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MANIPULATION OF OVERWINTERING HABITATS FOR INVERTEBRATE PREDATORS ON FARMLAND

by

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Dedicated To My Parents

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ABSTRACT

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MANIPULATION OF OVERWINTERING HABITATS FOR INVERTEBRATE PREDATORS ON FARMLAND

by Matthew Brian Thomas

Data are presented from a three-year study on the creation of overwintering habitats in farmland for the arthropod natural enemies of cereal aphids. These new habitats, in the form of grass-sown raised banks, re-created those aspects of existing field boundaries which had previously been shown to favour predator overwintering.

During the first year of establishment, the new habitats provided overwintering refuge sites for many spiders (Araneae), ground beetles (Carabidae) and rove beetles (Staphylinidae), with ground-zone searches producing total densities of these polyphagous predators up to 150m^{-2}. In the second and third years, destructive sampling revealed much higher predator numbers, peak densities exceeding 1500m^{-2} in some grass treatments in the second year. Identification of individual predator species revealed a shift in community structure, with spiders and ground beetles showing successional changes from pioneer to more specialised species as the newly created habitats matured. Beyond this, a range of biotic and abiotic factors were shown to be involved in the processes of successful overwintering and overwintering site selection.

Predator sampling studies in the spring showed that the overwintering predator populations in the new habitats could influence subsequent dispersal patterns into the crop, providing an even spread of predators throughout the field early in the season.

The results of the study are discussed in the context of the current social and economic climate within European agriculture, and it is suggested that dynamic land management, by enhancing natural pest control, could provide a means of reducing the present-day reliance on chemical pest control measures.

CHAPTER 1. GENERAL INTRODUCTION

1.1 Cereal aphids in the UK

The aphids Sitobion avenae (F.), Metopolophium dirhodum (Walker) and Rhopalosiphum padi (L.) are important pests of cereals in the UK, although the damage they cause varies from year to year (McLean et al. 1977; Vickerman & Wratten 1979; Carter et al. 1980).

Aphid damage may be a direct result of feeding due to the transmission of viruses or via honeydew contamination reducing photosynthetic rate (Rabbinge et al. 1980). Grain weight and percentage protein content of the grain can be reduced (Wratten 1975) and a reduction in "baking quality" may result from infestations (Lee, Stevens, Stokes and Wratten 1981). Direct damage due to aphid infestation can result in yield loss up to 14% (Watt, Vickerman & Wratten 1984) while wheat infected by barley yellow dwarf virus (BYDV) (Oswald & Houston 1953), during tillering or stem extension growth stages, can lead to a reduction in yield of 30% (Vickerman & Wratten 1979).

In years when aphids are abundant in cereals, insecticides are widely used, with many farmers spraying prophylactically (Potts 1977). Wratten, Watt, Carter & Entwistle (1990) reported the results of a survey carried out in 1984 on the use of aphicides in winter wheat. Data from more than 60,000 ha revealed that many crops were treated too late (by which time any crop damage had already taken place), dimethoate, affecting a wide range of "non-target" beneficial arthropods (Vickerman et al. 1987), was the insecticide most frequently used, tank mixes with fungicides were common, and there were great regional differences in spray timing and pesticide usage. In a similar survey of 115,000 ha of winter wheat in 1988, Wratten & Mann (1988) revealed that aphicides were still applied inappropriately, many crops being sprayed too late, or the aphid infestation was too late or too small to cause enough damage to justify the cost of spraying.

Accurate forecasting and advice on spraying, as well as biological techniques for reducing aphid survivorship would enable farmers to decrease such applications of pesticide. This would help delay the potential onset of resistance to aphicides and increase survivorship (and hence effectiveness) of the natural enemy complex (Burn, Coaker & Jepson 1987). An Integrated Pest Management (IPM) approach (maximising the use of natural pest control agents allied to a combination of other pest suppression techniques such as cultural methods, resistant crop varieties and selective use of pesticides) could therefore provide an economically justifiable alternative for aphid control, consequently reducing the environmental side effects associated with the intensive use of pesticides.

1.2 Natural enemies of cereal aphids.

Aphid-specific predators

Cereal aphids are attacked by a wide range of aphid-specific predators such as parasitic Hymenoptera, Coccinellidae (Coleoptera), Syrphidae (Diptera), and Chrysopidae (Neuroptera) (Vickerman & Wratten 1979). In the parasitic Hymenoptera for example, seven primary parasitoid and seven hyperparasitoid (using the primary parasitoids as hosts) species regularly attack aphids on cereal crops in Britain (Powell 1982). Most of these occur simultaneously in the same fields, forming a complex parasitoid community associated with cereal aphid populations (Wratten & Powell 1991). Parasitoids need to be active in the crop early in the year if they are to play a significant role in the control of summer aphid populations (a high parasitoid : aphid ratio early in the season has been shown to slow down the initial growth rate of the aphid population) (Powell 1983; Vorley 1986; Fougeroux et al. 1988). For example, field surveys in northern France in 1983 and 1984 demonstrated an inverse relationship between early levels of parasitism in cereal fields and subsequent peak aphid densities (Fougeroux et al. 1988). Similarly, Vorley & Wratten (1985) demonstrated, using simulation modelling in late-sown winter and spring-sown crops, that with early-season immigration, parasitoids could keep grain aphid populations at a level one seventh of that which they would have been if the parasitoids were absent.

Predator manipulative studies (involving predator exclusion techniques), have shown that other aphid-specific predators can also influence aphid numbers. For example, numbers of aphids were about eight times higher in experiments of Chambers et al. (1983) when cages were used to exclude Coccinellidae and Syrphidae in particular. Computer based modelling by Chambers & Adams (1986) has also implicated hoverflies in aphid control. However, although the aphid-specific predator complex is valued for reducing peak levels, or to hasten the "crash" of aphid populations (Vickerman & Wratten 1979; Chambers et al. 1983), other work has shown that because of their variability in abundance, often occurring in low numbers only (Potts & Vickerman 1974), they are unlikely to control aphid populations on their own; other predatory groups being of equal importance in many situations.

Polyphagous predators

Polyphagous predators such as certain species of Carabidae (Coleoptera), Staphylinidae (Coleoptera), Araneae and Dermaptera (specifically the earwig Forficula auricularia (L.)) are able to persist in the crop even when aphid numbers are low since they exploit a wide spectrum of prey types (Edwards, Sunderland & George 1979). The potential of these predominantly ground-zone predators to influence cereal aphid populations is theoretically high, as several workers have shown that cereal aphids frequently fall from the crop canopy. Sunderland, Fraser and Dixon (1986) showed that up to 90% of the aphid population per shoot fall to the ground each day. Similarly, between 4% and 71% of an aphid population have been recorded on the ground at any one time (Griffiths 1983; Sopp, Sunderland & Coombes 1987), while Holmes (1988) showed that no individuals of S. avenae reached adulthood on the same plant on which it was born.

From suction sample and pitfall trap surveys of cereal crops between the years of 1968 and 1972, Potts and Vickerman (1974) produced one of the first studies to implicate polyphagous predators in aphid biocontrol. They reported significant negative correlations between the number of aphids and an index of overall invertebrate faunal diversity excluding aphids. Further analysis relating the diversity index to the proportion of the predatory individuals captured, produced a positive correlation. Low populations of aphid specific predators at the time of sampling implicated polyphagous predators in the initial aphid number-diversity relationship. Further circumstantial evidence was provided by Chambers et al. (1982) who observed reduced early-summer aphid population densities towards field boundaries in early-sown fields but no difference between field centre and field edge populations in late-sown fields. Higher numbers of polyphagous predators were observed in pitfall catches at the field edges compared to mid-field trap numbers in the early-sown fields but not in the late-sown fields, again implicating these organisms in reducing the aphid numbers. In contrast, the numbers of aphid-specific predators in the early-sown fields positively correlated with the numbers of their prey, although prey rate of increase was correlated negatively with numbers of aphid specific predators.

Following the survey-based studies discussed above, a variety of alternative approaches have been employed to quantify the potential importance of polyphagous predators in cereals and other arable crops:

(i) In manipulation experiments where polyphagous predator numbers were reduced in exclusion plots, aphid populations subsequently increased above those of unenclosed areas (Edwards et al. 1979; Wratten & Pearson 1982; Chiverton 1986; Winder 1990).

(ii) Sunderland and Vickerman (1980) used gut dissection techniques to assess the proportion of predators containing aphid remains. This proportion was multiplied by the predator densities during the aphid increase phase to give a predation index which ranked 16 predators in order of importance. The carabids Demetrias atricapillus (L.) and Agonum dorsale (Pont.) and the earwig Forficula auricularia attained the top three positions in this crude ranking.

(iii) Further work has been carried out to gain a greater understanding of predator-prey interactions and expand upon Sunderland and Vickerman's preliminary ranking. For example, laboratory consumption rates of aphids were studied for many species of the predators from the original ranking (Griffiths, 1983; Carrillo, 1985; Sopp & Wratten, 1986; Coombes, 1987). These lab-based investigations on consumption rates were largely confirmed in the field by Mauremootoo (1991) who used the same predator species but Drosophila pupae and Musca eggs as "prey". Sunderland et al. (1987) and Sopp (1987) aimed to quantify predation rates of field collected predators using enzyme-linked-immunosorbent assay (ELISA) with antibodies specific to certain cereal aphid species. Predator groups such as Staphylinidae and Linyphiidae which were ranked low in earlier dissection-based rankings, assumed a higher importance as cereal aphid predators.

(iv) Indirect attempts to quantify foraging in the field have also been carried out. For example, Bryan and Wratten (1984) demonstrated various levels of aggregation by carabid and staphylinid beetles to high density (artificially created) patches of aphids. More recently, Winder (1990) showed that ground zone predators significantly reduce the rate at which displaced aphids recolonise the crop canopy. This is particularly significant as only those non-climbing predators that consume living aphids which would otherwise return to the crop, contribute to aphid control.

Having established that polyphagous predators appear to have the potential to influence aphid numbers, research can be directed towards gaining a greater understanding of the ecology of the arable system with the ultimate aim of enhancing the effectiveness of natural enemies, for example by selection of less toxic agrochemicals or by manipulating crop or non crop areas (Wratten et al. 1984).

1.3 Overwintering of polyphagous predators

Field boundaries have long been considered important overwintering sites for beetles and other invertebrates. Pollard (1968a) demonstrated that a hawthorn hedgerow provided a variety of different habitats. The effect of removing the bottom flora of a hedgerow (by applying the herbicide "Preeglone") was to decrease the abundance of several species of overwintering carabid beetle including Agonum dorsale, Harpalus rufipes (Degeer), Loricera pilicornis (F.), since shown to be potential aphid predators (Sunderland & Vickerman 1980). Similarly, Gorny (1970) and Bonkowska (1970) both identified shelterbelts (mature boundary habitats dominated by tree and shrub species; 14-17m high with an average breadth of 36m in the example of Bonkowska (1970)) as important permanent features of the agricultural environment providing alternative habitats for several species of predatory carabid.

Luff (1966a, 1966b) established for grasslands, that tussock forming grasses Dactylis glomerata (L.) and Deschampsia caespitosa (L.) harboured large communities of beetles both in summer and winter. It was demonstrated that a temperature of at least -17°C outside the tussock would be needed before the $LTemp_{50}$ (-8.5°C) of any of the overwintering species was reached inside the tussock, supporting the theory that many species of beetle (as well as other insects) have developed the habit of overwintering in grass tussocks in order to obtain shelter from cold conditions. Desender & D'Hulster (1982) and D'Hulster & Desender (1983), studying the hibernation of staphylinids in field edge sites, also concluded that dense vegetation, a deep aerated sod and a well developed litter layer provided a buffering of temperature fluctuations and made such a biotope a suitable overwintering site. Furthermore, in a boundary study on the overwintering of the carabid beetles A. dorsale, Bembidion lampros (Herbst) and D. atricapillus, Desender (1982) established positive correlations between the densities of the overwintering predators and the biomass of living and dead grass, and the mean depth of the compact sod layer.

Sotherton (1984, 1985) and Wallin (1985, 1986) demonstrated that many polyphagous predators overwinter almost exclusively in field boundaries. Boundary quality differed markedly between boundaries, with habitats such as raised banks with rough grass cover (which form hedge banks and post and wire boundaries in many parts of Europe (Greaves & Marshall 1987)) being the preferred habitat types (Sotherton 1985).

Coombes and Sotherton (1986) studied the phenology of crop invasion by the boundary overwintering predators in the spring. They revealed that although some species of Staphylinidae and Linyphiidae could invade the crop using aerial dispersal mechanisms, certain species of Carabidae entered the crop by walking only and as such, significant numbers of individuals of the carabid species studied were not found at the field centres until June.

In modern arable systems the accommodation of increasingly large machinery has led to the removal of hedges to produce larger fields (Davies & Dunford 1962; Edwards 1970). This process accelerated rapidly in the late 1940s as a result of government policy and the introduction of grants for hedgerow removal. Over the last 50 years c.40% of the hedges that were recorded in lowland Britain in 1940 have disappeared (Anon 1991). Despite new plantings, it is estimated that there is still an annual net loss of hedgerows in England and Wales (Anon 1986; Greaves & Marshall 1987). Accompanying this the incidence of spraying herbicides to control weeds in hedgerows has increased (Boatman 1989) reducing boundary quality as sites for overwintering predators. This environmental degradation has two major consequences for aphid biocontrol:

(i) With increasingly large fields, spring colonisation of field centres by non-flying predators such as many Carabidae could be impaired, especially at a time when their control potential is most beneficial (Wratten et al. 1984; Coombes & Sotherton 1986; Wratten 1988) i.e. reduced predation rates in the field centres during the normal time of aphid colonisation (Chambers et al. 1982). Related to this, field scale applications of broad-spectrum insecticides have been shown to result in aphid resurgence due to reduced predator pressure (a product of limited predator re-colonisation) at the field centre (Duffield & Baker 1990).

(ii) With the small boundary:field area ratio of large fields and reduced availability of non-crop habitats, the overall densities of polyphagous predators in arable ecosystems may become reduced, and their potential to influence pest numbers limited accordingly.

The above outline shows that some of the factors which could limit the effectiveness of native natural enemies have been identified. With this knowledge it may be possible to augment their densities within an integrated control programme and thus raise the natural enemy:pest ratio (van Emden 1988; van Emden & Wratten 1991).

