direct quadrat counts and soil sifting may be precluded by low density of arthropods (Greenslade, 1964) or by the resultant site destruction (likely, for example, in ridged potato crops), and pitfall trapping appears to be the method of choice. Pitfall trapping is commonly used because it is relatively cheap and not labour intensive (Luff, 1975). Results must be interpreted, however, with discretion due to the many factors which may influence catch. This subject was recently reviewed by Adis (1979).

The sampling method is essentially passive; containers are set in the ground and an animal intercepting one falls in and is unable to escape. Catches depend not only on the density of the study population but also on the activity of individuals in that population (Mitchell, 1963b; Edwards et al, 1979; Brunsting, 1983): a more active individual is more likely than a less active one to encounter a trap. Activity, and thus catch, can itself be affected by temperature (Briggs, 1960), hunger-status (Baars, 1979), mating and oviposition (Briggs, 1960), and type and/or density of vegetation in the trap vicinity (Greenslade, 1964). If a high activity level increases the effectiveness of a predator, a sampling method incorporating activity assessment may be desirable in predator studies.

Trapping efficiency can be influenced by other factors. Luff (1975) measured efficiencies of capture of 24-90 per cent in laboratory tests of traps different in size, shape and material of composition. Preservatives sometimes added to eliminate within-trap predation, can influence catch. Formalin appears to be attractive to some species of ground and rove beetles (Luff, 1968), although Ericson (1979) found no difference in overall catches of Pterostichus cupreus in winter wheat using dry traps or traps containing 5 per cent formalin. Pitfall traps are inefficient at catching some ground beetles, rove beetles, earwigs and linyphiid spiders (Sunderland and Chambers, 1983), possibly because of the animals' small size, flight ability, long tarsal claws or relatively long legs.

Comparisons of pitfall trap catches between years, different sites and different crops are best undertaken with caution. Despite their drawbacks pitfall traps do allow relative comparisons between different areas of a habitat within the same sampling period (Adis, 1979). They are thus adequate for use in monoculture crop situations where relative comparisons are required between plots in a field, as in the present study.

4-1-2 ARACHNIDA

(a) Spiders (Araneae)

Approximately 500,000 species of spider have been described worldwide, and about 600 are known from Britain. Most spiders make webs to catch the "animal plankton" and all are predatory and will eat one another (Jones, 1983). Longevity varies from a few months to several years and individuals may continue to moult after reaching maturity (Savory, 1977). Spiders in northern regions may take longer to complete their life-cycles than in the south (Edgar, 1971).

A small proportion of species migrates by "ballooning", where silk secreted from spinnerets is drawn out to a thread which is taken by the wind (Savory, 1977). Large fluctuations in numbers may occur, and sudden falls in population densities of spiders which commonly "balloon" (eg Foster, 1972) make data on effects of pesticides from field studies difficult to interpret. However, in an experiment in Israel wolf spiders were found in untreated apple orchards only (Mansour et al, 1983) and in the laboratory Erigone spp (Linyphiidae) were highly susceptible to pirimicarb, cypermethrin and methyl parathion (Brown et al, 1983).

Digestion in spiders is external (Jones, 1983), and they are in general opportunistic feeders particularly of flies, aphids, springtails and other insects (Aitchison, 1984). Many spiders, including web-builders and hunters, are known to eat pest aphids (Shiga, 1966; Vickerman and Sunderland, 1975; Nyffeler, 1983; Leathwick and Winterbourn, 1984; Sunderland et al, 1986). In China spiders are considered important in regulation of rice-hopper populations (Shibang, 1983). Few reports of spiders in potato fields were seen: Foster (1972) stated that certain Linyphiidae eat pest aphids in potato and Boiteau

(1983b) suggested a relationship between spider numbers in potato fields in Canada and abundance of the potato aphid.

The potential for web capture of aphids may be high because they cannot shed their legs, their long appendages increase the surface area available for entanglement and alatae are weak fliers (Nentwig, 1980). Capture efficiency probably varies depending on whether or not webs are "sticky", their size and their placement. Natural enemies of aphids may be killed by spiders (Foster, 1972). A review of the potential of spiders in biological control is given by Riechert and Lockley (1984).

(b) Harvestmen (Opiliones)

Harvestmen constitute the third largest order of the Arachnida, the Opiliones (Jones, 1983). Of 3500 species worldwide, only 22 occur in the United Kingdom (Sankey and Savory, 1974). They are distinctive animals, the majority characterised by extremely long legs. This, as well as other attributes, prompted their description by Savory (1977) as "the comedians of the Arachnida". Savory (1977) continued:

> "(harvestmen are) animals with rotund bodies ornamented with little spikes, with two eyes perched atop, back to back, like two faces of a clock tower, with ungainly legs insecurely attached, with feeble jaws and an undying thirst - a queer assortment of characters, even among queer folk".

Harvestmen are nocturnal (Jones, 1983) and live for about one year (Sankey and Savory, 1974). Eggs are laid in clusters, below the surface of damp soil (Savory, 1948), under stones and in cracks in wood (Todd, 1949). Most British species oviposit in autumn and the young hatch in the spring and early summer (Savory, 1948). Mating is frequent, requiring no courtship and, although sexual reproduction is usual, parthenogenesis may also occur (Sankey and Savory, 1974). Adults are most common in autumn and it was probably their abundance at "harvest-time" which earned the order its common name.

Harvestmen consume chitinous remains (Savory, 1977) and, although omnivorous (Jones, 1983), they mainly eat live animal prey (Todd, 1950). Recorded food items include calliphorid flies (Todd, 1950), bird-droppings, mushrooms, earthworms, earwigs, psyllids, spiders and noctuid moth larvae

(Bristowe, 1949). Reports of harvestmen eating aphids have been few possibly because this group has been somewhat neglected. Leiobunum rotundum (Todd, 1950) and Phalangium opilio (Bristowe, 1949) have, however, been observed preying on aphids. Wratten and Pearson (1982) stated that harvestmen were common in sugar beet fields but were fluid-feeders!

Harvestmen eat one another (Bristowe, 1949; Todd, 1950), although they are apparently distasteful to other arthropods, possibly due to an odoriferous fluid which they spray from thoracic glands (Blum and Edgar, 1971).

Little work appears to have been done on the effects of pesticides on harvestmen except that of Dempster (1967) who recorded Phalangium opilio in particular as sensitive to DDT sprays in Brussels sprouts.

4-1-3 INSECTA

(a) Rove beetles (Staphylinidae)

Nearly 1000 species of rove beetles occur in Britain, but the family is in general a neglected group (Tottenham, 1954). Rove beetles usually live in the top few centimetres of soil, in leaf litter and similar places, and most are active predators of a wide range of insects and other arthropods (Rotheray, 1986). Their habits are diverse, however, and staphylinids may be found in nests, among decaying organic matter and on moss, fungi and vegetation (Tottenham, 1954). Tachyporus spp, particularly T hypnorum, appear to be the commonest rove beetles in arable habitats including cereals (Vickerman and Sunderland, 1975; Sotherton, 1982; Shires, 1985) and sugar beet (Pietraszko and de Clercq, 1983a). Philonthus spp are also common (Feeney, 1983) and in potato fields in eastern Canada 97 per cent of staphylinids belonged to this genus (Boiteau, 1983b).

Tachyporus hypnorum is a spring-breeder, with larvae present during the summer and new adults occurring in the autumn (Speight, 1976). Larvae and adults climb plants readily (Feeney, 1983) and adults are active fliers (Speight, 1976). Tachyporus spp are univoltine in Britain (Dicker, 1944).

Larvae and adults of Tachyporus spp are predators of various insects including cabbage root fly (Coaker and Williams, 1963), the chrysomelid beetle Gastrophysa polygoni (Sotherton, 1982), and aphids (Dicker, 1944; Sunderland, 1975; Vickerman and Sunderland, 1975; Feeney, 1983). Unlike most staphylinids, Tachyporus spp are not exclusively fluid-feeders (Sunderland and Vickerman, 1980).

The effects of organophosphorous insecticides on rove beetles have been measured in plots of winter wheat treated in June with dimethoate (at 0.35 l ai/ha). Sprays reduced the number of adults captured in pitfall traps compared with those in untreated plots for up to 8 days (Powell et al, 1985). In spring wheat plots treated in June with parathion-methyl (at 1.0 kg ai/ha) the number of adult staphylinids recorded was less than 10 per cent of those in untreated plots (Shires, 1985). No reports of laboratory tests of pesticide toxicity to rove beetles were found by the author.

(b) Ground beetles (Carabidae)

The Carabidae is one of the world's largest insect families with over 40,000 described species (Thiele, 1977), 342 of which occur in Great Britain and Ireland (Luff, 1982b). Pterostichus melanarius is the most widespread carabid in European arable crops (Thiele, 1977) and often constitutes the majority of specimens caught in pitfall traps (Speight, 1976; Lyngby and Nielsen, 1981; Pietraszko and de Clercq, 1983b). Harpalus rufipes is common (Jones, 1979), as are Pterostichus madidus (Edwards et al, 1979), Bembidion spp (Coaker and Williams, 1963; Mitchell, 1963a; Jones, 1976) and Agonum dorsale (Edwards et al, 1979).

(i) Life history

In temperate climates ground beetles are univoltine (Thiele, 1977) and most have one of 2 types of life cycle. The majority are "spring-breeders" which overwinter as adults and emerge in spring to mate. Larvae are present in mid-summer when adults are scarce (Lindroth, 1974; Speight, 1976). "Autumn-breeders" like P melanarius, P madidus and Trechus quadristriatus overwinter mainly as larvae (Mitchell, 1963a; Luff, 1973; Hůrka, 1975), and adults emerge in mid-summer (Luff, 1973). Many ground beetles live for just one year, although Luff (1973) estimates that up to 25 per cent of adult ♀ P madidus overwinter and may lay eggs the following spring. A proportion of

P melanarius adults also successfully overwinters (Ericson, 1978). The eggs (Mitchell, 1963a), larvae (Jones, 1979) and pupal chambers of most carabid species are found in the soil, and adults shelter in cracks in the soil (Ericson, 1977).

(ii) Diet

The food of ground beetles is varied (Briggs, 1960; Luff, 1974a; Sunderland, 1975) and, although the family is considered overall to be carnivorous, herbivory and omnivory occur (Davies, 1953). Certain species are crop pests: Harpalus rufipes (Briggs, 1960), Pterostichus madidus will eat strawberries (Luff, 1974b).

Some carabids exhibit extreme polyphagy (see Table 18) which may enable them to persist in crops with low pest density. Polyphagy can, however, lessen their effectiveness as pest control agents, through predation of beneficial species. P melanarius adults will kill and consume adult P madidus in the laboratory even when provided with an alternative food supply (P L Dixon, unpublished). P melanarius will eat linyphiid spiders and rove beetles (Sunderland, 1975), and P madidus may take earwigs (Gradwell, 1954), Bembidion spp, Nebria brevicollis and rove beetle larvae (Luff, 1974a). Ground beetle adults (Hagley et al, 1982) and larvae (Thiele, 1977) are cannibalistic. Larvae are also highly predatory (Tomlin, 1975). Many species are opportunists and diet changes throughout a season (Chiverton, 1984) may simply reflect prey availability. Some carabids will consume dead insects (Young, 1984) but the frequency and importance of this activity is unknown.

Information regarding ground beetle diets is, however, currently limited as the nocturnal habits of many species make direct observation of predation very difficult (Grant and Shepard, 1985), and available laboratory techniques have shortcomings (see Chapter 5). Nonetheless, many species have been recorded as either containing aphid remains or as having eaten aphids in the laboratory (Table 19), and they may have great potential as predators of pest aphids.

(iii) Natural enemies

Predators:

Records of predators of ground beetles are few, although Thiele (1977)

Table 18

Some food items of Pterostichus melanarius exemplifying the extreme polyphagy of some ground beetles

(L = Laboratory, F = Field)

Site	Food Item	Source
L	Aphis fabae nymphs	Dunning et al, 1975
L	Wheat bulbfly (Delia coarctata) pupae	Ryan, 1975
L	Euxesta notata (Diptera : Ortalidae)	Tomlin, 1975
L	Northern corn rootworm (Coleoptera : Chrysomelidae) larvae and eggs	Tyler & Ellis, 1979
L	Scarabid beetle larvae; codling moth larvae + eggs; earthworms; weed seeds	Hagley et al, 1982
F	Strawberries	Briggs, 1960
F	Cabbage root fly (Delia radicum)	Coaker & Williams, 1963
F	Trechus quadristriatus (Coleoptera : Carabidae)	Mitchell, 1963b
F	Cereal aphids, "flies", Erigone atra (Araneae : Linyphiidae) Philonthus spp (Coleoptera : Staphylinidae) larvae	Sunderland, 1975
F	Gastrophysa polygoni (Coleoptera : Chrysomelidae) larvae + adults	Sotherton, 1982
F	Bembidion spp (Coleoptera : Carabidae), ladybeetle larvae, hoverfly larvae, Rhopalosiphum padi	Chiverton, 1984

Table 19

Ground beetles recorded as aphid predators in either laboratory (L) or field (F)

Site	Aphid	Ground Beetle	Source
L	Rhopalosiphum padi	Bembidion lampros	Scheller, 1984
F	cereal aphids	Pterostichus melanarius, Harpalus rufipes, Agonum dorsale, B lampros	Sunderland, 1975
F	"	A dorsale, B lampros, Trechus quadristriatus	Vickerman and Sunderland, 1975
F	"	16 species including A dorsale, Synuchus nivalis, Demetrias atricapillas	Sunderland and Vickerman, 1980
F	"	A dorsale	Griffiths, 1982
F	"	Bembidion obtusum	Feeney, 1983
F	"	H rufipes	Loughridge and Luff, 1983
F	"	A dorsale, B lampros, P melanarius, Loricera pilicornis	Scheller, 1984
F	Rhopalosiphum padi	P melanarius	Chiverton, 1984
L	Aphis fabae	Bembidion spp, P melanarius, H rufipes, Harpalus aeneus	Dunning et al, 1975
L	Myzus persicae	H rufipes	Loughridge and Luff, 1983
F	Strawberry aphid	A dorsale	Dicker, 1951
F	aphids	Nebria brevicollis	Penney, 1966
F	aphids	Pterostichus madidus	Luff, 1974a

states they are eaten by birds and probably by hedgehogs and shrews.

Parasitoids:

Parasitoids recorded from Carabidae include Hymenoptera (Rivard, 1964; Luff, 1975, 1976, 1982a), mermithid nematodes (Rivard, 1964; Jones, 1979) and tachinid larvae (Rivard, 1964, Jones, 1979). Luff (1982a) recorded 20.3 per cent of Harpalus rufipes larvae collected by spring soil sampling as parasitised by Proctotrupes gladiator (Hymenoptera : Proctotrupidae) and up to 27 per cent by Microctonus caudatus (Hymenoptera : Braconidae) (Luff, 1976). Rates of infection of less than 1 per cent have been recorded, however, for Nebria brevicollis (Luff, 1975).

Percentage parasitism of beetles may be underestimated. During at least the later stages of parasitism it is probable that beetle activity is decreased. If population assessment is via pitfall trapping, parasitised beetles are less likely to be trapped than unparasitised ones.

(iv) Effects of pesticides

According to Thiele (1977) carabid beetles appear to be much more susceptible to the effects of pesticides than are other insects. A review of the literature reveals this to be an overgeneralization: susceptibility varies with species, pesticide and mode of exposure. Even different formulations of the same active ingredient may vary in their level of effect. In a laboratory experiment, carbofuran sprayed on to soil killed 100 per cent of carabids tested whereas exposure to carbofuran granules induced a level of mortality similar to that in the untreated beetles (Gholson et al, 1978).

Laboratory studies tend to confirm ground beetle susceptibility (eg Brown et al, 1983). A variety of chemicals in both granular and liquid formulations has been reported as toxic to carabids including members of the organochlorine, organophosphate, carbamate and pyrethroid insecticide groups (Mowat and Coaker, 1967; Tomlin, 1975b; Hagley et al, 1980; Brown et al, 1983). Application methods are not consistent in laboratory studies and as beetle susceptibility is known to vary with mode of exposure (Wilkinson, 1983), comparison of results is difficult. For example, Brown et al (1983) exposed beetles to a dry film of insecticide on glass whereas Hagley et al (1980) applied materials directly using a micro-applicator.

Laboratory results are valuable nevertheless, for example in illustrating differences in susceptibility between species. Agonum dorsale is consistently reported as susceptible to a variety of insecticides (Mowat and Coaker, 1967; Wilkinson, 1980; Brown et al, 1983). Mortality of Pterostichus melanarius treated with pesticides may be very low (eg Hagley et al, 1980), although acephate, demephion and demeton-S-methyl killed over 90 per cent of adult P melanarius when beetles were totally immersed for one second in the aphicide solution, or fed contaminated food (Dunning et al, 1982).

Differences in susceptibility of species to insecticides may be caused by a number of factors. Factors influencing beetle activity level and thus exposure and mortality, include temperature, age and hunger status (Critchley, 1972). Cuticular thickness may also affect susceptibility (M Luff, pers comm). Susceptibility is apparently inversely related to beetle size (Hagley et al, 1980). Critchley (1972), for example, recorded that small carabids of the size of Bembidion lampros succumb 12-13 times as rapidly as P melanarius. Size and susceptibility are not always inversely related (Mowat and Coaker, 1967).

Extrapolation of laboratory results to field situations must be done with caution. Exposure to foliar sprays may be very low due to the secretive and nocturnal habits of many carabids, particularly if ground cover by the crop canopy is extensive. Also, toxicity in the laboratory may be exaggerated due to a build-up of vapour pressure in test chambers (Brown et al, 1983).

In field investigations into the effects of pesticides, the numbers of carabid beetles in pitfall traps in sprayed areas are often lower than those in unsprayed areas, after treatment. Catches in treated plots usually subsequently "recover" (eg Sekulić and Dedić, 1983; Chiverton, 1984; Powell et al, 1985; Shires, 1985). This is often attributed to pesticide toxicity followed by a re-invasion of treated areas by beetles from outside. Other explanations have, however, been proposed (eg Feeney, 1983; Chiverton, 1984) and are discussed in Chapter 7.

4-2 MATERIALS AND METHODS

4-2-1 EARWIG TRAPS

White, opaque plastic pots, 13.4 cm high with a fluid capacity of 650 ml

(Sweets Services Ltd, Edinburgh) were inverted and fixed with drawing pins to bamboo canes (Plate 1). Each cane was pushed into the soil until the mouth of the pot was held 10 cm above the soil surface. A piece of crumpled blank newsprint was inserted into each pot to provide a suitable resting place for earwigs.

In 1983, 5 traps were placed in each plot but due to low numbers caught a single trap per plot only was used in 1984 (Figure 10). Earwig traps were examined weekly from the beginning (29 April and 15 May in 1983 and 1984 respectively) to the end (14 September, 11 September) of each trial. Wet or missing paper was replaced. Earwig traps were not used in 1985.

4-2-2 PITFALL TRAPS

Pitfall traps were used to sample ground-based arthropods and consisted of a container (perimeter: 25 cm; depth: 12 cm) and a cover to exclude rainfall (Plate 1). Containers were clear polystyrene no 16 "Pioneer" polypots (A and W Gregory Co Ltd, Glynde Street, London). Covers were 10 cm x 10 cm squares of hardboard, with 4 nails per cover as legs. Hardboard and nails were dipped in "Ronseal" polyurethane outdoor wood seal varnish.

Polypots were placed in holes dug in the furrows such that their rims were level with the soil. Forty-five ml of 10 per cent formalin and a drop of detergent to reduce surface tension were added to each container on each sampling occasion. Covers were positioned centrally 2 cm above the polypots.

Five traps were placed in each plot in 1983; 7 traps in each plot in 1984 and 1985 (Figure 10). In all years trapped arthropods collected in the field were placed in styrofoam cups and returned to the laboratory for identification and relevant analysis.

Pitfall traps containing formalin were examined at approximate weekly intervals in 1983 and 1984. In 1983, traps were in position and operating for 7 days prior to each sample being taken (ie they were constantly in operation, give or take a day or two needed for access of tractors and sprayers to apply fungicide). The single exception was the first sample after treatment which was taken at 5 days. In 1984, traps were in operation over 24 hour periods

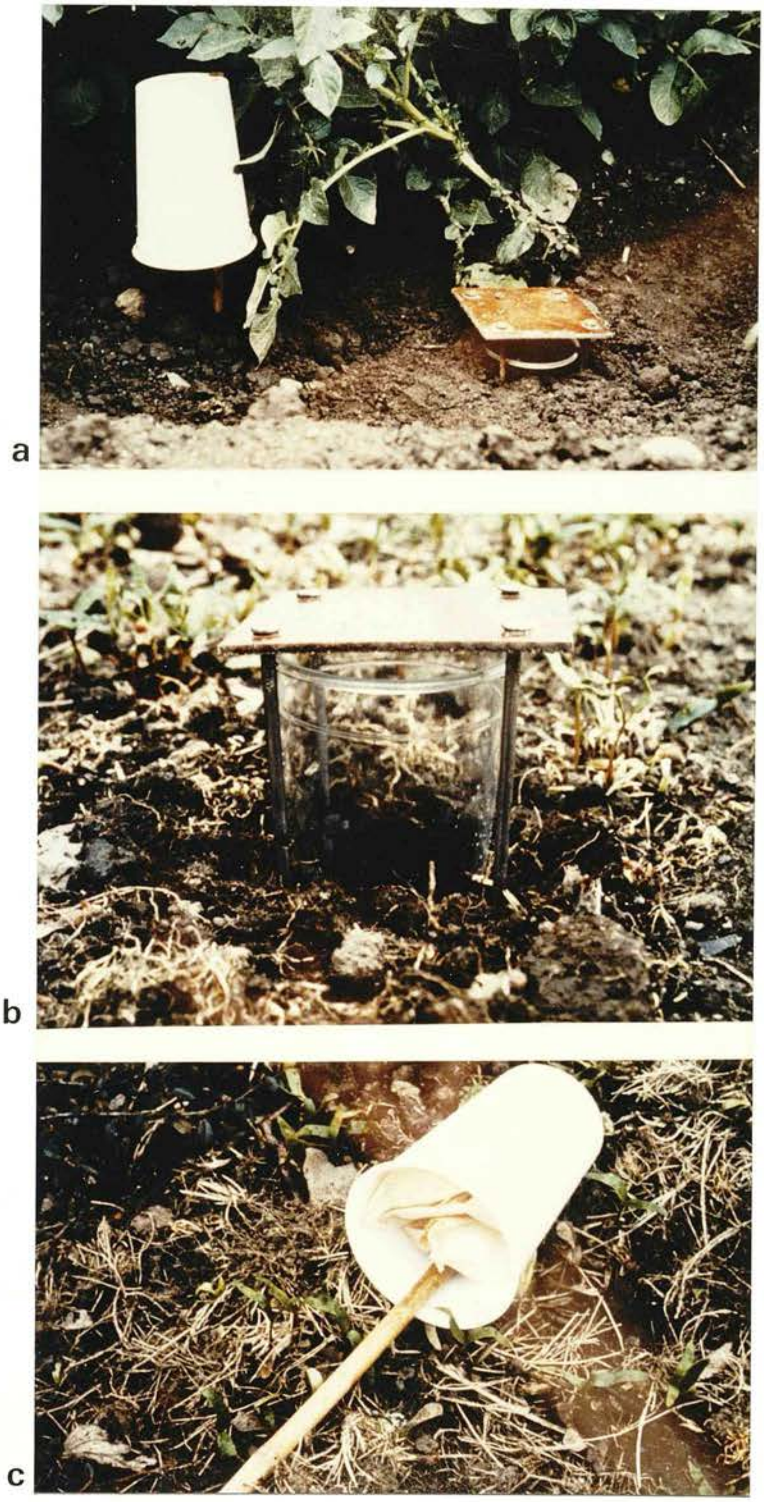


Plate 1: Examples of traps used to sample epigeal arthropods (a = earwig trap (left) and pitfall trap with rain cover, in position in furrow; b = exploded view of a pitfall trap; c = earwig trap showing paper inside container).

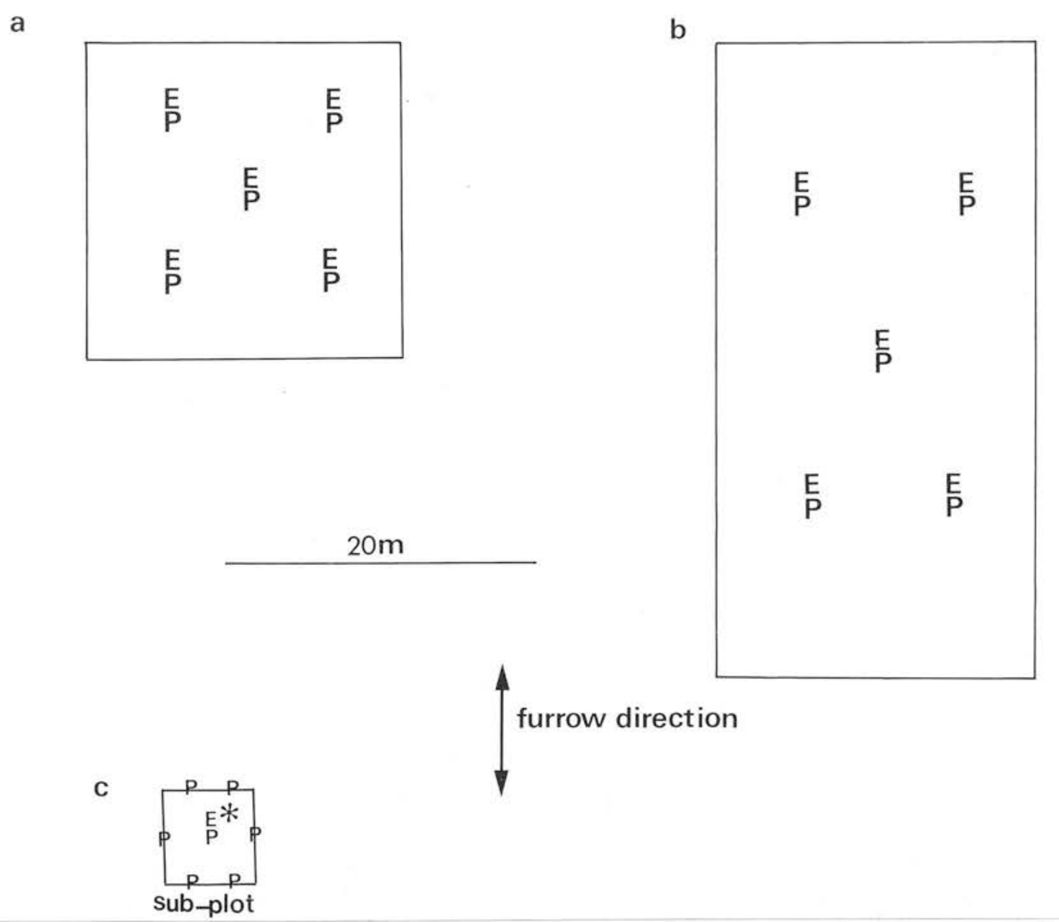


Figure 10: Layout of pitfall (P) and earwig (E) traps in field plots.
(a = 1983 (small plot); b = 1983 (large plot); c = 1984 and 1985).
(* - 1984 only).

only except during the 2 spraying occasions when sampling intensity was increased. At the first spray (12 July) all types of sample were taken immediately before as well as at 2, 4, 7, 24, 48 and 72 hours after treatment. Samples taken at the second spray (7 August) were again taken prior to application and at 24, 48, 72 hours afterwards. After the second treatment, pitfall traps were checked at 01:00 on 8 August, 11 hours post-spray. This sample was taken as it was estimated to be about midway through the activity cycle of the Pterostichus species under study (Luff, 1978).

In 1985, all types of sample were taken immediately pre-spray and at 24, 48 and 72 hour, and 1 and 2 week post-spray intervals only, at each of the 2 spraying occasions.

4-3 RESULTS AND DISCUSSION

4-3-1 EARWIG TRAPS

No earwigs were caught in earwig traps. One Forficula auricularia only was caught in a pitfall trap.

4-3-2 PITFALL TRAPS

(a) General

Over 11,000 animals were caught in pitfall traps during the 3 years. Of these, 89 per cent were insects, and 80 per cent of these were ground beetles. Percentages of some of the commonest groups are given in Table 20. Many taxa were represented by single or very few individuals and others were of sporadic occurrence. These are not discussed in detail but total numbers of all animals caught in each year are given in Appendix 1.

Arthropods considered to be potential aphid predators were identified to species level where possible but several were taken to higher taxa only. Some staphylinids are particularly difficult to identify (R Lszykowski, pers comm). The linyphiid spiders were also difficult to identify because the male palps had opened in the formalin-filled traps, and many specimens were immature.

Table 20

Per cent of total animals caught in pitfall traps, comprised of various taxonomic groups in 1983, 1984 and 1985 and overall in the 3 years

Percent of total

Animal \ Year	1983	1984	1985	Overall per cent
Total insects	85.1	88.6	92.2	88.6
Ground beetles	76.3	82.0	81.0	79.8
Rove beetles	2.6	2.6	10.2	5.1
Harvestmen	2.0	3.0	0	1.7
Spiders	9.8	8.1	6.7	8.2

Coccinellid larvae were present in pitfall traps in 1984, after aphid numbers had declined, and were probably searching for food. Many flies were found in traps. Most were teneral and presumably had pupated in the potato fields. The majority was detritivores or pests of crops other than potato (eg the onion fly and the cabbage root fly). The earthworms recorded in 1983 were mainly trapped on a single occasion and after heavy rainfall.

Throughout most of this chapter and elsewhere as appropriate pitfall trap catches are given as mean numbers per trap per 24 hours. This adjustment was made to compensate for the different numbers of traps and the different time periods traps were in operation in each year. If few individuals were caught, total numbers are presented.

(b) Spiders

Fifty hunting spiders and nearly 1000 Linyphiidae were trapped over the 3 years (Table 21, Figure 11). Most of the hunting spiders were of the Lycosidae, the wolf spiders and some were identified as Pardosa pullata. A single Agroeca proxima (Liocranidae) was trapped in 1983.

Wolf spiders, except those in 2 genera, do not build webs for prey capture but forage among low vegetation or on the ground (Stratton, 1985). Pardosa spp are poor climbers (Leathwick and Winterbourn, 1984) and are probably restricted to aphids on the ground. Pardosa pullata is characterised as a field species (Itämies and Ruotsalainen, 1985) and comprised 1.5 per cent of the spider catch for various habitats in Finland (Itämies and Ruotsalainen, 1984). Too few wolf spiders were caught to allow comment on treatment effects but overall, similar numbers were trapped in all plots each year.

Of the Linyphiidae, 713, 232 and 43 individuals were trapped in 1983, 1984 and 1985 respectively. Six specimens trapped in 1983 were identified as Lepthyphantes zimmermani. Populations were erratic with many peaks in 1983 and 1984 (Figure 11). These obscured any effects of the pesticides and may have been due to ballooning migrations. Numbers were similar in treated and untreated areas in all years and overall, increases in numbers were observed after treatment in 1983 and 1984 (Figure 11). These increases were not consistent, however: in 1983, numbers trapped rose from 3 to 6 before

Table 21

Total numbers of hunting spiders caught in pitfall traps in treated and untreated plots

	Total Number		
Month \ Year	1983	1984	1985
May	3	6	-
June	4	5	-
July	9	6	1
August	6	2	0
September	8	0	-
Total number	30	19	1

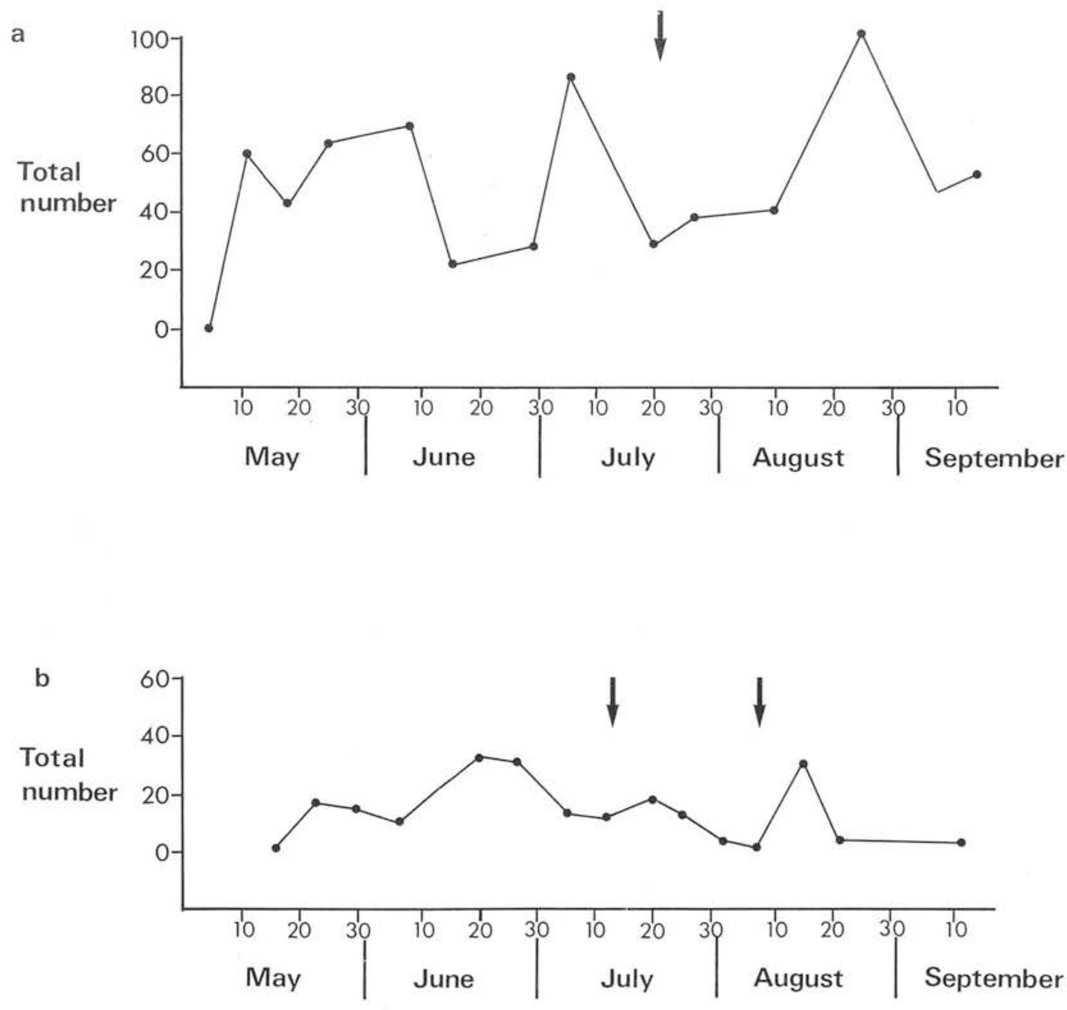


Figure 11: Total numbers of money-spiders from all plots during 1983 (a) and 1984 (b). Arrows indicate dates of pesticide application.

and after treatment with thiometon and methiocarb together, but fell from 9 to 2 after treatment with thiometon alone. In 1985, few were caught. Twenty-two of the total of 43 specimens were trapped on 17 August in 1985, and totals were 25 and 18 in treated and untreated plots respectively.