1.4 Environmental manipulation for the encouragement of natural enemies

Several studies have demonstrated that increasing intra-crop diversity may cause decreases in pest numbers. For example, intercropping or the presence of weeds frequently causes a dramatic decrease in pest numbers on crops (Van Emden, 1988). Vickerman (1974) found more than ten times the number of staphylinid beetles in winter barley plots with grass weeds than barley plots without. Aphid populations were 25% smaller in the weedy plots. Similarly, Powell et al. (1981) comparing seven species of polyphagous beetle predators caught in pitfall traps in unweeded and "clean" plots of winter wheat, found significantly higher numbers of four species in the weedy areas. Coaker (1990) cites numerous examples demonstrating increases in predator species in intercrop systems compared with monocultures. For example, Gavarra & Raros (1975) found spiders to be more effective against corn borers in a corn/groundnut intercrop system, and Dempster & Coaker (1974), O'Donnell & Coaker (1975) and Ryan et al. (1980) recorded higher populations of carabids and staphylinids in brassicas intercropped with clover. Beyond these ideas, "conservation headlands" have been established along field margins in cereals by the Game Conservancy Trust, as a means of increasing insect diversity and abundance to provide chick food for the grey partridge, Perdix perdix (L.). These habitats are created by selective applications of pesticides (herbicides, fungicides and insecticides) to 6m wide strips at the edges of cereal fields. This allows the less ecologically valuable and more agriculturally damaging weed species to be removed without affecting the more "desirable" species (those species that act as host plants of preferred chick-food insects) (Boatman et al. 1989). As well as enriching the general insect fauna outside the commercial crop (Rands 1985) (including effects on butterflies (Dover 1989)), it appears that there may be beneficial effects on polyphagous predators (Chiverton 1991) and aphidophagous hoverflies (Cowgill 1991) into the cropped area.

Several studies have also suggested that as well as intra-crop manipulation, management of crop edges and adjacent non-crop field boundary habitats could represent a possible tool towards the goal of integrated methods for biocontrol in cereals and other crops. For example, Von Klinger (1987) investigated the effects of margin-strips of Sinapsis alba L. and Phacelia tanacetifolia Benth. along a winter wheat field. Significantly higher numbers of species and individuals of different predatory groups were found in or near the margin-strips, compared with the wheat plot without the sown margin-strip. In particular, polyphagous predators such as carabid beetles occurred in increased numbers in the margin-strips and adjacent parts of the wheat field. The results of a separate field manipulation experiment using margin-strips of Phacelia tanacetifolia (by workers at Southampton University, reported in Farmers Weekly (9.11.) 1990) also suggested beneficial effects for aphid predators; this time as a potential pollen source for certain species of hoverfly.

Augmentation of beneficial arthropods by strip management was also studied by Nentwig (1988,1989). The effects of narrow unmown strips in a mixed grass meadow, and successional strips of vegetation in a field of winter wheat were analyzed in comparison with areas with conventional management. In combination with an increase in species number and diversity of beneficial arthropods, the degree of stability (defined as a relative constant abundance in successive years) increased in the strip managed areas.

Effects of increased spatial heterogeneity within the arable landscape were investigated by creating an experimental corridor system consisting of several small woodlots on intensively used agricultural land (Mader 1988). The results suggested an increase in species richness and diversity in the new habitats compared with neighbouring fields, and there was an indication that predatory animals inhabiting the woodlots spread into the neighbouring fields and to some extent exerted regulatory effects on their prey populations.

The overall conclusion of these studies was that increased structural diversity within the agro-ecosystem tended to lead to community stability, and predator populations from edge habitats were able to influence, to some extent, densities of their prey populations in the adjacent fields.

1.5 Aims of the project

From the above literature it is concluded that inadequate provision of overwintering habitat such as hedgerows with grassy underbanks, coupled with limited powers of spring dispersal of certain predator species, can reduce the effectiveness of many polyphagous predators as control agents of cereal aphids in the cereal ecosystem. The aim of this project therefore, is to attempt to redress the balance of hedgerow removal associated with farming intensification, by creating new habitats to provide improved overwintering conditions for polyphagous predators in arable land. Rather than just manipulate or create habitats at the field boundary, it is intended to reduce field size by creating linear "island" habitats representing what are effectively facsimiles of hedgerow bases at the field centres. The latter aspect should enable predators with low rates of dispersal to reach the field centre earlier in the spring than they would otherwise do (Wratten et al. 1984). Colonisation of the new habitats will be monitored through time and any effects on predator dispersal into the crop in the spring recorded. Beyond this, studies will be carried out to investigate the biotic and abiotic factors influencing habitat selection and overwintering success of certain predator species. This should provide a greater understanding of the mechanisms associated with overwintering and potentially allow the development of management guidelines aimed at optimising biocontrol by native natural enemies, ideally as part of an IPM approach to cereal pest control, in which host plant resistance and rational pesticide use also play a part.

CHAPTER 2. CREATION OF "ISLAND" HABITATS IN FARMLAND TO MANIPULATE POPULATIONS OF BENEFICIAL ARTHROPODS.

SUMMARY

(1) Data are presented from a three year study on the creation of overwintering habitats in farmland for the arthropod natural enemies of cereal aphids. These new habitats, in the form of grass-sown raised banks, re-created those aspects of existing field boundaries which had previously been shown to favour predator overwintering.

(2) During the first year of establishment, the new habitats provided overwintering refuge sites for many Araneae, Carabidae and Staphylinidae. Ground-zone searches produced total polyphagous predator densities of up to $150m^{-2}$.

(3) In the second and third years, destructive sampling revealed higher predator numbers; peak densities exceeding $1500m^{-2}$ in some grass treatments in the second year.

(4) During the course of the study, densities of individual predator species varied considerably, with Araneae and Carabidae showing successional changes from pioneer to more specialised species as the newly created habitats matured.

(5) The role of such a habitat creation scheme in increased stability and enhanced biocontrol within the agro-ecosystem is discussed.

2.1 INTRODUCTION

The abundance and diversity of predatory insects within fields are closely related to the nature of the surrounding vegetation (Altieri & Letourneau 1982). Replacement of areas of natural vegetation by crop monocultures can eliminate many indigenous biocontrol agents that are dependent on the presence and diversity of wild plants in the agricultural landscape (van Emden 1965,1981) for at least part of the year.

Desender (1982), Sotherton (1984, 1985) and Wallin (1985, 1986) have shown that some field boundary types are of particular importance in providing overwintering refuges for many species of polyphagous invertebrate predator in arable field systems which then disperse into the crops in the following spring (Wallin 1985; Coombes & Sotherton 1986). Experimental manipulative studies have demonstrated the role of these groups in reducing the numbers of aphid pests of arable crops (Edwards, Sunderland & George 1979; Wratten & Pearson 1982; Chiverton 1986; Winder 1990). Many features of the boundaries in which these groups overwinter (such as the aerial components of hedge or shelterbelt) are relatively unimportant to their role as reservoirs of these natural enemies (Wratten 1988a; Wratten & Thomas 1990). Of greater importance is the nature of the ground flora and physical structure of the hedge or boundary base. Habitats such as raised banks with rough grass cover (grass tussocks especially (Luff 1966a)) may support high densities of Carabidae and Staphylinidae (Coleoptera), Dermaptera and Araneae. Without such non-crop habitats, the overall densities of polyphagous predators in arable farming ecosystems may become reduced, and their potential to influence pest numbers limited accordingly.

In modern arable systems the accommodation of increasingly large machinery has led to the removal of hedges to produce larger fields (Davies & Dunford 1962; Edwards 1970). Rapid spring colonisation of field centres by non-flying predators such as many Carabidae could therefore be impaired, especially at a time when their control potential is most beneficial (Wratten et al. 1984; Coombes & Sotherton 1986; Wratten 1988b). Also, with the small boundary:field area ratio of large fields, the final density in the crop of predators originating from the non-cropped boundary areas could be lower than in similar but smaller fields. The subject of this chapter therefore, is to present the results of a study which aimed to create artificially, overwintering habitats on farmland which would favour the development of high populations of predators. Also, by the same method, to reduce field size experimentally by creating new within-field overwintering refuges, with the aim of enhancing field colonisation in the spring by predators with low rates of dispersal.

2.2 MATERIALS AND METHODS

Creation of "island" habitats

The new within-field refuges used in this study took the form of three raised earth banks created by two-directional ploughing during the normal autumn cultivation period. Ridge 1 and ridge 2 (both 0.4m high, 1.5m wide, 290m long) bisected fields of 7 ha (field 1) and 20 ha (field 2) respectively on a mixed/arable farm in north Hampshire, U.K.. Ridge 3 (0.4m high, 1.5m wide, 680m long) crossed a field of 51 ha (field 3) on a second mixed/arable farm in central Hampshire, U.K.. Both farms shared similar chalk/flint soils. The banks did not extend completely to the existing field margins; areas of cultivated crop (20m wide in field 1, 50m wide in field 2 and 70m in field 3) were left at each end to allow movement of farm machinery from one field side to the other, without damaging the bank.

All fields had a recent history of growing cereals prior to the onset of the experiment. At the time of ridge establishment, field 2 was in winter wheat but was sown to fodder peas and winter rape in the second and third winters respectively. Field 3 was initially sown to spring barley and then to vining peas for two years. Field 1 was the only field to remain in cereals, being sown to winter wheat for the three years of the study.

Following an application of a broad-spectrum herbicide (glyphosate), at recommended field rate (1440 g ai ha^{-1}), to remove broadleaved weeds that colonised the banks following ploughing, sections of each new bank were hand sown at commercial sowing rates (spring 1987) with various grass species in a linearly randomised block design, with six blocks per bank. Each block contained one replicate of each of eight treatments, each replicate being 6m long on ridges 1 & 2 and 14m long on ridge 3 (diagramatic representations of the randomised block designs are given in Appendix I). The grasses and seed rates were Dactylis glomerata L. (Cock's-foot) 3 g m^{-2}, Lolium perenne L. (Perennial rye-grass) 3 g m^{-2}, Agrostis stolonifera L. (Creeping bent) 8 g m^{-2}, and Holcus lanatus L. (Yorkshire fog) 4 g m^{-2}, and were selected for their qualities of fast growth and good winter cover, requiring little maintenance; they included both matt-forming (L. perenne and A. stolonifera) and tussock-forming (D. glomerata and H. lanatus) species. These species were also those that would not be considered by the farmer as invasive, aggressive weeds of the crop so that the earth banks could not be considered as foci of pernicious weeds. As well as single-species treatments, mixtures of three (A. stolonifera excluded) and the four species (to study the effects of seed "cocktails") were sown. Bare ground controls (maintained by hand weeding or the use of glyphosate at the same rate as above) and treatments of flowering plants to provide pollen and nectar for aphid-specific predators such as Syrphidae and parasitoid wasps (as part of a study not directly concerned with the overwintering project) were also included.

Assessment of predator community composition

Winter 1987/88

During the winter of 1987/88 (November to the end of February), ground-zone surface-searching for predators was carried out on ridges 1 & 2 and in the field surrounding each ridge. Six 0.1 m^2 quadrats were used per replicate on the ridges. Four blocks were searched on each ridge. Twelve quadrats were also randomly placed at distances at least 40m from the ridges or existing boundaries for each mid-field predator density estimate, there being one mid-field recording for each block searched i.e. a total of 48 mid-field quadrats. An aspirator was used to collect insects on the soil surface and amongst grass stems and leaves which were teased apart (but not removed) with the finger tips.

Winter 1988/89

Ground-zone surface-searching was also carried out during the second winter of the study (again from November to the end of February). However, greater structural development of the grasses made thorough examination very difficult. For this reason only four blocks of ridge 1, together with the accompanying field were examined in this way. The remaining sampling (throughout the same period) was destructive; turves ($0.04m^2$ and 0.1m deep) were dug up and placed in polythene bags, thoroughly broken up in white photographic trays in the laboratory, and their fauna hand sorted. This method was considered to give a far more accurate estimate of actual predator densities at this time. However, as the area of each plot was only 9 m^2, limited numbers of destructive samples could be taken. Furthermore, only the single grass species treatments were sampled, as one $0.04m^2$ quadrat within the grass-mixture treatments was likely to be dominated by a single grass species and therefore not give a true representation of the mosaic of grasses of which the treatment comprised. Two destructive samples were taken from each replicate of the single grass species treatments on the ridge that had already been surface-searched. As the second ridge (ridge 2) had not already been sampled in this year, three destructive samples were taken from the same treatments as those sampled on ridge 1. Twenty within-field destructive samples were taken from each of the adjacent field sites away from any influence of boundary/ridge habitats.

Winter 1989/90

Destructive sampling for predators was carried out on all three ridges in this winter season, during the same sampling period described previously. Four destructive samples were taken from each replicate of the single grass species treatments in each block of ridges 1 & 2. Six samples were taken from each replicate of the same treatments of four blocks of ridge 3.

During this period, natural field boundaries were also sampled. Ten destructive samples (at 5m intervals) were taken from a representative 50m section of each the four boundaries surrounding fields 1 & 2.

2.3 RESULTS

Densities of predatory groups

Winter 1987/88

Randomised block analysis of variance (log (numbers+1/quadrat)) followed by Tukey's (1949) test revealed significantly different surface-search densities of total predators (ridge 1 $F_{6,140} = 9.16$, $\underline{P} < 0.01$; ridge 2 $F_{6,140} = 23.45$, $\underline{P} < 0.01$), predatory Carabidae (ridge 1 $F_{6,140} = 6.15$, $\underline{P} < 0.05$; ridge 2 $F_{6,140} = 9.32$, $\underline{P} < 0.01$), predatory Staphylinidae (ridge 1 $F_{6,140} = 3.01$, $\underline{P} < 0.01$; ridge 2 $F_{6,140} = 21.10$, $\underline{P} < 0.01$) and Araneae (ridge 1 $F_{6,140} = 15.53$, $\underline{P} < 0.01$; ridge 2 $F_{6,140} = 22.95$, $\underline{P} < 0.01$) between treatments in the 1987/88 winter on ridges 1 & 2 (Table 2.1). These differences occurred at a time when percentage grass cover in the plots was approximately 60%, with individual tussocks having little dead plant material at their base. With the exception of the Staphylinidae in treatments sown with Agrostis stolonifera and Dactylis glomerata on ridge 1, densities in the grass-sown treatments of both ridges exceeded those in the respective open-field areas, for each of the predator groups.

Winter 1988/89

Surface-search data from the second winter showed a similar pattern (total predators $F_{6,140} = 27.34$, $\underline{P} < 0.01$; predatory Carabidae $F_{6,140} = 10.95$, $\underline{P} < 0.01$; predatory Staphylinidae $F_{6,140} = 10.27$, $\underline{P} < 0.01$; Araneae $F_{6,140} = 28.418$, $\underline{P} < 0.01$) , with, however, increased predator densities in most sown plots compared with the bare ground treatment on the ridge and the open-field areas, with respect to the previous year's densities (Table 2.1).

Destructive sampling revealed predator densities far in excess of those recorded by surface-searching on both ridges (Table 2.2). Open-field densities however, remained at a similar level. On ridge 1, D. glomerata and H. lanatus supported significantly higher densities of all combined predatory groups than did the other treatments (total predators $F_{3,24} = 21.76$, $P < 0.001$; predatory Carabidae $F_{3,24} = 27.09$, $P < 0.001$; predatory Staphylinidae $F_{3,24} = 7.86$, $P < 0.001$; Araneae $F_{3,24} = 10.86$, $P < 0.001$). On ridge 2, H. lanatus supported higher densities of predators than did the other three treatments (total predators $F_{3,48} = 14.95$, $P < 0.001$; predatory Carabidae $F_{3,48} = 12.15$, $P < 0.001$; predatory Staphylinidae $F_{3,48} = 7.46$, $P < 0.001$; Araneae $F_{3,48} = 4.91$, $P < 0.01$).

Winter 1989/90

The densities of the combined predatory groups obtained by destructive sampling from all three ridges are presented in Table 2.3. Although predator densities were reduced slightly in some treatments compared to the previous year (most markedly in the Carabidae on ridge 1), ridges 1 & 2 showed significant between-treatment differences for each of the predatory groups except for the predatory Staphylinidae on ridge 1, and the predatory Staphylinidae and total predators on ridge 2 (ridge 1: total predators $F_{3,72} = 5.35$, $P < 0.01$; Carabidae $F_{3,72} = 18.53$, $P < 0.001$; predatory Staphylinidae $F_{3,72} = 1.89$, $P = 0.14$; Araneae $F_{3,72} = 6.85$, $P < 0.001$; and ridge 2 total predators $F_{3,72} = 1.82$, $P = 0.15$; Carabidae $F_{3,72} = 10.25$, $P < 0.001$; predatory Staphylinidae $F_{3,72} = 0.73$, $P = 0.54$; Araneae $F_{3,72} = 2.93$, $P < 0.05$).

On ridge 3, significant between treatment differences were observed for the total predators ($F_{3,80} = 4.95$, $P < 0.01$), Carabidae ($F_{3,80} = 5.99$, $P < 0.001$) and the predatory Staphylinidae ($F_{3,80} = 5.16$, $P < 0.01$). No significant between-treatment differences were observed for the Areanae ($F_{3,80} = 1.16$, $P = 0.33$).

On all three ridges, treatments sown with the tussock- forming grass D. glomerata appeared to support the highest denisties of Carabidae. For the predatory Staphylinidae, densities were high on all three ridges during the final winter, and H. lanatus, although not always significant, appeared to provide one of the most suitable overwintering habitats. No individual grass treatment however, consistently supported highest densities of Araneae.

Predator species composition

The most abundant predatory Carabidae and Staphylinidae were identified to genus or species level. As this project was originally designed to manipulate overwintering habitats for predatory Coleoptera (the families studied in detail by Sotherton (1984, 1985)), the Araneae were identified only to family level.

Although all treatments were sampled on ridges 1 & 2 in winter 1987/88, data for only the four single-grass species treatments are presented; these were the only treatments sampled in all winters.

Densities of the most common species of predator overwintering in the four single-grass species treatments on the within-field ridges 1 & 2 during the first three winters following establishment are given in Tables 2.4 - 2.6. Data for the final winter on ridge 3 are presented in Table 2.7. Randomised block analysis of variance (log (n+1) transformation) followed by Tukey's test was carried out for each ridge to identify any between-treatment differences. Only the most abundant predator species are tabulated and so the totals of the various predatory groups (Tables 2.1 - 2.3) may exceed the sum of the individual species listed in the Tables 2.4 - 2.7. Furthermore, some species may not be represented consistently due to between-year and between-site variation in community structure.

Carabidae

The same species dominated the whole predator group on ridges 1 & 2 for all years of the study. The species found on the second farm on ridge 3 during the final year were similar to those on the principal study farm. *Bembidion lampros* (Herbst.), *Bembidion obtusum* (Serville), *Demetrias atricapillus* (L.) and *Trechus quadristriatus* (Shrank) were common to all sites in all years. *Notiophilus bigutattus* (F.) was present on ridges 1 & 2 during the 1987/88 winter but was virtually absent in the following years. Conversely, species of the genus *Amara* were not present until the second winter (1988/89) of the study and even by the third winter were not abundant enough to allow analysis at the single species level. *Agonum dorsale* (Pont.), with the exception of ridge 2 during 1988/89, was encountered infrequently. *Demetrias atricapillus* reached peak densities on ridge 1 during the second winter and dominated the total Carabidae catch in the *Dactylis glomerata* and *Holcus lanatus* treatments (overall *D. atricapillus* accounted for 77.9% of the total predatory carabid beetles caught on ridge 1 and 47.8% on ridge 2 at this time). Significant between-treatment differences for individual carabid species were more apparent during the second and third winters than in the first. Furthermore, total carabid densities in the most favourable treatments on ridges 1 & 2 were comparable with the overall carabid densities from the natural field boundaries surrounding the adjacent fields at the end of the study (Table 2.6).

Staphylinidae

As with the Carabidae, a small number of species dominated the predatory Staphylinidae for all three winters. Tachyporus hypnorum (Fabricius) was the most abundant single species for all years of the study; this was most pronounced on ridges 1 & 2 during 1988/89 (accounting for 49.2% and 56.0% of the total predatory staphylinids, respectively) and 1989/90 (accounting for 45.9% and 39.7% respectively) winters. Similarly, T. hypnorum dominated the predatory Staphylinidae on ridge 3 during 1989/90 (48.4% of the total). Holcus lanatus appeared to support the highest densities of T. hypnorum at all three sites during the 1989/90 winter, although this was not always statistically significant. Other species of the genus Tachyporus were Tachyporus chrysomelinus (L.), Tachyporus obtusus (L.) with some Tachyporus nitidulus (Fabricius). Species of the genus Stenus were found on all ridges in relatively low numbers with the exception of ridge 1 in 1988/89, where densities in plots sown with H. lanatus and D. glomerata exceeded $200m^{-2}$. As for the Carabidae, total predatory staphylinid densities on ridges 1 & 2 were comparable with the overall densities in the natural boundaries of the adjacent fields (Table 2.6).

Araneae

The Araneae were dominated by the families Linyphiidae and Lycosidae. Agrostis stolonifera tended to support the lowest densities of Lycosidae on ridges 1 & 2 throughout the study and on ridge 3 during winter 1989/90, although these differences were not always significant. There were no consistent distribution patterns for the Linyphiidae throughout the study, although some significant between-treatment differences did exist (Tables 2.4-2.6). During the 1989/90 winter, Araneae densities on ridges 1 & 2 were comparable with those observed in the adjacent field boundaries (Table 2.6).

Changes in predator community structure

As data for ridge 3 were not available until the final study year, details of community structure are presented in full for ridges 1 & 2 only.

Carabidae

The Carabidae were divided into "boundary" carabids (those species that were largely dependent on boundary habitats as overwintering refuge sites e.g. Agonum dorsale, Bembidion lampros, Demetrias atricapillus and certain Amara spp. (Sotherton 1984, 1985)) and "open-field" carabids (i.e. those species that had regular patterns of dispersion in agricultural land and were present at the field centres even during the winter period e.g. Bembidion obtusum, Notiophilus bigutattus and Trechus quadristriatus (Sotherton 1984,1985)). The proportion of boundary and open-field carabids in the different treatments over the three winters on ridge 1, together with the average proportion of boundary and open-field carabids from the four natural boundaries surrounding field 1 sampled during the 1989/90 winter, are presented in Fig. 2.1. The carabid population was dominated by open-field species during the first winter, with few boundary carabid species at this time. In the second and third winters, there was a significant increase in the proportions of boundary carabids in the four treatments (two-way analysis of variance on the mean proportion of boundary carabids (√arcsine transformation) for each treatment between blocks and years, followed by Tukey's test). The highest proportions tended to occur in winter 1988/89, although proportions in winter 1989/90 were significantly higher than those of winter 1987/88 (A. stolonifera $F_{2,10} = 16.3$, $P < 0.001$; D. glomerata $F_{2,10} = 28.2$, $P < 0.001$; H. lanatus $F_{2,10} = 25.9$, $P < 0.001$; L. perenne $F_{2,10} = 6.1$, $P < 0.05$). Comparison of proportions of "boundary" carabids (√arcsine transformation) in the ridge treatments (mean per block) and in the natural boundaries (mean per boundary) surrounding field 1 showed there was no significant difference between the ridge treatment and the natural boundary communities taken as a whole, during winter 1989/90 ($F_{4,23} = 1.6$, $P = 0.21$).

The proportion of boundary and open-field carabids over the three winters on ridge 2, together with the average proportion of boundary and open-field carabids in the natural boundaries of field 2 during winter 1989/90, are presented in Fig. 2.2. As for ridge 1, the ridge 2 carabid population was dominated by open-field species during the first winter. In the following winter, there was a significant increase in the proportion of boundary carabids. In the final winter, proportions of boundary carabids were at their highest in all treatments except for L. perenne, which did not differ significantly between second and third winters (A. stolonifera $F_{2,10} = 33.3$, $P < 0.001$; D. glomerata $F_{2,10} = 25.9$, $P < 0.001$; H. lanatus $F_{2,10} = 71.9$, $P < 0.001$; L. perenne $F_{2,10} = 21.6$, $P < 0.001$). Comparison between proportions of boundary carabids in the ridge treatments and proportions in the natural boundaries surrounding field 2, showed there was no significant difference between the ridge treatment and the existing boundary communities during the final winter ($F_{4,23} = 0.8$, $P = 0.49$).

Temporal changes in the proportion of lycosid spiders out of the Linyphiidae + Lycosidae total, in the various treatments on ridges 1 & 2 are presented in Figs. 2.3 & 2.4 respectively. Two-way analysis of variance revealed a significant increase through time in the proportion (√arcsine transformation) of Lycosidae in the four treatments on both ridges (ridge 1 : A. stolonifera $F_{2,10} = 18.9$, $P < 0.001$; D. glomerata $F_{2,10} = 23.0$, $P < 0.001$; H. lanatus $F_{2,10} = 17.1$, $P < 0.001$; L. perenne $F_{2,10} = 24.7$, $P < 0.001$. Ridge 2 : A. stolonifera $F_{2,10} = 4.5$, $P < 0.05$; D. glomerata $F_{2,10} = 36.6$, $P < 0.001$; H. lanatus $F_{2,10} = 58.2$, $P < 0.001$; L. perenne $F_{2,10} = 12.5$, $P < 0.001$).

There was no significant difference between the ridge treatment and natural boundary lycosid proportions in field system 1 or 2 by the end of the study ($F_{4,23} = 1.6$, $P = 0.21$ and $F_{4,23} = 0.9$, $P = 0.47$ respectively).

Table 2.1. Mean densities (m^{-2}) of groups of polyphagous predators sampled by surface-searching, winter 1987/88 (year 1) and 1988/89 (year 2). Treatments within a year with the same letter do not differ significantly at the 5% level (randomised block analysis of variance followed by Tukey's (1949) test).

		No. predators (m^{-2})							
Treatment	Year	Carabidae		Staphylinidae		Araneae		Total predators	
Ridge 1									
A. stolonifera	1	29.1	(a)	0.4	(b)	9.2	(c)	38.7	(b)
D. glomerata	1	38.3	(a)	3.5	(b)	24.6	(b)	66.4	(a)
H. lanatus	1	34.6	(a)	7.1	(a)	46.7	(ab)	88.4	(a)
L. perenne	1	42.1	(a)	10.8	(a)	48.8	(a)	101.7	(a)
3 species	1	45.0	(a)	5.4	(ab)	25.0	(b)	75.4	(a)
4 species	1	41.7	(a)	4.2	(ab)	25.4	(b)	71.3	(a)
Bare ground	1	23.8	(a)	0.4	(b)	5.8	(c)	30.0	(b)
Field 1	1	21.4		3.8		8.3		33.5	
A. stolonifera	2	70.8	(a)	7.9	(cd)	45.4	(bc)	124.1	(b)
D. glomerata	2	60.8	(a)	24.2	(ab)	65.8	(abc)	150.8	(ab)
H. lanatus	2	47.9	(a)	19.2	(abc)	71.7	(ab)	138.8	(ab)
L. perenne	2	37.1	(a)	12.1	(bc)	48.3	(abc)	97.5	(b)
3 species	2	60.0	(a)	36.7	(a)	91.7	(a)	188.4	(a)
4 species	2	49.6	(a)	14.2	(abc)	39.2	(c)	103.0	(b)
Bare ground	2	2.4	(b)	0.4	(d)	2.5	(d)	5.3	(c)
Field 1	2	11.0		0.0		5.1		16.1	
Ridge 2									
A. stolonifera	1	70.0	(a)	14.1	(b)	37.6	(a)	121.7	(a)
D. glomerata	1	70.6	(a)	22.5	(a)	57.1	(a)	150.2	(a)
H. lanatus	1	56.7	(ab)	27.2	(a)	72.2	(a)	156.1	(a)
L. perenne	1	53.3	(ab)	23.3	(a)	45.0	(a)	121.6	(a)
3 species	1	52.8	(ab)	22.2	(a)	43.9	(a)	118.9	(a)
4 species	1	50.6	(ab)	27.3	(a)	57.3	(a)	135.2	(a)
Bare ground	1	24.4	(b)	0.0	(c)	5.0	(b)	29.4	(b)
Field 2	1	38.9		2.5		7.1		48.5	

Table 2.2. Mean densities (m^{-2}) of groups of polyphagous predators obtained by destructive sampling from ridges 1 & 2, winter 1988/89. See Table 2.1.