Linyphiids are small (approximately 2 mm) spiders which hang inverted below sheet webs and comprise about 40 per cent of British species (Jones, 1983). They may have greater potential than wolf spiders in aphid control because they are able to climb plants and spin webs. Linyphiids were common on potatoes in Essex where 3 species preyed on young nymphs of Myzus persicae, M ornatus and Aulacorthum solani (Foster, 1972).

In 1983, sheet webs were occasionally seen on potato foliage, particularly at hill bases between groups of haulms. On 4 July 1984 100 hills (50 from each of treated and untreated areas) were examined. Fifty per cent of hills in each area had sheet webs at their bases and, although this was not studied further, it suggests that some aphid mortality is due to entanglement in spider webs. Linyphiid webs in winter wheat covered over 50 per cent of the ground area in early August and many aphids were present and attacked on the webs by spiders (Sunderland et al, 1986).

(c) Harvestmen

Eight species of harvestmen were trapped during 1983 and 1984. No opilionids were caught in 1985.

Of a total of 233 specimens, 126 (54 per cent) were Phalangium opilio. This is a long-legged, highly active species which normally inhabits woodland, long herbage and bushes (Sankey and Savory, 1974). The first P opilio were trapped on 8 and 13 June in 1983 and 1984 respectively, although it is likely that some of the immature (and unidentified) harvestmen present before this were P opilio.

Catches declined in all treatments in the week following insecticide application in 1983 (Figure 12). This may be due to toxic effects being obscured by redistribution but data are few. In 1984, the first demeton-S-methyl spray had no apparent effect on numbers trapped, although at the

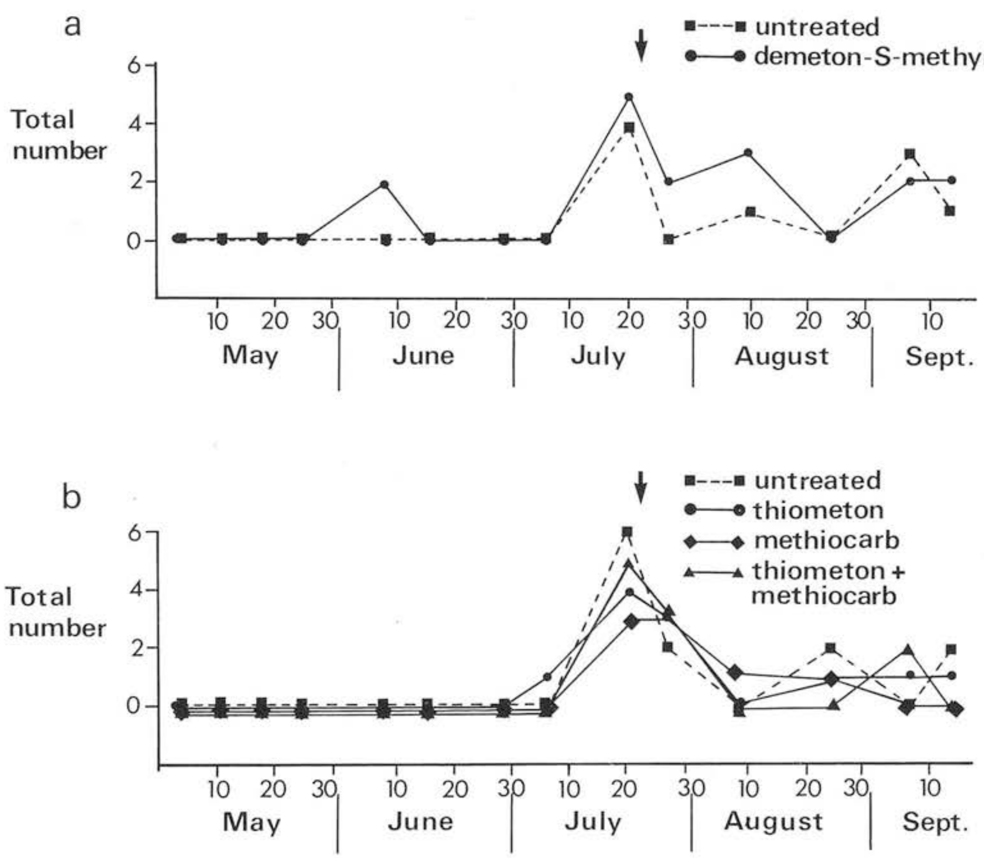


Figure 12: Total numbers of Phalangium opilio in 1983. Arrows indicate dates of treatment application.

second spray in August more were caught in treated plots (Figure 13). Whether this is a real effect is unclear due to low counts.

P opilio has been recorded from potato fields in Essex (Foster, 1972) and is described as a "cornfield" species by Todd (1949). Dempster (1967) says P opilio was an important predator in Brussels sprouts, where it spends the day in litter under plants. In general, this harvestman is numerous and well-distributed through the United Kingdom (Sankey and Savory, 1974).

Other species were uncommon during the time of pesticide application. In 1983, 43 Opilio saxatilis and 11 Paroligolophus agrestis were trapped in September, and 14 Mitopus morio in June. In 1984, 5 M morio were caught in August, 2 in September. O saxatilis is commonest on sand dunes but is also found on low vegetation (Jones, 1983). P agrestis is very common, particularly in trees, and M morio is widely distributed and often abundant, especially among grass and low herbage (Sankey and Savory, 1974). Data for uncommon species are given in Appendix 1.

It is possible that numbers of harvestmen present in potato fields were underestimated. Sankey and Savory (1974) suggest beating, sweeping and funnels (eg Berlese, Tullgren) as sampling methods but do not mention pitfall trapping. Harvestmen, with their long legs, may be able to avoid or escape from pitfall traps.

(d) Rove beetles

Approximately 350 rove beetles were trapped between 1983 and 1985 (Appendix 1), with over half trapped in 1983. Staphylinids were so few that effects of insecticides cannot be determined and Tachyporus spp only are discussed in detail.

Five species of Tachyporus were trapped in 1983, 4 in 1984 and one in 1985 (Appendix 1). T hypnorum was the most numerous overall, particularly in May 1983 and was present in each year. Other species were less common (Appendix 1). In 1984, only 9 Tachyporus specimens were trapped: 2 T hypnorum in May and one in June, 4 T chrysomelinus in May and one each of T pallidus and T pusillus in June. In 1985, one T hypnorum was present in a

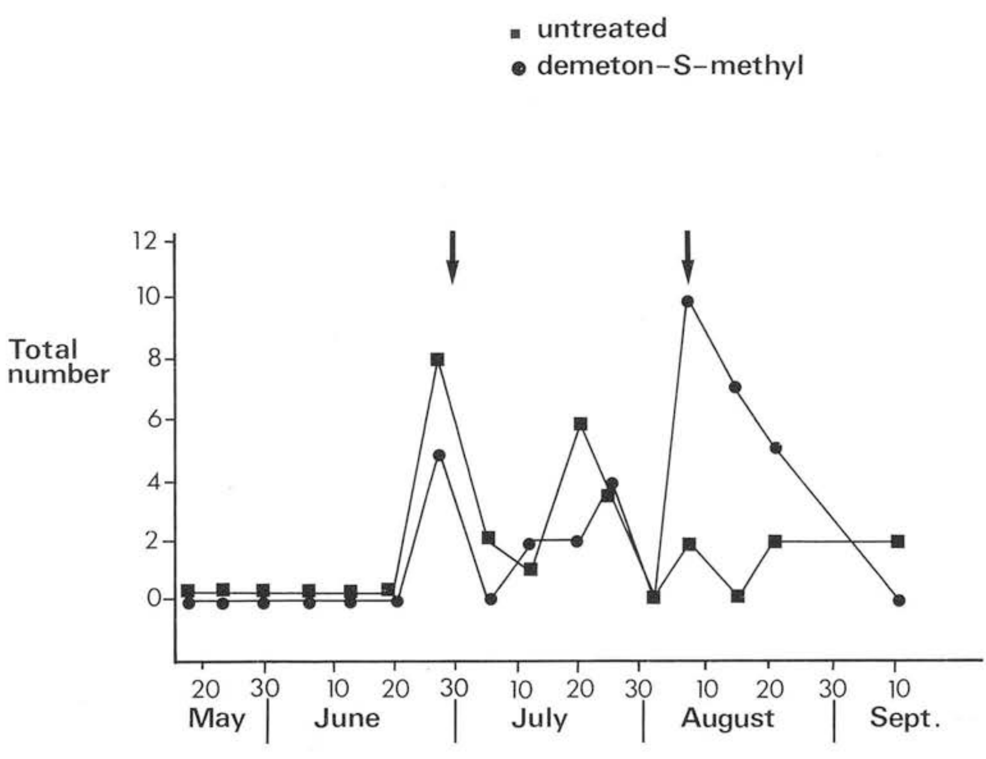


Figure 13: Total numbers of Phalangium opilio in 1984. Arrows indicate treatment application.

pitfall trap in July and 5 were trapped in August.

Single specimens of the widespread but local rove beetle (Tottenham, 1954), Deleaster dichrous were caught in 1984 and 1985. Xantholinus linearis was trapped in 1983 only: 48 specimens, of which 43 occurred in May. Twenty of the 30 Oxytelus spp trapped in 1984 were present in May and June.

Thirty-three specimens caught in each of 1983 and 1984 (total = 66) were not identified. These are small, taxonomically difficult beetles (R Lszykowski, pers comm), and again most occurred in the spring. In 1985, 67 rove beetles were trapped, the majority (35) on 17 August. Of the overall total of 67 individuals, 66 were from untreated plots. This may indicate an effect due to demeton-S-methyl application but data are inconclusive due to low numbers.

Tachyporus spp were seen on potato plants on several occasions in 1983 and 1984, and on 4 July 1984 2 small, black (unidentified) rove beetles were observed on lower leaves.

Data suggest that rove beetles may not have great potential as control agents of aphids on potato, partly because they occur mainly in the spring. Results must, however, be interpreted with caution. Luff (1968) found that formalin was attractive to certain staphylinids and this may have affected catches in the current study. Also, pitfall traps may not be an efficient sampling method for Tachyporus spp. Sunderland and Vickerman (1980) found this genus poorly represented in pitfall traps even when numerous in ground-search samples.

(e) Ground beetles

Nineteen species of ground beetle were collected over the 3 years but most were uncommon (Table 22). Pterostichus melanarius was overall the most abundant, representing 68 per cent of all specimens trapped. The ground beetle fauna was dominated by a few genera, 96 per cent of the catch being comprised of Trechus and Pterostichus. A similar situation was reported from Canadian potato fields (Boiteau, 1983a,b) where 4 genera, including Pterostichus and Harpalus constituted 91-95 per cent of all carabids collected. Harpalus spp, uncommon in the present study, are often abundant in

Table 22

Total numbers of each species of ground beetle caught in pitfall traps in 1983, 1984 and 1985

Species / Year	Total number 1983	1984	1985
Calathus melanocephalus	0	0	1
Nebria brevicollis	0	11	6
Notiophilus biguttatus	2	1	0
Clivina fossor	83	4	1
Trechus quadristriatus	327	1345	60
Bembidion lampros	0	13	3
Bembidion femoratum	2	0	0
Bembidion tetracolum	0	1	0
Bembidion obtusum	9	37	6
Bembidion guttula	15	69	3
Pterostichus adstrictus	1	1	0
Pterostichus madidus	56	887	29
Pterostichus melanarius	5248	417	406
Pterostichus niger	41	1	6
Calathus fuscipes	3	0	0
Agonum dorsale	22	20	1
Amara apricaria	1	4	1
Harpalus rufipes	1	5	9
Harpalus aeneus	1	0	2
Total number specimens	5812	2816	534
Total number species	15	15	14
Number 'trap days' *	11,760	1232	672

* Number 'trap days' = total number traps x number 24 h periods traps operational

agricultural habitats (Thiele, 1977; Pietraszko and de Clercq, 1983b). Only those species of which at least 20 individuals were trapped in any one year are discussed further. Data for other species are given in Appendix 1.

(i) Clivina fossor

This species was abundant in spring 1983 only (Table 23) too early to be a major predator of aphids on potato. C fossor is common and widespread throughout the United Kingdom, and is mostly found in pasture and other open habitats (Luff, 1982a). It was abundant in winter wheat in England (Jones, 1976) and is a predator of cabbage root fly eggs (Coaker and Williams, 1963).

(ii) Trechus quadristriatus

This beetle was most abundant in 1984 (Table 24). Peak catches in 1983 and 1984 were in September (Tables 23 and 24). In 1985, none was trapped until August, when 60 were caught.

T quadristriatus is a small (3.4-5 mm), nocturnal (Luff, 1978) ground beetle common in dry, open country (Lindroth, 1974). It is common on agricultural land, particularly from late August to October (Coaker and Williams, 1963; Jones, 1979; Purvis and Curry, 1984).

Counts were too low during pesticide application for determination of treatment effects. This species seems of little importance as a predator of aphids on potato due to the lack of temporal synchronization but has been implicated as a major predator of other pest species (eg Coaker and Williams, 1963; Mitchell, 1963a; Pietraszko and de Clercq, 1983b).

(iii) Bembidion spp

Five species of Bembidion were captured (Table 22), and B obtusum and B guttula were most abundant. In each year most were trapped in May and June (Table 24) before both field treatment and aphid infestation. They are therefore not major aphid predators in the fields studied. Only 3 B obtusum and 6 B guttula were caught in 1985.

Bembidion is the largest carabid genus in the United Kingdom and consists

Table 23

Total numbers of various ground beetles caught in pitfall traps during May - September, 1983

Total number

Species / Month	*Clivina fossor*	*Trechus quadristriatus*	*Agonum dorsale*	*Pterostichus niger*	Number 'trap days'*
May	56	4	15	0	3360
June	25	0	4	0	2520
July	2	11	3	10	2520
August	0	121	0	20	1680
September	0	191	0	11	1680
Total	83	327	22	41	11,760

* Number 'trap days' = total number traps x number 24 h periods traps operational

Table 24

Total numbers of various ground beetles caught in pitfall traps during May - September, 1984

Total number

Species / Month	*Trechus quadristriatus*	*Agonum dorsale*	*Bembidion obtusum*	*Bembidion guttula*	Number 'trap days'*
May	0	9	13	35	168
June	15	11	16	27	224
July	10	0	1	5	392
August	904	0	7	2	392
September	416	0	0	0	56
Total	1345	20	37	69	1232

* Number 'trap days' = total number traps x number 24 h periods traps operational

of small (3-3.5 mm) beetles which generally overwinter as adults and are thus common in spring (Lindroth, 1974). B lampros, although rare in this study, is often common on arable land (Jones, 1976). B obtusum feeds on aphids (Feeney, 1983) and the Bembidiini in general are omnivorous (Davies, 1953).

(iv) Agonum dorsale

A dorsale was trapped in low numbers in each year and was largely absent after June (Tables 23 and 24). It was not present in traps at times of insecticide application and was not temporally synchronized with aphids on potato.

A dorsale is a spring breeder (Griffiths, 1982) and overwinters in aggregates in hedgerows and field boundaries (Sotherton, 1984). It was abundant in hedgerows at Sheriffhall Mains in June 1984. In cereals this ground beetle is considered a major aphid predator (Sunderland and Vickerman, 1980; Griffiths, 1982; Scheller, 1984), and is often abundant and active sufficiently early in the season to prey on spring infestations of aphids in winter-sown cereals (Edwards et al, 1979).

(v) Pterostichus spp

Four species were trapped between 1983 and 1985 (Table 22). P adstrictus was rare and is usually associated with mountainous country (Lindroth, 1974). P melanarius, P madidus and P niger are common and widely distributed in Britain (Luff, 1982b).

P niger

P niger was rare in 1984 and 1985: 1 and 6 individuals respectively were caught (Table 22). In 1983, peak numbers in pitfall traps were recorded in August (Table 23). Counts were too low for statistical analysis but were similar in all plots on each sampling occasion. P niger is a large (15-20.5 mm) macropterous species (Lindroth, 1974) which appears not to have received much attention.

P melanarius and P madidus

Differences between treatments and sexes were tested statistically by analyses of variance (ANOVAs) using the "Genstat" statistical package. Data followed a Poisson distribution and, as means and variances were proportional, were transformed to square roots before analysis. Means and associated confidence intervals are back-transformed. Where counts were low (early in each spring, overall in 1985) ANOVAs were not performed and either actual means and associated standard error estimates or total numbers are presented.

General

P melanarius was numerically dominant in 1983 and 1985 and common in 1984 (Table 22). P madidus was abundant in 1984 only (Table 22). Both species are large (12-18 mm), black and nocturnal, and apparently brachypterous in the United Kingdom (Lindroth, 1974).

In 1983 and 1984, both species were present in May when sampling began (Tables 25 and 26). Corresponding data are not available for 1985 as sampling began in July. Peak numbers in traps in 1983 and 1984 occurred in July and August (P madidus: Table 26, Figure 14; P melanarius: Figures 15-17). These peaks may have been induced through insecticidal interference with the natural system (see p.94).

1983

P melanarius

Catches of P melanarius in the experiment using methiocarb and thiometon were not significantly different between treatments on any sampling occasion (F tests, $p > 0.05$) (Figure 15). In the demeton-S-methyl trial counts of P melanarius were significantly different between treatments on 2 dates only: there were fewer ($F = 6.49$, $p \leq 0.05$) trapped in treated plots at the first sample (27 July) after spraying and more ($F = 6.81$, $p \leq 0.05$) trapped in treated areas on 7 September (Figure 16).

The number of P melanarius caught was lower in all 24 plots (ie in both trials) at the first sample after treatment. There was an apparent partial recovery in numbers by the next sampling date (Figures 15 and 16). Counts were thought to be lower in all plots including untreated controls on 27 July due to redistribution by this highly mobile beetle. Small plots and a 5 day interval

Table 25

Total numbers of Pterostichus melanarius in pitfall traps at various sampling occasions in 1983 and 1984

1983		1984	
Date	Total number	Date	Total number
4 May	6	16 May	0
11 "	7	23 "	1
18 "	9	30 "	2
25 "	7	6 June	0
8 June	2	13 "	0
15 "	3	20 "	18
29 "	264	27 "	49
14 September	209	11 September	31

Table 26

Total numbers of Pterostichus madidus in pitfall traps at various sampling occasions in 1983 and 1984

1983		1984	
Date	Total number	Date	Total number
4 May	0	16 May	1
11 "	1	23 "	6
18 "	1	30 "	14
25 "	0	6 June	3
8 June	0	13 "	1
15 "	0	20 "	13
29 "	0	27 "	21
6 July	12		
20 "	12	11 September	18
27 "	4		
10 August	17		
24 "	4		
7 September	3		
14 "	1		

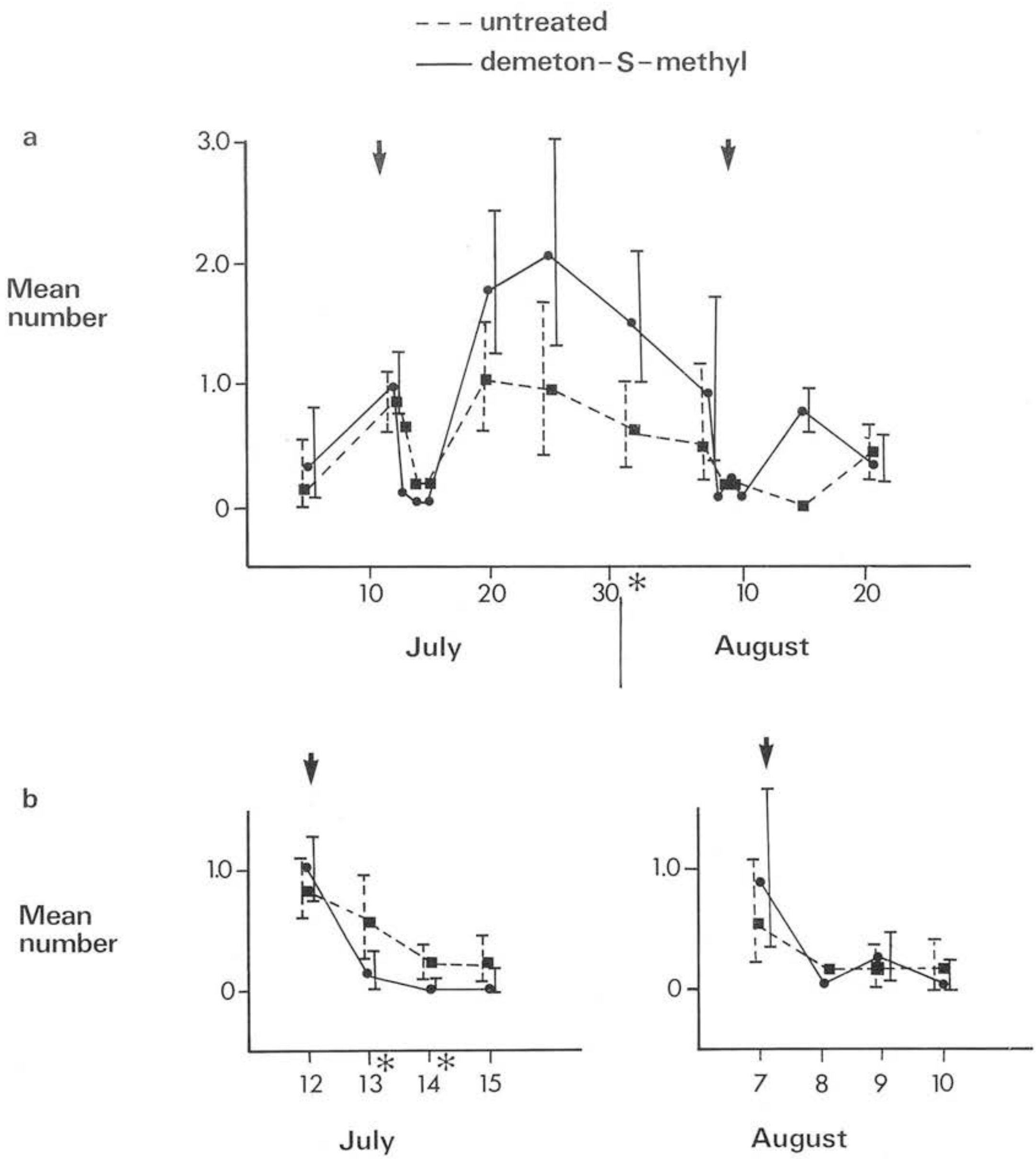


Figure 14: Back-transformed means per trap per 24 hours and associated 95 per cent confidence intervals of ⚥ <u>Pterostichus madidus</u> in 1984. Confidence intervals for data collected during intensive sampling are given on b and c only. "*"s indicate significant differences at $p \leq 0.05$, arrows indicate dates of treatment. (a = overall results; b = intensive sampling at spray 1; c = intensive sampling at spray 2).

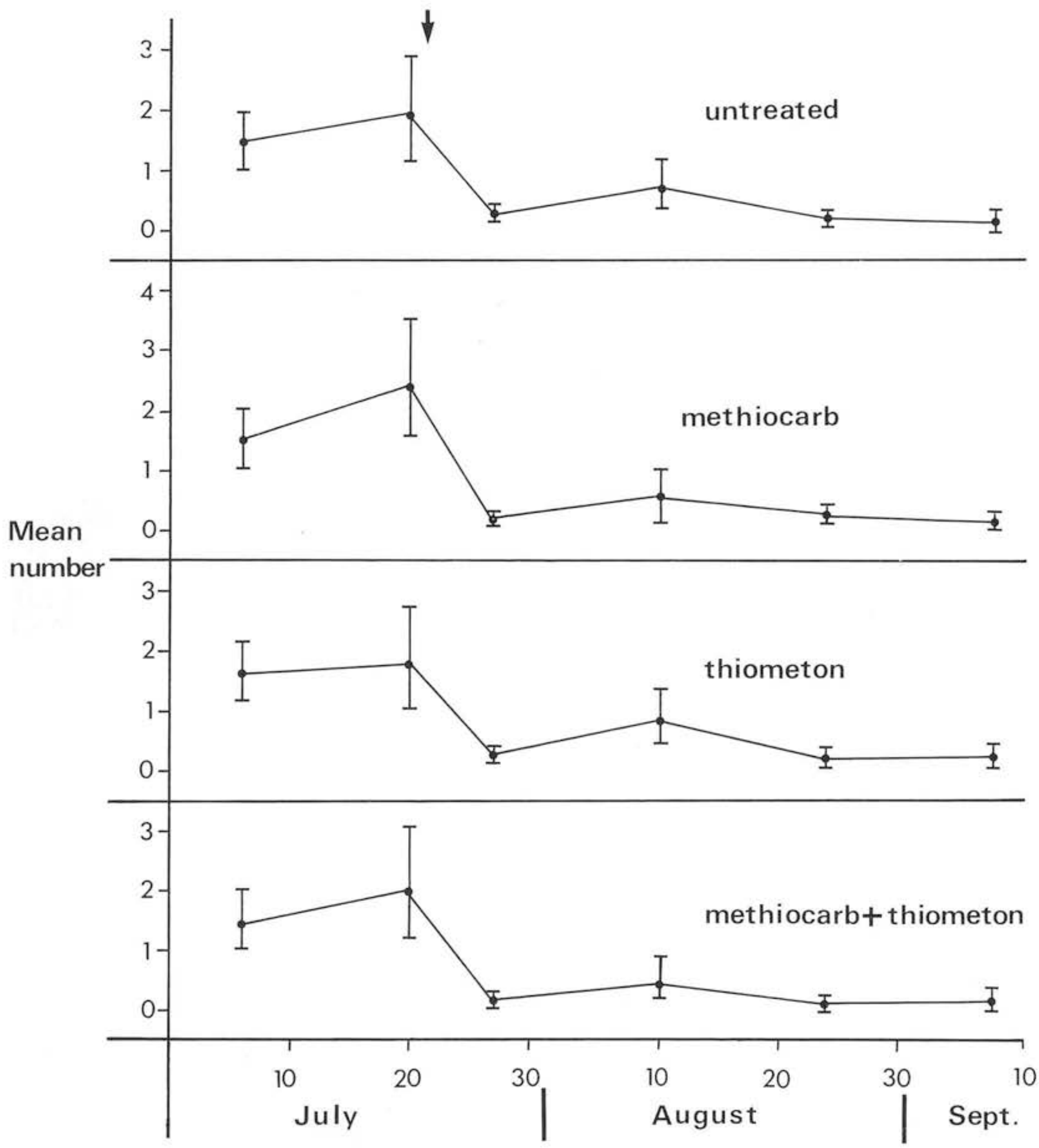


Figure 15: Back-transformed means per trap per 24 hours and associated confidence intervals of <u>Pterostichus melanarius</u> (sexes combined) in the "manipulative" trial, 1983. Arrow indicates treatment application.

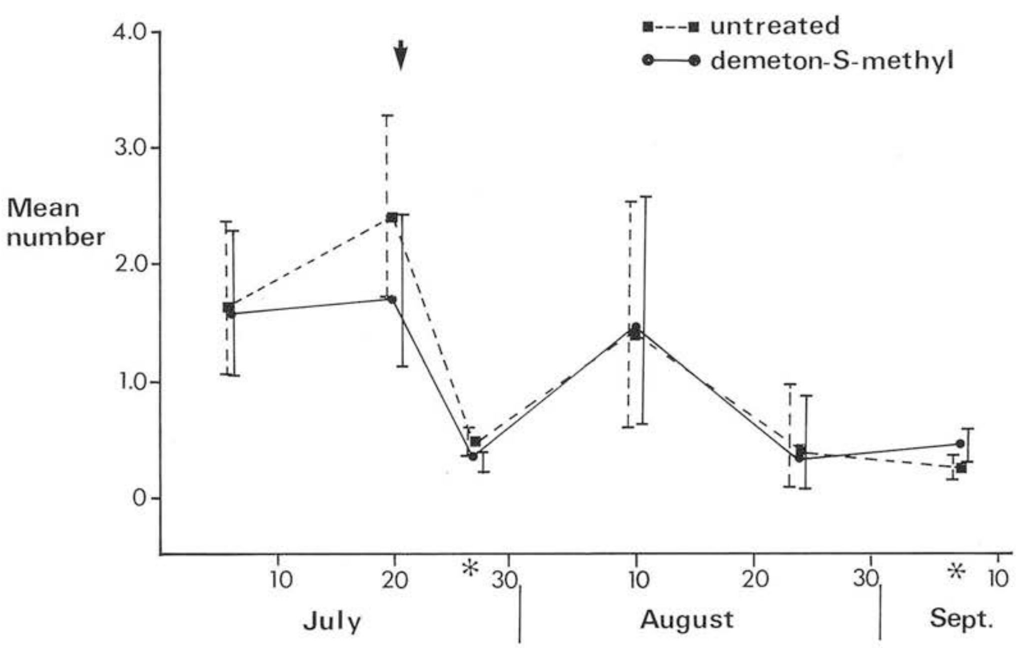


Figure 16: Back-transformed means per trap per 24 hours and associated confidence intervals of Pterostichus melanarius (sexes combined), in the demeton-S-methyl trial in 1983. Arrow indicates date of treatment; "*"s indicate significant differences at $p \leq 0.05$.

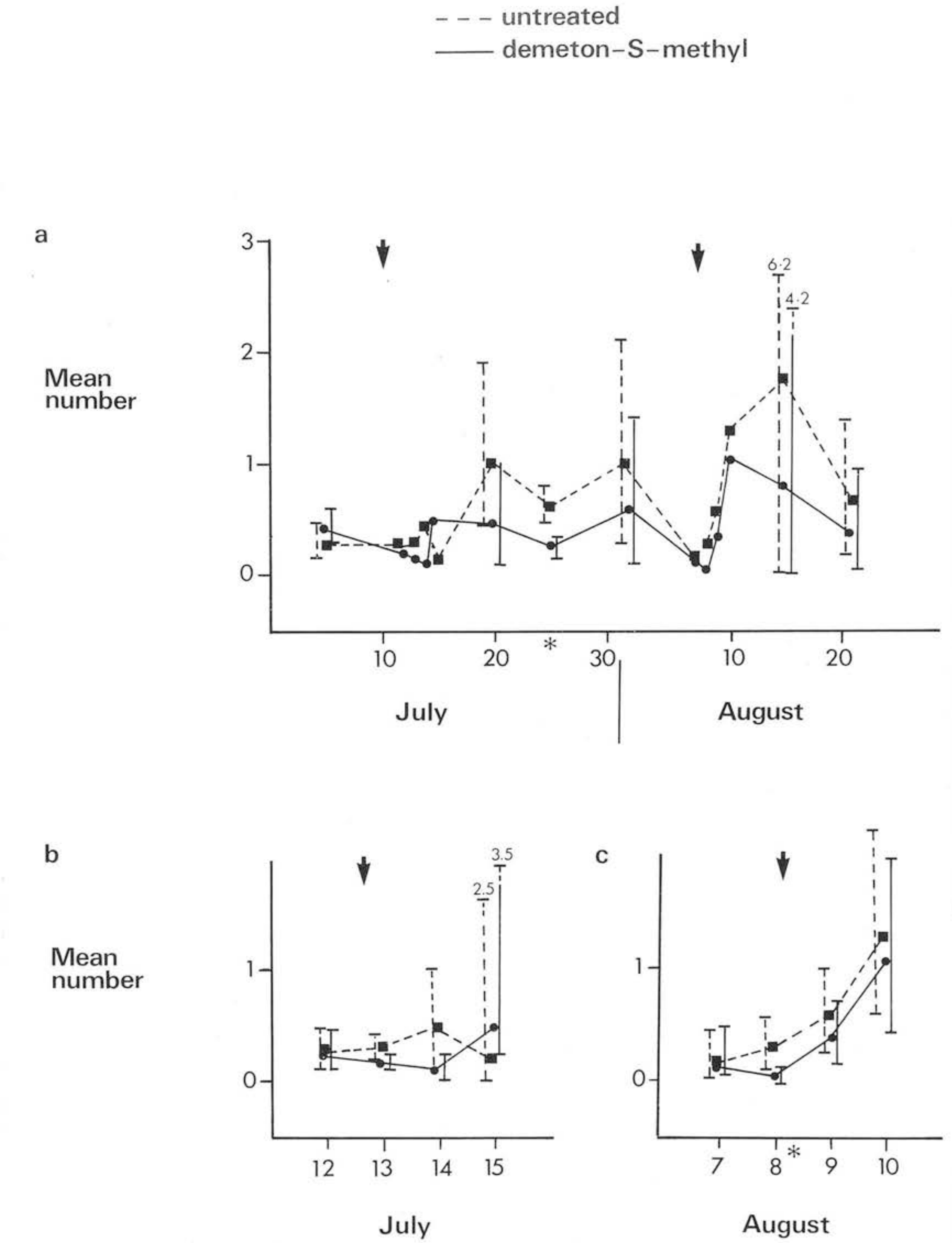


Figure 17: Back-transformed means per trap per 24 hours and associated 95 per cent confidence intervals of Pterostichus melanarius (sexes combined), 1984. Confidence intervals for data collected during intensive sampling are given on b and c only. Arrows indicate treatment application; "*"s indicate significant differences at $p \leq 0.05$.
(a = overall results; b = intensive sampling at spray one; c = intensive sampling at spray two).

to the first sample after treatment had allowed beetles to move into plots other than those they were in during treatment, obscuring any effect of the pesticides. That significant differences between treatments were detected in the larger plots of the demeton-S-methyl experiment supports this hypothesis.

P madidus

Numbers of P madidus trapped were also reduced after treatment in 1983 but catches were low and thus inconclusive. Total catches on all 24 plots for each sampling occasion only are given (Table 26).

1984

General

In 1984, trapping was done over 24 hour periods only. Plots were each 50 m x 50 m with pitfall traps in 6 m^2 "sub-plots" in the centres of the larger ones (see General Materials and Methods). The effectiveness of field trials depended on the majority of Pterostichus spp being unable to travel more than 22 m, the distance between the edge of a sub-plot and the margin of its associated larger plot, in 24 hours. A mark-release study done in 1984 to check this assumption (see Chapter 6) showed average daily distances travelled of 5.1-11.4 m for both species. Plot sizes were thus considered adequate at least for samples at 24 hours after demeton-S-methyl application.