	No. predators (m^{-2})			
Treatment	Total Carabidae	Total Staphylinidae	Total Araneae	Total predators
Ridge 1				
A. stolonifera	157.5 (b)	160.3 (ab)	170.0 (bc)	487.8 (b)
D. glomerata	1112.5 (a)	152.5 (b)	222.5 (ab)	1487.5 (a)
H. lanatus	765.0 (a)	272.4 (a)	360.3 (a)	1397.7 (a)
L. perenne	107.4 (b)	50.6 (b)	117.7 (c)	275.7 (b)
Field 1	10.0	3.1	10.0	25.6
Ridge 2				
A. stolonifera	111.0 (bc)	88.8 (b)	73.5 (ab)	273.3 (bc)
D. glomerata	97.0 (c)	69.3 (b)	51.3 (b)	217.6 (c)
H. lanatus	301.3 (a)	206.8 (a)	140.3 (a)	648.4 (a)
L. perenne	200.0 (ab)	98.5 (b)	95.7 (ab)	394.2 (ab)
Field 2	18.0	4.0	6.7	28.7

Table 2.3. Mean densities (m^{-2}) of groups of polyphagous predators obtained by destructive sampling from ridges 1, 2 & 3, together with field boundaries surrounding fields 1 & 2, winter 1989/90. See Table 2.1.

	No. predators (m^{-2})			
Treatment	Total Carabidae	Total Staphylinidae	Total Araneae	Total predators
Ridge 1				
A. stolonifera	58.3 (b)	293.8 (a)	152.1 (ab)	504.2 (ab)
D. glomerata	220.1 (a)	297.9 (a)	263.6 (a)	763.6 (a)
H. lanatus	57.3 (bc)	357.3 (a)	158.3 (ab)	572.9 (a)
L. perenne	30.2 (c)	219.8 (a)	108.3 (b)	358.3 (b)
Field 1	7.5	4.2	8.0	19.7
Existing boundaries	221.9	200.6	118.8	541.3
Ridge 2				
A. stolonifera	151.2 (ab)	179.2 (a)	81.3 (b)	411.5 (a)
D. glomerata	241.3 (a)	181.5 (a)	130.4 (ab)	553.3 (a)
H. lanatus	85.4 (b)	215.6 (a)	131.3 (ab)	432.3 (a)
L. perenne	98.95 (b)	277.1 (a)	165.6 (a)	541.7 (a)
Field 2	12.0	2.1	6.5	20.6
Existing boundaries	308.1	187.5	73.8	569.4
Ridge 3				
A. stolonifera	16.7 (b)	180.2 (b)	169.8 (a)	397.9 (b)
D. glomerata	69.8 (a)	242.8 (ab)	219.8 (a)	555.2 (ab)
H. lanatus	47.9 (ab)	446.9 (a)	220.8 (a)	756.3 (a)
L. perenne	34.4 (ab)	257.3 (ab)	233.3 (a)	529.2 (ab)
Field 3	6.5	3.8	10.5	20.8

Table 2.4. Mean predator densities (m^{-2}) obtained by surface-searching from the four single grass treatments on ridges 1 & 2, winter 1987/88. Treatments in the same row sharing the same letter do not differ significantly at the 5% level for individual predatory groups (randomised block analysis of variance (log (n+1)) followed by Tukey's test). Absence of letters for particular predator groups indicates that numbers were too low for analysis.

		Number of predators (m^{-2})							
	Predatory group	*Agrostis stolonifera*		*Dactylis glomerata*		*Holcus lanatus*		*Lolium perenne*	
Ridge 1	*Bembidion lampros*	1.3	(a)	1.3	(a)	0.8	(a)	1.3	(a)
	Bembidion obtusum	21.3	(a)	33.3	(a)	24.2	(a)	24.6	(a)
	Demetrias atricapillus	0.4	(a)	4.2	(a)	0.8	(a)	3.3	(a)
	Notiophilus biguttatus	2.1	(a)	1.7	(a)	4.6	(a)	3.3	(a)
	Trechus quadristriatus	0.4	(a)	2.0	(a)	1.7	(a)	2.5	(a)
	Total Carabidae	29.2	(a)	38.3	(a)	34.6	(a)	42.1	(a)
	Stenus spp.	0.0		0.4		0.4		0.0	
	Tachyporus hypnorum	0.4	(b)	2.9	(ab)	6.3	(a)	6.7	(a)
	Other *Tachyporus* spp.	0.0		0.0		0.4	(a)	2.5	(a)
	Total Staphylinidae	0.4	(b)	3.8	(ab)	7.1	(a)	10.8	(a)
	Linyphiidae	9.2	(c)	21.9	(b)	42.0	(ab)	47.5	(a)
	Lycosidae	0.0		1.7	(ab)	3.8	(a)	1.3	(ab)
	Total Araneae	9.2	(c)	24.6	(b)	46.7	(ab)	48.8	(a)
	Total predators	38.8	(b)	66.7	(a)	88.3	(a)	101.2	(a)
Ridge 2	*Bembidion lampros*	0.8	(b)	5.4	(a)	0.8	(b)	0.8	(b)
	Bembidion obtusum	51.6	(a)	44.2	(ab)	32.1	(ab)	24.6	(b)
	Demetrias atricapillus	0.8	(b)	15.0	(a)	15.0	(a)	8.3	(a)
	Notiophilus biguttatus	14.6	(a)	7.9	(a)	10.0	(a)	9.2	(a)
	Trechus quadristriatus	1.7	(a)	3.3	(a)	4.6	(a)	0.8	(a)
	Total Carabidae	70.8	(a)	60.8	(a)	47.9	(a)	37.1	(a)
	Stenus spp.	2.5	(a)	6.7	(a)	6.7	(a)	2.1	(a)
	Tachyporus hypnorum	3.8	(a)	9.2	(a)	7.0	(a)	2.9	(a)
	Other *Tachyporus* spp.	1.7	(a)	4.2	(a)	1.3	(a)	0.0	
	Total Staphylinidae	7.9	(b)	24.2	(a)	19.2	(ab)	12.1	(ab)
	Linyphiidae	45.4	(a)	61.1	(a)	67.9	(a)	48.3	(a)
	Lycosidae	0.0		3.8	(a)	2.9	(a)	0.0	
	Total Araneae	45.4	(a)	65.8	(a)	71.7	(a)	48.3	(a)
	Total predators	124.2	(a)	150.1	(a)	138.8	(a)	97.5	(a)

Table 2.5. Mean predator densities (m^{-2}) obtained by destructive sampling from the four single grass species treatments on ridges 1 & 2, winter 1988/89. See Table 2.4.

		Number of predators (m^{-2})							
	Predatory group	*Agrostis stolonifera*		*Dactylis glomerata*		*Holcus lanatus*		*Lolium perenne*	
Ridge 1	*Amara* spp.	6.3	(a)	2.1	(a)	2.1	(a)	2.1	(a)
	Bembidion lampros	45.8	(a)	35.4	(ab)	18.8	(ab)	8.3	(b)
	Bembidion obtusum	68.8	(a)	116.7	(a)	62.5	(a)	20.8	(a)
	Demetrias atricapillus	8.3	(c)	922.9	(a)	662.5	(a)	64.6	(b)
	Trechus quadristriatus	22.9	(a)	27.1	(a)	14.6	(a)	18.8	(a)
	Total Carabidae	154.2	(b)	1104.2	(a)	760.4	(a)	114.6	(b)
	Stenus spp.	0.0		214.6	(a)	247.9	(a)	131.3	(a)
	Tachyporus hypnorum	129.2	(a)	120.8	(a)	227.1	(a)	33.3	(b)
	Other *Tachyporus* spp.	31.3	(a)	31.3	(a)	45.8	(a)	16.7	(a)
	Total Staphylinidae	160.4	(b)	366.7	(ab)	520.8	(a)	181.3	(b)
	Linyphiidae	164.1	(bc)	210.4	(ab)	340.6	(a)	97.9	(c)
	Lycosidae	6.3	(a)	12.5	(a)	18.8	(a)	18.8	(a)
	Total Araneae	170.8	(bc)	222.9	(ab)	360.4	(a)	116.8	(c)
	Total predators	485.4	(b)	1693.8	(a)	1641.7	(a)	412.5	(b)
Ridge 2	*Agonum dorsale*	22.2	(a)	6.9	(a)	34.7	(a)	27.8	(a)
	Amara spp.	1.4	(a)	2.8	(a)	4.2	(a)	0.0	
	Bembidion lampros	0.0		9.7	(a)	1.4	(b)	0.0	
	Bembidion obtusum	6.9	(a)	1.4	(a)	5.6	(a)	11.1	(a)
	Demetrias atricapillus	29.2	(c)	36.1	(bc)	177.8	(a)	83.3	(ab)
	Trechus quadristriatus	38.8	(a)	27.8	(a)	38.9	(a)	47.2	(a)
	Total Carabidae	111.0	(bc)	97.2	(c)	301.4	(a)	200.0	(ab)
	Stenus spp.	2.8	(a)	12.5	(a)	11.1	(a)	15.2	(a)
	Tachyporus hypnorum	51.4	(a)	47.2	(a)	97.2	(a)	47.2	(a)
	Other *Tachyporus* spp.	13.9	(bc)	1.4	(c)	75.0	(a)	25.0	(ab)
	Total Staphylinidae	88.8	(b)	69.3	(b)	206.8	(a)	98.5	(b)
	Linyphiidae	62.5	(ab)	45.8	(b)	113.9	(a)	83.3	(ab)
	Lycosidae	8.2	(a)	6.9	(b)	19.5	(b)	31.9	(ab)
	Total Araneae	73.5	(ab)	51.3	(b)	140.3	(a)	95.7	(ab)
	Total predators	273.5	(bc)	217.5	(c)	648.3	(a)	394.2	(b)

Table 2.6. Mean predator densities (m^{-2}) obtained by destructive sampling from ridges 1 & 2 and field boundaries surrounding fields 1 & 2, winter 1989/90. Letters are absent from the natural boundaries column as these values were not included in the analysis of variance. See Table 2.4.

		Number of predators (m^{-2})				
	Predatory group	*Agrostis stolonifera*	*Dactylis glomerata*	*Holcus lanatus*	*Lolium perenne*	Natural boundaries
Ridge 1 / Field 1	*Amara* spp.	5.2 (a)	0.0	3.1 (a)	4.2 (a)	2.5
	Bembidion lampros	9.4 (a)	2.1 (a)	1.1 (a)	2.1 (a)	20.6
	Bembidion obtusum	20.8 (a)	27.1 (a)	22.9 (a)	11.5 (a)	97.5
	Demetrias atricapillus	2.1 (b)	154.2 (a)	17.7 (b)	9.4 (b)	73.1
	Trechus quadristriatus	10.4 (a)	11.5 (a)	5.2 (a)	7.3 (a)	4.4
	Total Carabidae	58.3 (b)	220.1 (a)	57.3 (bc)	30.2 (c)	221.9
	Stenus spp.	17.7 (a)	37.5 (a)	19.8 (a)	17.7 (a)	26.3
	Tachyporus hypnorum	158.5 (b)	153.1 (a)	168.8 (a)	57.3 (b)	133.1
	Other *Tachyporus* spp.	120.8 (a)	99.0 (a)	161.5 (a)	141.7 (a)	35.6
	Total Staphylinidae	293.8 (a)	297.9 (a)	357.3 (a)	219.8 (a)	200.6
	Linyphiidae	115.6 (ab)	141.8 (a)	79.2 (ab)	69.8 (b)	53.1
	Lycosidae	36.5 (b)	117.8 (a)	78.0 (ab)	39.6 (b)	62.8
	Total Araneae	152.1 (ab)	263.6 (a)	158.3 (ab)	108.3 (b)	118.8
	Total predators	504.2 (ab)	763.6 (a)	572.9 (a)	358.3 (b)	541.3
Ridge 2 / Field 2	*Amara* spp.	5.2 (a)	2.2 (a)	7.3 (a)	1.1 (a)	1.9
	Bembidion lampros	120.8 (a)	121.7 (a)	61.5 (b)	84.4 (ab)	246.9
	Bembidion obtusum	18.8 (ab)	53.3 (a)	4.2 (b)	6.3 (ab)	30.6
	Demetrias atricapillus	2.1 (b)	61.9 (a)	7.3 (b)	7.3 (b)	13.1
	Trechus quadristriatus	0.0	1.1	0.0	0.0	0.6
	Total Carabidae	151.2 (ab)	241.3 (a)	85.4 (b)	98.9 (b)	308.1
	Stenus spp.	0.0	8.7 (a)	0.0	9.4 (a)	1.9
	Tachyporus hypnorum	92.7 (a)	69.6 (a)	106.3 (a)	69.8 (a)	130.0
	Other *Tachyporus* spp.	82.3 (a)	98.9 (a)	102.1 (a)	194.8 (a)	40.6
	Total Staphylinidae	179.2 (a)	181.5 (a)	215.6 (a)	277.1 (a)	187.5
	Linyphiidae	48.9 (a)	64.1 (a)	66.7 (a)	90.0 (a)	31.0
	Lycosidae	30.3 (a)	64.1 (a)	62.1 (a)	70.9 (a)	41.5
	Total Araneae	81.3 (b)	130.4 (ab)	131.3 (ab)	165.6 (a)	73.8
	Total predators	411.5 (a)	553.3 (a)	432.3 (a)	541.7 (a)	569.4

Table 2.7. Mean predator densities (m^{-2}) obtained by destructive sampling from ridge 3, winter 1989/90. See Table 2.4.