P madidus

Numbers of P madidus were similar in treated and untreated areas immediately before the first demeton-S-methyl application on 12 July 1984 ($F = 1.16$, $p > 0.05$), but were significantly lower in sprayed plots at 24 ($F = 9.88$, $p \leq 0.05$) and 48 ($F = 8.70$, $p \leq 0.05$) hours after treatment (Figure 14). On 15 July, 72 hours after spray application, fewer P madidus were trapped in treated than untreated plots (Figure 14) but the difference was not significant ($F = 4.60$, $p > 0.05$). More beetles were caught in treated than untreated plots on 20 and 25 July but again differences were not significant ($F = 5.64$, 5.90 respectively, $p > 0.05$) (Figure 14). At the next sampling date, 1 August, more P madidus were trapped in sprayed than unsprayed areas ($F = 10.23$, $p \leq 0.05$) (Figure 14).

Results of predator gut dissections (Chapter 5) suggested that aphids in sprayed plots fall to the ground after treatment, where they are available as prey. "Fed" beetles from treated plots are less active than "hungry" ones from untreated areas where aphids on foliage are relatively inaccessible. This reduced activity level is reflected in lower trap catches after treatment followed by higher catches due to increased activity as aphid prey on the ground was depleted (for further explanation see Chapter 5).

On 7 August in 1984, demeton-S-methyl was applied to the same plots as on 12 July. If the reduction in beetle numbers was due to aphids on the ground after treatment, a second spray should produce little response as aphid populations were low. Trap catches were not significantly different between treatments before ($F = 1.05$, $p > 0.05$) or at any time after ($p > 0.05$) demeton-S-methyl application on 7 August (Figure 14). Twenty-four hours after the second treatment there were fewer P madidus trapped in treated areas. The reduction was not significant ($F = 4.84$, $p > 0.05$) but suggests that a reduction in activity level due to abundance of aphids on the ground is not the entire explanation.

P melanarius

Numbers of P melanarius caught immediately before the first spray in 1984 were similar in each treatment ($F = 0.05$, $p > 0.05$) (Figure 17). At 24 and 48 hours after the spray fewer were trapped in treated plots but differences were not significant ($F = 4.95$, 5.10 respectively, $p > 0.05$). Numbers were also similar before the second spray ($F = 0.01$, $p > 0.05$) followed by a significant reduction in catches of P melanarius in treated areas 24 ($F = 11.62$, $p \leq 0.05$) but not 48 ($F = 1.21$, $p > 0.05$) hours after treatment (Figure 17).

The catch pattern for P melanarius was similar to that of P madidus with a reduction in numbers in treated plots after spraying. Unlike P madidus a subsequent increase in trap catches in treated plots did not, however, occur. Instead, significantly more P melanarius were trapped in untreated areas after the first spray ($F = 14.29$, $p \leq 0.05$) and on other sampling occasions differences were not significant ($p > 0.05$).

Catches were so low that statistical analyses are not robust. Perhaps P melanarius is a more catholic feeder than P madidus and thus exhibited a weaker response. The reduction in numbers trapped in sprayed areas after the second treatment suggests, as with P madidus, that differences in activity level due to hunger status are not the sole explanation.

Short-term variations in weather may influence beetle activity and thus trap catch. Figure 18 shows mean trap catches of P madidus and P melanarius, mean air temperatures and total rainfall on the 4 days around each treatment in 1984. Numbers of P madidus but not P melanarius followed a pattern similar to that of air temperature in July. In August numbers of P madidus decreased, however, immediately after treatment, whereas air temperatures increased slightly. On 9 August, air temperatures were lower than on the previous day but catches of P madidus increased in treated plots. P melanarius catches did not follow air temperature trends at any time. Catches of both species were apparently not influenced by rainfall. Changes in numbers of beetles trapped in the periods around spraying were probably related to the treatment in some way: they were not greatly influenced by weather conditions.

1985

Field experiments in 1985 were as in 1984 except sampling was done around treatment applications only, and the 2 sprays were applied on separate areas. The 2 treatment applications were replicates of one another and different sites had therefore to be used so that aphids would be present in plots treated at the second spray. Two separate areas of a single aphid-infested field were used.

Numbers of both P melanarius and P madidus trapped were so few (Tables 27 and 28) that statistical analyses were not performed. Data for P melanarius are actual means and standard errors as counts were not transformed. A pattern similar to but weaker than that observed in 1984 was evident in P melanarius catches after the first treatment. Numbers trapped were slightly lower at 24 hours and slightly higher at one week after spray application in treated than untreated areas (Table 27).

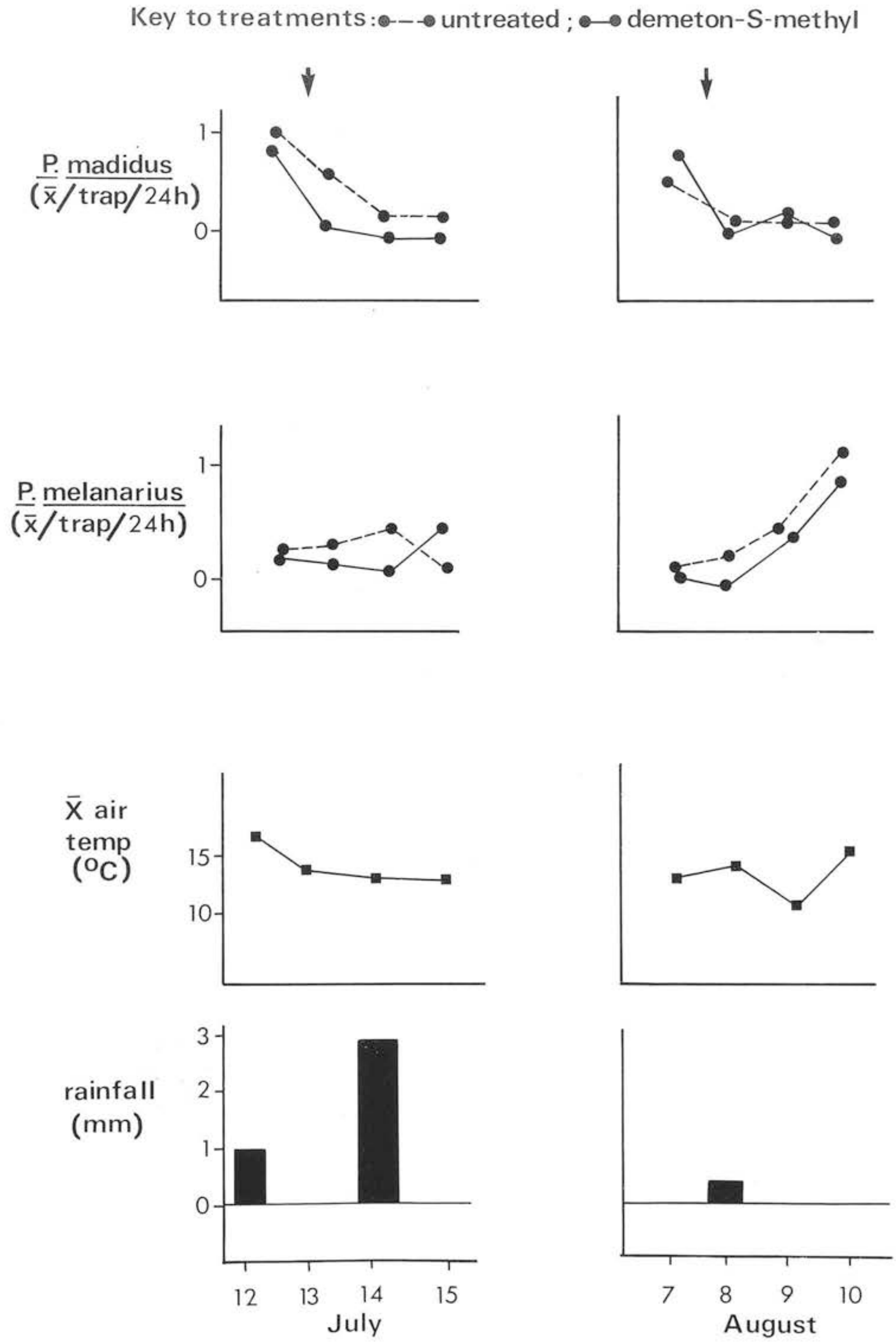


Figure 18: Catches of Pterostichus melanarius and Pterostichus madidus around times of treatment in 1984, and some associated weather data. Arrows indicate treatment application.

Table 27

Mean number/trap/24h ± SE_{95} ⚥ Pterostichus melanarius in 1985

Arrows indicate demeton-S-methyl application

	Number beetles	
Date	Untreated	Treated
25 July	0.26 ± 0.06	0.26 ± 0.04
→ 26 "	0.22 ± 0.06	0.18 ± 0.03
27 "	0.01 ± 0.01	0.02 ± 0.01
28 "	0.14 ± 0.03	0.13 ± 0.06
1 August	0.50 ± 0.04	0.60 ± 0.05
8 "	0.32 ± 0.04	0.25 ± 0.02
14 August	0.10 ± 0.03	0.06 ± 0.00
→ 15 "	0.01 ± 0.01	0.06 ± 0.03
16 "	0.05 ± 0.02	0.03 ± 0.01
17 "	0.09 ± 0.03	0.04 ± 0.02
21 "	0.11 ± 0.03	0.19 ± 0.05
28 "	0.01 ± 0.01	0.01 ± 0.01

Table 28

Total numbers ⚥ Pterostichus madidus in 1985
Arrows indicate demeton-S-methyl application

	Number beetles	
Date	Untreated	Treated
25 July	3	10
→ 26 "	0	0
27 "	0	0
28 "	0	1
1 August	2	5
8 "	0	2
14 August	2	2
→ 15 "	0	1
16 "	0	0
17 "	0	1
21 "	0	0
28 "	0	0

Sex of beetles

The sex of trapped P melanarius and P madidus was not determined in 1983 except for those used for gut dissections. Counts of ♀ and ♂ P melanarius in 1984 and 1985 and of P madidus in 1985 were combined due to low numbers trapped. Catches of P madidus in 1984 only were sufficient that data for sexes could be analysed separately.

In 1984, trap catches were analysed using ANOVA after square root transformation. The sex-spray interaction was not significant ($p > 0.05$) on any date tested (all dates after 27 June), indicating that demeton-S-methyl did not affect catches of ♂♂ and ♀♀ differently.

More ♂♂ than ♀♀ were trapped on the following dates:

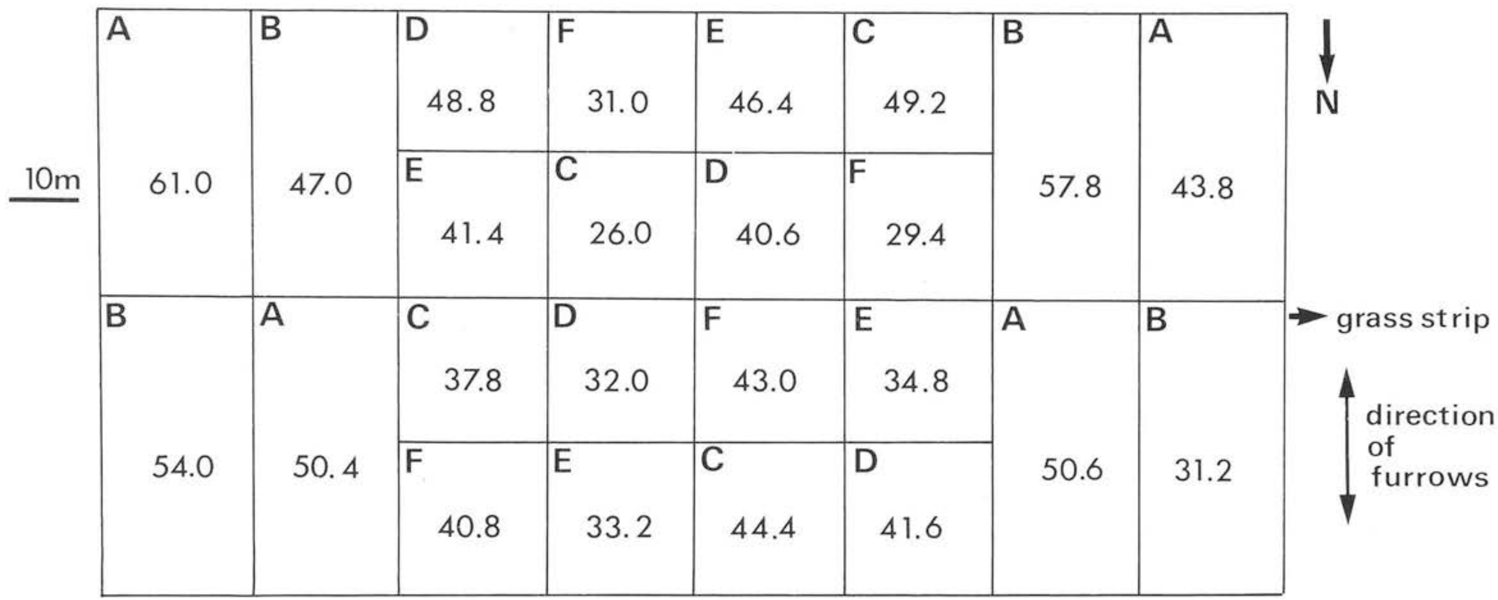
8 August	F	=	7.68	($p \leq 0.05$)
9 "	"	=	44.07	"
10 "	"	=	30.20	"
15 "	"	=	10.77	"
21 "	"	=	22.10	"

These data may reflect actual differences in population structure and/or differences in activity levels. On the last sampling date (11 September) numbers of ♂♂ and ♀♀ caught were similar ($F = 0.80$, $p > 0.05$).

Effect of plot position

Field sites were adjacent to a grass strip in 1983 (see Figure 2) and a hedge ran along 3 sides in 1984 (see Figure 3). The possibility that plot position in the field affected beetle catch was considered and the mean numbers per trap of P melanarius in 1983 and P madidus in 1984, over the entire season, were calculated for each plot (Figures 19 an d 20).

In 1983 (Figure 19), numbers per plot varied widely but there was no obvious pattern in catch with regard to proximity to the grass strip. In 1984, each of the 4 plots adjacent to the hedge and road were considered a "pair" with the adjoining plot to the NE (Figure 20). Numbers of P madidus trapped in each plot adjacent to the hedge and road were higher than those caught in each respective "paired-plot", although this difference between pairs was not



Key to Treatments	
demeton-S-methyl trial	'manipulative' trial
A – untreated	C – untreated
B – treated	D – methiocarb
	E – thiometon
	F – methiocarb + thiometon

Figure 19: Layout of field trials in 1983. Numbers indicate the mean number of Pterostichus melanarius per trap over the entire season in each plot.

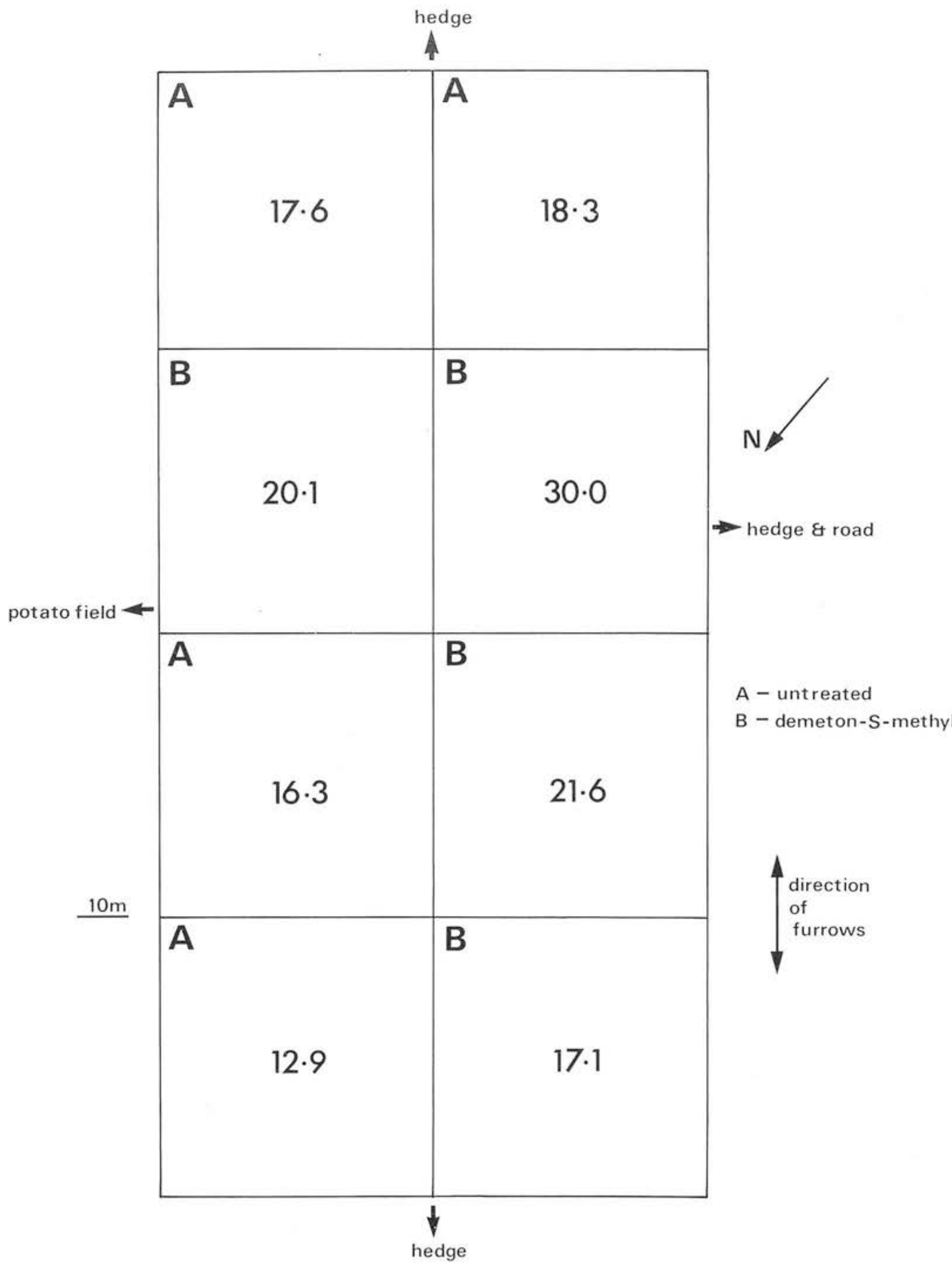


Figure 20: Layout of field trials in 1984. Numbers indicate mean number Pterostichus madidus caught per trap over the entire season in each plot.

significant (paired t-test = 2.64, 3 df, NS $p > 0.05$). It is possible that the hedge was influencing beetle numbers or activity, although apparently not significantly. This difference due to proximity to a hedge may have contributed to variation in trap catches in the field experiment but as replicates were randomly assigned, treatment effects should not have been affected.

CHAPTER 5

POLYPHAGOUS PREDATORS

PREY/INSECTICIDES (LABORATORY)

5-1 GUT DISSECTIONS

5-1-1 INTRODUCTION

The occurrence together in a field of a pest and a predator does not prove that the pest is eaten by that predator. Evaluation of the predatory potential of polyphagous arthropods in potatoes must first establish that the predator will eat aphid pests of potato.

Gut dissection is a simple and common method of prey assessment which relies on the presence of observable remains like exoskeleton. Many epigeal predators ingest, however, mainly liquid (Savory, 1977) and pre-orally digested food is not detectable by gut dissection. Serological techniques are suitable for detection of liquid or solid food. They involve the use of rabbits to produce a specific antibody to prey species, and a licence is required to carry this out (A Burn, pers comm). Ready-made cereal aphid, but not potato aphid, antiserum was available (A Burn, K Sunderland, pers comm) and as cereal aphid antiserum elicits very weak cross-reactions with potato aphids it is unsuitable for detecting potato aphids in predators (K Sunderland, pers comm).

During 3 nocturnal observation sessions in the potato field in July 1983, few fluid-feeding predators were seen and the decision not to become involved in serological work was therefore taken. It is, however, recognized that certain fluid-feeding taxa, like linyphiid spiders, may be important aphid predators. The species of most interest in the present study, adult Pterostichus melanarius, Pterostichus madidus and harvestmen, consume hard remains detectable by gut dissection and this method was used (see Davies, 1953; Penney, 1966; Luff, 1974a; Griffiths, 1982).

No method other than direct observation is able to differentiate between primary and secondary predation. Direct observation is time-consuming and difficult particularly with nocturnal predators, and secondary predation must be considered when evaluating prey items by less direct methods.

5-1-2 MATERIALS AND METHODS

Specimens were dissected in alcohol with the aid of a binocular microscope. A ventral, longitudinal incision was made in the abdomen and thorax, exposing the gut. This method was time-consuming and for Pterostichus spp only in 1984 and 1985, crops were obtained by teasing the body apart at the junction of prothorax and elytra. Crops were usually easily pulled out through the "neck". In Coleoptera the crop, and in harvestmen the stomach and gastric caecae were removed and placed in 40 per cent glycerine on slides (Loughridge and Luff, 1983). Crops only were examined in beetles as aphid remains in the mid- and hind-guts are difficult to assess (M Luff, pers comm).

Stomach contents were examined at x100 bright-field magnification and aphid remnants including siphunculi, legs, rostra, eyes with triommatidia and caudae (Plate 2) were counted. Siphunculi were identified to species when possible.

Specimens of certain species of epigeal arthropods, and ladybird adults and larvae from pitfall traps, were examined. In 1983, dissections of P melanarius were begun with individuals trapped on 6 July. Up to 50 beetles on each date were examined in each treatment in the demeton-S-methyl trial, and up to 50 in each treatment in the "manipulative" trial on the dates immediately before and after treatment application. Dissections were not continued in the manipulative trial because redistribution had obscured pesticide effects. Less than 50 beetles were dissected if less than 50 were trapped.

In 1984, all specimens of selected beetle species trapped when aphids were present in the field were examined, and in 1985 all predatory beetles were dissected. All harvestmen were dissected in each year except those trapped in late August/early September when aphids were not present.

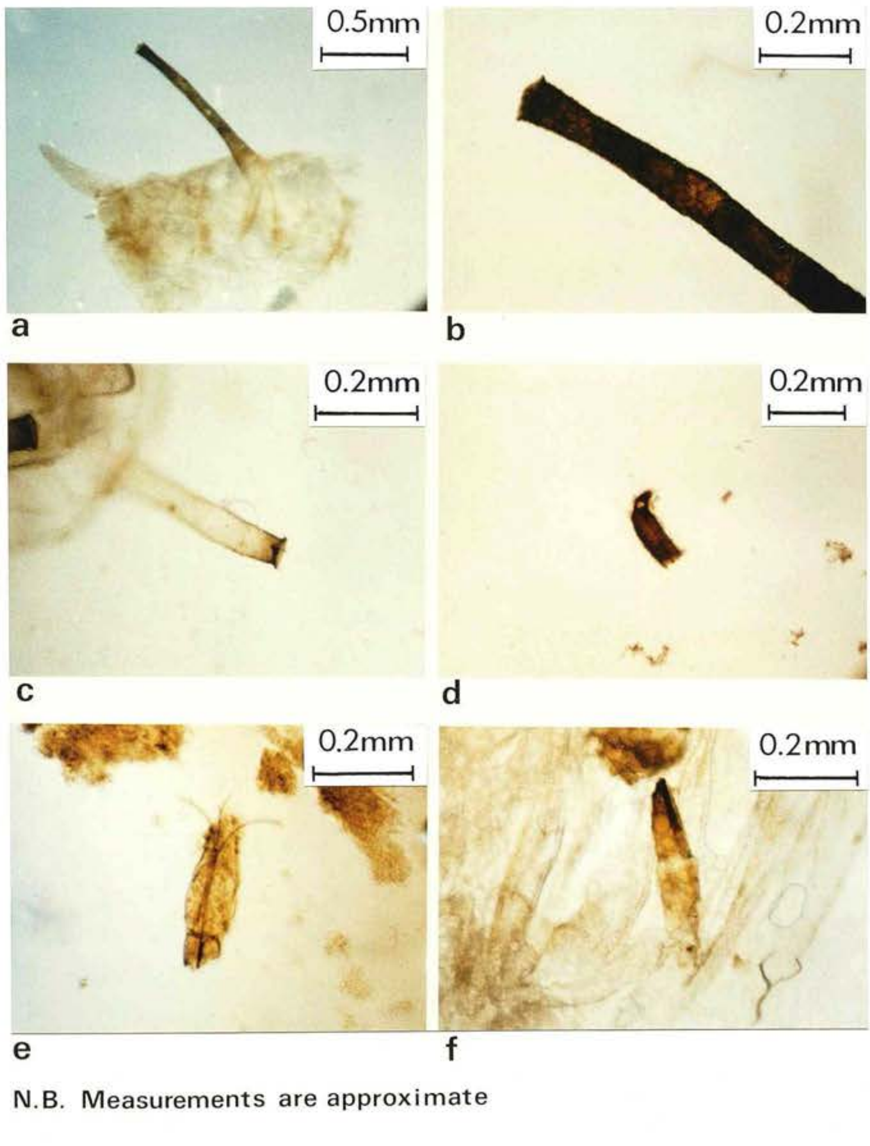


Plate 2: Examples of aphid remnants observed in guts of dissected arthropods (a, b, c = siphunculi, b showing reticulated pattern characteristic of Macrosiphum euphorbiae; d = last tarsal segment and claws: e, f = rostra, e showing extruded stylets).

Data analysis

When sufficient numbers were dissected, data were analysed by X^2 tests with treatments and presence or absence of aphid remains as categories. Data are presented as percentages of dissected specimens which contained at least one aphid fragment. Percentages are rounded to the nearest whole number and are based on treatment not plot totals due to low numbers. Data for ♂♂ and ♀♀ are combined due either to low numbers caught or because results were not significantly different.

5-1-3 RESULTS AND DISCUSSION

Types of aphid fragment in guts

The crops of approximately 2800 beetles and the stomachs and gastric caecae of about 200 harvestmen were examined. Legs were the commonest remnant in each year, followed by rostra, siphunculi, caudae and eyes (Table 29). Eighty per cent of the siphunculi were from Macrosiphum euphorbiae. The rest were either damaged and not identified or were not from M euphorbiae. The number of aphid body parts in digestive tracts varied from a single leg or rostrum to a maximum of 67 remnants in a ♂ P madidus from untreated plots on 25 July 1984. This individual contained 45 legs, 15 rostra, 6 siphunculi and one eye, indicating it had eaten at least 15 aphids. The maximum number of aphid parts found in a harvestman was in a P opilio which contained 30 legs, 4 siphunculi and 3 rostra, a minimum of 5 aphids. Some beetles contained an entire aphid nymph.

Gut contents other than aphids

Unidentified mites were sometimes found in P melanarius crops with a maximum of 25 in one beetle. In 1985, a juvenile rhabditid nematode was seen in a ♂ P melanarius. These nematodes feed on fungi (A Spaull, pers comm). P niger crops generally contained abundant material resembling soil or finely ground vegetation. Pollen was often observed in crops, particularly in P madidus and T quadristriatus. Fragments of unidentified beetles were occasionally seen but many crops were apparently empty of all chitinous remains. The majority of guts with aphid remnants contained only remnants of aphids. It is thus unlikely that much aphid predation was

Table 29

Percentages of total aphid fragments counted in each year represented by various types of chitinous remains

Aphid remnant / Year	Percentage of total: Legs with claws	Rostra	Siphunculi	Eyes	Caudae
1983	54	24	19	1	0
1984	67	18	12	1	1
1985	55	19	21	3	2

NB: Percentages do not always total 100 as they are rounded secondary as, if so, the remains of the aphid predator should have been present.

In the following sections results of gut dissections of the most numerous predators, P melanarius and P madidus are discussed in detail:

(a) Pterostichus melanarius

Out of a 3 year total exceeding 1800 dissected specimens, 260 (14.4 per cent) contained aphid remains.

1983

In the manipulative trial in 1983, the percentage of P melanarius guts with aphid remnants was not significantly different between any treatments in the manipulative trial either immediately before ($X^2 = 5.40$, df = 3, $p > 0.05$), or after ($X^2 = 2.05$, df = 3, $p > 0.05$) pesticide application (Table 30). When data were pooled over treatments, however, dissection results for immediately before and after treatment were significantly different ($X^2 = 38.16$, df = 1, $p \leq 0.05$). A greater proportion contained aphid remains after treatment.

Results of the demeton-S-methyl trial were similar. Numbers of beetles with aphid remains were similar in the 2 treatments both before ($X^2 = 0.61$, df = 1, $p > 0.05$) and after ($X^2 = 2.17$, df = 1, $p > 0.05$) spraying. When data were pooled across treatments a significantly higher proportion of beetles contained aphid remains immediately after spraying than before ($X^2 = 7.80$, df = 1, $p \leq 0.05$) (Table 31). In the manipulative trial this pattern may be due to redistribution of beetles masking a treatment effect, as probably occurred with the pitfall trap catches. Gut dissection and trap catch results are, however, inversely related: after treatment, catches were reduced but the proportion of the catch with aphid remains increased.

This pattern was not observed in the demeton-S-methyl plots. In these plots the numbers of P melanarius caught were significantly lower in treated than untreated areas on 27 July, the first sampling occasion after treatment. The gut dissections did not, however, reveal a significant difference in the

Table 30

Numbers of *Pterostichus melanarius* (sexes combined) with aphid remains, from the manipulative trial, 1983
Percentages of beetles with aphid remains in parentheses

Treatment / Sampling occasion	untreated		methiocarb		thiometon		methiocarb and thiometon		Total	
	a [+]	b *	a	b	a	b	a	b	a	b
20 July	50	7 (14)	50	4 (8)	50	1 (2)	50	3 (6)	200	15 (7)
treatment →										
27 July	38	14 (37)	32	13 (41)	26	10 (38)	25	6 (24)	121	43 (35)

[+] a : Number dissected   * b : Number with aphid remains

Table 31

Numbers of Pterostichus melanarius (sexes combined) with aphid remains, from the demeton-S-methyl trial, 1983
Percentages of beetles with aphid remains in parentheses

Treatment / Sampling occasion	untreated		demeton-S-methyl	
	Number dissected	Number with aphid remains	Number dissected	Number with aphid remains
20 July	100	13 (13)	100	18 (18)
treatment ——>				
27 July	50	15 (30)	46	14 (30)
10 August	50	6 (12)	50	3 (6)
24 August	47	1 (2)	53	2 (4)
7 September	37	0	50	0
14 September	36	0	47	0
Total	320	35 (11)	246	37 (15)

proportion of beetles with aphid remains between treatments on 27 July. Catches were only slightly lower in treated plots (Chapter 4) and it is possible that redistribution also affected gut dissection results in the demeton-S-methyl trial. If redistribution had not occurred, the proportion of beetles with aphid remains might have been significantly higher in treated plots on 27 July.

1984 and 1985

Too few P melanarius were trapped in 1984 to allow robust analysis (Table 32). Overall, 10.6 per cent of dissected beetles contained aphid remains but catches around spray dates were so low that detection of any treatment effects is not possible. Catches, and thus dissections, in 1985 were also few (Table 33). Chi-square tests on selected dates revealed no significant differences between treatments in the proportions of beetles containing aphid remains on 1 and 8 August in 1984 and 25 and 26 July in 1985 (X^2 = 3.50, df = 1, 0.42, 0.19, 3.02 respectively, $p > 0.05$).

(b) Pterostichus madidus

Over the 3 years, 278 (30.5 per cent) of the 910 P madidus dissected contained aphid remnants. In 1983 and 1985, few specimens were caught. Of 32 individuals trapped in 1983, 10 contained aphid remains (31 per cent) and of 31 dissected in 1985, 6 were "positive" (19 per cent).

1984

Over 800 P madidus were dissected in 1984. Two hundred and sixty (31 per cent) contained aphid fragments (Table 34). Immediately before the first demeton-S-methyl spray on 12 July, the proportion of beetle crops with aphid remains was not significantly different between treated and untreated areas (X^2 = 0.00, df = 1, $p > 0.05$). On 13 July, immediately after treatment, a higher percentage of beetles from treated plots contained aphids (X^2 = 7.32, df = 1, $p \leq 0.05$), compared to untreated plots. Percentages were thereafter similar in both treatments until 25 July. At that time a higher proportion of beetles from untreated areas contained aphid remains (X^2 = 25.34, df = 1, $p \leq 0.05$). Similarly on 1 and 7 August, more beetles from unsprayed plots were "positive" (X^2 = 14.98, df = 1, 11.57 respectively,

Table 32

Numbers of Pterostichus melanarius (sexes combined) with aphid remains, 1984. Total numbers dissected are numerators, numbers with remains are denominators. Percentages with remains in parentheses.

Treatment \ Date	12 July (Treatment ↓)	13 July	14 July	15 July	20 July	25 July	1 August	7 August (Treatment ↓)	8 August (10h)	8 August (24h)	9 August	10 August	15 August	Total
untreated	0/7	0/4	0/4	-	4/19	0/14	1/7	1/17	1/5	0/3	0/1	0/10	1/33	8/124
					(21)		(14)	(6)	(20)				(3)	(6)
demeton-S-methyl	0/8	0/9	0/14	1/2	3/7	6/30	6/18	0/30	4/6	3/8	1/8	1/17	1/40	26/197
				(50)	(43)	(20)	(33)		(67)	(37)	(12)	(6)	(2)	(13)

Table 33

Numbers of Pterostichus melanarius (sexes combined) with aphid remains, 1985. Total numbers dissected are numerators, numbers with remains are denominators. Percentages with remains in parentheses.

Treatment \ Date	25 July (Treatment ↓)	26 July	27 July	28 July	1 August	8 August	Total	14 August (Treatment ↓)	15 August	16 August	17 August	21 August	28 August	Total
untreated	$^{5}/_{23}$	$^{9}/_{26}$	$^{0}/_{2}$	$^{4}/_{14}$	$^{11}/_{56}$	$^{4}/_{36}$	$^{33}/_{157}$	$^{6}/_{11}$	$^{3}/_{4}$	$^{1}/_{6}$	$^{4}/_{/}$	$(^{7}/_{9})$	$^{0}/_{1}$	$^{21}/_{38}$
	(22)	(35)		(29)	(20)	(11)	(21)	(54)	(75)	(17)	(50)	(78)		(55)
demeton-S-methyl	$^{3}/_{29}$	$^{13}/_{20}$	$^{1}/_{2}$	$^{4}/_{14}$	$^{4}/_{62}$	$^{1}/_{28}$	$^{26}/_{155}$	$^{5}/_{6}$	$^{2}/_{5}$	$^{2}/_{3}$	$^{0}/_{5}$	$^{7}/_{22}$	-	$^{16}/_{41}$
	(10)	(65)	(50)	(29)	(6)	(4)	(17)	(83)	(40)	(67)		(32)		(39)

Table 34

Numbers of Pterostichus madidus (sexes combined) with aphid remains, 1984
Percentages of beetles with aphid remains in parentheses

Treatment / Sampling occasion	untreated		demeton-S-methyl	
	Number dissected	Number with aphid remains	Number dissected	Number with aphid remains
12 July	48	7 (15)	57	7 (12)
T ⟶				
13 " *	35	8 (23)	9	7 (78)
14 "	14	3 (21)	4	1 (25)
15 "	16	8 (50)	5	3 (60)
20 "	60	34 (57)	104	52 (50)
25 " *	57	36 (63)	118	27 (23)
1 August *	38	19 (50)	86	13 (15)
7 " *	37	18 (49)	52	7 (13)
T ⟶				
8 " (10 hours after spraying)	10	2 (20)	10	2 (20)
8 " (24 hours after spraying)	17	5 (29)	7	0
9 "	21	5 (24)	20	3 (15)
10 "	14	1 (7)	8	0
Total	367	138 (38)	480	122 (25)

* indicates significant differences between treatments, $p \leq 0.05$

T = treatment

$p \leq 0.05$). On 8 August, 24 hours after the second demeton-S-methyl spray, the percentages of P madidus with aphid fragments were similar in all plots ($X^2 = 0.10$, df = 1, $p > 0.05$).

Gut dissection results, particularly for P melanarius in 1983 and P madidus in 1984, prompted the idea that aphids fall from potato foliage to the ground after treatment. They are there available as prey but are usually largely unavailable as these large carabids appear not to climb potato plants. Beetles in treated areas feed on these "fallen" aphids and are thus less hungry in treated than untreated plots. Pterostichus spp in untreated plots will be relatively more active, having eaten less aphids than those in treated plots; hungry beetles are known to be more active than less hungry ones (Baars, 1979). The number of specimens caught in pitfall traps is therefore greater in untreated areas and proportionally fewer have eaten aphids.

Data indicate that this effect lasts about 24 hours only after treatment (see Table 34), perhaps because aphids on the ground have been eaten, or have deteriorated by then. Aphids do fall to the ground after treatment with demeton-S-methyl (Chapter 2). Figure 21 shows the percentage of P madidus with aphid remains and the numbers of aphids on petri plates after the first spray in 1984. On 13 July in particular, 24 hours after treatment, the proportions of beetles with remains and the numbers of aphids on plates appear to correspond.

At the second spray in 1984 plots treated with demeton-S-methyl on 12 July were re-sprayed. Few aphids were present to fall to the ground and after the second spray, beetle numbers in traps were not significantly lower nor did a higher proportion contain aphids in treated compared with untreated plots. These observations lend support to the hypothesis of increased feeding leading to decreased activity/catch because when few aphids were available, the pattern did not occur.

Two weeks after the first spray in 1984, beetle catch was higher in treated areas but the proportion with aphids was higher in untreated plots. At this time few aphids were present in treated plots but populations were rapidly increasing in untreated areas. Beetles in treated areas may have been more

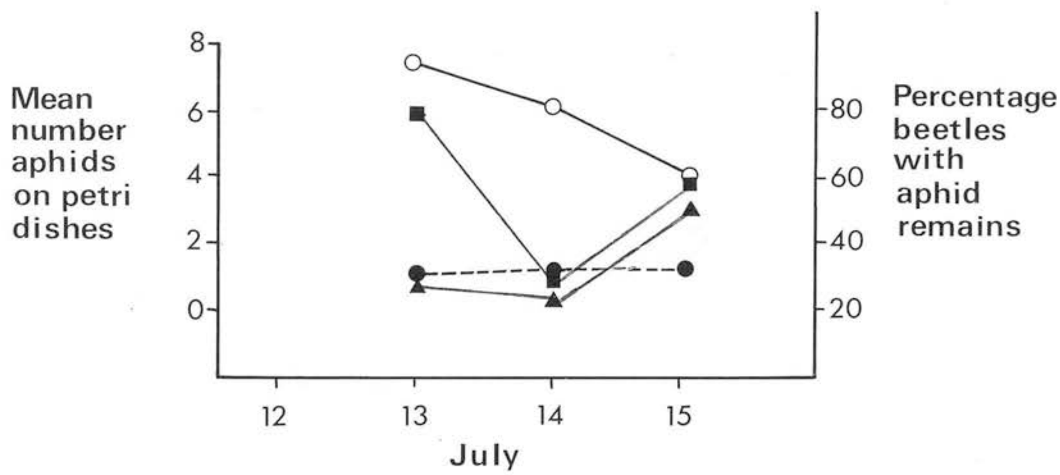


Figure 21: Mean number Macrosiphum euphorbiae on petri plates in treated (○—○) and untreated (●----●) plots, and percentage Pterostichus madidus with aphid remains in treated (■—■) and untreated (▲) plots in 1984. Demeton-S-methyl was applied on 12 July.

active due to hunger, than those in untreated areas. This hunger may have been induced by insecticidal death of prey, whether aphids or other unassessed animals. Chiverton (1984) observed significant increases in catches of P melanarius in treated compared with untreated plots of spring barley several weeks after insecticide treatment. He suggested that prey populations were reduced by the insecticide, resulting in hungrier and more active beetles and consequently higher trap catches. A similar situation appears to exist in potatoes treated with demeton-S-methyl.

In late July 1984 large aphid populations in untreated plots may have led to aphids falling to the ground as a result of increased activity induced by overcrowding. Aphids probably do fall to the ground and are eaten on occasions other than after pesticide treatment as some beetles contained aphid remains even before spray application (Tables 30-34). On 20 July 1984, over a week after treatment, 50 per cent of dissected P madidus from treated plots contained aphid remains. This may be because aphids on the ground are still available or there are small numbers of aphids still on the crop in treated areas. Beetles may also be eating aphids in untreated areas and then moving into treated plots.

(c) Miscellaneous Coleoptera

Specimens of carabids other than Pterostichus spp, of ladybird adults and larvae and of the staphylinid genus Tachyporus, were also dissected. Numbers dissected do not always correspond with numbers trapped either because they were caught when aphids were not present in the field or because they were unfamiliar species and mounted for identification. Many species included in this section were uncommon in pitfall traps and data are pooled over treatments.

In 1983, few beetles contained aphid remains (Table 35). Trechus quadristriatus is a fluid-feeder (Mitchell, 1963a) and predation by this species may have been underestimated. Crops of T quadristriatus and Bembidion spp generally contained brown, amorphous material with no recognizable chitinous remains. Five of 31 (16 per cent) Pterostichus niger had eaten aphids as had a large proportion of Coccinella septempunctata. Most Tachyporus dissected contained material resembling oil droplets, although one T obtusus captured on 20 July contained aphid fragments.

Table 35

Gut dissection results of Coleoptera uncommon in pitfall traps in 1983
Data represent numbers dissected and numbers which contained aphid fragments, ie $^0/_4$ indicates of 4 beetles dissected 0 contained aphids
(- indicates none dissected)

Animal \ Date	6 July	20 July	27 July	10 Aug	24 Aug	7 Sept	14 Sept
Carabidae							
Trechus quadristriatus	-	$^0/_4$	$^0/_3$	$^0/_{41}$	$^0/_{43}$	-	-
Bembidion obtusum	-	-	-	$^0/_2$	-	-	-
Bembidion guttula	-	-	-	$^0/_1$	-	-	-
Pterostichus niger	$^0/_2$	$^1/_5$	$^0/_1$	$^3/_{11}$	$^1/_{12}$	-	-
Agonum dorsale	-	-	-	-	$^0/_1$	-	-
Staphylinidae							
Tachyporus hypnorum	-	$^0/_3$	$^0/_4$	$^0/_1$	-	-	-
Tachyporus obtusus	-	$^1/_1$	$^0/_1$	$^0/_1$	-	-	-
Tachyporus pallidus	-	-	$^0/_2$	-	-	-	-
Coccinellidae							
Coccinella septempunctata (adults)	$^2/_3$	$^1/_2$	$^1/_2$	$^1/_1$	-	-	-

In 1984, T quadristriatus, Bembidion spp and the staphylinids were not dissected. The single P niger collected (on 8 August) contained aphid remnants. Two of 3 adult C septempunctata and 2 of 4 coccinellid larvae also contained aphid remains. No other beetles were dissected in 1984.

Table 36 gives results for 1985. Several species of ground beetle were examined but numbers trapped were low. Of those dissected, Nebria brevicollis (1 of 4), Harpalus rufipes (3 of 9) and Calathus melanocephalus (1 of 1) contained aphid remains. Two of 3 C septempunctata also contained aphid fragments.

(d) Harvestmen

Phalangium opilio

One hundred and thirteen Phalangium opilio were dissected in 1983 and 1984, and of these 61 specimens (54 per cent) contained aphid remains (Tables 37 and 38). A higher proportion of the catch had eaten aphids in 1983 (71 per cent) than in 1984 (39 per cent), although numbers were low. Few were trapped on dates near spraying occasions. Overall, proportions of stomachs and gastric caecae with aphid remains were similar in treated and untreated areas in both years.

Few harvestmen of other species were collected and results for 1983 are pooled over time (Table 39). Five of the 6 species apparently ate aphids. In 1984, only P opilio was trapped when aphids were present in the field and other species were not dissected. No harvestmen were trapped in 1985.

5-2 RETENTION TIME OF APHID PREY IN PTEROSTICHUS SPP

5-2-1 INTRODUCTION

In gut dissections, some beetles from sprayed areas contained aphid remains, although trapped up to 3 weeks after treatment. Aphid numbers on plants were very low after spray application and it seemed possible that beetles were feeding on aphids in untreated plots but dispersing to treated areas where they were captured. If this was so, effects of demeton-S-methyl

Table 36

Gut dissection results of miscellaneous beetles trapped in 1985
(Data: eg $^0/_1$ indicates 1 beetle dissected, no aphid remains in crop; - indicates no specimens dissected)

Animal \ Date*	25 July	26 July	28 July	1 Aug	14 Aug	15 Aug	16 Aug	17 Aug	28 Aug
Carabidae									
Nebria brevicollis	-	-	-	-	$^0/_1$	$^1/_1$	-	-	$^0/_2$
Clivina fossor	-	-	-	-	-	-	-	$^0/_1$	-
Calathus melanocephalus	-	-	$^1/_1$	-	-	-	-	-	-
Agonum dorsale	-	$^0/_1$	-	-	-	-	-	-	-
Amara apicaria	-	-	$^0/_1$	-	-	-	-	-	-
Harpalus aeneus	-	$^0/_2$	-	-	-	-	-	-	-
Harpalus rufipes	$^1/_1$	$^0/_2$	-	$^0/_1$	$^1/_1$	$^1/_1$	$^0/_2$	$^0/_1$	-
Coccinellidae									
Coccinella septempunctata (adults)	-	$^2/_3$	-	-	-	-	-	-	-

* (Only dates when animals collected are given)

Table 37

Gut dissection results of Phalangium opilio, 1983
Data represent numbers with aphid remains (numerator) and numbers dissected (denominator) (- indicates no specimens dissected)

Treatment \ Date	8 June	15 June	29 June	6 July	20 July	27 July	10 Aug	24 Aug	7 Sept	14 Sept
manipulative trial:										
untreated	-	-	-	-	4/6	2/2	-	1/1	-	1/2
methiocarb	-	-	-	-	2/2	3/3	-	0/1	-	-
thiometon	-	-	-	1/1	4/4	3/3	-	1/1	0/1	0/1
methiocarb + thiometon	-	-	-	-	3/3	2/2	-	-	1/1	-
demeton-S-methyl trial:										
untreated	-	-	-	-	4/4	-	-	-	0/2	0/1
demeton-S-methyl	2/2	-	-	-	3/5	1/2	2/2	-	0/1	0/2
Totals	2/2	-	-	1/1	20/24	11/12	2/2	2/3	1/7	1/7

Table 38

Gut dissection results of Phalangium opilio, 1984
(For explanation of symbols see above)

Treatment \ Date	12 Jul	13 Jul	14 Jul	15 Jul	20 Jul	25 Jul	1 Aug	7 Aug	8^{+} Aug	8* Aug	9 Aug	10 Aug	15 Aug
untreated	1/2	-	0/1	3/5	4/5	3/3	1/1	0/2	2/2	-	0/3	-	-
demeton-S -methyl	1/1	1/1	1/1	0/1	2/2	0/4	0/1	1/10	1/1	0/1	1/2	1/3	0/7
Total	2/3	1/1	1/2	3/6	6/7	3/7	1/2	1/12	3/3	0/1	1/5	1/3	0/7

$^{+}$ 1.00 am * 10.00 am

Table 39

Gut dissection results of harvestmen trapped infrequently in 1983
Data represent numbers dissected with aphid fragments in gut (numerator) and total numbers dissected (denominator)
(- indicates no specimens dissected)

Treatment / Species	Manipulative trial				demeton-S-methyl trial	
	Untreated	methiocarb	thiometon	methiocarb + thiometon	untreated	demeton-S -methyl
Mitopus morio	2/2	2/2	-	-	2/4	2/7
Oligolophus tridens	-	-	-	0/1	-	-
Paroligolophus agrestis	-	-	-	-	0/4	1/8
Opilio parietinus	1/1	-	-	-	-	-
Opilio saxatilis	0/3	0/1	1/3	2/3	5/27	2/14
Leiobunum rotundum	-	-	-	-	1/1	-

on predation of aphids would be obscured as the origin of prey was uncertain. A series of laboratory experiments was done in 1984 and 1985 to determine the length of time an aphid meal is held in the digestive tract. This would indicate the length of time between feeding and capture.

5-2-2 MATERIALS AND METHODS

Beetles were caught in dry pitfall traps in an area of the potato field outside the main trial at Sheriffhall Mains in 1984 and in a field of early potatoes at Sheriffhall Mains in 1985. Beetles were kept at about 4°C in a darkened cold store in plastic washing-up bowls containing dog-meal and water. Seven days before the start of the experiment in each year, carabids were kept individually in 9 cm plastic petri dishes, provided with water only, and stored at approximately 20°C with a natural light regime. After 7 days each beetle was offered a live, apterous 4th instar or adult Macrosiphum euphorbiae or Myzus persicae. Each beetle was offered an aphid a maximum of 5 times, each occasion lasting 10 seconds with an interval of about one minute between each. If after this time the carabid had not eaten an aphid it was deprived of food for a further 3 days, after which the process was repeated. Numbers of each species and sex of beetle used were as available. Beetles which had taken an aphid were frozen at various "post-feeding" intervals.

In 1984 males were killed at half-hourly intervals from 1-10 hours and at 18, 24, 36 and 48 hours after feeding. Females were frozen at hourly intervals from 2½-9½ hours after eating. In all cases a single individual only was killed at any one time, except when one of each sex was frozen. In early July 1985, 11 P madidus (6 ♀♀, 5 ♂♂) were killed 24 hours after feeding. On 18 August 1985, specimens of P madidus and P melanarius were killed at intervals of 6, 12 and 24 hours after eating. In each case 4 ♀ P melanarius and 2 of each sex of P madidus were tested.

Carabids were frozen, then placed in 70 per cent alcohol. The digestive tract of each was later removed and placed in 40 per cent glycerine on a slide. Foregut, midgut and hindgut (after Crowson, 1981) were each examined separately for the remnants of the earlier aphid meal. If no aphid remains were seen, slides were re-examined. Aphid position in the digestive tract was recorded.

5-2-3 RESULTS AND DISCUSSION

In slides examined twice, no aphid remains were seen at the second examination. Results of the 1984 experiment were inconsistent (Table 40) - aphid remains were present in one midgut within 2 hours and in a hindgut within 4½ hours of feeding. At 10 hours, remnants were observed in the foregut of one ♂ only but at intervals exceeding 10 hours, no remains were present in either gut section. This suggests that passage through the alimentary canal occurs at between 10 and 18 hours after feeding.

Due to the variability of the 1984 data, in 1985 several beetles were used at each feeding interval. This necessitated a reduction in the number of intervals tested. In the experiment where 11 P madidus were killed after 24 hours, aphid remains were found in the foreguts of 2 ♀♀ and the midgut of one ♂. The guts of the other 8 specimens were empty. In the second experiment in 1985, the numbers of beetles used were too low (2 of each sex of P madidus and 4 ♀ P melanarius) to allow comparison of species or sexes (Table 41). After 12 hours aphid remnants were present in foreguts but by 24 hours remains were detected in hindguts only. Remains were present in hindguts of 6 of the 8 specimens within 6 hours of feeding, indicating fairly rapid movement through the gut.

The few studies of retention time of prey in the digestive tracts of ground beetles suggest passage generally occurs within about 30 hours. Rhopalosiphum padi was retained in the digestive tract of Bembidion lampros for a mean of 27 hours (Scheller, 1984). The interval between consumption of fall armyworm (Spodoptera fungiperda) larvae by the carabid Calosoma sayi, and the appearance of prey in beetle faeces varied from 7.5-23 hours (Young and Hamm, 1986). Loughridge and Luff (1983) found that a significantly higher percentage of Harpalus rufipes caught in formalin-filled pitfall traps contained aphid remains than those caught in dry pitfall traps. This observation implies that a significant amount of digestion occurs in beetle guts in dry traps, and as the traps were operated over 24 hour periods, significant digestion must have occurred within that time.

Overall, the evidence is that prey is retained for about one day or less. If these results can be extrapolated to the field, most aphids in guts of beetles

Table 40

<u>Pterostichus</u> <u>madidus</u> containing aphid remains (+) or not (-) in foregut, midgut or hindgut at various intervals after consumption of an aphid in the laboratory. A single specimen was used at each interval.

Time from feeding-death (hours)	Part of digestive tract		
	Foregut	Midgut	Hindgut
(a) ♀♀			
2½	+	+	-
3½	-	+	-
4½	-	-	+
5½	-	+	-
6½	+	+	-
7½	-	-	+
8½	-	+	-
9½	-	+	-
(b) ♂♂			
1	+	-	-
1½	+	+	-
2	+	+	-
2½	+	-	-
3	-	-	-
3½	-	+	-
4	+	+	-
4½	-	+	-
5	-	-	-
5½	+	-	+
6	-	-	+
6½	+	-	-
7	-	+	-
7½	-	+	-
8	+	+	-
8½	-	-	-
9	-	-	-
9½	+	-	+
10	+	+	-
18	-	-	-
24	-	-	-
36	-	-	-
48 (x2)	-	-	-

Table 41

Pterostichus spp containing aphid remains (+) or not (-) in foregut, midgut or hindgut 6, 12 or 24 hours after consumption of an aphid
(Each horizontal set of 3 symbols (+/-) represents a single beetle)

	Time between feeding and death (hours)								
	6			12			24		
Part of gut* / Species	F	M	H	F	M	H	F	M	H
Pterostichus madidus ♀♀	-	-	+	+	-	-	-	-	-
	-	-	+	-	-	-	-	-	+
Pterostichus madidus ♂♂	+	-	+	+	-	-	-	-	+
	-	-	+	-	+	-	-	-	-
Pterostichus melanarius ♀♀	+	-	+	-	-	+	-	-	+
	+	-	-	-	-	+	-	-	-
	+	+	-	-	+	+	-	-	-
	+	-	+	+	-	-	-	-	-

* F = foregut, M = midgut, H = hindgut

trapped in the field were eaten within the 24 hours before capture. P madidus and P melanarius travel an average of 9 m in 24 hours (Chapter 6). An aphid was therefore likely to have been eaten in the plot of capture, particularly in 1984 and 1985 when plots were larger than in 1983.

The hunger status of Pterostichus spp used in these experiments was unknown, but may affect retention time of prey. Rate of prey digestion in larvae of Poecilus cupreus increased as the period of starvation before feeding increased (Lövei et al, 1985). If laboratory beetles were "hungrier" than field-collected ones, the latter may have retained prey longer and some aphids recorded from crops may have been eaten in a plot other than that of capture. The rate of aphid passage through the guts of "fed" beetles was not determined in the laboratory as aphids were not accepted unless the beetles were "hungry".

5-3 CLIMBING OF POTATO PLANTS BY CARABIDAE

5-3-1 INTRODUCTION

Some species of ground beetles are known regularly to climb plants: Zabrus tenebroides climbs cereal stalks and feeds on grain, and Agra tristis climbs trees in the Brazilian rain forest (Thiele, 1977). Little is known about the plant-climbing ability of most carabids (Lövei and Szentkirályi, 1984). Agonum dorsale has been casually observed to climb on winter wheat but rarely to a height sufficient to feed on aphids (Griffiths, 1982; Griffiths et al, 1985). The same species, as well as Amara and Risophilus (Vickerman and Sunderland, 1975), and Harpalus rufipes (Loughridge and Luff, 1983), have been swept from cereal plants. Lövei and Szentkirályi (1984) placed traps on maize stalks and over 3 years only 10 ground beetles were trapped, all of which were macropterous. The apparent consensus is that most ground beetles infrequently, if ever, climb on vegetation (Kirk, 1971; Griffiths, 1982), and Kirk (1982) concluded:

> "after 15 summers spent studying (carabids) in the field both day and night, I have never seen a ground beetle on a standing cornstalk".

However, in a laboratory study Dunning et al (1975) found P melanarius and A dorsale to be active climbers on sugar beet plants, and in a field study Foster (1972) observed a specimen of Pterostichus strenua on a potato haulm.

The situation was ambiguous and experiments were done to determine whether ground beetles, particularly Pterostichus spp, climb potato plants.

5-3-2 MATERIALS AND METHODS

(a) Field

(i) On 9 August 1984, bioadhesive tape designed to trap caterpillars ("Ecoland", Milan, Italy) was applied to the stems of 3 potato haulms but was unmanageably sticky and not used further. On 10 August 1984, "sticktite" was thickly applied in a 10 cm wide band at 10 cm above soil level to 5 haulms in each of 5 groups of 5 hills (125 haulms in total). These were examined daily over 7 days for beetles trapped in the sticktite. The ground around each hill was examined for insects which might have encountered the sticktite and fallen or walked away.

(ii) Twice during 1984 and once during 1985 trial sites were visited at midnight and casual observations made of nocturnal predators.

(b) Laboratory

Tests were made in 1984 to determine whether Pterostichus encountering sticktite would be trapped.

(i) Sticktite was applied thickly to the insides of 3 9 cm plastic petri dishes. Two adult ♀ P madidus were placed in one dish; 2 ♂♂ in each of the others. All beetles were monitored for 10 minutes.

(ii) Three potato haulms were obtained from the field and leaves removed in the laboratory. The haulm bases were inserted into a cardboard box such that the haulms were vertical. A 10 cm wide sticktite band was applied to the upper portion of each stem. Two P melanarius (1 ♀, 1 ♂) and 2 P madidus (1 ♀, 1 ♂) were placed individually on the sticktite bands. Each beetle was monitored for 10 minutes.

5-3-3 RESULTS AND DISCUSSION

(a) Field

No large carabids were trapped in the sticktite bands placed on 125 potato haulms. Over the 7 days, a total of 6 hoverfly adults, 6 Bembidion spp, 2 adult Coccinella septempunctata and one adult Coccinella undecimpunctata, as well as many small, unidentified flies and wasps, was trapped. The absence of large ground beetles may be because they do not climb potato haulms, they are not trapped by sticktite, or they are repelled by sticktite.

(b) Laboratory

Experiments to determine whether beetles are trapped or repelled by sticktite were largely inconclusive. In the test with 6 P madidus placed on sticktite-covered petri plates, 2 waded about in it and 4 were immediately immobilized. All eventually died. The plates were, however, slippery and it is possible that had beetles been able to "grip" the surface they may have been able to climb out.

In the laboratory trial with sticktite-covered haulms each individual fell off after a few seconds. This result may not be representative of the field as handling "disturbed" the beetles and they "struggled" when put on the sticktite.

No carabids were ever observed on foliage examined during nocturnal field visits. Trechus spp and Bembidion spp were occasionally observed on leaves during the day. On several occasions in the field, Pterostichus spp captured in dry traps were placed carefully on middle and upper leaves of potato plants. In every case they immediately slipped about the foliage and fell to the ground. Their behaviour was most likely to have been abnormal at these times.

5-4 INSECTICIDES : LABORATORY STUDIES

5-4-1 INTRODUCTION

Results of field experiments suggested 3 possible explanations for reductions in catches of Pterostichus spp in treated areas:

1. beetle mortality due to direct exposure to the insecticide;

2. a decrease in activity level of beetles due to a decrease in level of hunger in treated but not untreated areas; this results from feeding on aphids fallen to the ground after treatment;

3. beetle mortality due to the consumption of aphids contaminated with insecticide.

To determine whether any of these hypotheses, or a combination of them, was correct a number of questions had first to be answered:

1. does direct exposure to demeton-S-methyl kill these beetles;

2. do treated aphids fall to the ground;

3. do Pterostichus spp eat these aphids and, if so, is beetle mortality a result?

Various laboratory and field experiments were done in an attempt to answer these questions.

5-4-2 MORTALITY DUE TO DIRECT EXPOSURE

(a) Field experiments

(i) Two dry pitfall traps were placed in each plot before the second spray in 1984. Live beetles caught could be monitored to assess percentage mortality of those from treated and untreated areas. Traps were examined at 11, 24, 48 and 72 hours after treatment. Trapped Pterostichus spp were returned to the laboratory and kept separately in petri dishes supplied with food and water. Beetles were maintained at about 20°C and with natural light, and monitored once daily for seven days.

Results

Few beetles were caught in dry traps. At 11 hours after treatment

3 P melanarius and one P madidus were trapped in untreated plots; 3 P madidus only in treated plots. At 24 hours 2 P melanarius and one P madidus were present in untreated plots and 3 P madidus and one P melanarius in treated plots. At 48 hours after treatment one beetle only, a P madidus, was caught in an untreated area. None was trapped 72 hours after spraying. Of captured beetles, 2 individuals only died: one of each species, each collected on 8 August (24 hours after treatment) in sprayed areas, and each died on 13 August.

A similar experiment was done at the first spray in July 1985. No beetles were captured.

(ii) Little information was obtained using dry traps to catch "treated" and "untreated" Pterostichus spp in 1984 and 1985 so an experiment was done where known numbers of beetles were introduced into plots before spraying. On 13 August 1985, 3 plastic washing-up bowls were each filled with approximately 800 g soil. Ten ♀ P melanarius and 5 of each sex of P madidus were introduced into each bowl, provided with moistened dog meal and kept in the laboratory overnight at about 20°C. One hour before the field spray on 14 August, the dog meal was removed and bowls with beetles placed in furrows in the field: one in each of 2 plots to be treated, one in an untreated plot. Two hours after treatment bowls were returned to the laboratory and beetles provided with fresh dog meal and moistened paper-towelling. Bowls were maintained at about 20°C and with a natural light regime and beetle mortality was monitored at 24 hour intervals for 8 days.

Results

No mortality occurred during the experiment. At 24 hours after treatment a ♀ P melanarius from a sprayed plot was "semi-active", able to take a few steps when prodded but unsteady and slow. She had apparently recovered by 48 hours after insecticide application.

(b) Potter Tower experiments

(i) Introduction

A "Potter Precision Laboratory Spray Tower" (Burkard Manufacturing

Co, Hertfordshire) with a detachable atomizer and pneumatic spray table was used to assess the effects of demeton-S-methyl on Agonum dorsale, Pterostichus melanarius and P madidus.

Beetles, collected in dry pitfall traps outside the field experiment area at Sheriffhall Mains (1984) or Turnhouse Farm (1985) were kept either in groups of 5 in ventilated 9 cm plastic petri dishes (A dorsale), or in groups of 40 in plastic washing-up bowls (Pterostichus spp). All were provided with water and moistened dog meal and kept at about 4°C in a darkened cold store. Twenty-four hours before experiments insects were maintained at 20°C in natural light. The Potter Tower was used to expose beetles to insecticide either directly or indirectly. Insufficient beetles were available to relate response to dose (probit analysis). Experiments were done instead to relate response to time.

(ii) Agonum dorsale

Beetles were treated in 1984 only. In the indirect treatment 9 cm plastic petri dishes with 16.5 g soil (from Sheriffhall Mains) were sprayed with demeton-S-methyl at field rate (420 ml/ha in 200 l water) or at half that rate. Twenty dishes were treated in each category. A single untreated unsexed beetle was placed in each dish after soil treatment.

For direct treatment individuals were placed in 9 cm petri dishes with covers removed, and were sprayed singly with demeton-S-methyl at either full or half rate. Twenty specimens were treated in each category. Immediately after exposure beetles were placed in 9 cm petri dishes each of which contained 16.5 g untreated soil.

The control treatment using water only was applied directly to beetles in petri plates containing 16.5 g soil rather than treating soil and beetles separately as was done with demeton-S-methyl. This was because numbers of beetles were low and water was assumed to be non-toxic.

Twenty-two individuals remained following allocation of the above 100 beetles. To dishes already containing beetles 11 of the remaining 22 were added to 11 dishes with soil sprayed at half rate and 11 to 11 dishes with soil sprayed at full rate. Thus 22 dishes contained 2 individuals, the rest one, and each treatment was replicated either 20 or 31 times.

All beetles were maintained after treatment in 9 cm plastic petri dishes at 20°C and provided with water and moistened dog meal. Beetles were examined at the following "post-treatment" intervals (hours): 2, 4, 6, 8, 10, 12, 18, 24, 48, 72, 96, 120, 144 and 168. Records were kept of numbers of individuals dead, moribund, semi-active or active. A dead beetle did not move when prodded with forceps; a moribund individual twitched when touched but did not walk. A semi-active carabid was able to take a few steps only and an active beetle ran about in the dish when prodded.

Results

Data for A dorsale mortality are shown in Figure 22. Per cent mortality was very high when beetles were treated directly with either rate, or with full rate on soil. Full rate on beetles elicited the fastest response with 75 per cent dead in 6 hours and 90 per cent in 2 days. Full rate on soil produced a slower response possibly because the effective dose increased with time as beetles moved about and contacted the pesticide residue. The differences between these treatments are not, however, great - a 5 per cent difference in mortality may reflect only a single individual. Direct treatment and full rate on soil produced 95-100 per cent mortality in 7 days. Half rate on soil had little effect and no beetles died when treated with water.

Demeton-S-methyl toxicity data for A dorsale are not strictly relevant to potato fields in Scotland as this species is mainly present in the spring (Chapter 4) and is unlikely to be abundant when crops are treated. Results may, however, be relevant to other cropping situations such as in cereals where A dorsale is more likely to be exposed to insecticides. In the present study A dorsale was used to test the "experimental system" because, unlike other species of carabids, it was abundant at the time of the test.

Ware potatoes receiving foliar insecticidal sprays are likely to be treated in July and/or August in Scotland, a time when the crop canopy is extensive.

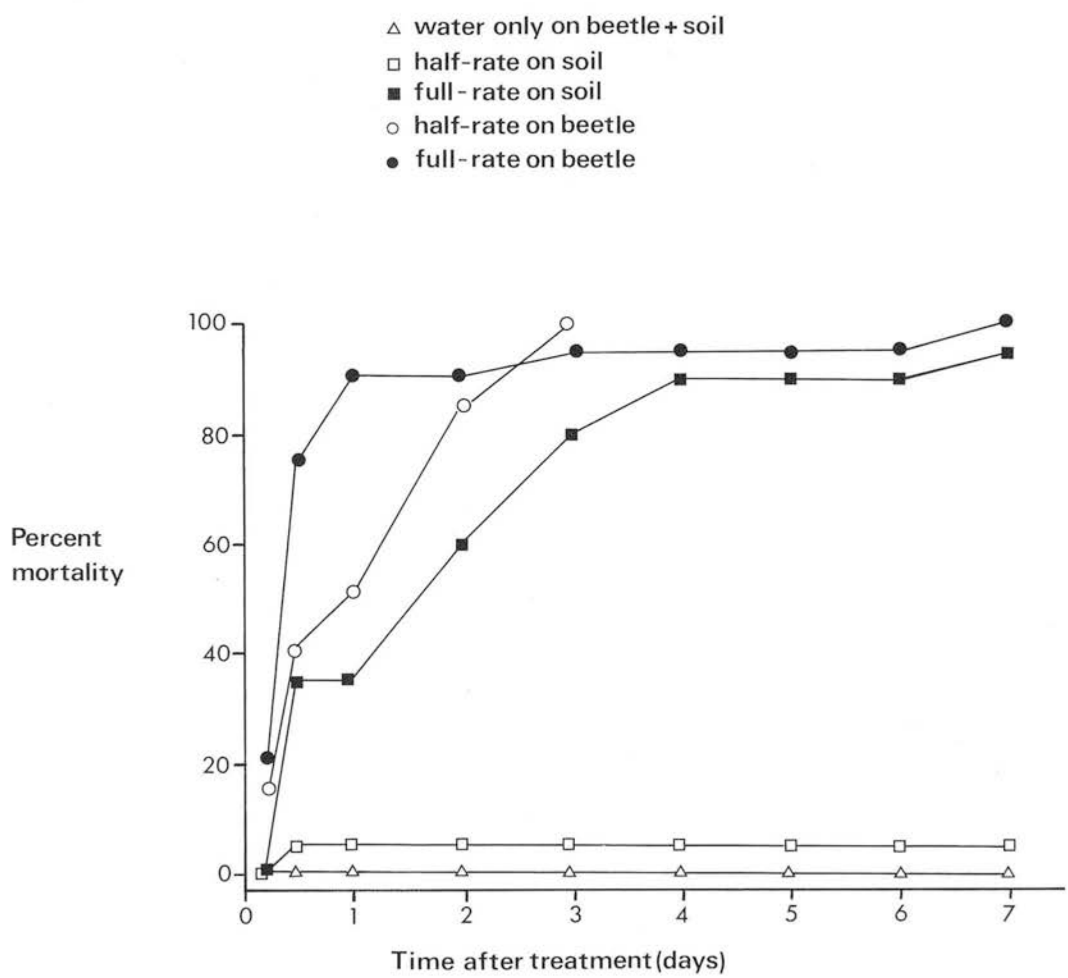


Figure 22: Percentage mortality Agonum dorsale adults (sexes combined) against time (days) from treatment in the laboratory with demeton-S-methyl.