		Number of predators (m^{-2})							
	Predatory group	*Agrostis stolonifera*		*Dactylis glomerata*		*Holcus lanatus*		*Lolium perenne*	
Ridge 3	*Amara* spp.	3.1	(a)	9.4	(a)	2.1	(a)	1.0	(a)
	Bembidion lampros	1.0	(b)	13.5	(a)	15.6	(a)	9.4	(a)
	Bembidion obtusum	4.2	(a)	13.5	(a)	3.1	(a)	8.3	(a)
	Demetrias atricapillus	0.0		12.5	(a)	2.1	(a)	2.0	(a)
	Trechus quadristriatus	8.3	(a)	13.6	(a)	19.2	(a)	7.3	(a)
	Total Carabidae	16.7	(b)	69.8	(a)	47.9	(ab)	34.4	(ab)
	Stenus spp.	2.1	(a)	6.3	(a)	9.4	(a)	5.2	(a)
	Tachyporus hypnorum	102.1	(a)	111.5	(a)	220.8	(a)	112.5	(a)
	Other *Tachyporus* spp.	68.8	(b)	112.5	(a)	211.5	(a)	135.4	(ab)
	Total Staphylinidae	180.2	(b)	242.8	(a)	446.9	(ab)	257.3	(a)
	Linyphiidae	140.7	(a)	176.1	(a)	173.5	(a)	165.7	(a)
	Lycosidae	27.1	(b)	41.7	(ab)	44.8	(a)	66.2	(a)
	Total Araneae	169.8	(a)	219.8	(a)	220.8	(a)	233.3	(a)
	Total predators	397.9	(b)	555.2	(ab)	756.3	(a)	529.2	(ab)

Figure 2.1. Mean proportions of "boundary" and "open-field" carabids overwintering on within-field ridge 1 during 1987/88, 1988/89, 1989/90 winters. Different letters indicate significant between-year differences in the proportion of "boundary" carabids within individual treatments at the 5% level (two-way analysis of variance (√arcsine transformation), followed by Tukey's test). As = Agrostis stolonifera; Dg = Dactylis glomerata; Hl = Holcus lanatus; Lp = Lolium perenne; NB = Natural boundaries (sampled during winter 1989/90); ▨ "boundary" carabids; ☐ "open-field" carabids.

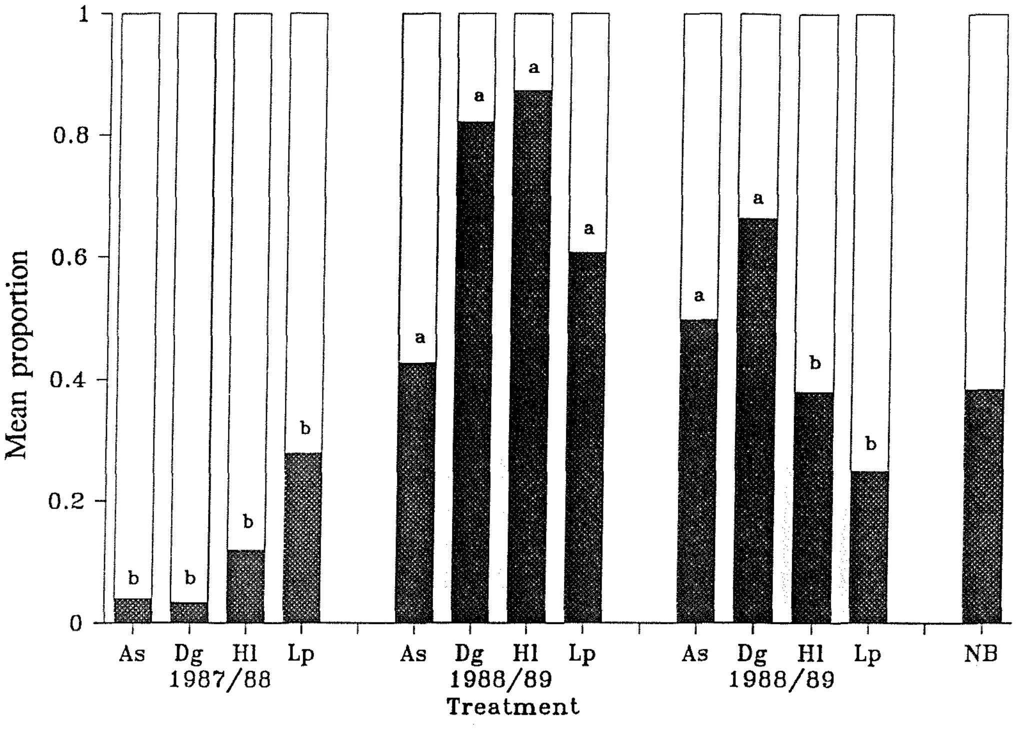


Figure 2.2. Mean proportion of "boundary" and "open-field" carabids overwintering on within-field ridge 2 during 1987/88, 1988/89, 1989/90 winters. See Fig.2.1.

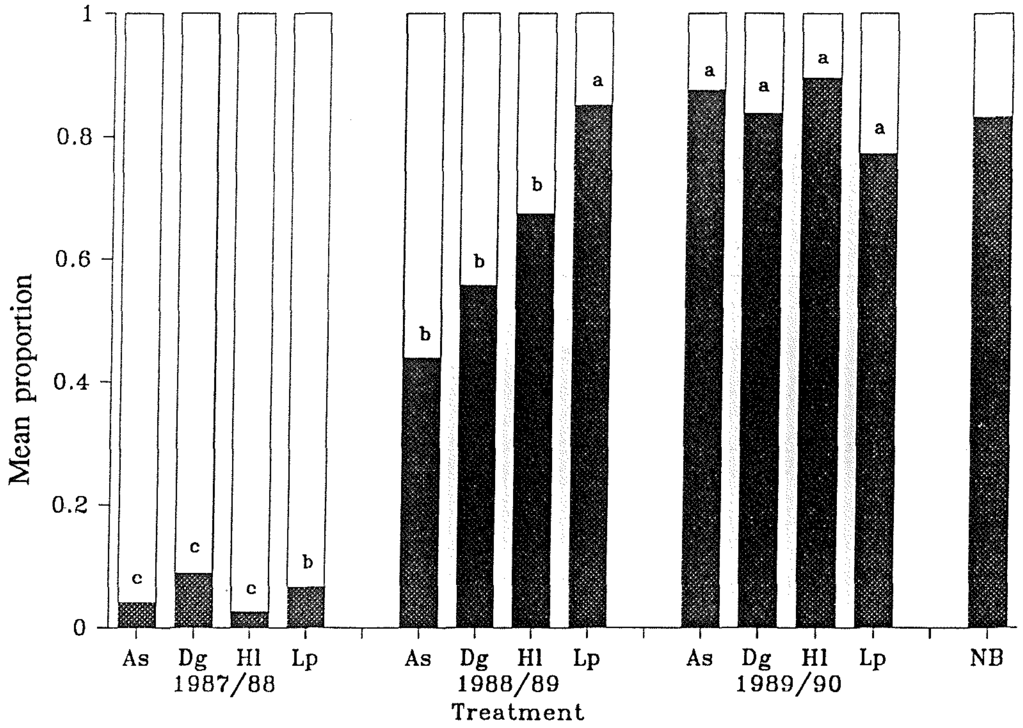


Figure 2.3. Lycosid (▨) and linyphiid (☐) spiders, expressed as a mean proportion of the lycosid+linyphiid total, overwintering on within-field ridge 1 during 1987/88, 1988/89, 1989/90 winters. See Fig.2.1.

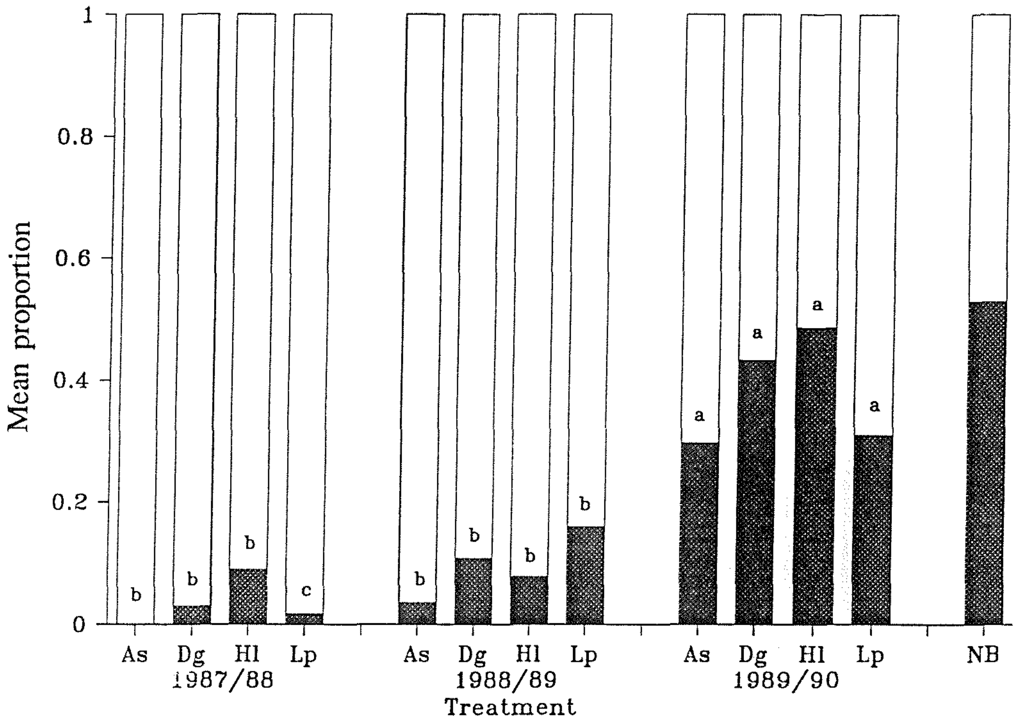
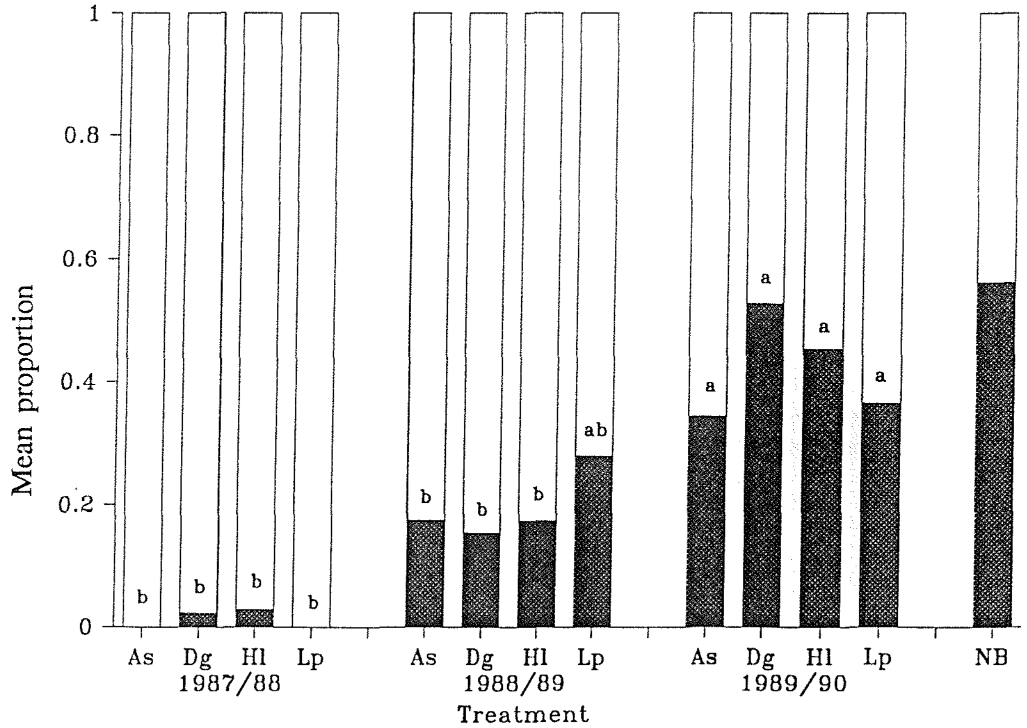


Figure 2.4. Lycosid (▨) and linyphiid (☐) spiders, expressed as a mean proportion of the lycosid+linyphiid total, overwintering on within-field ridge 2 during 1987/88, 1988/89, 1989/90 winters. See Fig.2.1.



2.4 DISCUSSION

Predator densities

The overwintering predator densities achieved during the first year of ridge establishment were not atypical of those found in other field boundary types in Hampshire (Sotherton 1985). Although relatively poor grass establishment and maturity allowed thorough examination of the different grass ridge treatments (i.e. surface-searching was considered to provide a good estimate of predator densities at this time), there were no consistent significant differences between treatments.

Surface searching during the second winter was hindered by the high percentage grass cover and areas of dense tussocky vegetation. It was perhaps not surprising therefore that no significant differences occurred in predator densities between grass treatments when this sampling method was used. Destructive sampling, however, revealed that D. glomerata and H. lanatus for ridge 1, and H. lanatus and L. perenne for ridge 2, produced very high predator densities and appeared to provide the most suitable overwintering habitats for all of the predatory groups during the second winter. The between-ridge treatment differences were primarily due to the very high densities of Demetrias atricapillus on ridge 1 compared with ridge 2. This species appeared to aggregate in the tussock forming grasses and thus, due to its high abundance, led to Dactylis glomerata being the most favourable treatment on ridge 1. The lower Demetrias atricapillus densities on ridge 2, in contrast, reduced the carabid and hence total predator densities, most markedly in the Dactylis glomerata treatments, creating the observed between-ridge differences.

Similar between-treatment distribution patterns to those of the 1988/89 winter were observed in the following winter on ridges 1 & 2. The between-ridge treatment differences were less marked however, due to a decline in Demetrias atricapillus numbers in the third winter. Overall therefore, apart from the influence of Demetrias atricapillus densities, there were no large differences in the predator densities between ridges 1 & 2 during the three winters of the study. Destructive sampling showed that predator densities in certain treatments exceeded those recorded in the most favourable existing boundaries. Densities of $1000 m^{-2}$ in existing field boundaries were considered to be very high by Sotherton (1985), yet in only the second year of this study, densities in D. glomerata on ridge 1 reached over $1500 m^{-2}$. Although numbers were reduced slightly in the third winter, the overall predator densities on both ridges were still very high, and compared favourably with predator densities in the existing boundaries of the adjacent fields.

The between-treatment predator distribution patterns observed on ridge 3, also suggested H. lanatus, together with D. glomerata and L. perenne, to provide the most suitable overwintering habitats. However, although the total predator densities on ridge 3 were quite high, the overall carabid densities were very low at this site. Lack of data from the previous winters, or from natural boundaries at this site during the final winter, precluded any thorough explanation. As there were no structural or vegetational reasons why this ridge should be less suitable as an overwintering habitat than the other two ridges, it is likely that an impoverished carabid fauna (possibly resulting from a more severe recent insecticide regime) coupled with the larger field, were responsible for reducing the overwintering carabid densities at this site.

Succession of predator communities

Carabidae

The insect communities in the grass treatments with the highest densities of carabids during the study were dominated by boundary species by the final winter of the study i.e. those species that in the absence of the ridges, would not be present at the field centres at this time.