It was considered that a proportion of applied material would be intercepted by foliage. Ground beetles, particularly nocturnal species, would therefore be unlikely to receive a full dose of insecticide. At the time of the experiment with A dorsale, the rate reaching the ground (ground-rate) was not known and the half-rate used to represent this was arbitrarily chosen. Time constraints resulted in Pterostichus spp not being tested in the Potter Tower in 1984, and laboratory susceptibility of Pterostichus spp to demeton-S-methyl was instead examined in 1985. Before 1985 trials, field experiments were done to determine the proportion of demeton-S-methyl reaching ground level. These experiments are described below, followed by details of experiments to determine whether Pterostichus spp are killed by direct exposure to demeton-S-methyl.

(c) Pesticide penetration of crop canopy

Two experiments were done during the first field spray on 25 July 1985. Insecticide penetration was measured at 3 levels in the foliage, although the proportion reaching the ground was of most interest in the present study. At the time of these experiments the potatoes had developed a complete canopy of foliage.

(i) On 24 July, 80 7.0 cm x 2.5 cm rectangles of water-sensitive paper (manufactured by Ciba-Geigy, available from C T (London) Ltd, Guildford, Surrey, England) were fixed with "Blu-Tak" to the insides of the bottom halves of 80, 9 cm plastic petri dishes. Water-sensitive paper is yellow when unexposed: after exposure to liquid it turns blue, and the proportion of blue paper provides a relative indication of spray penetration.

Four petri plates were attached to single bamboo canes at points equivalent to various levels above potato ridges: 50 cm ("upper" leaves), 35 cm ("middle" leaves), 10 cm ("lower" leaves) and 0 cm (at soil level). Plates were positioned on canes at 90° to one another so overlap was minimized. Four canes each with 4 petri plates were placed immediately before treatment within foliage in the 6 m x 6 m subplot area of each plot to be sprayed. Four plates per subplot to be treated were also placed on the ground under foliage in the furrows. After plot treatment dishes were collected, covered and taken to the laboratory where samples of the water-sensitive paper were photographed.

Results

Plate 3 shows samples of water-sensitive paper after treatment in the field. The samples were chosen visually and represent average results for each canopy position. There is an obvious trend towards lesser spray penetration of lower foliage and the soil in the furrows.

Humidity caused the background diffuse blue colour which is particularly noticeable on the papers from the furrow, where foliage was most dense. Had this been foreseen, paper could have been placed in unsprayed plots as well, and the differences compared. Nevertheless, it is is still possible to discern the discrete marks indicating insecticide impingement.

(ii) In early July 1985, thin-layer grade silica-gel powder was mixed with water to form a slurry which was spread on 20 cm x 5 cm glass plates at the Department of Agriculture and Fisheries for Scotland (DAFS), East Craigs, Edinburgh.

On 24 July groups of 4 silica-gel plates were clamped at 90° to one another to single bamboo canes and at the same levels as the petri plates discussed above. Four canes were positioned within foliage in each subplot to be treated, immediately before spraying. Plates at 50 cm above ridges were not placed under leaves. Four plates per "treated" subplot were also placed under foliage in furrows. Immediately after insecticide application a 200 ml sample was taken from the spray tank.

One hour after spraying, plates were collected and taken to DAFS where the silica-gel was scraped into volumetric flasks. Each plate was washed with 50 ml acetone. Extracts containing acetone and gel were injected into a "Perkin Elmer F33" gas chromatograph with a flame photometric detector. The detector cell measured the wavelengths emitted by heated phosphorous (the phosphorous in the demeton-S-methyl). Each extract was assessed against a standard (analytical grade demeton-S-methyl) and the concentration of active ingredient in each was calculated. The tank mixture was diluted in acetone, injected into the gas chromatograph and analysed

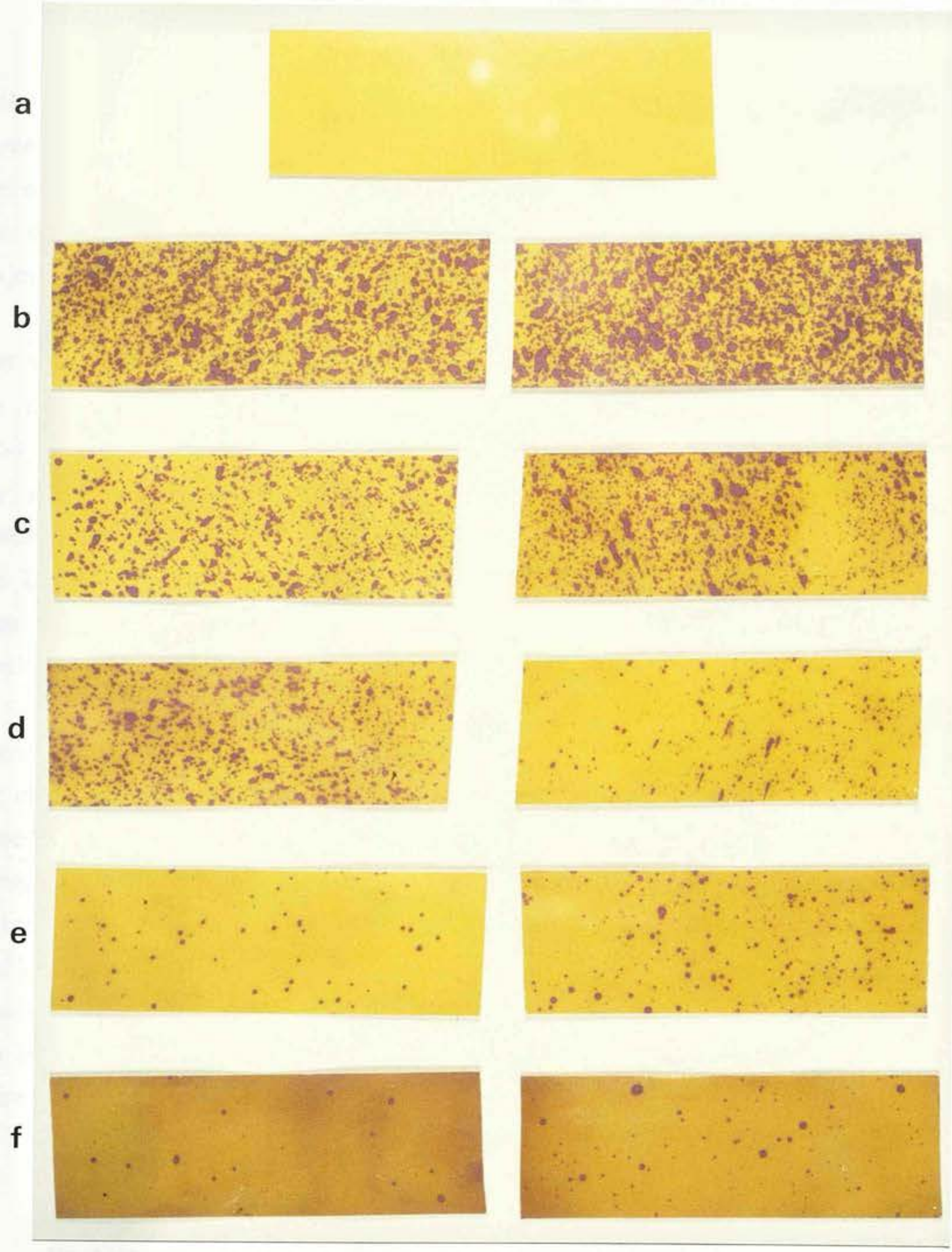


Plate 3: Samples of water-sensitive paper from various positions within the potato canopy after treatment with demeton-S-methyl and an untreated sample.
(a = untreated; b = upper leaf level; c = middle leaf level; d = lower leaf level; e = on soil, on ridge; f = on soil, in furrow).

as above.

Results

The amount of demeton-S-methyl deposit on silica-gel plates increased with increasing distance of plates from soil level (Figure 23). The overall percentage deposition was low with even upper leaf positions receiving an average of one-fifth of the theoretically applied rate. Reasons for this are unknown but spray drift away from plates is unlikely to have been a major factor as the weather was calm on the day of spraying (see Appendix 2).

The tank mixture sample contained 495.5 g/ha of active ingredient, twice the theoretical rate of 244 g/ha. Duplicated tests of the tank sample gave good agreement on this figure so presumably the analysis was accurate. For the sprayer used, each full tank of demeton-S-methyl at recommended concentration contains 500 ml of concentrate originating from 1 l bottles. The likely explanation for the double-rate tank mixture is that the full rather than half litre was used, although this was refuted by the farm worker involved.

Nonetheless, Pterostichus melanarius and P madidus, which probably do not climb plants, are unlikely to receive a dose of demeton-S-methyl exceeding 4 or 5 per cent of the recommended rate (Figure 23). The percentage deposition data given are based on g/ha of active ingredient on silica-gel plates in relation to a theoretical application of 244 g/ha. If the actual applied rate was twice the theoretical, then percentage deposition figures should be halved and the percentage of insecticide reaching Pterostichus spp is less than 5 per cent. Five per cent was chosen as the "ground-rate" to be tested using the Potter Tower.

(d) Potter Tower : Pterostichus spp

Beetles used in Potter Tower experiments in 1985 were treated either directly or indirectly with full-rate (244 g/ha), or 5 per cent of full-rate (12.2 g/ha) demeton-S-methyl. Soil used was from Turnhouse Farm and in all respects other than application rates and species used, 1985 experiments were the same as those of 1984 with Agonum dorsale. Table 42 shows the quantity of each sex and species used in each treatment, numbers used being

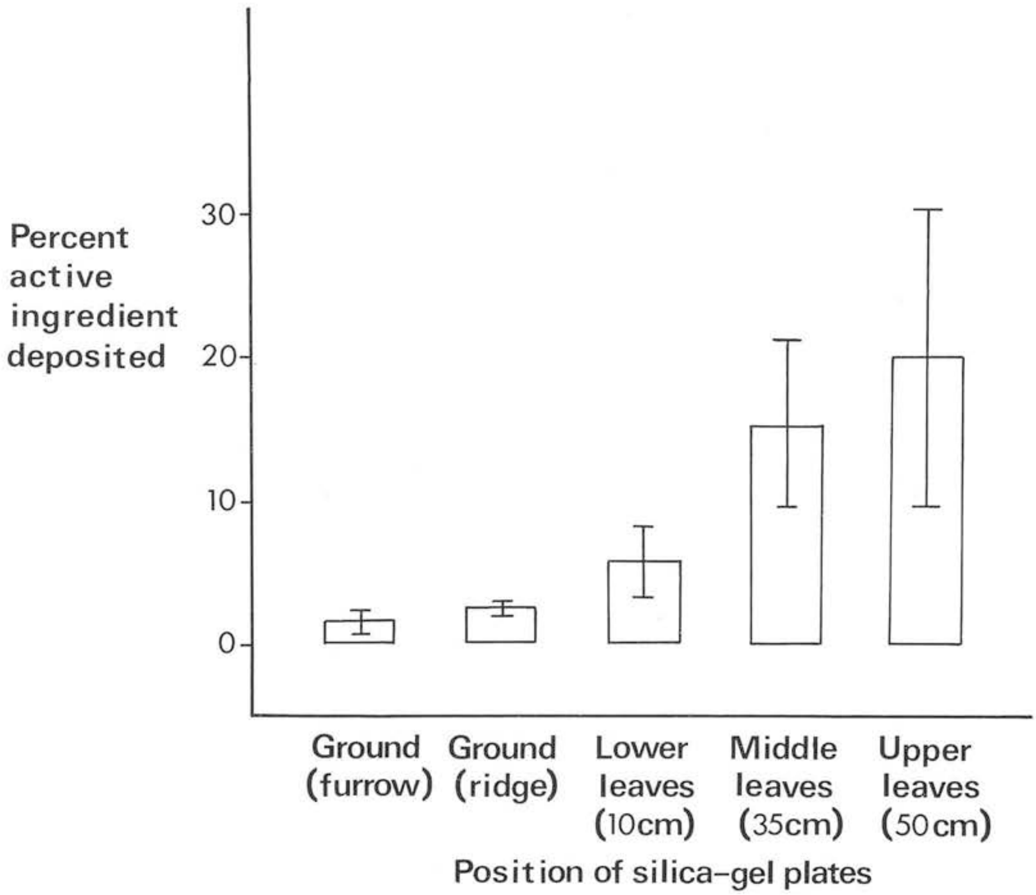


Figure 23: Mean percentage and 95 per cent confidence intervals of theoretical applied rate (244 g a.i. per ha) of demeton-S-methyl deposited at various levels in a potato crop, as measured on silica-gel plates.

Table 42

Numbers of Pterostichus melanarius and Pterostichus madidus exposed either directly or via treated soil to various rates of demeton-S-methyl using a Potter Tower. The totals dead in each category at the end of the experiment are in parentheses.

Treatment	Sex	Number individuals treated (no dead at end of experiment)			
	Species	Pterostichus melanarius		Pterostichus madidus	
		♀	♂	♀	♂
on beetle	Water	10 (0)	0 -	5 (0)	5 (1)
	Full-rate	20 (0)	5 (0)	5 (0)	5 (3)
	Ground-rate	20 (1)	10 (0)	5 (0)	5 (0)
on soil	Full-rate	20 (3)	5 (0)	5 (1)	5 (1)
	Ground-rate	20 (0)	10 (0)	5 (0)	5 (0)
Total		90 (4)	30 (0)	25 (1)	25 (5)
Overall per cent mortality		4.4	0	4.0	20.0

governed by availability. Fewer beetles were allocated to the control as few deaths were expected. As beetles were sprayed individually, each specimen represents a replicate of a particular treatment.

Results

Demeton-S-methyl appears not to be very toxic to P melanarius or P madidus (Table 42), although ♂ P madidus seem somewhat susceptible, particularly to direct application at full-rate. Three ♀ P melanarius died after exposure to full-rate on soil, one after 2 days, the others after 5. The "lag period" may be explained by the time necessary to accumulate a lethal dose as beetles moved about and contacted treated soil; certainly the individual which died after 2 days had been "semi-active" from 6 hours after treatment, although no moribund state was observed. The 2 beetles which were dead at 5 days were recorded as active at 4 with no observed intermediate states.

Of the 3 ♂ P madidus which died after direct treatment with full-rate demeton -S-methyl, one was dead within 18 hours, one after 2 days and one after 3 days. In these cases soil was untreated and the lag period between spray application and death was not due to an accumulated dose. Perhaps a minimum period is required following exposure before lethal effects are expressed. It is possible that a higher level of mortality would have been detected had the insects been monitored for a longer period; in general, however, ground beetles may take up to 2 days to show effects, with additional mortality after 4 days being rare (P J Edwards, pers comm).

The P madidus which died between 12 and 18 hours after treatment was semi-active at 2 hours, made an apparent recovery at 4 hours and was recorded as active until 10 hours when it was moribund. The others died after being last recorded as active, with again no observed intermediate stages.

Overall, mortality was low (0-20 per cent) and the death of a ♂ P madidus 6 days after exposure to water only suggests the occurrence of some natural death. This low mortality did not occur when P melanarius was treated with demeton-S-methyl in the laboratory in Suffolk (Dunning et al, 1982). Beetles were treated with a concentration commercially recommended for aphid control on sugar beet, either by total immersion for one second, by soil contact or by food contamination. Mortality after 100 hours was 85, 48 and 95 per cent respectively.

5-4-3 REDUCTION IN BEETLE ACTIVITY LEVELS

The possibility of beetles feeding on aphids fallen to the ground after insecticide treatment, with a consequent reduction in activity level and trap catch, is discussed in section 5-1.

5-4-4 BEETLE MORTALITY DUE TO EATING CONTAMINATED APHIDS

Pterostichus melanarius (6 ♀♀, 5 ♂♂) and P madidus (5 ♀♀, 5 ♂♂) collected from dry pitfall traps at Turnhouse Farm in 1985 were kept in a darkened cold store at 4°C and with moistened dog meal and water for several days. On 3 August, beetles were kept separately in petri dishes and, so they would be hungry, were provided with water only.

On 10 August, the upper sides of leaves of Chinese cabbage (Brassica oleracea cv chinensis) infested with Myzus persicae (from a laboratory culture) were sprayed with the field-recommended rate of demeton-S-methyl (420 ml/ha in 200 l water), using a Potter Tower. Leaves were detached from stems and placed in 9 cm petri dishes before treatment, and were left in dishes for 2 hours after treatment.

After 2 hours, 15 treated 4th instar or adult apterous M persicae were placed on each of several squares of damp filter paper. Each beetle was provided with 15 treated aphids. Over the next 4 hours, dishes were examined every 30 minutes; if all 15 aphids had been eaten they were replaced by another 15 treated aphids.

Beetles were then provided water and dog meal and kept at about 20°C in a natural light regimen. They were examined at intervals of 4, 12, 18 and 24 hours after the first offering of treated aphids, then at 24 hour intervals for 9 days. Numbers of dead, moribund and active individuals at each check, and of the quantity of treated aphids consumed by each beetle, were recorded. Six individuals (3 ♀♀ P melanarius, 3 ♀♀ P madidus) were fed as above but with untreated aphids.

Results

The number of aphids eaten per beetle ranged from 0-105 and averaged 62 (±6). One individual only consumed no aphids: a ♂ P melanarius.

Overall mortality was 19.1 per cent (4/21). Two ♂♂ P madidus and 2 ♀♀ P melanarius died, although there was no apparent pattern in either length of time between consumption and death, or in quantity of treated aphids eaten and death. Both P madidus died between 24 and 48 hours after first being offered aphids. One of these beetles was moribund within 4 hours of having eaten 15 aphids and consumed no others. The second beetle was semi-active after 2 meals (at 12 hours after first offering) but accepted and ate another 15 aphids. Several P madidus (both sexes) exhibited twitching leg movements during the experiment, from within 12 hours to 4 days after the first meal, but all apparently recovered.

No obvious symptoms of insecticide-poisoning were observed in any P melanarius except in the deaths of 2 females. Of these, one died 3 days after its first meal (having eaten 6 meals = 90 aphids), the other after 10 days and 3 meals (45 aphids). None of the beetles fed untreated aphids died or exhibited symptoms of insecticide-poisoning.

P melanarius and P madidus will obviously eat treated aphids, with an average mortality of approximately 20 per cent. This level of mortality does not preclude more subtle effects (eg a decrease in fecundity), which were not monitored in this experiment and which could affect beetle populations over a longer term. Beetles used in this study were "hungry" and had no alternate prey: whether treated aphids would be as readily consumed in the field is unknown.

Mortalities of 93-98 per cent were recorded in the laboratory 100 hours after P melanarius ate powdered bran and dried meat contaminated with demeton-S-methyl, acephate or demephion (Dunning et al, 1982). These mortalities are higher than observed in the present study but amounts of food consumed were not stated. The situation is, however, complex:

deltamethrin killed 80 per cent of *P melanarius* exposed to treated soil but only 3 per cent of *P melanarius* which had eaten treated food (Dunning *et al*, 1982). Gholson *et al* (1978) fed larvae of the black cutworm *Agrotis ipsilon* treated with various insecticides, to 4 species of carabid beetle, including *Pterostichus chalcites*. Results for all species were combined and mortality varied from 2.5 to 82.5 per cent of beetles fed with toxaphene- or carbofuran-treated cutworm larvae respectively. In the same experiment 100 per cent of carabids died when confined on carbofuran-treated soil and 21-95 per cent after exposure to soil treated with toxaphene. Route of exposure is obviously important in carabid susceptibility to pesticides and warrants further attention.

CHAPTER 6

POLYPHAGOUS PREDATORS

MISCELLANEOUS

6-1 ALARM PHEROMONE EXPERIMENT

6-1-1 INTRODUCTION

Pheromones are semiochemicals which act generally intra-specifically and in aphids the 3 main types are aggregative, sexual and alarm (Herrbach, 1985). Alarm pheromones volatilize from the cornicle secretions produced when aphids are attacked or irritated (Pickett et al, 1982). (E)-ß-farnesene is the alarm pheromone of many species of aphid including Macrosiphum euphorbiae and Myzus persicae (D Griffiths, pers comm).

Alarm pheromone production is induced by a variety of factors including predation, vibration and certain insecticides. Individuals in the vicinity of an aphid caught by a predator will walk away or drop from the plant (Montgomery and Nault, 1977; Gut and van Oosten, 1985). Demeton-S-methyl and pirimicarb, but not deltamethrin, induce cornicle secretion and therefore alarm pheromone release in some aphids (Rice et al, 1983).

Aphid alarm pheromones may be used in future crop protection as repellents, preventing alate aphids from landing (Herrbach, 1985). Alarm pheromones used in combination with certain insecticides enhance aphid kill by increasing activity and thus exposure to the chemical (Pickett et al, 1982), and (E)-ß-farnesene may be important in biological control as it is probably not toxic to the natural enemy fauna (Herrbach, 1985). However, (E)-ß-farnesene is volatile and persists poorly in crops, although some of its derivatives may be more persistent (Pickett et al, 1982). Also, if alarm pheromones are employed in the same "shotgun approach" to pest management as biocidal compounds, aphids are likely to be selected with a reduced response to alarm pheromone (B Roitberg, pers comm).

In the current study, ground-based predators in potato fields probably eat aphids mainly when aphids fall on to the soil, as after treatment with pesticides. (E)-ß-farnesene was used to determine whether the availability of aphids to epigeal predators could be increased, compared with untreated, using a material other than toxic insecticides.

6-1-2 MATERIALS AND METHODS

On 10 June 1985, Maris Piper VTSC unchitted tubers were planted singly in plastic pots with a 3:1 mixture of a standard potting compost and peat. Pots were kept outside in a sunny, sheltered position and watered as required. On 29 August 1985, 660 g of soil from Turnhouse Farm were placed in each of 5 plastic washing-up bowls. Three of each sex of Pterostichus melanarius and P madidus were added to each of 3 bowls. All bowls were kept at about 20°C in natural light, and those with beetles provided with moistened dog meal and water. Also on 29 August, 10 leaves were removed from the middle regions of the potatoes planted previously. Two leaves were put in each of 5 plastic cups containing water. Pieces of Chinese cabbage with insecticide-susceptible Myzus persicae from a laboratory culture, were placed on the potato leaves and as the cabbage deteriorated, aphids moved to the potatoes. Approximately 50 aphids were transferred to each leaf in this way.

On 31 August, 2-sided sticky tape was applied in a continuous strip to the inside rims of the washing-up bowls. This was to trap any aphids falling to the soil and subsequently climbing the bowls, after treatment. Two leaves with aphids were placed, upper surfaces uppermost, on each of 5 enamel trays such that foliage hung outside tray edges and did not overlap horizontally. Leaves were held in place by sticky tape. Leaf bases were wrapped in wet cotton wool. Trays were positioned over plastic bowls so that leaf tips hung approximately 10 cm from the soil surface.

Leaves were treated with either water alone, (E)-ß-farnesene or demeton-S-methyl. Spraying was done with a small domestic spray atomizer (fluid capacity 300 ml) used for moistening plant leaves. One depression of the atomizer plunger released c 1.2 ml of fluid. During application, atomizers were held at 25 cm from leaf surfaces and the 3 treatments were done in separate rooms to minimize contamination. Water was applied to leaves over a tub containing beetles; (E)-ß-farnesene and demeton-S-methyl were each applied to leaves over 2 tubs, one with and one without beetles.

Application rates (approximations only):

(i) water: c 11 ml/m^2

(ii) (E)-ß-farnesene: synthetic alarm pheromone was provided by Dr D Griffiths, Rothamsted Experimental Station. It was dissolved in hexane (1 mg/ml) in 12 drawn glass tubes sealed under nitrogen. Each tube contained about 800 ul (E)-ß-farnesene. In a preliminary trial no reaction was observed when undiluted material from 2 tubes was sprayed on a Chinese cabbage plant infested with Myzus persicae. In the present experiment therefore all the remaining 8 ml of (E)-ß-farnesene was used in an attempt to induce a reaction, a rate of about 36 ml/m^2.

(iii) demeton-S-methyl: the commercial product was diluted according to the manufacturer's recommendation. The volume of diluted demeton-S-methyl applied was similar to that of the (E)-ß-farnesene → 8.4 ml (7 depressions of the plunger). To meet the recommended rate of 420 ml/ha, this volume should have been applied to about 7.4×10^{-4}m^2. It was actually applied to 2.2×10^{-1}m^2 and thus the rate used was much less than that recommended for field sprays.

All dog meal was removed before treatment. Numbers of aphids present on upper and lower surfaces of all leaves were counted before and after treatment. Numbers of aphids on the soil and on the sticky tape were counted after treatment. All beetles were killed after 24 hours and crops examined as described in Chapter 5.

6-1-3 RESULTS AND DISCUSSION

Before treatments were applied, most aphids were on the lower surfaces of the potato leaves (Table 43). Most aphids treated with demeton-S-methyl fell from leaves, particularly those on lower surfaces, despite the applied rate having been low. Aphids on the upper surfaces of the leaves may have died on the leaf and remained there. Data indicate that beetles may have

Table 43

Numbers of Myzus persicae on potato leaves before treatment and on leaves, soil and sticky tape 24 h after treatment with water, demeton-S-methyl or (E)-ß-farnesene in the laboratory. Treatments done over tubs with or without Pterostichus melanarius and Pterostichus madidus.

	Treatment \ Location	Before treatment	After treatment			Difference in numbers of aphids on leaves before, and on leaves, soil and tape after treatment
		On Leaves	On Leaves	On Soil	On Tape	
Tubs with beetles	Water	U* - 28 L - 116	U - 42 L - 128	0	2	+28
	demeton-S-methyl	U - 55 L - 153	U - (27)** L - (4)	(12)	(1)	-164
	(E)-ß-farnesene	U - 95 L - 130	U - 24 L - 158	1	16	-26
Tubs without beetles	demeton-S-methyl	U - 76 L - 71	U - (24) L - (3)	(51)	0	-69
	(E)-ß-farnesene	U - 17 L - 123	U - 17 L - 122	0	14	+13

* U = upper leaf surface, L = lower leaf surface ** (n) : dead aphids

eaten aphids on the soil: there were 51 dead aphids on the soil in tubs without beetles but only 12 aphids on soil in tubs with beetles. Also, there was a net reduction in numbers of dead and living aphids of 164 in tubs with, and of 69 in tubs without, beetles. One individual only was present on the sticky tape. Crops of dissected beetles from tubs treated with demeton-S-methyl were empty.

Aphid numbers on leaves were similar before and after treatment with (E)-ß-farnesene (Table 43). Aphids were unable to reclimb leaves from which they had fallen. Thus apparently they generally did not fall in response to the alarm pheromone. This may have been because the alarm pheromone was ineffective, although highest numbers of aphids on sticky tape were from these tubs. Laboratory cultures sometimes exhibit diminished responsiveness to alarm pheromone, particularly if old, and some species of aphid appear to require vibration of their substrate before many respond (Clegg and Barlow, 1982). Whatever the reason for the lack of response, results from the (E)-ß-farnesene experiment are inconclusive. The crop of one ♀ P madidus only from the alarm pheromone-exposed tub contained aphid remains.

Water appeared to have little effect on aphids, although 2 were on sticky tape. The highest net increase in numbers occurred in the tub treated with water and this was probably due to reproduction. No beetles from this tub contained aphid remains in their crops.

The crop of one beetle, of a total in all treatments of 26, contained aphid remains. This may have been because beetles did not eat fallen aphids, although the numbers of aphids on the soil in tubs treated with demeton-S-methyl was higher in tubs without beetles than with them. Crops of those beetles which ate aphids may have been empty because prey retention time was low.

6-2 MARK-RELEASE EXPERIMENT

6-2-1 INTRODUCTION

The effectiveness of the 1984 and 1985 field trials depended on individuals of Pterostichus spp not being able to travel more than 22 m in 24 hours. A mark-release study was done in 1984 to determine whether this distance was sufficient. Mark-release techniques are well established for determining population estimates and dispersal abilities of insects (Rivard, 1965; Fletcher, 1974; Robinson and Luff, 1979). They involve measuring the time taken from the simultaneous release of large numbers of marked individuals from a central location to their subsequent recapture at predetermined capture points extending out, often radially, from the central location. The standard technique seemed to present two problems in the current study: the radial geometry of the spatial layout when potatoes are planted in parallel ridges; and the need for large numbers of insects to release when the numbers of P madidus and P melanarius available were relatively small. An alternative mark-release layout was designed for use in potato fields.

6-2-2 MATERIALS AND METHODS

Eighteen adjacent furrows in a part of the field other than the main trial area were used. Release points formed a line 21.5 m from the field edge at right angles to the furrows (Figure 24). Black plastic "no 5 BEF" growers pots (perimeter 40 cm) were positioned in the furrows at distances between 0.5 m to 21.0 m from the release points, 4 traps at each distance, the traps forming a parallelogram. This parallelogram layout was adopted because it was considered that released beetles were more likely to move along furrows than across ridges and the experimental area would thus be "enclosed" with ridges acting as barriers. With the diamond-shaped trap arrangement any beetles moving across ridges were more likely to encounter a trap in the adjacent furrows than if the traps had been laid out in a different manner (ie an "X" shape). On each of the corners of the parallelogram near the release points, 2 additional 0.5 m traps were placed as safeguards against any beetles crossing ridges near the edge release points. As the width of a furrow was greater than the trap diameter, a 10 cm x 15 cm rectangle of 1.0 mm wire mesh was positioned on either side of each trap to prevent beetle escape round the sides of the traps (Plate 4).

Adult P melanarius and P madidus trapped in July in dry pitfall traps baited with strawberries, were kept in large plastic washing-up bowls, 40 beetles per bowl. These were lined with damp paper towelling and stocked with

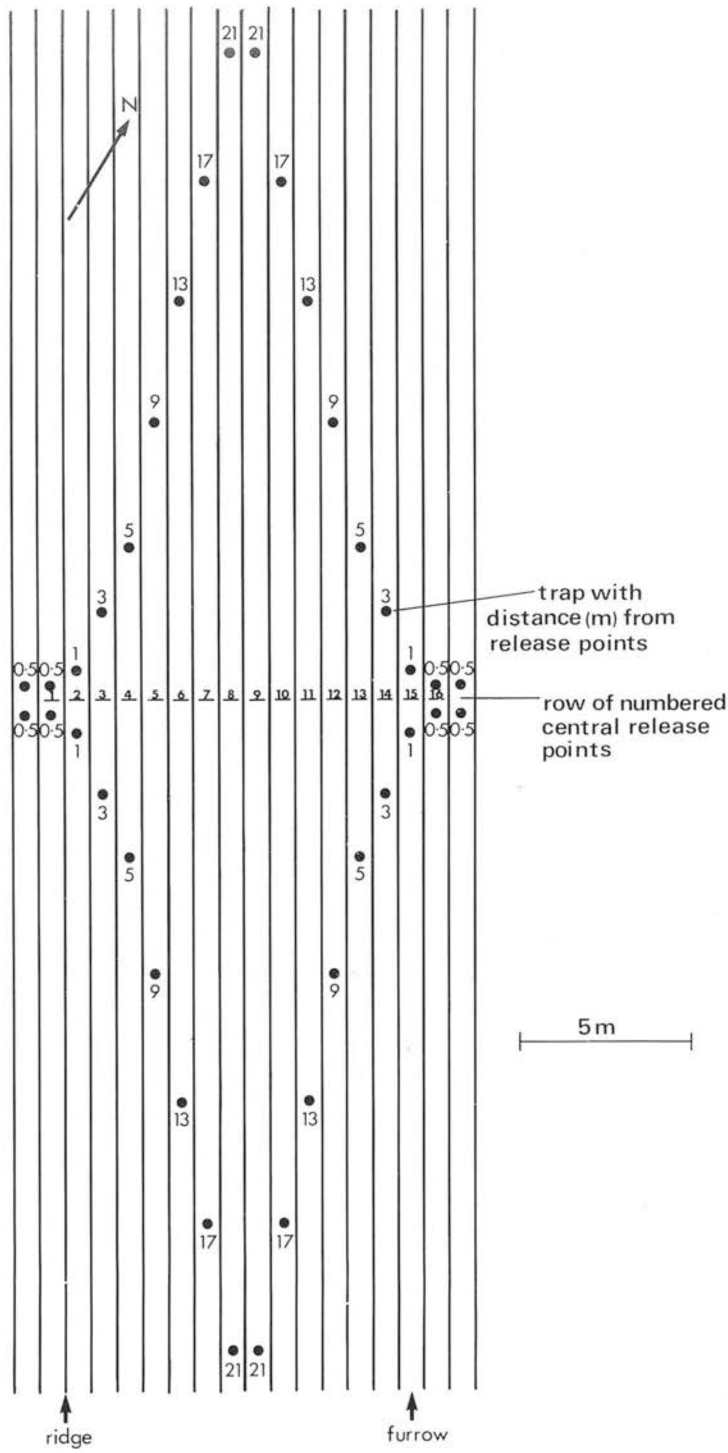


Figure 24 Layout of mark-release experiment. See text for details.

Plate 4: Trap used in mark-release experiment. Wire mesh was used to reduce the likelihood of beetle escape round the sides of the traps.

water and dog meal. To reduce cannibalism, beetles were kept in a darkened store at 4°C until 2 days before release. At this time they were placed in plastic petri dishes (3 individuals of one sex of one species per dish) and provided with water only. Dishes were maintained at about 20°C in natural light. Depriving beetles of food for 2 days, ie releasing "hungry" insects, was an attempt to obtain, over the experimental period, maximum estimates of natural movement ability; patterns and rates of beetle movement are known to vary with degree of hunger (Baars, 1979). Starved individuals move much farther, and in a straight line, than fed individuals which move randomly over short distances.

Twenty-four hours before release beetles were marked with "Humbrol" coloured enamel paint such that the sex and release point of each recaptured insect could be determined. Spots of coloured paint were placed on the thorax and elytra according to intended release position. Thoracic spots enabled sex determination and individuals were recognizable by elytral mark position (Figure 25).

Releases were made on 1 August 1984, during the inactive period (15:00-16:00 hours) of these nocturnal animals. This was to minimize the artificially high level of activity often observed immediately after release (Southwood, 1978). Six ♀ and 6 ♂ P madidus were released at each central point, a total of 192 beetles. Fewer P melanarius were available: of the 44 ♀♀ and 36 ♂♂, 6 of each sex were released at central points 4, 6, 8, 9, 11 and 13; 4 further ♀♀ were released at each of points 2 and 15 (Figure 24). Traps were examined at 2, 24, 48, 72, 96 and 120 hours after release. Records were kept of captured marked and unmarked animals. Recaptured beetles were re-released at original release points.

The distances moved by individual beetles were determined using the Pythagorean theorem: the square of the maximum distance travelled was assumed equal to the sum of the square of the linear distance between the central line of release points and the trap of capture, and the square of the number of ridges between release point and trap. Because any haphazard wanderings by beetles between points of release and capture were unknown, distances travelled are minimum estimates. Due to this imprecision, the non-linear component of the potato ridge-furrow profile has not been

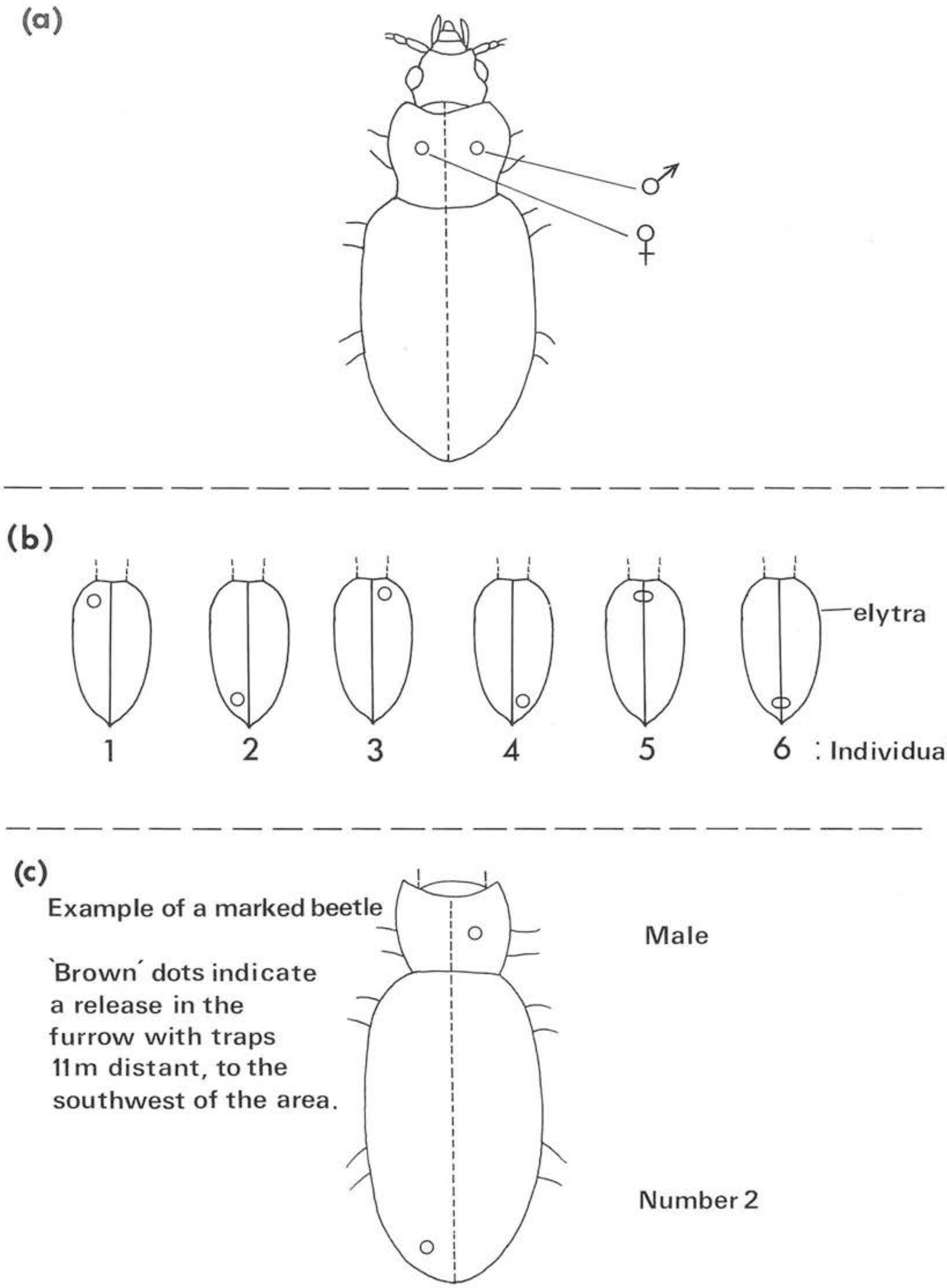


Figure 25: Diagram to show the markings used on beetles in the mark-release experiment.
(a = dots indicating sex; b = dots indicating individual number; c = example).

considered.

Numbers of beetles moving in each of 4 directions (NW, NE, SW, SE) between release and recapture, were calculated for each sampling occasion. These data were used to determine whether movement was "random" with respect to direction.

6-2-3 RESULTS AND DISCUSSION

(a) Recaptures

A total of 38 beetles was recaptured (14.0 per cent), only one of which was a multiple recapture. This beetle was a ♂ P melanarius recaptured at 48 and 120 hours after release. Two hours after release a single beetle was caught: in a 0.5 m trap. The carabids were observed to move little immediately upon release - rather they ran underneath stones or into soil fissures.

Due to low counts at 120 hours, recapture data for 96 and 120 hours were combined for X^2 analysis. Overall recapture rates of P madidus of 14.6 per cent and P melanarius of 12.8 per cent were not significantly different ($X^2 = 1.77$, df = 3, $p > 0.05$) and, although rates were higher for males than females (Table 44), the difference was not significant ($X^2 = 4.68$, df = 3, $p > 0.05$). Recaptures of each sex of either species were not considered separately because numbers caught were too low.

Beetles indigenous to the area were often trapped, and the proportion of marked animals in the total catch decreased with time (Figure 26), probably due to a "dilution" of marked beetles as they mixed with local populations or moved outside the trapping area.

(b) Distances travelled

The mean "daily" distance travelled by all recaptured beetles during the experiment was 8.7 m. The average distances between points of release and recapture at each sampling time ranged from 5.1 m - 11.4 m (Table 45). These data must be interpreted carefully as a beetle caught in a trap 21 m from its release point 4 days after release, may have moved 5 or 6 m/day

Table 44

Numbers released and total numbers recaptured of female and male *Pterostichus madidus* and *Pterostichus melanarius* in mark-release experiment

	Sex	Number released	Number recaptured	Recapture rate (%)	Total number captured*
Pterostichus madidus	♀	96	10	10.4	19
	♂	96	18	18.8	36
Pterostichus melanarius	♀	44	4	9.1	7
	♂	36	6	16.6	25

* Includes recaptured marked and captured unmarked beetles

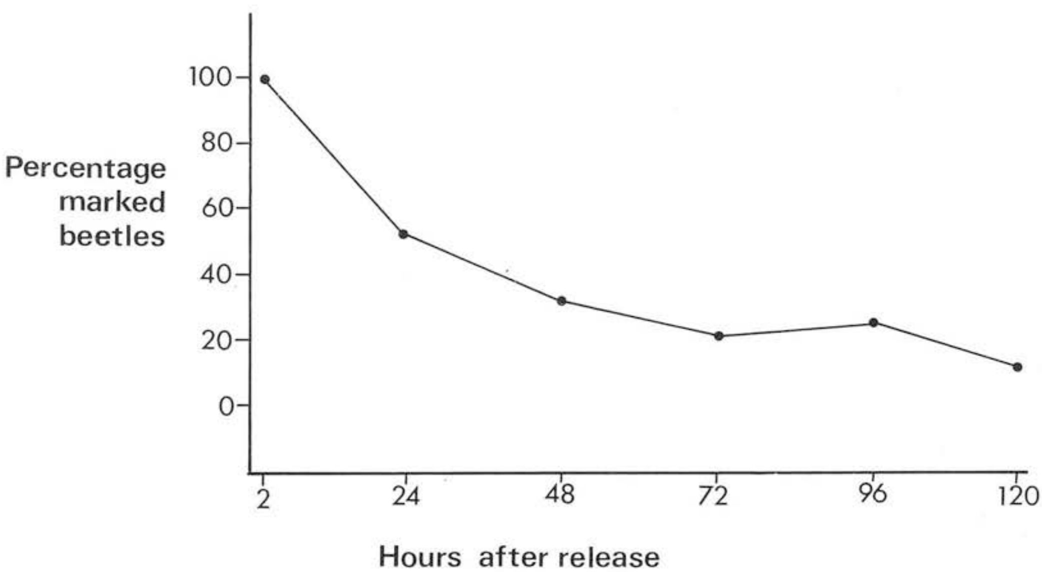


Figure 26: Percentage of the total number of beetles caught in the mark-release experiment, comprised of marked individuals.

Table 45

Mean daily distance travelled by recaptured Pterostichus spp at 24, 48, 72, 96 and 120 h after release

Time after release (h)	Mean distance travelled (m) $\pm$ SE_{95}
24	9.1 ± 1.47 (n = 13)
48	5.1 ± 1.15 (n = 7)
72	8.3 ± 2.24 (n = 6)
96	11.4 ± 2.17 (n = 9)
120	9.0 ± 0.02 (n = 2)
Overall	8.7 ± 0.88 (n = 37)

only. As this information was not known, calculations were based on distances moved between release and capture in 24 hours regardless of day of capture, and some calculated distances are probably over-estimates. Distances moved between release and capture divided by the number of days between release and capture are given in Appendix 4. Calculated this way, the mean daily distance travelled by all recaptured beetles was 4.9 m. Distances discussed in the rest of this thesis are those not divided by the number of days between release and recapture. These results compare well with those of J Cory (pers comm) who reported mean daily distances travelled in winter wheat by P madidus of 1.1 m - 6.5 m and by P melanarius of 1.1 m - 10.0 m, depending on trap spacing.

Activity level, represented as the total number of recaptures and the mean distance travelled in each post-release interval, appeared to be related to temperature (Figure 27). It would be interesting to determine the strength of these relationships but 5 days of capture results is too short a period for statistical analysis; a 14 day minimum is probably required to assess the influence of weather on carabid beetle dispersal (P den Boer, pers comm). Using radioactive Pterostichus oblongopunctatus, Brunsting (1983), in a laboratory study, found the percentage of active animals to be independent of temperature but the speed of movement was positively correlated.

(c) Direction of movement

The original hypothesis was that the potato ridges would act as barriers, discouraging dispersal over them and forcing beetles to move along the furrows only. Beetles would in effect be confined to straight tracks along which they could travel for distances varying from 0.5 m - 21.0 m before encountering a trap. Recapture rates should thus be high and fewer individuals need be used than is usual with mark-release studies.

When numbers of beetles (summed over time) moving in each of 4 directions (corresponding to movement across-ridge or along-furrow) were examined, however, there was no indication that beetles moved preferentially in any one direction ($X^2 = 2.89$, df = 3, $p > 0.05$); rather they appeared to travel equally within furrows and across ridges.

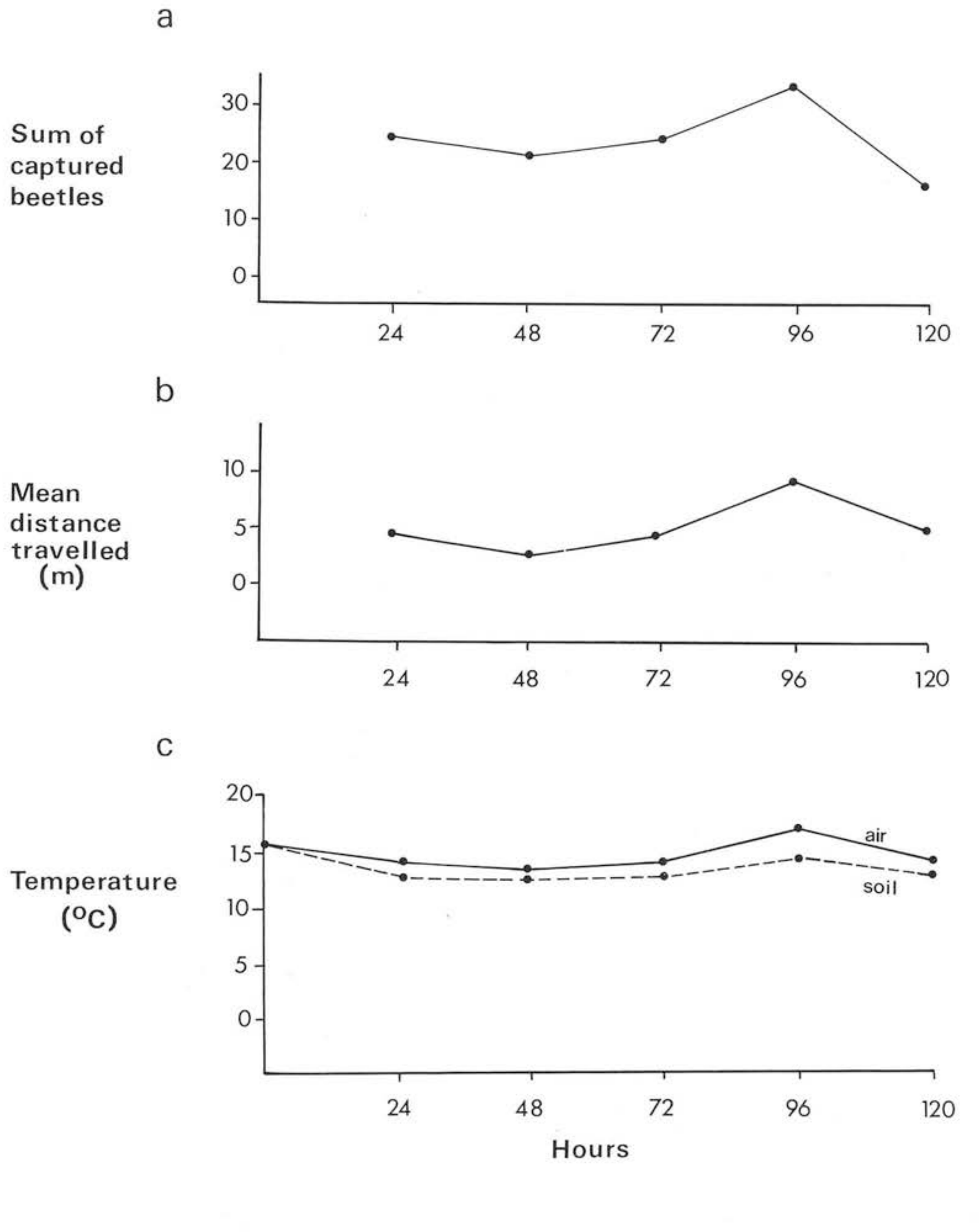


Figure 27: Total number of beetles captured (a) and mean distance travelled (b) of Pterostichus spp at post-release intervals of 24, 48, 72, 96 and 120 hours. Soil (at 5 cm) and air temperatures (°C) from Pathhead Meteorological Station are given in (c).

Appendix 4 gives details of beetle movement: lines connect the point of release and the trap of capture for each individual recaptured at the various post-release intervals. That beetles moved across ridges as well as along furrows is evident. Apparent "non-directional" movement has been observed in other ground beetles. Baars (1979) found that the directions in which Pterostichus versicolor and Calathus melanocephalus started after release were random, and Weseloh (1985) stated that Calosoma sycophanta appeared to have no preferred direction of dispersal.

Recaptures were so few that statistical tests have low power. Nevertheless, ridges are apparently not barriers to movement. "Allometry", the biology of body size (Calder, 1984), says that uphill travel is relatively more demanding for larger animals and that smaller animals climb hills at steeper angles than larger ones. Small animals optimise the use of their shorter lifetimes by minimizing time of movement and allowing more time for pursuits such as foraging (Calder, 1984).

Movement across ridges reduced the effectiveness of the mark-release design but in the context of the larger study the ability to climb ridges may be an important attribute of a potential predator in potato crops. Such an ability would increase the possibility of a predator contacting prey on the foliage, especially when the plants are small.

Despite dispersal being non-directional in the present study, recapture rates were of the order of 13-14 per cent. These rates, which compare favourably with those of standard mark-release techniques (Rivard, 1965; Ericson, 1977; J Cory, pers comm), were obtained by releasing comparatively few insects. It is likely that the distance travelled by the majority of these beetles is less than the distance between the margins of large and small plots in the insecticide field trial. Thus beetles trapped in a plot 24 hours after spray application are almost certain to have been in that plot during treatment.

6-3 DENSITY-CATCH EXPERIMENT

6-3-1 INTRODUCTION

Evaluation of the "predator potential" of an animal requires some indication of the absolute numbers of that species present in a crop. Information of this nature was desired for Pterostichus melanarius and P madidus in potato fields. Pitfall traps give measures of relative densities of a species but because trapping efficiency is affected by many factors (see Chapter 4), catches cannot be directly related to absolute densities. Direct sampling of soil using cores or quadrats was considered excessively site-disruptive and instead a field experiment using concrete "boxes" was done to try to relate beetle density in a defined area with catch in pitfall traps.

6-3-2 MATERIALS AND METHODS

Forty-eight soil-filled concrete boxes measuring 1 m x 1 m x 1 m (Figure 28) were available at the "Bush Estate" (Edinburgh School of Agriculture field station, Penicuik (NT245634)). Built for use in potato cyst nematode studies, these had not been used for several years. Boxes were open at top and bottom and a 15-18 cm rim protruded above soil level. It was assumed that the beetles would be unable to escape from the enclosures which would in effect be barriered plots but this was not tested before the study due to lack of time. Although larger experimental areas would have been desirable, the boxes were available in sufficient quantity that a replicated trial was possible; the construction of larger arenas would have necessitated a reduction in replicates.

Before the experiment, boxes were weeded as required. On 21 May 1985 soil samples were taken: 6 random samples, each approximately 17 g and from a depth of 5-6 cm, were taken from each of the 48 boxes. A single sample from all 48 areas combined was sent to the College soils laboratory for analysis.

To provide shelter for released insects, an unchitted potato tuber was planted in 2 corners of each box on 4 June 1985, at 20 cm depth and 10 cm from each side (Figure 28). A majority sprouted but in late July most were killed by accidental herbicide drift from an adjacent field trial. Surviving plants were removed by hand on 3 August.

All P melanarius and P madidus used in the experiment were provided by Dr M Luff of the University of Newcastle because insufficient numbers

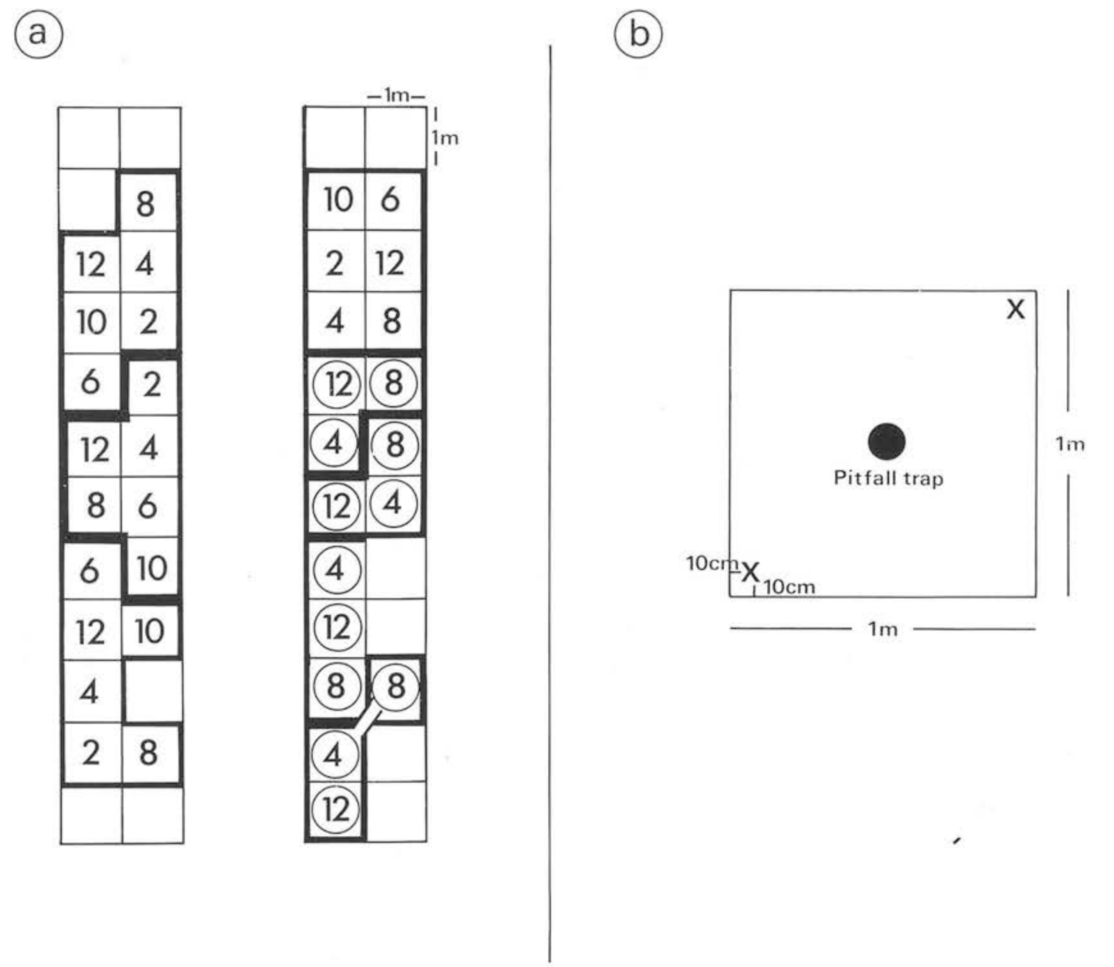


Figure 28: Layout of density-catch experiment to determine pitfall trap efficiency, at Bush Estate, 1985. (a = general layout, n - numbers of Pterostichus melanarius released in a particular box, ⓝ- numbers of Pterostichus madidus released; b = single concrete box, x - placement of potato tubers).

were available from trapping locally. Beetles were received on 26 July 1985 and were maintained at about 4°C in a dark store-room and provided with food and water. As indigenous Pterostichus spp were present in the boxes, released specimens were marked. A soldering iron with a fine tip was used to make 2 horizontal grooves covering 6 or 7 elytral intervals on the left elytron of each beetle.

One pitfall trap (as used in routine field sampling) was placed in the centre of each box on 3 August 1985. A large net (mesh: 2.5 cm), supported by canes 1 m above ground level, was positioned over the entire site to reduce predation of released beetles by birds. Thirty-six boxes only were used in the trial as the corners of some had deteriorated such that beetle escape was possible. Also not all were required due to low numbers of P madidus available for release.

Releases were made at 15:00 hours on 4 August with various numbers (always 1:1 sex ratio) of beetles released per box: P melanarius at 12, 10, 8, 6, 4 or 2, P madidus at 12, 8 or 4 per box. Each density of each species was replicated 4 times in a randomized block design (Figure 28). At 19:00 hours on 4 August, 4 hours after beetles were released, 45 ml of 10 per cent formalin and a drop of liquid detergent were added to each trap to approximate field sampling conditions. Traps were checked at 24, 48, 72, 96, 120, 144 and 168 hours after release. To maintain beetle density, captured individuals were replaced.

Nearly 40 per cent of released P melanarius were captured at the 24 hour sample. Insufficient insects were available to maintain this order of replacement over several days, so after 24 hours P melanarius were replaced only in boxes with 12, 8 or 4 released beetles. Boxes with 10, 6 or 2 individuals were monitored but captures not replaced. All captured P madidus were replaced. Records were kept of all captured marked and unmarked beetles. Associated temperature data are given in Appendix 2.

6-3-3 RESULTS AND DISCUSSION

At 24 hours after release a significant ($F = 8.856$, $df = 1,22$, $p \leq 0.05$) relationship between catch in pitfall traps and original release density of

P melanarius was observed, despite high variation within density replicates (Figure 29). No such relationship was observed for P madidus.

Marked individuals of both species (3 P madidus, 2 P melanarius) were captured in boxes other than those in which they were released and as these beetles are unable to fly they must have climbed the sides of the boxes. The first beetles to escape from boxes in which they were released were captured at 96 hours, but this does not exclude the possibility of beetle escape earlier in the experiment. Capture data, particularly those obtained at more than 24 hours after release, were thus considered unreliable as initial densities were unknown, and the 24 hour results only are discussed.

An indication of the density-catch relationship may be calculated using Figure 29. For example, a catch of 3 P melanarius in a pitfall trap in operation over 24 hours, indicates an initial density of about 9 beetles/m^2. Extrapolation of these results to field conditions is, however, questionable. Data for one day only are reliable and repeated results over several days are required. Also, it is possible that catches in the first 24 hours are artificially high, as is sometimes observed in mark-release studies (Southwood, 1978). More importantly, the effective "catch area" of a pitfall trap (the extent of the area from which trapped beetles originate) in the field is unknown. Results of the present experiment refer to a catch area of 1 m^2 only and further studies are necessary to determine the effective catch area of pitfall traps in fields. Increased replication of each release-density is also desirable as standard errors were high in the Bush Estate study.

Factors affecting activity and thus catch, in the field, would also affect catches in this, or similar, experiments. Results would therefore need to be obtained for each species of interest individually, and observed relationships between beetle density and trap catch are restricted to the time of year of the experiment as beetle activity varies during a season. In the present study, lack of foliage cover due to the destruction of potato plants by herbicide drift may have increased beetle activity.

Soil animals, including collembola, other carabid beetles (Bembidion spp, Notiophilus spp) and earthworms, were present in the concrete boxes and presumably the released beetles would not have had to leave the boxes to find prey. Soil levels of phosphorous, potassium and magnesium were medium, and the pH was 5.3.

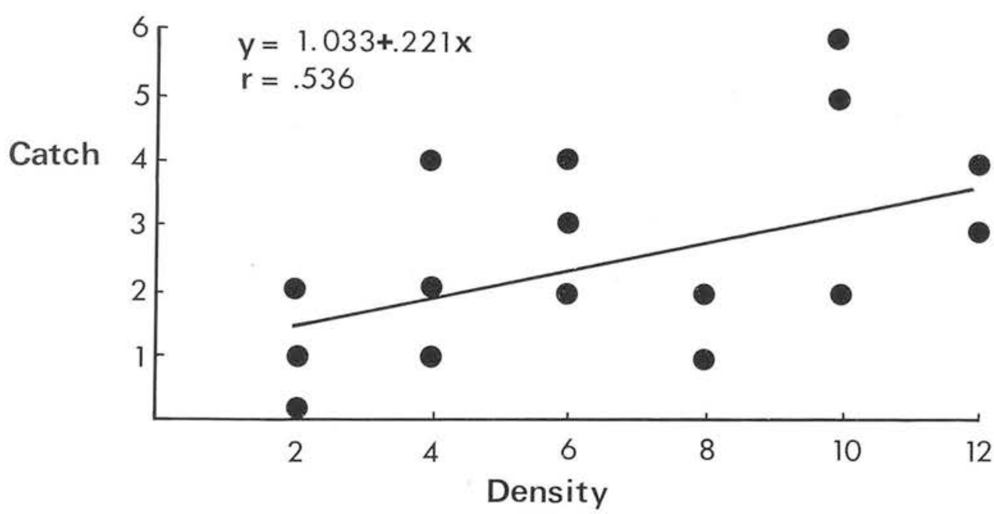


Figure 29: Relationship between catch in pitfall traps and original release density of Pterostichus melanarius 24 hours after release. ("r" is significant at $p \leq 0.05$).

CHAPTER 7

GENERAL DISCUSSION

7-1 GENERAL

The arthropod fauna under study was dominated by aphids and ground beetles (Table 46) but components of the fauna may be under-represented in the data due to the sampling methods used. Hoverfly larvae, for example, were counted during the day but many are nocturnal (Rotheray, 1984) and the problems derived from pitfall traps sampling the arthropod fauna differentially have already been discussed. Nevertheless, the high numbers of polyphagous predators in these potato crops is obvious.

Figures 30–33 show total numbers of the main taxa in untreated plots and some associated weather data in each of the 3 years. Absolute comparisons of numbers in the different taxa are not possible because it is not known how the different sampling methods relate to one another. Some patterns in the data are, however, evident.

Aphid mummies and aphid-pathogenic fungi were related in a density-dependent manner to aphid numbers. Ladybirds were present at low numbers in each year and were generally uncommon until after aphid populations had peaked. Catches of Pterostichus spp were often highest before peak aphid populations occurred and these carabids were generally present early in the season when aphids were apparently few.

7-2 INFLUENCE OF WEATHER

It is difficult to relate temperatures over a season with numbers of arthropods on plants or in traps because populations will vary over time anyway. Rainfall and temperature may, however, influence numbers over short periods, or may increase populations of natural enemies which, like fungi, require moisture for spread. Short-term catches of ground beetles may also be affected by weather. High temperatures are often associated

Table 46

Arthropod fauna of some potato fields in eastern Scotland surveyed using various methods (see text), 1983-1985

	Approximate total number
aphids	28,000
ground beetles	9,000
spiders	1,000
ladybird beetles	500
parasitic wasps	450
rove beetles	300
harvestmen	250
hoverflies	30
lacewings	25

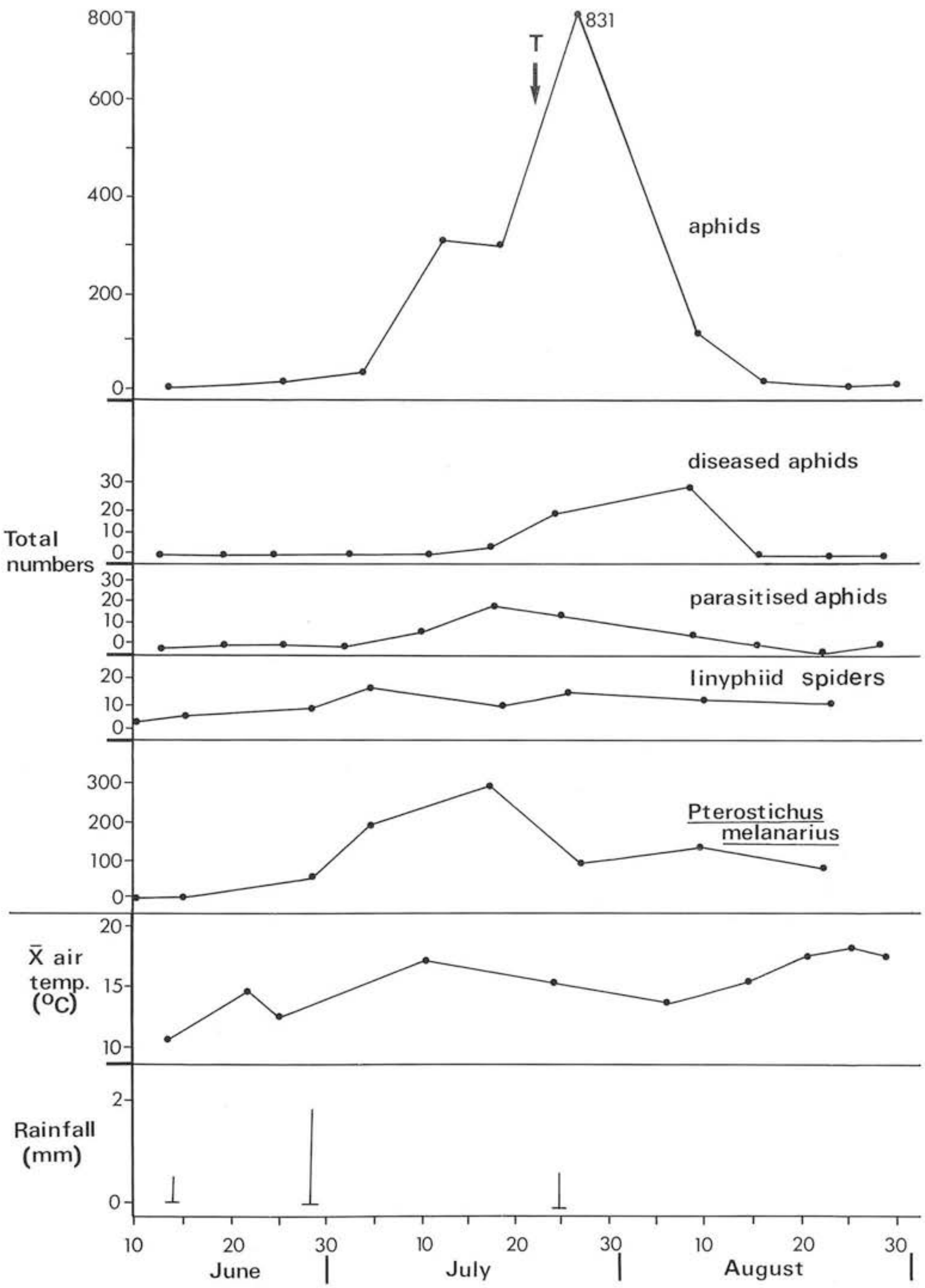


Figure 30: General population trends of Macrosiphum euphorbiae and selected natural enemies from untreated plots in the "manipulative" trial in 1983. Weather data also given.

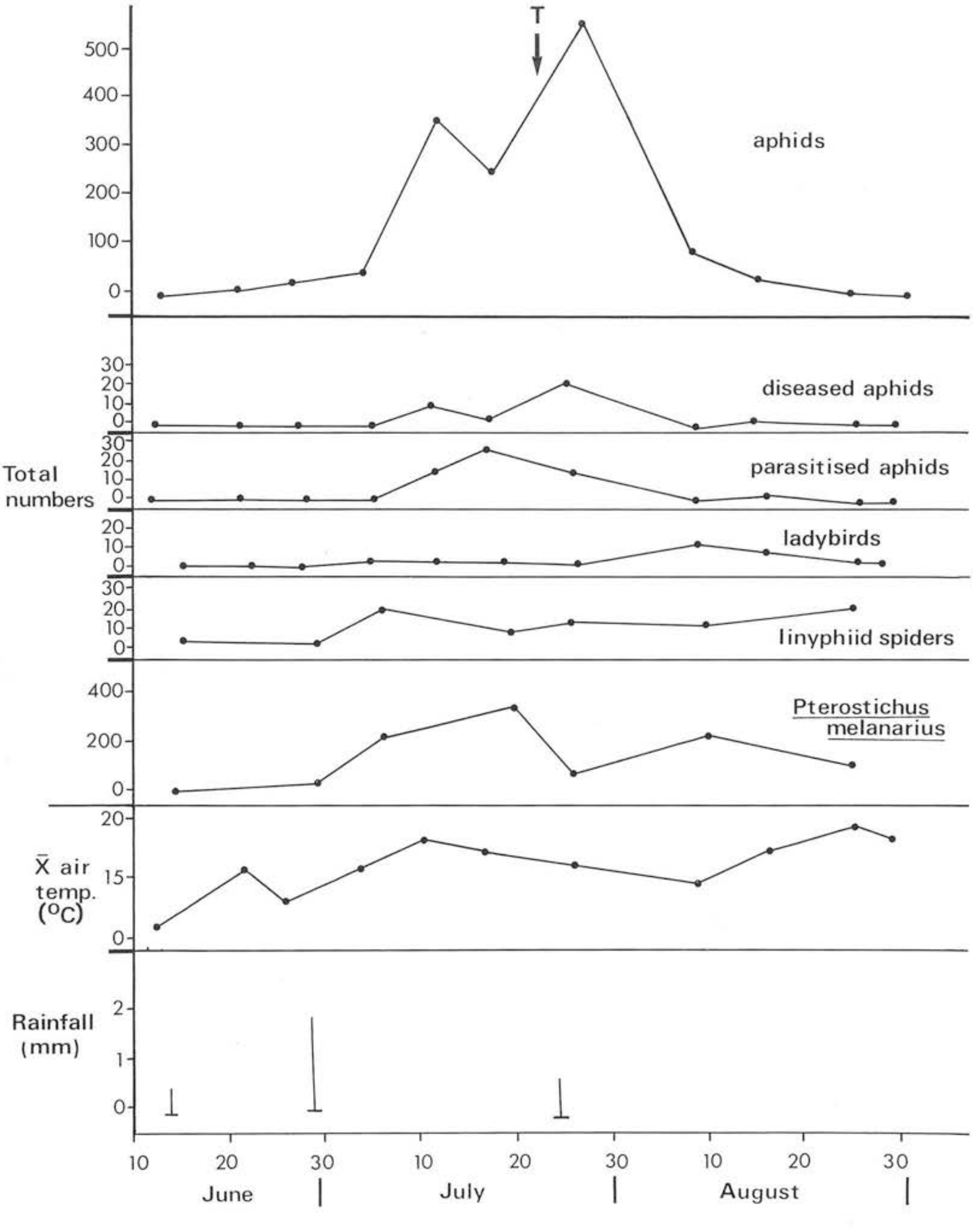


Figure 31: General population trends of Macrosiphum euphorbiae and selected natural enemies from untreated plots in the demeton-S-methyl trial in 1983. Weather data also given.