On ridge 2, the high proportion of boundary carabids in the third study year occurred after clear successional changes over the course of the study. On ridge 1 however, the highest proportions occurred in the second year. This was the result of peak D. atricapillus densities inflating the proportion of boundary carabids at this time. In the third year when this species was far less abundant (reduced densities in all treatments, plus low densities in the natural boundaries), the proportion of boundary carabids fell accordingly, but were equivalent to the proportions found in the adjacent field boundaries at this site. In other words, rather than losing their capacity as overwintering habitats, which would account for the fall in carabid densities that took place between second and third winters, the ridges in fact represented refuge sites at least as suitable as the existing natural habitats for boundary overwintering carabids.

These results support the findings of Mader (1988) who during a five year study, observed that the number and percentage of open-field species of carabid declined in favour of forest species as vegetation cover increased within a newly created woodlot plantation.

Araneae

Succession also occurred within the spider community. The low proportion of Lycosidae during the 1987/88 winter led to the Linyphiidae dominating on ridges 1 & 2 in the first year. Following this, the proportion increased until the final year, where the proportion of lycosids on both ridges did not differ significantly from the proportions in the natural boundaries bordering the respective adjacent fields. These results are similar to those reported in other studies on spider succession (Huhta 1971; Nentwig 1988). High powers of aerial dispersal among the Linyphiidae (Duffey 1956; Plagens 1986), allow rapid colonisation and succession (Nentwig 1988). The change in the ratio of Lycosidae:Linyphiidae therefore, probably reflected succession from pioneer species (r-strategists i.e. Linyphiidae) towards more permanent and specialised species (K-strategists i.e. Lycosidae) (Nentwig 1988).

Staphylinidae

Parameters that reflect community structure are more valuable as indicators of ecological change than abundance of individual species (Cairns 1974). With only a few species all sharing similar overwintering strategies therefore (unlike the Carabidae and Areaneae which could be dividied into sub-groups), detailed conclusions regarding successional change of the predatory Staphylinidae in this study are rather limited. All ridges supported fairly high densities in the final year of the study and there was evidence suggesting Holcus lanatus to be the most favourable treatment for certain species at least. Furthermore, densities on the within-field ridges were similar to those found in the natural boundaries bordering fields 1 & 2.

Conclusion

In the third winter after establishment, all ridges supported similar high total densities of polyphagous predators. However, although the role of Linyphiidae in aphid biocontrol has been highlighted (Sunderland et al. 1987), little is known about their dispersal dynamics or overwintering strategies. If, as is suggested, large populations remain within the open field or occupy areas of pasture (G. Thomas pers. comm.) and other uncultivated biotopes (Nyffeler & Benz 1982) over the winter period, the maintenance of a relatively small population (although high density) at the field centre may not be of great importance because high powers of aerial dispersal would allow rapid field recolonisation from other sources. Similarly, although the predatory role of spiders has been demonstrated in crops such as grain sorghums (Bailey & Chada 1968), alfalfa (Wheeler 1973) and rice

(Kiritani 1979), the predatory role of Lycosidae in cereals has still to be fully quantified. Furthermore, if only limited interaction with the open field takes place, there may be little benefit in supporting a high population density at the field centre. From a pest management perspective therefore, manipulation of the predatory Coleoptera may be of greatest value.

The successional changes which were observed as the ridge habitats matured indicated a shift away from initial dominance of open-field to that of boundary overwintering species of Carabidae and from pioneer r-selected species towards more permanent specialist K-selected species in the Araneae. Mader (1988) and Nentwig (1988) considered this small change within the r-K-continuum, provided by increased spatial heterogeneity, to be sufficient to provide an increase in stability of the agro-ecosystem as a whole. As conventional arable systems tend to provide fragmented and unstable environments (Wratten & Thomas 1990), such habitat creation schemes could provide a useful measure to strengthen natural control mechanisms disrupted by intensive farming methods (Mader 1988). Similarly, studies by Stern (1969) and more recently by Von Klinger (1987), Nentwig (1988, 1989), Mader (1988) and Wratten & Thomas (1990), all showed that manipulation of crop edges represented a possible management tool towards the goal of integrated methods for biocontrol in cereals and other crops. It is possible therefore, that such cultural techniques could help farmers decrease applications of pesticide, thus contributing to IPM systems whose long-term benefits might outweigh some of the shorter-term economic and environmental costs of present-day pest control methods (Coaker 1987).

CHAPTER 3. ASSESSMENT OF PREDATOR PENETRATION OF THE CROP IN THE SPRING

SUMMARY

(1) A variety of approaches were used to assess whether populations of predators from newly created overwintering habitats could influence penetration of the crop in the spring.

(2) The use of predation pressure (monitored using artificial prey) as in indicator of temporal and spatial changes in predator numbers was largely inconclusive.

(3) Methods which involved predator sampling however, showed that the overwintering predator populations in the new habitats could influence subsequent dispersal patterns in the spring, providing an even spread of predators throughout the crop early in the season.

3.1 INTRODUCTION

The results of Chapter 2 showed the possibility of manipulating the arable environment to maintain a "boundary" overwintering predator population at the field centre during the winter period. From a pest management perspective however, it is necessary that such populations influence subsequent predator dispersal patterns in the spring; a high density nucleus of predators at the field centre is of little benefit if invasion of the crop does not take place.

Coombes and Sotherton (1986) identified two types of dispersal pattern for predators leaving overwintering habitats and invading cereal fields in the spring. For predators with high mobility such as certain species of staphylinid beetle (e.g. Tachyporus spp. (thought to disperse by flight)), invasion of the crop was almost instantaneous with numbers rising simultaneously at all distances from the field boundary. Carabid beetles such as Bembidion lampros and Demetrias atricapillus however dispersed more slowly by walking and showed a "wave" of movement into the fields as the season progressed. Studies were carried out therefore to investigate whether any similar dispersal patterns could be observed by predators invading the crop from the within-field overwintering habitats. The previous studies of Coombes & Sotherton (1986) concentrated on predator emigration in the cereal ecosystem and as a result, little is known about dispersal patterns in crops such as peas or winter rape. For this reason, emigration was studied from within-field ridge 1, the only ridge to be in cereals for all the three years of the study.

3.2 MATERIALS AND METHODS

Predation pressure

To assess whether the within-field ridges and their predator populations influenced spring penetration, predation rates on artificial prey were monitored from April to late May 1988 and 1989. It was thought that this would give an index of predation pressure temporally and spatially linked to predator density, providing an indirect method of monitoring spatial patterns through time.

Small dishes (5cm diameter) of soil were inserted to soil surface level on ridge 1 and in its adjacent field. In 1988 each dish contained twenty freeze-killed pea aphids (Acyrthosiphon pisum Harris, third-fourth instar) and in 1989 twenty-five Drosophila melanogaster, Meigen pupae. Lids placed above each dish provided protection against rainfall.

In 1988, dishes of prey were placed in seven transects (one for each treatment type selected at random along the length of the ridge) running at right angles to the ridge at distances of 0m (on the ridge itself), 1m, 5m, and 15m into the adjacent field, with one dish at each distance. In 1989, dishes were placed in two grass treatments only (D. glomerata and H. lanatus, these treatments having the highest predator densities (Chapter 2)) in each of four blocks. Associated with each of these twelve grassy parts of the bank were transects of dishes progressing into the crop at 3m, 10m, 30m, and 60m from the bank (the 60m position being only 45m from an existing boundary). For both years, the numbers of prey items remaining in each dish after 24h exposure were recorded. Assessments of predation were made over one 24h period per week for seven weeks. Although temperature variation between dates could influence overall predation levels, such changes would be uniform along the transects thus making analyses of within date spatial patterns possible. Furthermore, although no predator marking was carried out, any spatial patterns which occurred at the field centre were assumed to be a result of dispersal of overwintered predators from the within-field ridge.

Predator sampling

Spring 1989

Accompanying the 1989 predation experiment, transects of vacuum-net (Thornhill, 1978) samples, the same as those in the predation experiment (progressing into the crop at 0m, 3m, 10m, 30m, and 60m from ridge 1) were taken at weekly intervals from April to late May 1989. Samples at each distance in an individual transect comprised 15 contiguous $0.1m^2$ sub-samples of 10 seconds' duration each, parallel to the ridge. Samples were taken from five transects running at right angles to the ridge adjacent to the Dactylis glomerata treatments in each of five blocks. No such samples were taken during the 1988 spring, as overwintering predator densities following the first year of ridge establishment were not considered high enough to have a detectable influence on spring dispersal patterns into the crop.

Spring 1990

For the final spring (1990) no artificial prey were used to monitor spatial changes in predation pressure associated with invasion of the crop through time. Instead, ten transects of barrier pitfall traps (Durkis & Reeves 1982) were placed at right angles to ridge 1 at equal intervals (25m) along its length. No particular grass treatments were selected. If however, a transect initially coincided with either a bare earth or "pollen and nectar source" treatment, it was repositioned adjacent to the nearest grass plot.

The barrier pitfall traps consisted of pairs of pitfall traps (diameter 9cm, depth 13cm) filled to 1/3 with water containing detergent. The traps in each pair were 1m apart and joined along one edge by a wooden barrier (1.4m long x 0.1m high) inserted 2-3cm into the soil. Traps were placed in the crop at 1m, 4m, 20m, and 50m from the edge of the ridge. The contents of each pair of pitfalls were pooled so each barrier catch comprised two pitfall catches (Wallin 1985). As the length of the barrier exceeded the distance between pitfalls, the barrier traps could be considered directional; they were therefore positioned facing towards the within-field ridge. Traps were set for one three-day period each week and then emptied at this interval throughout April and May 1990.

Vacuum-net samples were taken once again at weekly intervals from early April to late May. Samples were taken from five transects adjacent to the Dactylis glomerata treatments in each of five blocks. As in the previous spring, samples at each distance in an individual transect comprised 15 contiguous $0.1m^2$ sub-samples of 10 seconds' duration each, parallel to the ridge. Unlike the earlier study however, samples were taken at the same distances into the crop as the barrier pitfall traps (i.e. 1m, 4m, 10m, 20m, 50m).

3.3 RESULTS

Predation pressure

The results of the 1988 predation study are presented in Fig. 3.1. Although there were few significant differences between predation levels on the ridge and those in the transects into the field for particular dates (two-way analysis of variance (√arcsin transformation of proportion of prey removed/dish) against distance and transect per date with 3,18 d.f., followed by Tukey's test), a trend existed such that a peak of predatory activity appeared to move away from the ridge into the field through time.

For the 1989 study some data are missing because of damage caused by small mammals to the prey. No apparent increase in predatory activity appeared to penetrate the crop. Instead, the highest activity consistently occurred on the ridge itself (two-way analysis of variance on transformed data/date, with 4,28 d.f.) (Fig. 3.2).

Spring sampling of predators

Spring 1989

The results of the 1989 vacuum-net study for Demetrias atricapillus and Tachyporus hypnorum, the most abundant carabid and staphylinid beetles respectively, overwintering on ridge 1 are presented in Figs. 3.3 & 3.4. Two-way analysis of variance (numbers ($\log(n/1.5m^2 +1)$) against distance and transect per date with 4,16 d.f.) followed by Tukey's test was carried out to identify any spatial patterns in the crop. Proportions were used for graphical presentation to correct for between-date variation in abiotic factors, such as temperature and humidity, which can affect surface activity of invertebrates and thus influence the efficiency of vacuum-net sampling (Frampton 1989) and pitfall trapping (Greenslade 1964) as methods for studying epigeal fauna.

There were significantly higher numbers of D. atricapillus on or immediately adjacent to the ridge up until 3 May 1989 (mean density at 0-3m during this period = $12.2m^{-2}$), after which the numbers tended to become more evenly distributed with no significant differences between distances (mean density over 0-60m during this final period = $0.4m^{-2}$) (Fig. 3.3.). Two significant peaks of abundance (0m and 60m) of T. hypnorum were observed until 18 April 1989 (mean density at 0-3m = $10.5m^{-2}$) (Fig. 3.4). Although there were no consistent spatial patterns after this date, significantly lower numbers of T. hypnorum were found on the ridge than in the crop by the end of the study (mean density over 0-60m from 8 May - 22 May = $2.3m^{-2}$).

The results for linyphiid spiders suggested apparently limited invasion of the crop, with significantly higher numbers occurring on the ridge itself for all dates except 8 May 1989, on which no significant between-distance differences were observed (Fig. 3.5).

No other predator species or predator groups were caught in sufficient numbers to demonstrate any further invasion patterns (i.e. analysis was not carried out for species or groups with less than one individual/trap/date (Wratten et al. 1988)).

Spring 1990 - Barrier pitfall study

Using the same criterion for analysis described above (at least one individual/trap/date), no single boundary overwintering coleopteran species was caught in sufficient numbers to allow individual analysis in the barrier pitfall study. Species were grouped therefore, according to their dispersal characteristics (after Coombes & Sotherton 1986), i.e. slow wave-like crop invasion resulting from dispersal by walking (e.g. B. lampros, D. atricapillus and A. dorsale) and rapid invasion resulting from dispersal by flight of Tachyporus spp. (dominated by T. hypnorum, with some T. chrysomelinus and T.

obtusus). Two-way analysis of variance (numbers (log(n/trap+1)) against distance and transect per date with 4,36 d.f.) followed by Tukey's test was carried out to identify any spatial patterns in the crop. Once again, proportions were used for graphical presentation to correct for between-date variation in abiotic factors.

The slowly-dispersing carabids were not abundant enough in the crop to allow analysis for the first two weeks of the study or on 11 May. On the remaining dates, no significant between-distance differences were observed (Fig. 3.6).

The dispersal patterns of the Tachyporus spp. are presented in Fig. 3.7. Numbers were too low for analysis on 26 April and 3 May. Although some significant between-distance differences occurred, no consistent patterns of dispersal were evident on the remaining dates.

The adult overwintering carabid Bembidion obtusum (Sotherton 1985) and the larval overwinterer Nebria brevicollis F. (Penney 1966) were the only coleopteran species caught in sufficient numbers to allow analysis at the species level. B. obtusum were found at all distances into the crop from the beginning of the study, although between-date variation in spatial distribution did occur (Fig.3.8). N. brevicollis were not abundant until 22 April, after which they were captured at all distances, with perhaps a gradient (significant on 11 May) of higher numbers nearer to the ridge than at the field centre (Fig.3.9).