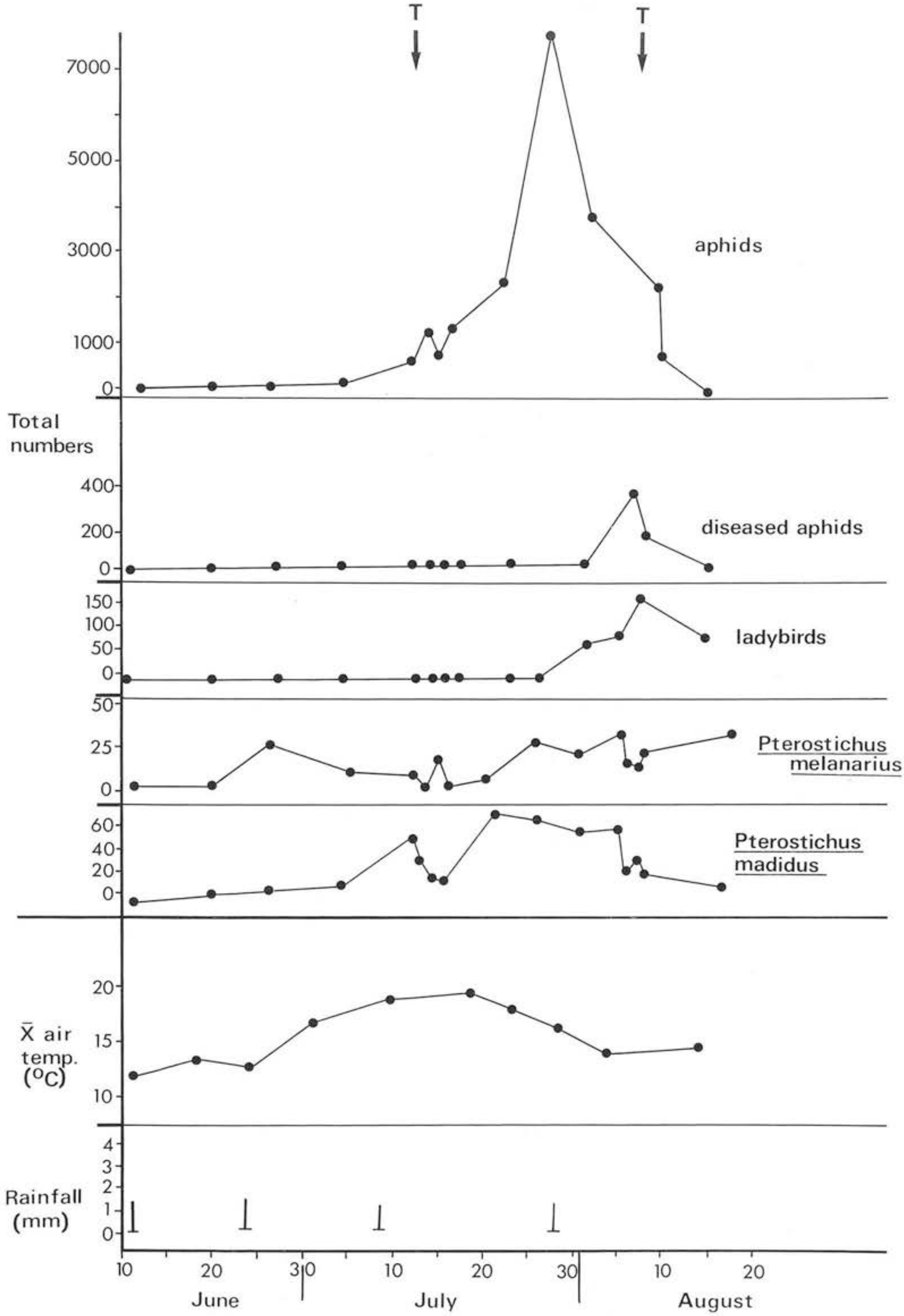


Figure 32: General population trends of Macrosiphum euphorbiae and selected natural enemies from untreated plots in 1984. Weather data also given.

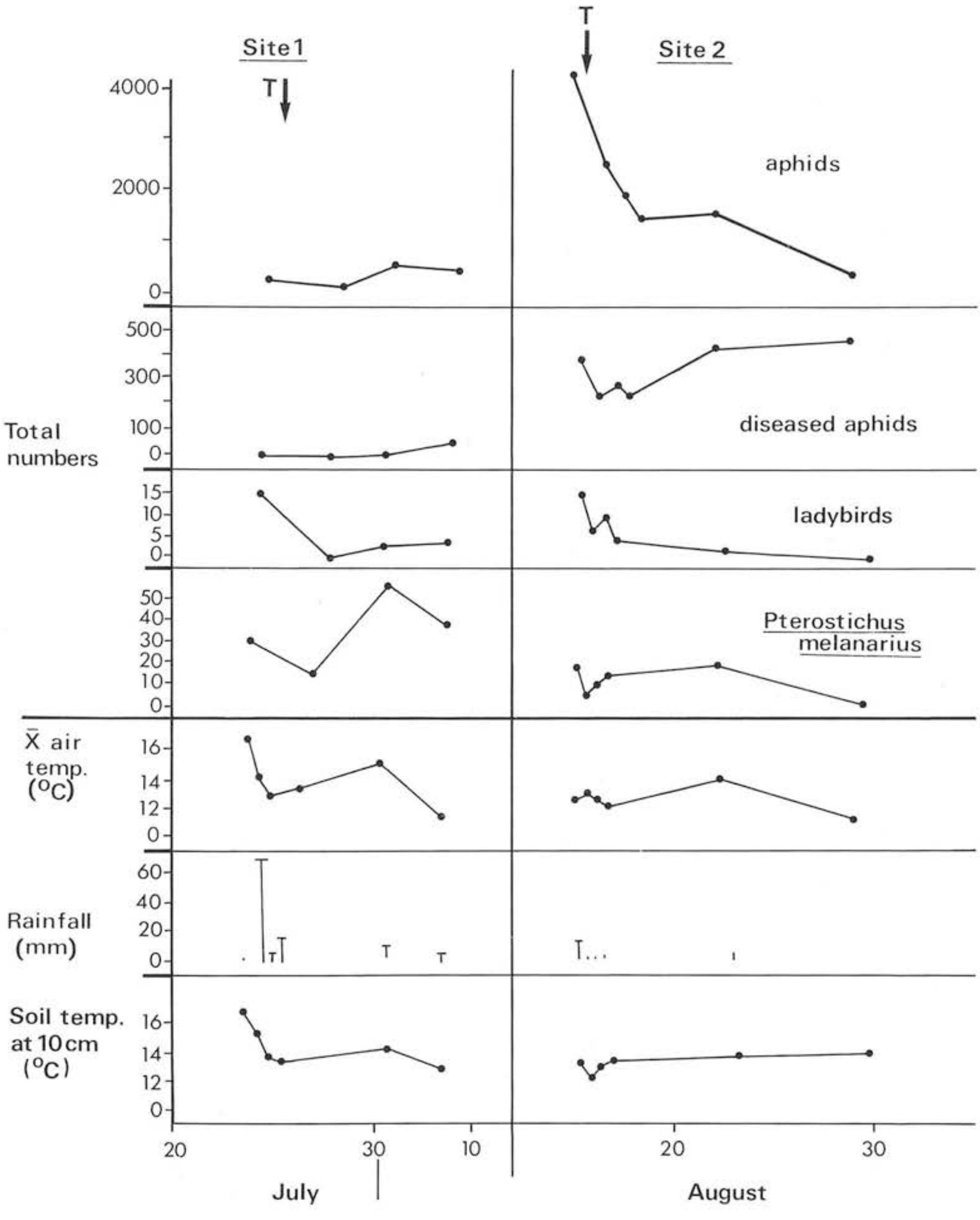


Figure 33: General population trends of Macrosiphum euphorbiae and selected natural enemies from untreated plots in sites one and two in 1985. Weather data also given.

with high catches of large carabids (Baars, 1979; Jones, 1979) because the duration of their activity period is lengthened and they move more quickly (Brunsting, 1983). It is unlikely that short-term temperatures varied sufficiently in this study to produce large differences in catch; even if they did, individuals in untreated and treated areas would presumably be similarly affected.

7-3 POLYPHAGOUS PREDATORS

Polyphagous predators have been implicated as important aphid control agents partly because they are present when other natural enemies are not. For example, the numbers of aphid-specific predators and parasitoids were positively correlated and the numbers of polyphagous predators highly negatively correlated with cereal aphids in England (Edwards et al, 1979). These authors considered early predation by polyphagous predators to be important in preventing the build-up of aphid populations. Chambers et al (1982) stated that aphid numbers in winter wheat were reduced early in the season by polyphagous species and the aphid-specific arthropods which appeared later prevented aphid numbers exceeding 3.9 per shoot.

The polyphagous predators associated with potato crops may have a similar potential for suppressing aphid populations early in the season. Certainly they were present at that time (Figures 30–33). Aphid-specific natural enemies and alate emigration were probably more important, however, in reducing aphid numbers during the decline phase in untreated plots.

7-3-1 POSSIBLE ROLE IN REDUCING VIRUS SPREAD

Assuming that polyphagous predators like Pterostichus spp do consume aphids on potato early in the season, they may exert a beneficial effect in at least 2 ways:

(i) They may slow the rate of increase of aphid populations if sufficient predation occurs early in the season (Figure 34). Under favourable conditions of weather and food supply, populations would probably peak at a level similar to that attained in the absence of early-season predation.

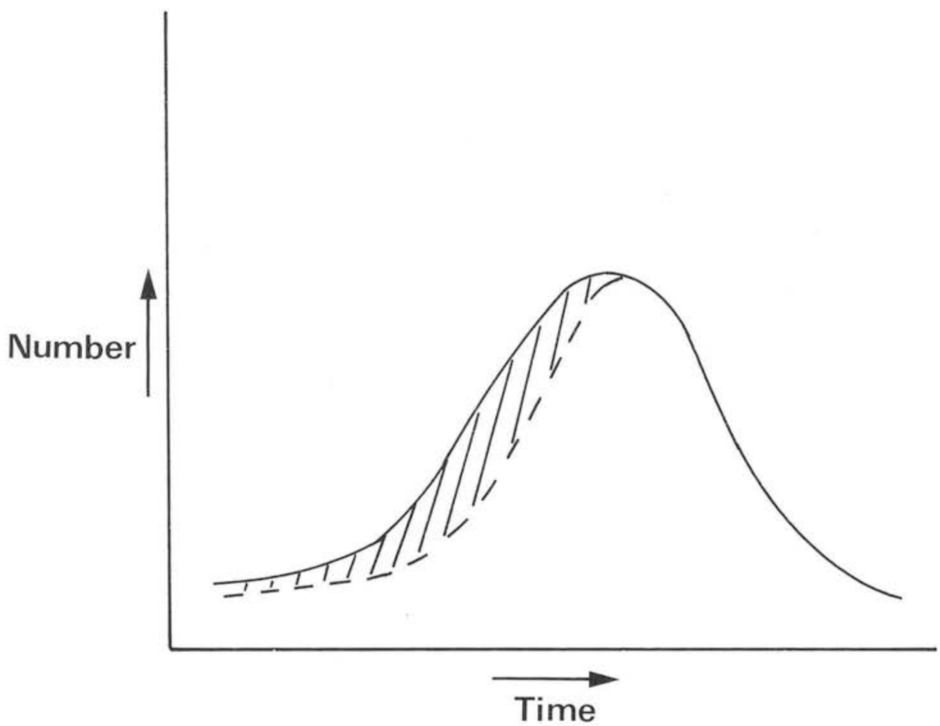


Figure 34: Possible patterns of development of populations of aphids on potato with (- - -) and without (——) early-season predation by polyphagous predators.

The lag which might be induced, however, may mean fewer aphids present at a time most crucial for virus spread; spread of potato viruses is often attributed to migrant alate aphids early in the season (Doncaster and Gregory, 1948), when potato plants are young and more susceptible to infection (Fisken, 1959b).

(ii) Myzus persicae, the principal vector of potato viruses (Shaw, 1976), usually occurs on lower leaves of potato (Bradley, 1952; Drübbisch, 1985). Lower leaves, particularly of young plants, appear to be a more potent virus source than middle or upper ones (Syller, 1980). Control of M persicae on lower leaves, particularly when plants are young, is therefore important and may be effected by polyphagous predators.

7-3-2 CARABIDAE

The most abundant polyphagous predators in this study were ground beetles and these may be important in aphid control in potatoes. Several species ate aphids and in fact the amount of predation was probably underestimated for two reasons. Pitfall traps selectively sample active individuals and ground beetles are more active when hungry (Baars, 1979): a hungry beetle is therefore more likely to be caught than a less hungry one. Also, crops only were examined in the gut dissections, and some beetles with empty crops may have contained aphid remnants elsewhere in their digestive tracts.

The number of species of carabids in pitfall traps on any sampling occasion in 1983 and 1984 varied from 5-15 (Table 47). The Berger-Parker dominance index, which expresses the proportion of the total catch due to the dominant species (Berker and Parker, 1970) shows that the community was most diverse early in each season. On 8 June 1983, 70 per cent of individuals trapped were Clivina fossor and at the end of the 1984 season, Trechus quadristriatus was the dominant species. The carabid fauna was dominated at all other times by Pterostichus spp: from 29 June to 14 September 1983, P melanarius represented 58-98 per cent of the total catch and in 1984 over half the trap catches between 5 July and 1 August were P madidus.

(a) Pterostichus spp

P melanarius and P madidus are widely distributed and common

Table 47

Dominance index (d) and species richness (S) of ground beetles caught by pitfall traps during 1983 and 1984 (for sample sizes see text)

1983			1984		
Sampling date	d	S	Sampling date	d	S
4 May	0.23	15	16 May	0.38	6
11 "	0.23	10	23 "	0.24	12
18 "	0.33	10	30 "	0.35	15
25 "	0.40	15	6 June	0.31	9
8 June	0.70	9	13 "	0.27	5
15 "	0.33	5	20 "	0.31	9
29 "	0.97	6	27 "	0.21	9
6 July	0.98	8	5 July	0.52	8
20 "	0.96	14	12 "	0.80	8
27 "	0.87	14	20 "	0.82	6
10 August	0.94	9	25 "	0.75	6
24 "	0.62	13	1 August	0.81	6
7 September	0.59	15	7 "	0.46	8
14 "	0.58	13	15 "	0.63	11
			21 "	0.62	7
			11 September	0.89	7

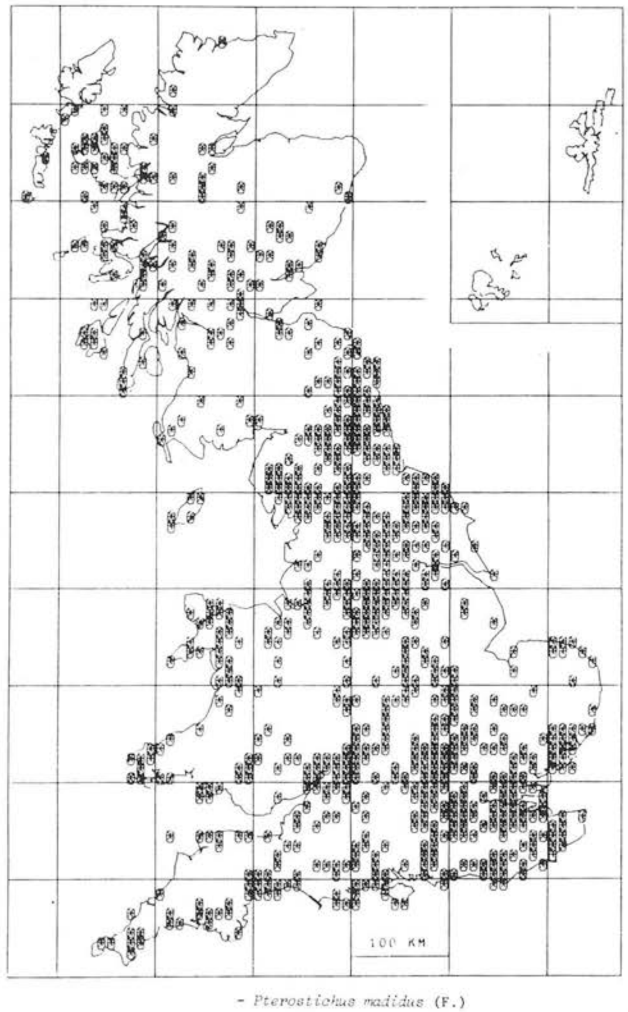
throughout Britain (Figure 35), positive attributes of species being considered as pest control agents. Their effectiveness in pest control depends, however, on a number of factors, including their voracity and density in fields.

In the current study, each tested beetle ate an average of 62 treated Myzus persicae in 4 hours. The number of M persicae eaten by P melanarius varied from 24-44 in 24 hours, depending on the duration of previous starvation (Crisostomo, 1984). In mark-release studies, reported densities of P melanarius in cereals ranged from 0.01 (J Cory, pers comm) to $0.73/m^2$ (Ericson, 1978). P madidus occurred at densities of $0.1-0.01/m^2$ in cereals (J Cory, pers comm). These densities seem low but must be related to voracity and mobility: the usefulness of hordes of inactive predators is questionable.

P melanarius and P madidus may have great potential as predators of aphids on potato. They are voracious, mobile and will kill prey even when satiated (Hagley et al, 1982). There are, however, difficulties to be considered in the evaluation of their effectiveness. Their diets are non-specific and the proportion of alternative prey eaten must be assessed. More importantly, the source of aphids taken must be determined.

Source of aphid prey

Most carabids and many staphylinids are thought not to climb plants, their predatory activity being restricted to aphids on the ground (Sunderland and Vickerman, 1980; Griffiths, 1982). The effectiveness of this activity depends on the proportion of the total aphid population on the ground and on the fate of these aphids in the absence of predation. In cereals, as much as 5 per cent of the aphid population may be on the soil at any one time (Loughridge and Luff, 1983). The situation in potatoes is not known but, if similar, predation of 5 per cent of the aphid population is unlikely to effect much control. The fate of aphids on the ground is also unknown but aphids knocked from potato foliage are probably able to return to at least the lower leaves. In the laboratory, more than one-third of M persicae and Hyadaphis erysinis did not return to turnip plants even when placed near stem bases (Montgomery and Nault, 1977). No aphids artificially knocked from winter wheat managed to reclimb the plants in a field



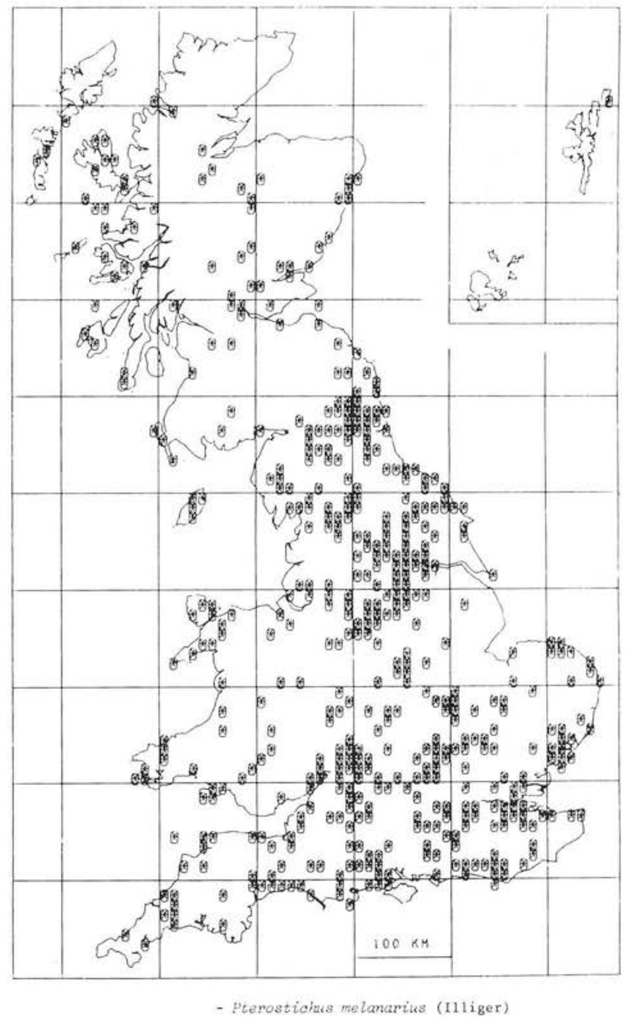


Figure 35: Distribution records of Pterostichus melanarius and Pterostichus madidus in Great Britain (after Luff, 1982b; with permission of the Biological Records Centre).

experiment (Griffiths, 1982). The fate of aphids on the ground in the absence of predation must be determined because if they would have died anyway, the benefit of predation in aphid control is negligible.

One way to increase the beneficial effect of polyphagous predators is to increase the numbers of aphids available on the soil.

Pesticides and (E)-ß-farnesene in aphid control

(i) Demeton-S-methyl induces the release of aphid alarm pheromone (Rice et al, 1983). Aphids on the ground after treatment may have responded either directly to the insecticide or to alarm pheromones. Ingestion of aphids contaminated with demeton-S-methyl can kill Pterostichus spp and as these aphids would have died anyway predation in this case would be detrimental. Ingestion of aphids which are on the ground in response to alarm pheromone would be beneficial if these aphids otherwise reclimb plants. Also, the use of alarm pheromone might increase the capture of aphids in spider webs.

(ii) The spread of virus disease may be increased by using aphid alarm pheromone alone or in conjunction with an insecticide. M persicae susceptible or resistant to organophosphate insecticides respond similarly to (E)-ß-farnesene and its derivatives (Gibson et al, 1984). Insecticide-susceptible aphids responding to alarm pheromone by increasing activity might survive insecticide exposure long enough to transmit non-persistent viruses. Persistent and non-persistent viruses may be spread by resistant aphids.

This potential for increased virus spread might severely limit the potential of (E)-ß-farnesene in integrated control. Again, however, the fate of aphids on the ground, the proportion which reclimb plants and the proportion eaten, must be determined.

7-4 MISCELLANEOUS

7-4-1 INTERPRETATION OF PITFALL TRAP CATCHES AFTER INSECTICIDE APPLICATION

The hypothesis is propounded in this study that beetles were less hungry and less active in sprayed than unsprayed areas immediately after pesticide application due to consumption of aphids which had fallen to the ground following treatment. This decreased activity resulted in fewer caught in traps. Subsequent increases in activity, and thus trap catch, are caused by prey depletion in sprayed areas.

Other authors have noted an initial decrease followed by an increase in carabid activity/catch after pesticide application but have offered different explanations: short-term toxicity followed by hyperactivity induced directly by the pesticide (Feeney, 1983) and direct mortality followed by re-invasion of the area from outside (Shires, 1985) are 2 interpretations. Re-invasion does not explain the fact that catches often increase in treated plots some weeks after treatment, compared with untreated plots.

The net result of feeding by carabids is decreased locomotor activity (Mitchell, 1963a). Conversely, starvation is a direct stimulus for locomotion (Baars, 1979; Brunsting, 1983). Hunger-state must therefore influence catch in pitfall traps and if hunger-state is affected by pesticide application then the hypothesis suggested here is probably at least a partial explanation for observed results.

Chiverton (1984) applied fenitrothion and fenvalerate to spring barley in Sweden. He recorded significant increases in pitfall trap catches of P melanarius in treated plots several weeks after treatment. At this time more beetles from untreated areas contained aphid remains. There were significant correlations between empty guts, low aphid numbers and high pitfall trap catches. In a study in potatoes in England, Crisostomo (1984) found the highest percentage of aphid remains in P melanarius caught 4 days after pirimicarb application. She observed a decrease in pitfall trap catch of carabids immediately after spray, followed by an increase in numbers trapped.

It is likely that insecticides can influence the trap catch of carabid beetles by altering their predatory activity. Caution should thus be exercised when interpreting pitfall-catch data from field experiments testing the effects of insecticides and gut dissections and laboratory tests of toxicity should be done in conjunction with field studies.

One of the original aims of the present study was to assess whether suppression of polyphagous predators results in increased aphid numbers. This was not determined due to the high level of mobility of the main species and the complication of pesticides possibly altering their predatory activity and thus trap catch. In this instance at least, pesticides were not an effective means of manipulating predator densities. Chiverton (1986) in a recent report concluded that differences in peak population levels of Rhopalosiphum padi in spring barley were caused by differences in numbers (manipulated by artificial barriers) of polyphagous predators. The use of artificial barriers or of small-scale laboratory studies seems essential if details of the mechanics of carabid-aphid interactions are to be ascertained and results are not to remain correlative.

7-4-2 ARE PTEROSTICHUS SPP BIENNIAL IN THE NORTH?

Numbers of P melanarius and P madidus trapped during this study generally alternated between high and low catches in successive years:

	Total catch		
	1983	1984	1985
P melanarius	5248	417	406
P madidus	56	887	29

This suggests that in Scotland these carabids may have a "biennial" life-cycle where adults do not breed in the year of their emergence from pupae but overwinter and breed in their second season. Luff (1980) reported that Harpalus rufipes in Northumberland had a biennial life-cycle and suggested the alternation of high and low catches in successive years was because the population consisted of 2 separate sub-populations which formed the bulk of the pitfall catch in alternate years.

In Scotland the breeding season may be too short to permit an annual life-cycle and, if so, one would expect similar data from other northern areas. In Norway there was a 2 year alternation of high and low numbers of P melanarius in swede turnips (Andersen, 1985). In England, a more southerly area, P melanarius (Luff, 1982a; Crisostomo, 1984) and P madidus (Luff, 1973; Shires, 1985) apparently have annual cycles. The reason why populations with a biennial cycle should fluctuate between high and low numbers is not known. It might be expected that half the total population would emerge or breed in each year, resulting in similar numbers each year.

A minimum of 4 years' data is required to establish whether these carabids do have biennial life-cycles (M Luff, pers comm) and thus the Scottish situation is currently unresolved. It is interesting that the alternation of high and low numbers recorded for P melanarius and P madidus was "staggered". This may be an adaptation to decrease competition between species of similar habits and from similar habitats.

7-5 CONCLUSIONS

Polyphagous predators, particularly ground beetles, were abundant in the fields studied. Many carabids fulfil certain criteria of "good" predators: they are voracious and mobile, they can withstand starvation and they eat alternate prey when pest numbers are low. Because of their high mobility they may be able to respond to pest outbreaks numerically via immigration, even if they are unable to respond by increased reproduction. Although polyphagous arthropods will feed on beneficial as well as pest species (Luff, 1974a; Sunderland, 1975), they will persist in crops during periods of low aphid density. This behaviour, together with their temporal synchronization with migrant aphids early in the season in potato fields, and their possible role as predators of M persicae on lower leaves, may result in their being better candidates than specific natural enemies, as control agents.

Their role in the control of aphids on potato is, however, currently speculative. The means of prey capture, the type of aggregative response, the voracity, the source of prey aphids and the proportion of alternate food in the diet must be determined for each candidate species before assessment of predator potential is possible. The present study indicated that polyphagous predators may be very important in aphid control, although further research to establish their exact potential is required.

7-6 SUGGESTIONS FOR FUTURE RESEARCH

In decreasing order of importance, I consider it essential:

1. to discover the source of the aphids eaten by Pterostichus spp, and their fate if not eaten;

2. to determine unequivocally whether Pterostichus spp climb on potato foliage in the field;

3. to determine the density of Pterostichus spp in the field, and their voracity;

4. to repeat the Potter Tower experiments with Pterostichus spp as results of the present study do not agree with those of Dunning et al (1982), and as, in common with some other laboratory trials in this study, few beetles were available to be tested;

5. to examine further the potential of (E)-ß-farnesene in increasing the availability of aphids to predation by polyphagous species, and to assess whether virus spread is enhanced through its use;

6. to assess further the potential of harvestmen as aphid control agents;

7. to assess further the potential of Tachyporus spp in aphid control;

8. to evaluate the different methods of assessment of aphid parasitism and determine which is most representative of the field situation.

CHAPTER 8

SUMMARY

1. Aphids, aphid-specific predators and epigeal arthropods were surveyed by visual sampling or pitfall trapping in potato fields in East Lothian, Scotland, between 1983 - 1985.

2. Over 90 per cent of aphids were Macrosiphum euphorbiae in each year. Demeton-S-methyl and thiometon were effective aphicides. M euphorbiae fell from potato plants treated with demeton-S-methyl.

3. Overall infection of aphids with aphid-pathogenic fungi was 6-7 per cent.

Overall level of parasitism was 1.1 per cent, with a maximum of 6.1 per cent in 1983. Seventy-eight per cent were primary parasitoids and most were Aphidius picipes. The majority of hyperparasitoids were Dendrocerus aphidum. Estimates of percentage parasitism differed depending on method of assessment.

4. Most of the c 600 ladybirds sampled were Coccinella septempunctata. Numbers in each year were low until after the aphid peak. Hoverflies and lacewings were rarely seen.

5. Approximately 11,000 animals were caught in pitfall traps. Eighty-nine per cent of these were insects and mostly ground beetles.

6. Many linyphiid spiders, harvestmen and rove beetles were trapped but populations were either low or erratic.

7. Nineteen species of ground beetles were caught but most were rare. Sixty-eight per cent of the total was Pterostichus melanarius.

8. In 1983, the effects of pesticides were obscured by redistribution of highly mobile species like harvestmen and Pterostichus spp. Larger plots

were used in 1984 and 1985.

9. Pitfall trap catches, particularly of Pterostichus madidus in 1984, were lower in treated than untreated areas for 3 days after the application of demeton-S-methyl. Numbers were significantly higher in treated plots 7-14 days after treatment. The hypothesis is suggested that beetles were less hungry in treated than untreated areas immediately after spraying due to feeding on aphids which had fallen on the ground. Subsequent increases in catches are due to hungry carabid beetles with higher activity as a result of reduction in prey populations by the insecticide. Pitfall trap data from field experiments on the effects of pesticides should therefore be interpreted with caution.

10. Gut dissections indicated that several species of ground beetles and harvestmen had eaten aphids. Aphid remains were also present in a single Tachyporus obtusus. Of c 2000 P melanarius dissected, 14.4 per cent contained aphid remains. Of c 900 P madidus dissected, 30.5 per cent had eaten aphids. Of 113 Phalangium opilio examined, 54.0 per cent contained aphid remnants.

11. Data were inconclusive but suggested that large carabids do not climb potato plants.

12. Penetration of the crop canopy by demeton-S-methyl was measured by gas chromatographic analysis of treated silica-gel plates. Upper leaves received about 20 per cent of the theoretical rate and the amount deposited on middle and lower leaves and on the soil was even less. Ground beetles were thus unlikely to receive a direct dose exceeding 4-5 per cent of the recommended rate.

13. Studies of field sprays on confined beetles and Potter Tower results suggested that direct applications of demeton-S-methyl at the recommended rate, or at 5 per cent of that rate, are not very toxic to Pterostichus spp.

14. Individual P melanarius and P madidus, previously starved for 7 days, ate an average of 62 Myzus persicae sprayed with demeton-S-methyl. Overall beetle mortality was 19.1 per cent when treated aphids were consumed, and 0 per cent when untreated aphids were eaten.

15. Fourteen per cent of P madidus and P melanarius were recaptured in a mark-release study. Released beetles travelled a mean daily distance of 8.7 m, and moved both along furrows and across ridges.

16. The significance and implications of these findings in relation to the potential of polyphagous predators in integrated control of aphids on potato are discussed. Suggestions for further research are given.