For the Linyphiidae, it was possible to see a shallow wave of emigration through time (Fig. 3.10). At the beginning of the study, highest numbers were found near the ridge (significant on 3 April and 22 April). Following this, no between-distance significance occurred until 11 May, after which significantly lower numbers were found immediately adjacent to the ridge habitat.

Once numbers were high enough to assess (from 12 April), the Lycosidae appeared to show limited crop invasion (Fig. 3.11). In fact, although present throughout the crop, significantly higher numbers were found immediately adjacent to the within-field ridge throughout the study period.

Spring 1990 - Vacuum-net study

The results of the 1990 vacuum-net study for D. atricapillus and Tachyporus spp. are presented in Figs. 3.12 & 3.13 respectively. Numbers of other predator species or predator groups were too low to demonstrate any further emigration patterns. Once again, two-way analysis of variance (log (n+1) transformation) was used.

The numbers of D. atricapillus were too low to analyse for three dates during the early part of the study. 22 April was the only assessable date of this period and showed significantly higher numbers of D. atricapillus within the first 4m of the crop. On 3 May and 11 May numbers increased significantly away from the ridge into the crop. On the remaining two dates, no significant spatial patterns existed (Fig. 3.12).

The vacuum-net study, like the barrier pitfall study, revealed no obvious patterns of dispersal for Tachyporus spp.. However, significantly lower numbers were caught adjacent to the ridge (1m) on 3 May and on the last two dates of the study, and joint lowest with 50m on 11 May (Fig. 3.13).

Figure 3.1. Mean number of pea aphids removed from the ridge and from the adjacent field at 1, 5, and 15 metres into the crop, spring 1988. Histograms within a week with the same letter do not differ significantly at the 5% level (two-way analysis of variance followed by Tukey's test). Distance from ridge: ▓ 0m, ▒ 1m, ░ 5m, ░ 15m.

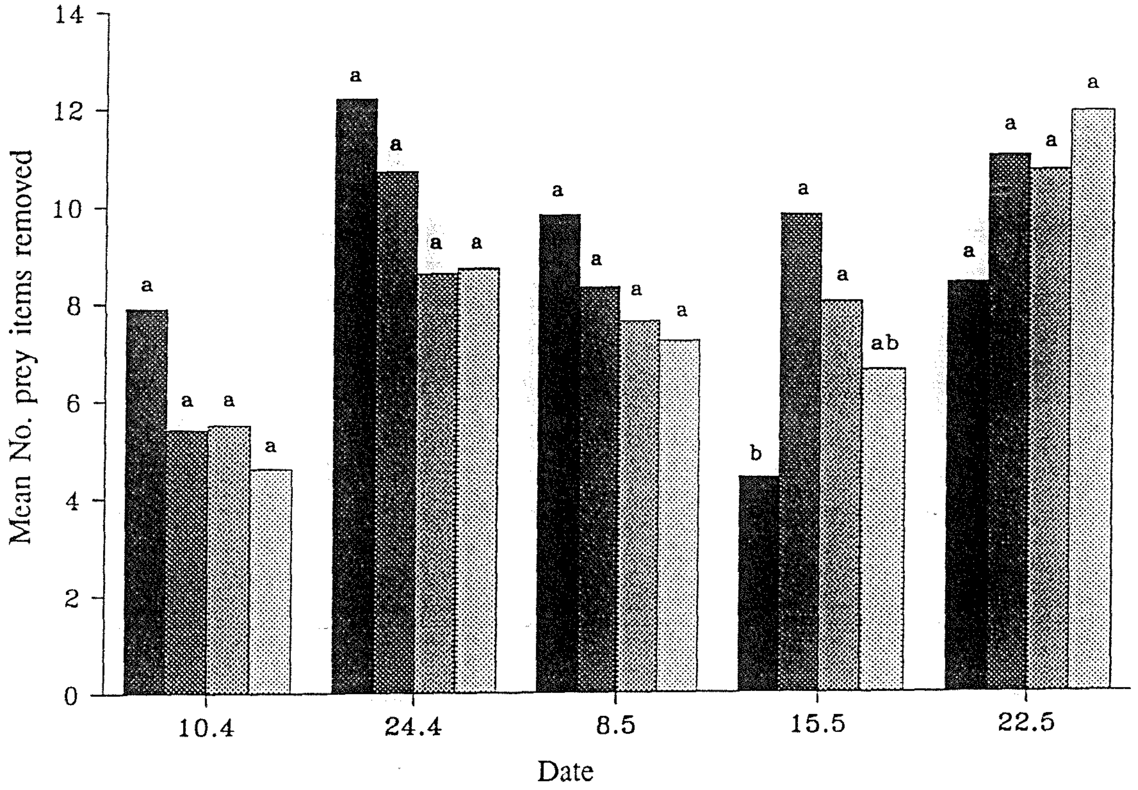


Figure 3.2. Mean number of Drosophila pupae removed from the ridge and from the adjacent field at 3, 10, 30, and 60 metres into the crop, spring 1989. See Figure 3.1. Incomplete data sets exist for two dates due to small-mammal disruption of the dishes of pupae. Distance from ridge: ▩ 0m, ▨ 3m, ▦ 10m, ░ 30m, ░ 60m.

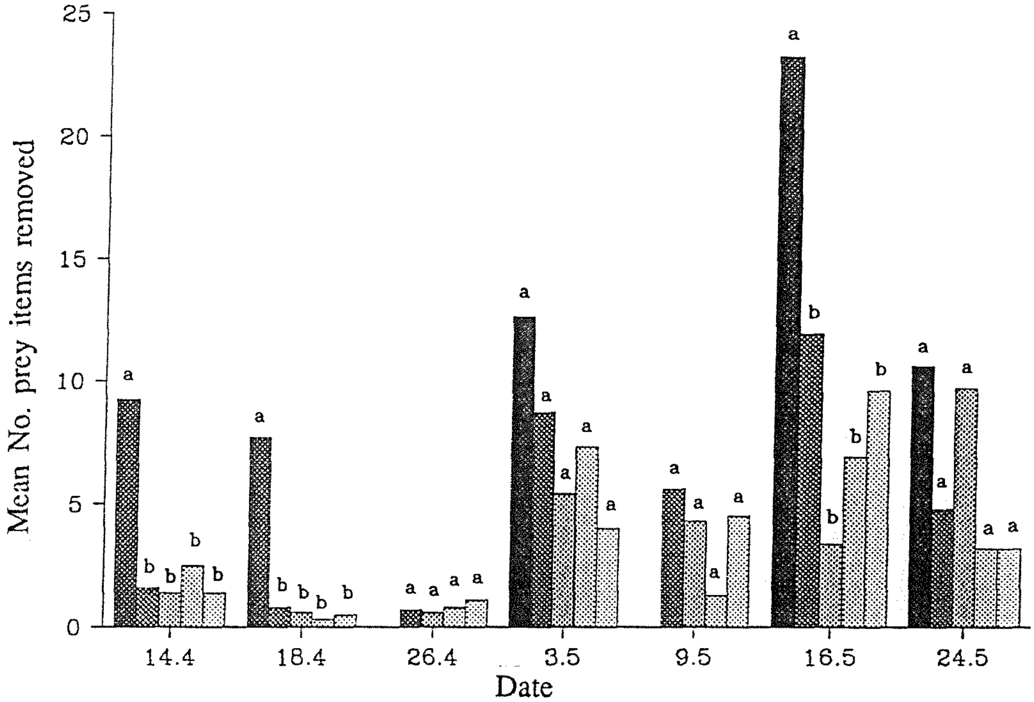


Figure 3.3. Emigration pattern of Demetrias atricapuillus from the spring 1989 vacuum-net study expressed as proportions of totals caught/date. * Denotes significant between-distance differences at the 5% level (two-way analysis of variance (log (numbers/trap +1)) followed by Tukey's test). Absence of histograms for particular dates indicates that numbers were too low for analysis.

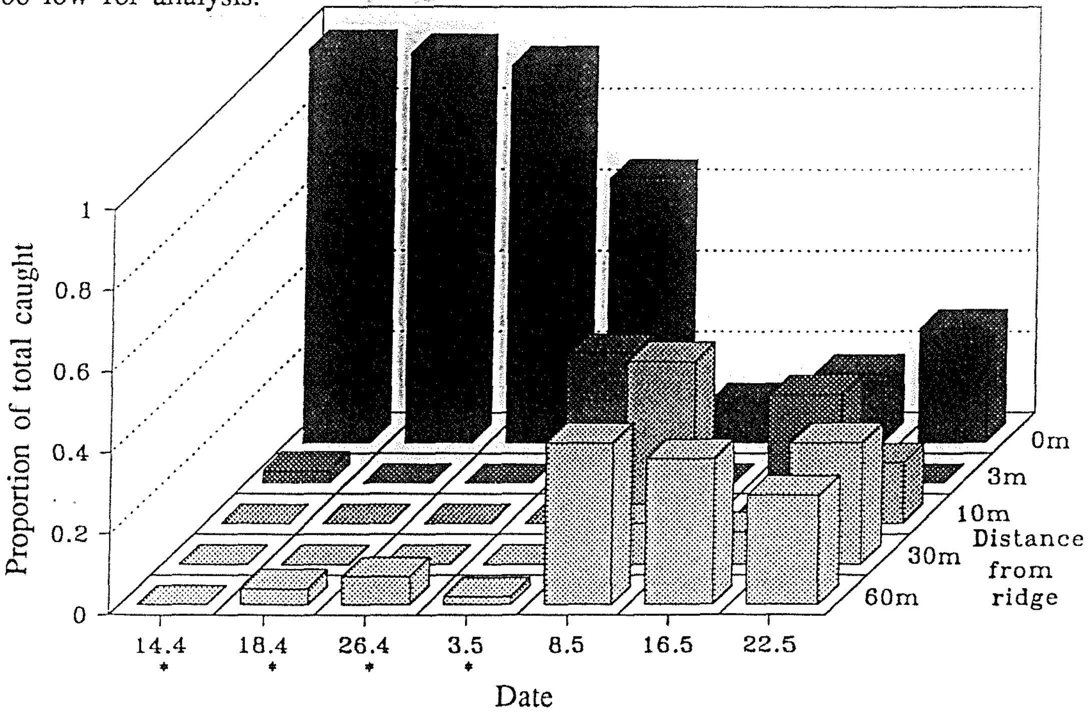


Figure 3.4. Emigration pattern of Tachyporus hypnorum from the spring 1989 vacuum-net study. See Fig.3.3

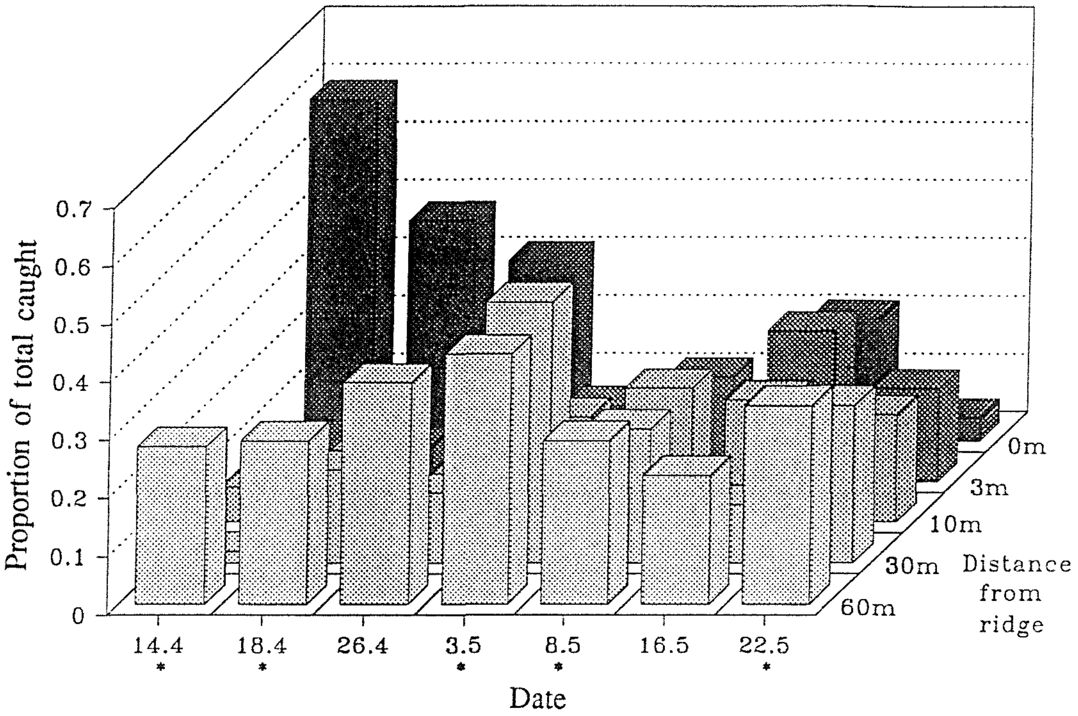


Figure 3.5. Emigration pattern of the Linyphiidae from the spring 1989 vacuum-net study. See Fig.3.3

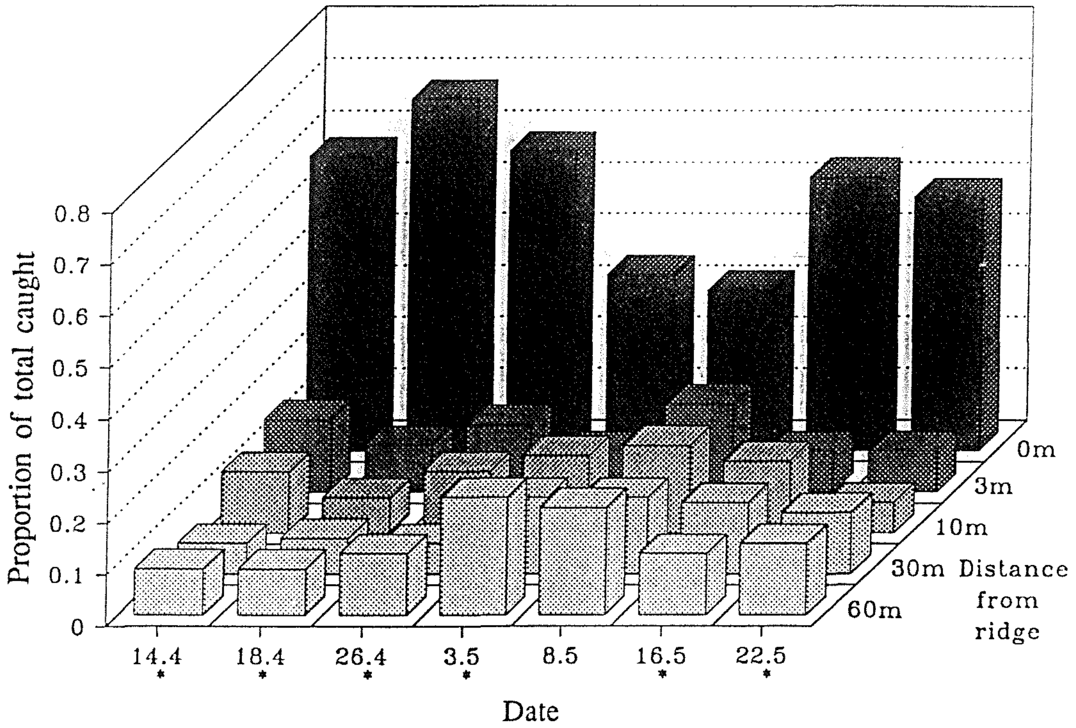


Figure 3.6. Emigration pattern of the boundary carabids from the spring 1990 barrier-pitfall study. See Fig.3.3.