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APPENDIX 1 - FAUNAL LIST

ANIMAL	TOTAL CATCH 1983	1984	1985
Phylum Annelida			
Class Oligochaeta			
Family Lumbricidae			
Allolobophora caliginosa (Savigny)	9	0	3
Lumbricus castaneus (Savigny)	1	0	0
immature specimens	98	0	0
unidentified adults	80	2	0
Phylum Arthropoda			
Class Arachnida			
Order Opiliones			
Family Phalangiidae			
Mitopus morio (Fabricius)	16	7	0
Oligolophus tridens (C L Koch)	1	0	0
Oligolophus sp C L Koch	0	1	0
Paroligolophus agrestis (Meade)	11	0	0
Phalangium opilio Linne	65	61	0
Opilio parietinus (Degeer)	1	0	0
Opilio saxatilis C L Koch	47	3	0
Leiobunum rotundum (Latreille)	1	1	0
immature specimens	0	18	0
Order Araneae			
Family Lycosidae	30	18	1
Family Linyphiidae	713	232	43
Class Diplopoda	26	0	0
Class Chilopoda	33	10	4
Class Insecta			
Order Collembola	79	23	0
Order Dermaptera			
Family Forficulidae	0	1	0

ANIMAL	TOTAL CATCH 1983	1984	1985
Order Plecoptera			
Family Nemouridae			
Nemoura cinera (Retzius)	0	2	0
Order Hemiptera			
Family Miridae			
Calocoris norvegicus (Gmelin)	11	0	0
unidentified specimens	2	5	0
Family Cicadellidae	3	0	0
Family Aphidiidae			
*Brachycaudus helichrysi (Kaltenbach)	0	2	0
*Myzus ascalonicus Doncaster	0	3	0
*Myzus ornatus Laing	1	0	0
*Myzus persicae (Sulzer)	196	66	611
*Aulacorthum solani (Kaltenbach)	0	19	648
*Macrosiphum euphorbiae (Thomas)	6185	20,087	16,617
Order Neuroptera			
Family Hemerobiidae			
Micromus variegatus (Fabricius)	1	0	0
Family Chrysopidae			
Chrysopa phyllochroma Wesmael	0	1	0
*unidentified larvae	18	1	0
*lacewing eggs	1	1	0
Order Coleoptera			
Family Carabidae			
Nebria brevicollis (Fabricius)	0	11	6
Notiophilus biguttatus (Fabricius)	2	1	0
Clivina fossor (Linnaeus)	83	4	1
Trechus quadristriatus (Schrank)	327	1069	59
Bembidion lampros (Herbst)	0	13	3
Bembidion femoratum Sturm	2	0	0
Bembidion tetracolum Say	0	1	0
Bembidion obtusum Serville	9	37	6
Bembidion guttula (Fabricius)	15	69	3

ANIMAL	TOTAL CATCH 1983	1984	1985
Pterostichus adstrictus Eschscholtz	1	1	0
+ Pterostichus madidus (Fabricius)	56	887	29
+ Pterostichus melanarius (Illiger)	5248	417	406
Pterostichus niger (Schaller)	41	1	6
Calathus fuscipes (Goeze)	3	0	0
Calathus melanocephalus (Linnaeus)	0	0	1
Agonum dorsale (Pontoppidan)	22	20	1
Amara apricaria (Paykull)	1	4	1
Harpalus aeneus (Fabricius)	1	0	2
Harpalus rufipes (Degeer)	1	5	9
Family Staphylinidae			
Deleaster dichrous (Gravenhorst)	0	1	1
Anotylus rugosus (Fabricius)	3	0	0
Oxytelus sp Gravenhorst	7	30	3
Lathrobium sp Gravenhorst	1	2	0
Xantholinus linearis (Oliver)	48	0	0
Philonthus cognatus Stephens	1	0	0
Philonthus sp Stephens	1	2	0
Tachyporus chrysomelinus (Linnaeus)	6	4	0
Tachyporus hypnorum (Fabricius)	35	3	7
Tachyporus obtusus (Linnaeus)	16	0	0
Tachyporus pallidus Sharp	11	1	0
Tachyporus pusillus Gravenhorst	7	1	0
Tachinus signatus Gravenhorst	6	3	0
Aloconota gregaria (Erichson)	16	0	0
Atheta euryptera (Stephens)	2	0	0
Atheta fungi (Gravenhorst)	2	0	0
Atheta (sg Acrotona) sp Thomson	2	0	0
Oxypoda sp Mannerheim	1	0	0
Aleochara bipustulata (Linnaeus)	2	0	0
Aleochara lanuginosa Gravenhorst	1	0	0
unidentified specimens	33	33	56
Family Elateridae			
Agriotes obscurus (Linnaeus)	0	1	0
Adrastus pallens (Fabricus)	0	1	0
Family Cantharidae			
Rhagonycha sp Eschscholtz	1	0	0
Family Nitidulidae			
Meligethes sp Stephens	2	8	0

ANIMAL	TOTAL CATCH 1983	1984	1985
Family Cryptophagidae			
Atomaria atricapilla Stephens	5	1	0
Atomaria fuscata (Schoenherr)	1	0	0
Family Coccinellidae			
*Adalia decempunctata (Linnaeus)	1	0	0
Coccinella septempunctata Linnaeus	13	8	3
*Coccinella septempunctata Linnaeus	119	46	75
*Coccinella undecimpunctata Linnaeus	2	7	0
coccinellid larvae	16	89	1
*coccinellid larvae + pupae	76	149	0
Family Lathridiidae			
Stephostethus lardarius (Degeer)	14	2	0
Family Chrysomelidae			
Oulema melanopa (Linnaeus)	4	0	0
Gastrophysa polygoni (Linnaeus)	1	0	0
Phyllotreta undulata Kutschera	0	2	0
Longitarsus kutscherae (Rye)	5	1	0
Chaetocnema concinna (Marsham)	3	2	1
Family Curculionidae			
Phyllobius sp Germar	4	0	0
unidentified specimens	5	0	0
Order Diptera			
Family Tipulidae	19	0	0
Family Psychodidae	2	0	- **
Family Chironomidae	1	0	-
Family Bibionidae	20	1	-
Family Mycetophilidae	9	0	-
Family Rhagionidae			
Rhagio tringarius (Linnaeus)	2	8	1
Family Phoridae	6	0	-

ANIMAL	TOTAL CATCH 1983	1984	1985
Family Syrphidae			
Syrphus vitripennis Meigen	0	1	0
Metasyrphus corollae (Fabricius)	2	0	0
Episyrphus balteatus (Degeer)	1	0	0
Eumerus strigatus (Fallen)	0	2	0
* syrphid larvae	2	2	
syrphid larvae	11	1	1
Family Heliomyzidae			
Geomyza sp Loew	1	0	-
unidentified specimens	1	2	-
Family Sphaeroceridae	3	0	-
Family Lonchaeidae	1	0	-
Family Chloropidae	1	0	-
Family Tachinidae	1	0	0
Family Calliphoridae			
Pollenia sp Robineau-Desvoidy	1	0	-
unidentified specimens	5	0	-
Family Scatophagidae	18	1	-
Family Anthomyiidae			
Pegohylemyia fugax (Meigen)	4	1	-
Delia antiqua (Meigen)	8	0	-
Delia brassicae Hoffmannsegg in Wiedemann	8	0	-
Delia coarctata (Fallen)	4	0	-
Delia florilega (Zettestedt)	1	0	-
Delia sp Robineau-Desvoidy	2	0	-
Nupedia aestiva (Meigen)	1	0	-
unidentified specimens	132	17	-
Family Muscidae	12	0	-
Order Hymenoptera			
Family Tenthredinidae			
Dolerus gonager (Fabricius)	9	0	0
Family Ichneumonidae			

ANIMAL	TOTAL CATCH 1983	1984	1985
Sub-family Phygadeuontinae	3	7	0
Sub-family Orthocentrinae	1	0	0
Family Braconidae			
Chorebus Haliday	3	0	0
Family Aphidiidae			
*Praon sp Haliday	0	11	0
*Aphidus picipes (Nees)	327	16	2
Family Pteromalidae			
*Asaphes vulgaris Walker	33	9	0
Family Diapriidae	2	0	0
Family Megaspilidae			
*Dendrocerus aphidum (Rondani)	48	5	0
*Dendrocerus carpenteri (Curtis)	4	0	0
*Dendrocerus sp	0	3	0
Family Formicidae			
Myrmica sp Latreille	1	0	0
Family Andrenidae	1	0	0
Family Apidae			
Bombus sp Latreille	1	0	0
Apis mellifera Linnaeus	0	1	0

* Indicates animals sampled by visual searches of foliage. All others were caught in pitfall traps.

** - Indicates animals in pitfall traps not identified (in 1985 only).

\+ Indicates specimens deposited in the Royal Museum of Scotland.

APPENDIX 2 - WEATHER DATA

Weather data were obtained from the Meteorological Office Climatological Services (Scotland), Edinburgh. Meteorological stations were chosen in each year for proximity or geographical similarity to field sites. Records from 2 stations are given for 1984: Pathhead is closest to the field site but is 160 m above sea level, 100 m higher than the field. East Craigs is further away but is at an altitude of approximately 60 m. The station at Turnhouse is very close to the 1985 field site and air temperature and rainfall data are taken from there in 1985. No soil temperature records were kept at Turnhouse and data used are instead from East Craigs. Record from the Bush Estate are also given for 1985. The station there was about 10 m from the concrete "boxes" used in the density-catch experiment (Chapter 6).

Air temperatures are averages of daily maximum and minimum temperatures. Soil temperature records were taken at depths of 30 cm in 1983 and at 10 cm in 1984 and 1985. Mean weekly soil and air temperatures and total weekly rainfall are given for 1983, to correspond with pitfall-trap operating periods of 7 days. Daily weather records for dates when pitfall traps or visual samples were taken only are given for all years.

Equipment used

Maximum and minimum self-regulating thermometers were exposed outdoors inside ventilated thermograph screens such that thermometer bulbs were 1.25 m above ground level. These were read by a Meterological Office observer daily at 09:00. Soil temperatures were also read at 09:00. Rainfall was measured with a rain gauge. Records were taken at 09:00 and reflect the total rainfall in the 24 hours since 09:00 the previous day.

Windspeeds

Windspeeds were taken at 09:00 on each date. Windspeeds for days on which treatments were applied are:

21 July	1983	-	8	kph
12 July	1984	-	35	kph
10 August	1984	-	10	kph
25 July	1985	-	0	kph
14 August	1985	-	16	kph

National Grid References of Meteorological Stations:

Royal Botanic Garden	:	NT 246756
Pathhead	:	NT 395644
East Craigs	:	NT 183736
Turnhouse	:	NT 159739
Bush Estate	:	NT 246635

Weather records from the Royal Botanic Garden, Edinburgh, 1983

Date	Air Temp (°C)	Rainfall (mm)
13 June	11.6	0.3
22 "	16.0	0
27 "	13.1	2.0
4 July	16.1	0
13 "	17.1	0
18 "	16.1	-*
25 "	16.8	0.5
8 August	14.4	0
16 "	16.7	0
25 "	18.4	0
30 "	17.5	0

* - = < 0.05 mm

Weather records from the Royal Botanic Garden, Edinburgh, 1983

1983

Date	Weekly means ± SE_{95} Air Temp (°C)	Soil Temp (at 30 cm) (°C)	Total Rainfall (mm)
28 April - 4 May	7.8 ± 0.8	8.5 ± 0.4	20.6
5-11 May	9.0 ± 1.1	10.0 ± 0.6	19.6
12-18 May	9.3 ± 1.4	10.5 ± 0.4	16.7
19-25 May	10.3 ± 1.0	12.4 ± 0.8	1.9
26 May - 1 June	9.0 ± 1.1	11.6 ± 0.8	71.0
2-8 June	10.7 ± 2.2	11.7 ± 1.3	12.1
9-15 June	12.7 ± 0.9	13.8 ± 0.2	1.7
16-22 June	14.7 ± 2.2	15.5 ± 1.2	0.4
23-29 June	13.4 ± 1.5	15.4 ± 0.6	5.0
30 June - 6 July	14.8 ± 2.1	15.6 ± 0.6	2.5
7-13 July	16.6 ± 1.2	17.1 ± 0.5	0.8
14-20 July	16.1 ± 1.6	17.0 ± 0.9	0
21-27 July	17.7 ± 0.7	17.9 ± 0.7	2.8
28 July - 3 August	15.5 ± 1.9	16.8 ± 1.0	7.2
4-10 August	16.3 ± 1.3	17.1 ± 0.8	0
11-17 August	17.7 ± 1.7	17.9 ± 0.4	4.2
18-24 August	15.7 ± 2.5	16.9 ± 1.0	15.2
25-31 August	16.5 ± 2.7	16.9 ± 1.0	5.0
1 August - 7 September	13.3 ± 1.8	14.5 ± 0.8	12.8

Weather records from East Craigs and Pathhead Meteorological Stations, 1984

Date	Air Temp (°C)		Soil Temp (°C) (at 10 cm)		Rainfall (mm)
	Pathhead	East Craigs	Pathhead	East Craigs	Pathhead
16 May	9.5	10.1	13.6	11.1	0.1
23 "	12.3	13.3	13.0	12.4	0
30 "	13.3	13.2	12.1	13.2	0
6 June	12.8	13.4	12.2	11.0	0.5
12 "	13.9	14.5	15.1	14.2	0.3
13 "	11.6	12.0	13.9	13.6	1.2
19 "	16.4	17.1	18.3	16.8	0
20 "	13.7	13.8	18.5	16.5	-*
26 "	15.5	15.8	16.2	14.2	0
27 "	13.9	11.8	17.2	16.0	1.2
4 July	14.2	15.6	16.9	16.6	0
5 "	15.5	16.2	18.6	18.2	0
12 "	16.4	17.6	18.0	16.8	1.0
13 "	14.2	14.6	17.0	16.2	-
14 "	13.1	13.7	17.4	16.4	2.8
15 "	13.1	13.5	16.0	15.6	-
20 "	17.5	18.9	19.3	17.8	0
21 "	14.4	15.7	20.5	18.5	0
25 "	17.2	17.3	20.7	19.5	0
1 August	15.5	15.8	14.6	14.1	1.4
7 "	12.5	13.4	14.5	13.8	-
8 "	16.0	15.3	14.4	15.1	0.3
9 "	11.0	10.8	15.5	15.0	-
10 "	15.4	15.4	13.1	13.8	0
14 "	14.7	15.8	17.9	16.6	0
15 "	14.2	13.8	17.0	15.2	0
20 "	20.1	18.9	17.7	17.4	0
21 "	19.6	17.6	18.7	17.6	0
10 September	11.9	12.3	12.2	11.8	0.2
11 "	12.9	13.5	12.1	12.2	0.3

* - = < 0.05 m

Weather records from East Craigs and Turnhouse Meteorological Stations, 1985

Date	Air Temp (°C) Turnhouse	Soil Temp (at 10 cm) (°C) East Craigs	Rainfall (mm) Turnhouse
25 July	16.2	16.8	0.1
26 "	13.2	15.8	64.3
27 "	12.2	13.9	3.4
28 "	12.7	13.8	12.2
1 August	14.1	14.0	3.1
8 "	10.7	12.7	0.8
14 "	13.2	13.1	12.2
15 "	13.8	11.9	0.6
16 "	13.1	12.9	0.9
17 "	12.7	13.3	0.9
21 "	14.0	13.3	1.6
28 "	11.2	13.5	-*

* - = < 0.05 mm

Weather records from Bush Estate, 1985

Date	Temperature (°C) Soil (at 10 cm)	Air
4 August	13.0	12.6
5 "	13.4	13.2
6 "	12.6	13.1
7 "	12.4	12.2
8 "	12.4	10.2
9 "	11.7	11.7
10 "	11.9	11.7
11 "	11.5	11.2

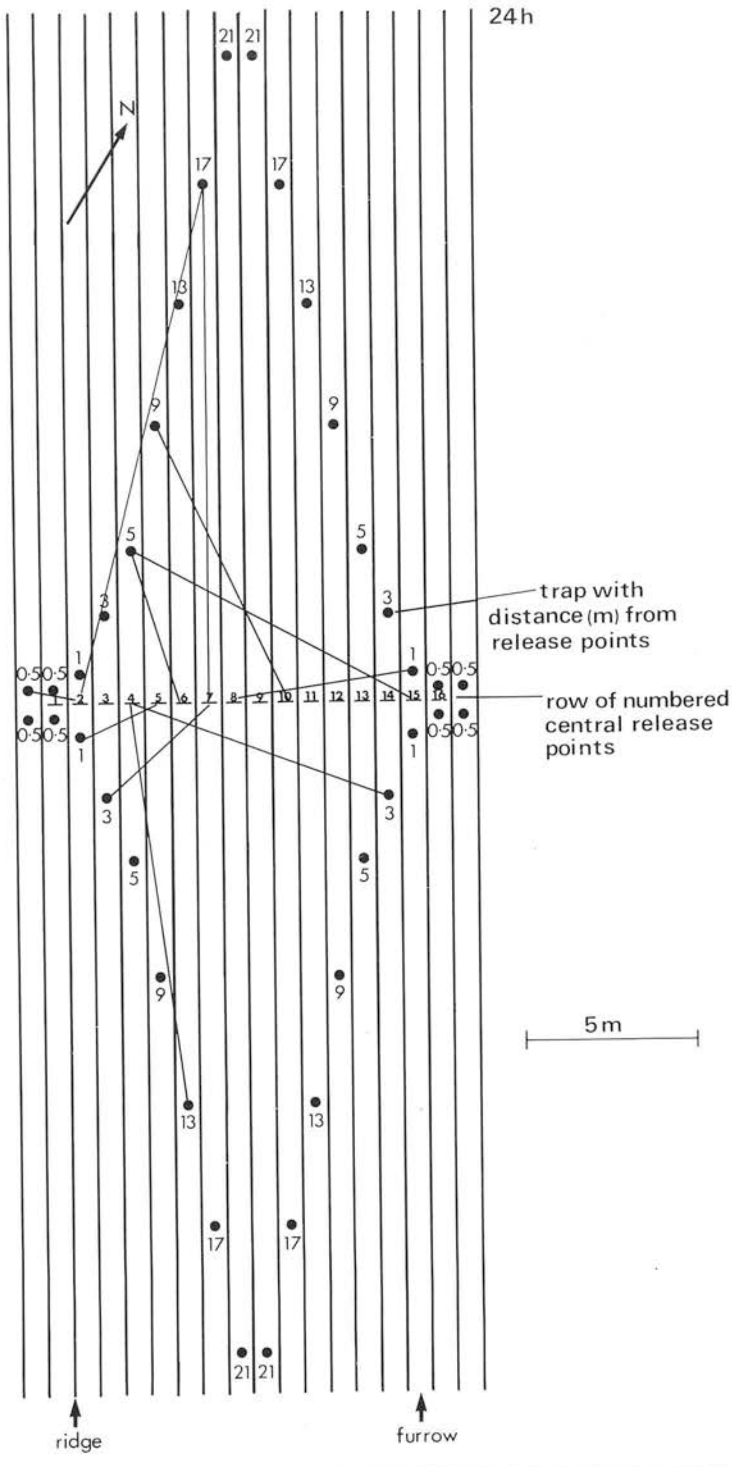
APPENDIX 3

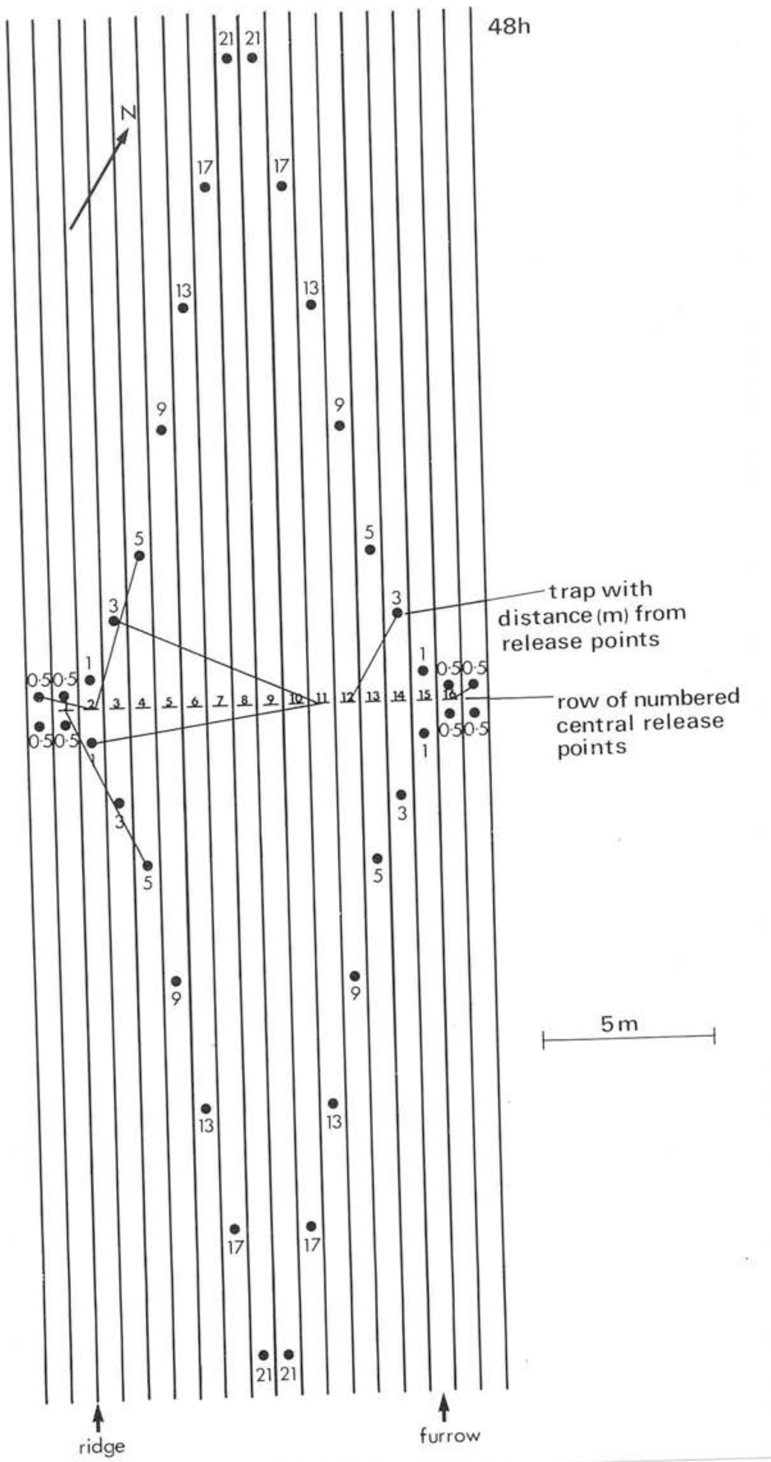
Total numbers of various parasitoids emerging from aphid mummies collected in 1984
(plots, leaf positions combined; U = untreated, T = treated)

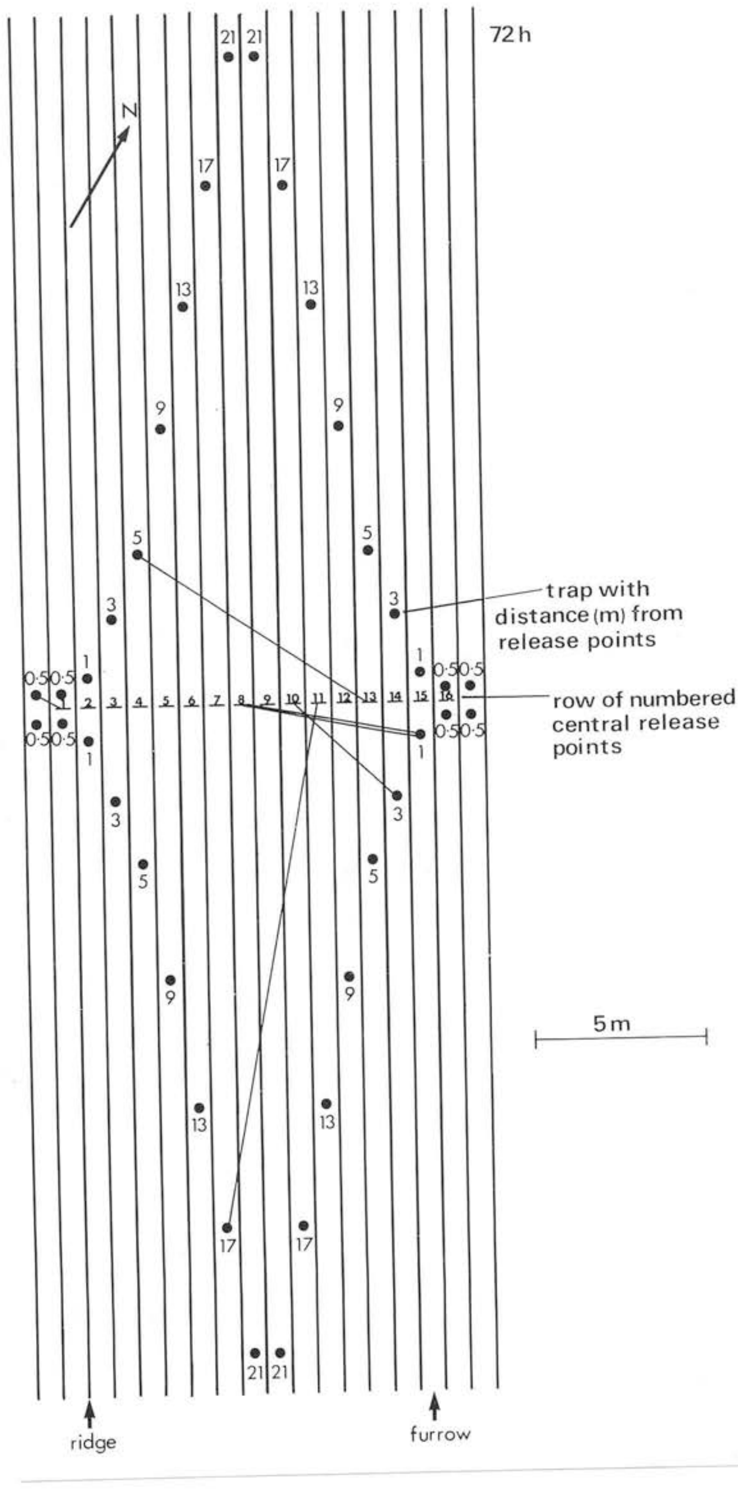
Species	Treatment	Date						
		25 July	1 Aug	7 Aug	8 Aug	14 Aug	20 Aug	10 Sept
Aphidius picipes	U	2	2	3	3	2	0	0
	T	0	1	1	1	0	0	0
Praon spp	U	1	3	1	3	0	0	0
	T	0	0	1	0	0	0	0
Asaphes vulgaris	U	0	3	1	4	0	0	0
	T	0	0	1	0	0	0	0
Dendrocerus aphidum	U	0	2	1	1	1	0	0
	T	0	0	0	0	0	0	0
Charipinae	U	0	0	1	0	0	0	0
	T	0	0	0	1	0	0	0

APPENDIX 4

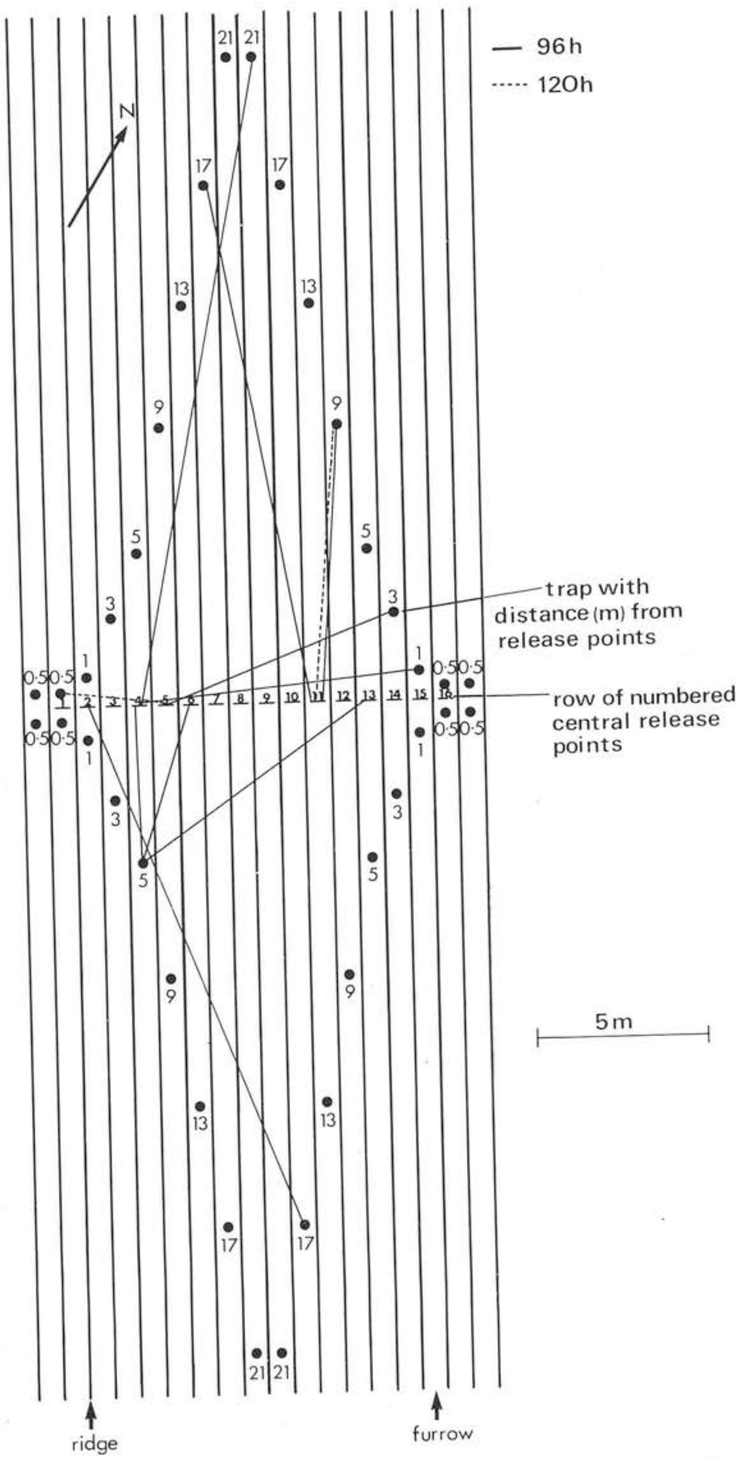
Layout of mark-release experiment with lines connecting original release point and trap of capture for each recaptured individual beetle, at each post-release interval.


24 h
N
trap with distance (m) from release points
row of numbered central release points
5 m
ridge
furrow


48h
N
trap with distance (m) from release points
row of numbered central release points
5 m
ridge
furrow



72 h
N
trap with distance (m) from release points
row of numbered central release points
5 m
ridge
furrow


— 96h
----- 120h
N
trap with distance (m) from release points
row of numbered central release points
5m
ridge
furrow

Appendix 4

(b) Mean distances moved by beetles between release and capture, divided by the number of days between release and capture

Time after release (h)	Mean distance travelled (m) $\pm$ SE_{95}
24	9.1 $\pm$ 1.47 (n = 13)
48	2.5 $\pm$ 0.58 (n = 7)
72	2.8 $\pm$ 0.75 (n = 6)
96	2.8 $\pm$ 0.54 (n = 9)
120	1.8 $\pm$ 0 (n = 2)
Overall	4.9 $\pm$ 0.74 (n = 37)

Dispersal of ground beetles in a potato crop; a mark-release study

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Keywords: Carabidae, *Pterostichus*, ground beetles, mark-release, potatoes

Introduction

Preliminary results of field investigations into the effects of insecticides on the natural enemies of potato aphids indicated that *Pterostichus madidus* (Fabricius) and *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae), the ground beetles most frequently caught in pitfall traps, redistributed rapidly after treatment. In order to determine the area of field plot which would accommodate this redistribution, a mark-release experiment was done to provide information on the likely mean daily distances travelled by the beetles.

Standard mark-release techniques for measurement of dispersal (Fletcher, 1974; Ericson, 1977) presented two problems: the need for large numbers of animals to release when the numbers of *P. madidus* and *P. melanarius* available were relatively small; and the radial geometry of the spatial layout when potatoes are planted in parallel ridges. This communication reports a mark-release study of ground beetles in a Scottish potato crop during 1984, using a parallelogram spatial layout and a few hundred insects only.

Methods and materials

Adult *P. madidus* and *P. melanarius* for marking were deprived of food two days before release so that they would be 'hungry', hungry carabids being known to travel farther than fed ones (Baars, 1979). Twenty-four h before release, beetles were marked with enamel paint. Releases were made at the centres of 16 adjacent furrows, release points forming a line 21.5 m from the field edge at right angles to the furrows. Pitfall traps were arranged overall as a parallelogram of equal length sides with the line of central release points forming one of the diagonals. The plastic pitfall traps (perimeter: 40 cm) were positioned at 0.5, 1, 3, 5, 9, 13, 17 and 21 m from the line of central release points. Four traps were positioned at each distance, two on either side of the line of release points.

Marked beetles were released mid-afternoon on 1 August. A total of 96 female and 96 male *P. madidus* was released but fewer *P. melanarius* were available: 44 ♀♀ and 36 ♂♂. Traps were examined at 2, 24, 48, 72, 96 and 120 h after release. Recaptured individuals were re-released at their original release points.

The distances moved by individual beetles were determined using the Pythagorean theorem: the square of the maximum distance travelled was assumed equal to the sum of the square of the linear distance between points of release and capture, and the square of the number of ridges between release point and trap. Because any haphazard wanderings by beetles between points of release and capture were unknown, distances travelled are minimum estimates. Due to this imprecision, the non-linear component of the potato ridge-furrow profile has not been considered.

Results and discussion

A total of 38 beetles was recaptured (14.0%), only one of which was a multiple recapture. Due to low counts at 120 h, recapture data for 96 and

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120 h were combined for χ^2 analysis. Overall recapture rates of *P. madidus* (14.6%) and *P. melanarius* (12.8%) were not significantly different (χ_3^2 = 1.77, $p < 0.05$), and although rates were higher for males than females (17.7% and 9.7% respectively) this difference was not significant (χ_3^2 = 4.68, $p < 0.05$). Recaptures of each sex of either species were not considered separately because too low numbers were caught.

The mean distance travelled by all recaptured beetles in this experiment, 8.6 m, compares well with the results of J. Cory (pers. comm.) who reported mean daily distances travelled in winter wheat by *P. madidus* of 1.1–6.5 m depending on trap spacing, and by *P. melanarius* of 10.0 m. The mean distances travelled by *Pterostichus* species between points of release and recapture at each sampling time are shown in Table 1. The maximum distance travelled by an individual in this study was 21.0 m.

Our original hypothesis was that the potato ridges would act as barriers, discouraging dispersal over them and forcing beetles to move only along the furrows. Beetles would in effect be confined to straight tracks along which they could travel for distances varying from 0.5 m to 21 m before encountering a trap. Recapture rate should thus be high and fewer individuals than is usual with mark-release studies, need be released. The results show that dispersal was nondirectional rather than primarily along furrows (χ^2 = 2.89, NS, $p < 0.05$), with ridges appearing not to be barriers to movement. Recapture rates were nevertheless of the order of 13–14%. These rates, which compare favourably with the recapture rates of standard mark-release techniques (Rivard, 1965; Ericson, 1977; Robinson & Luff, 1979; J. Cory, pers. comm.), were obtained by releasing comparatively few beetles.

Table 1. Mean distance travelled by recaptured *Pterostichus* spp. at various h after release.

Time after release (h)	Mean distance travelled (m) ± s.e.	n
24	9.1 ± 1.47	13
48	5.1 ± 1.15	7
72	8.3 ± 2.24	6
96	11.4 ± 2.17	9
120	9.0 ± 0.02	2

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