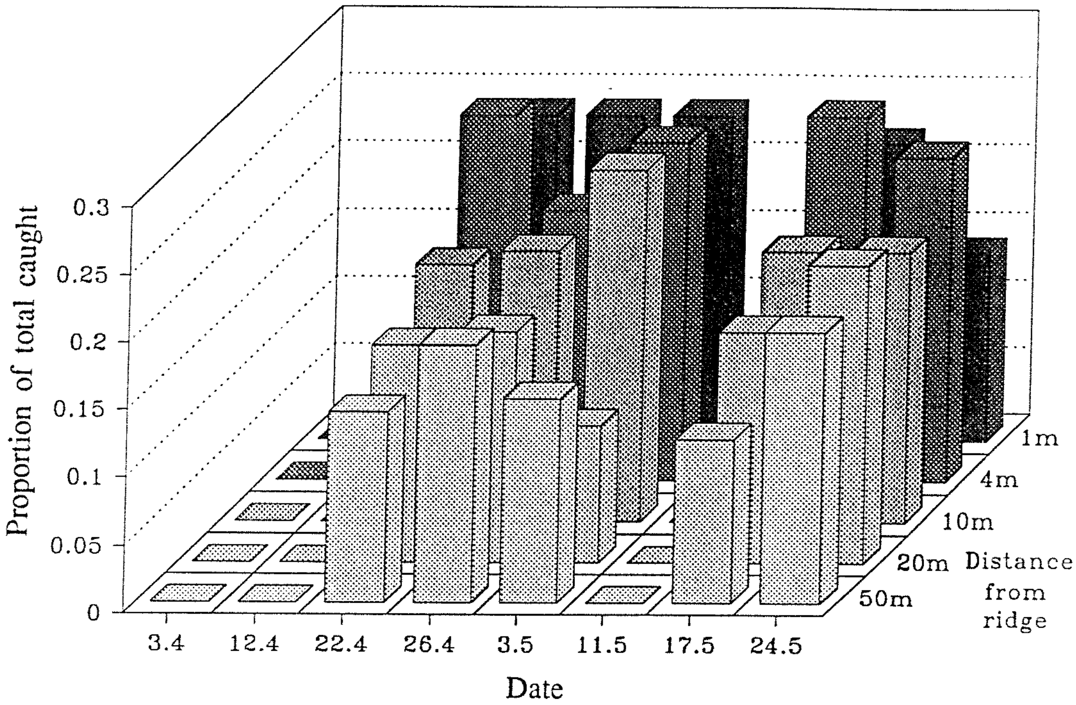


Figure 3.7. Emigration pattern of the Tachyporus spp. from the spring 1990 barrier-pitfall study. See Fig.3.3.

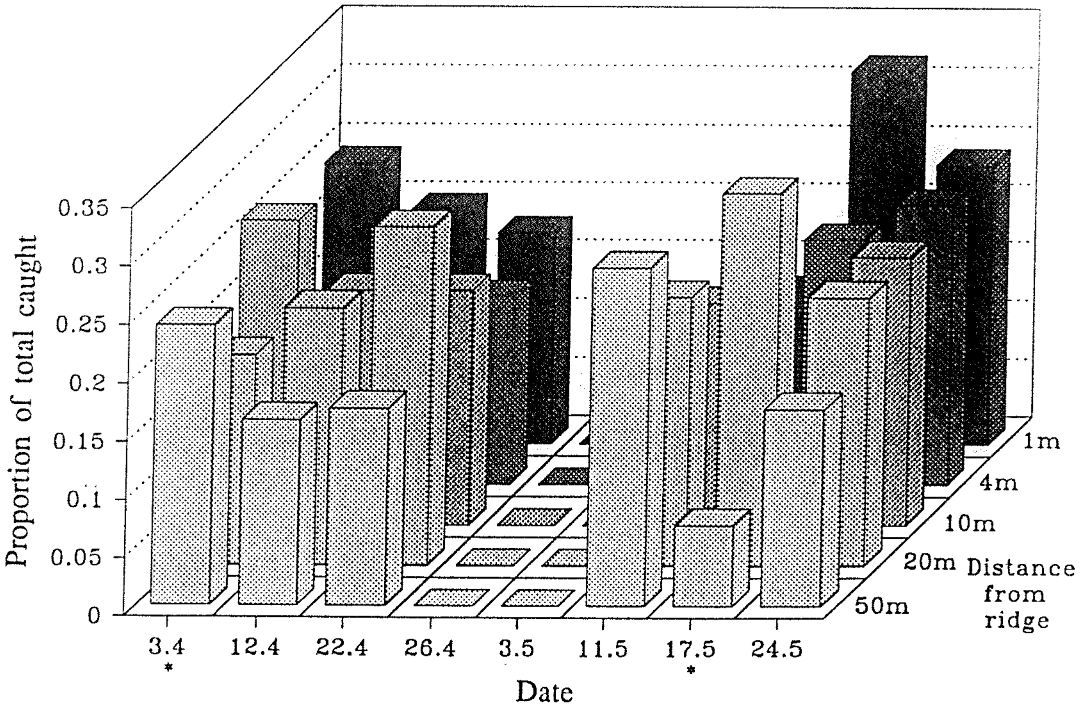


Figure 3.8. Emigration pattern of Bembidion obtusum from the spring 1990 barrier-pitfall study. See Fig.3.3.

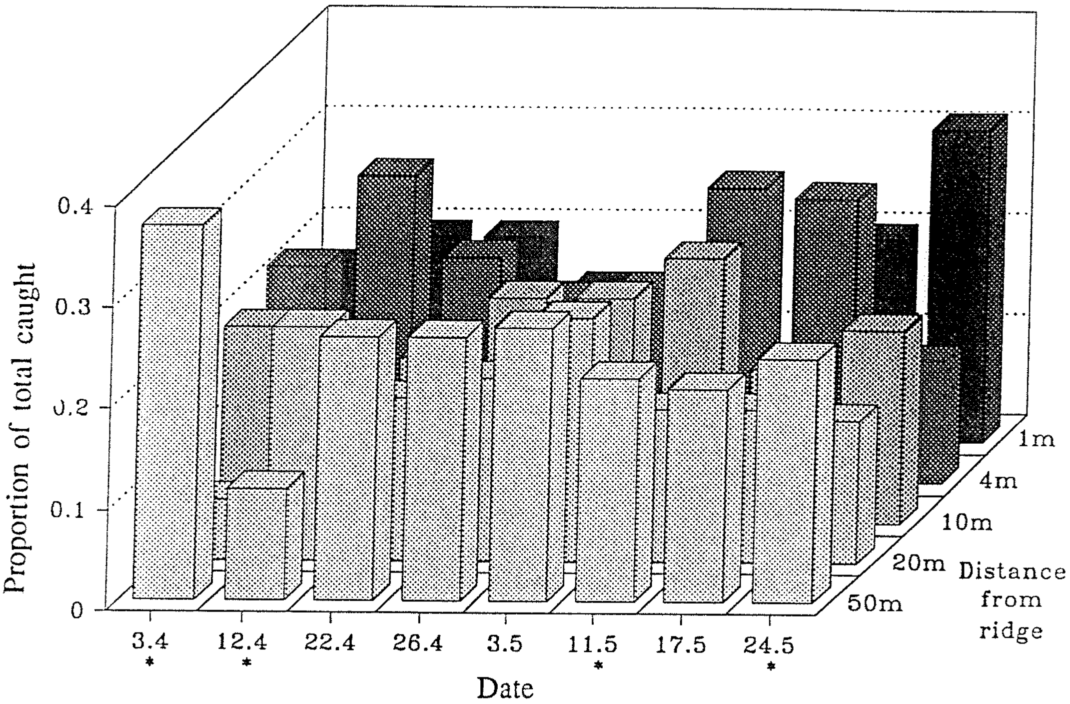


Figure 3.9. Emigration pattern of Nebria brevicollis from the spring 1990 barrier-pitfall study. See Fig.3.3.

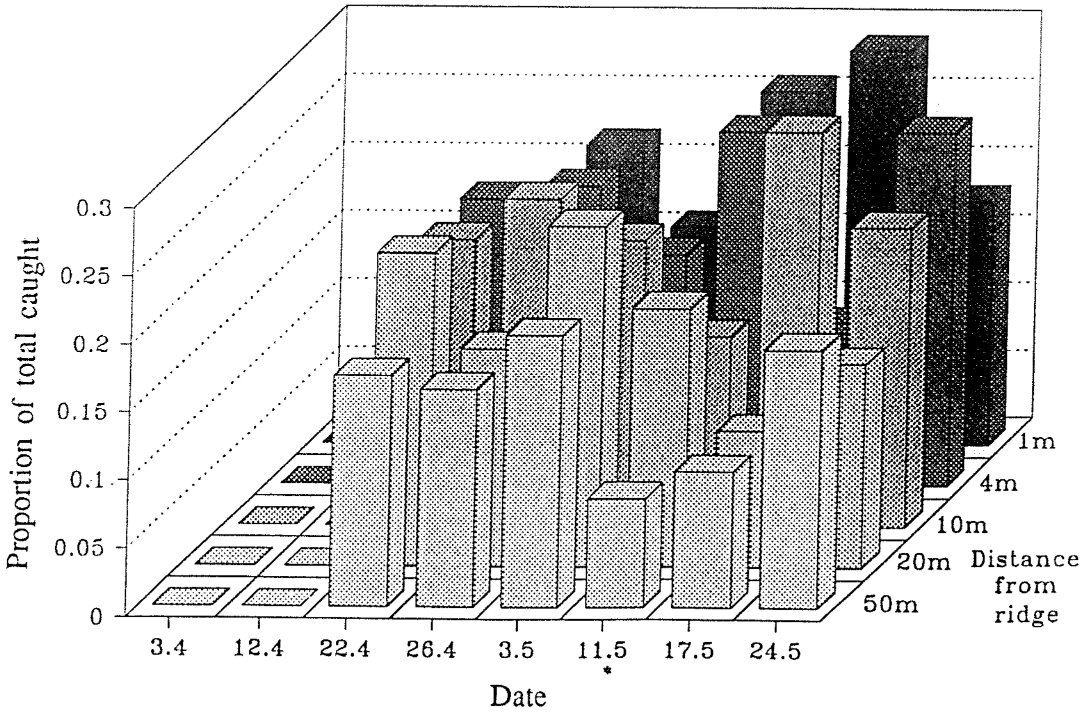


Figure 3.10. Emigration pattern of the Linyphiidae from the spring 1990 barrier-pitfall study. See Fig.3.3.

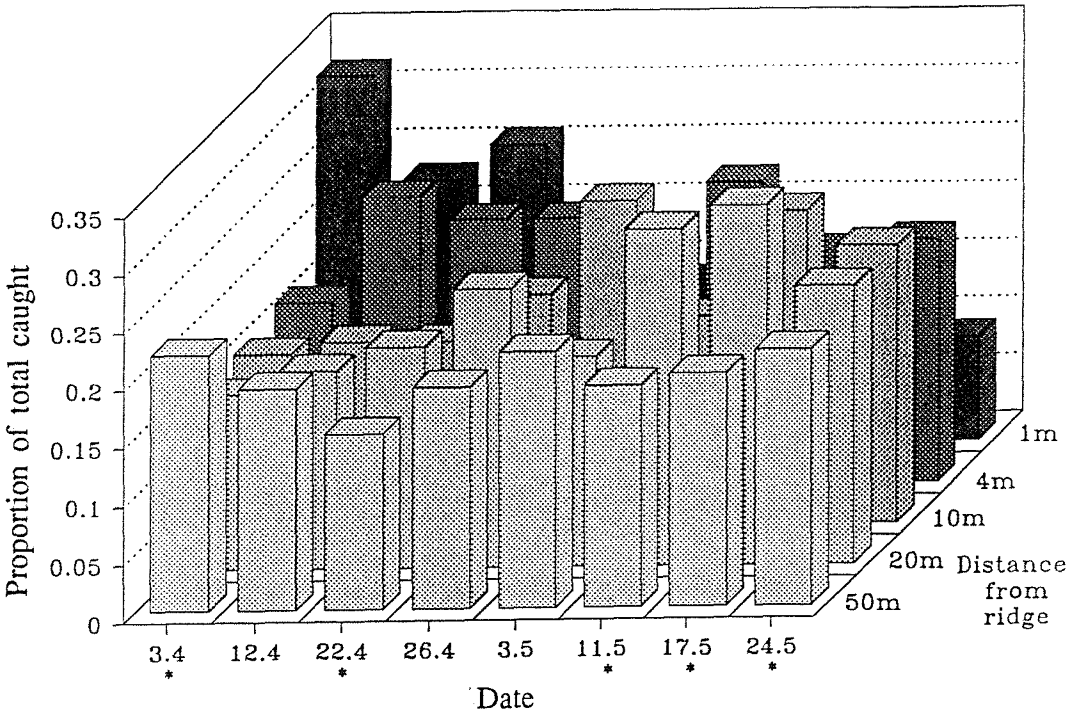


Figure 3.11. Emigration pattern of the Lycosidae from the spring 1990 barrier-pitfall study. See Fig.3.3.

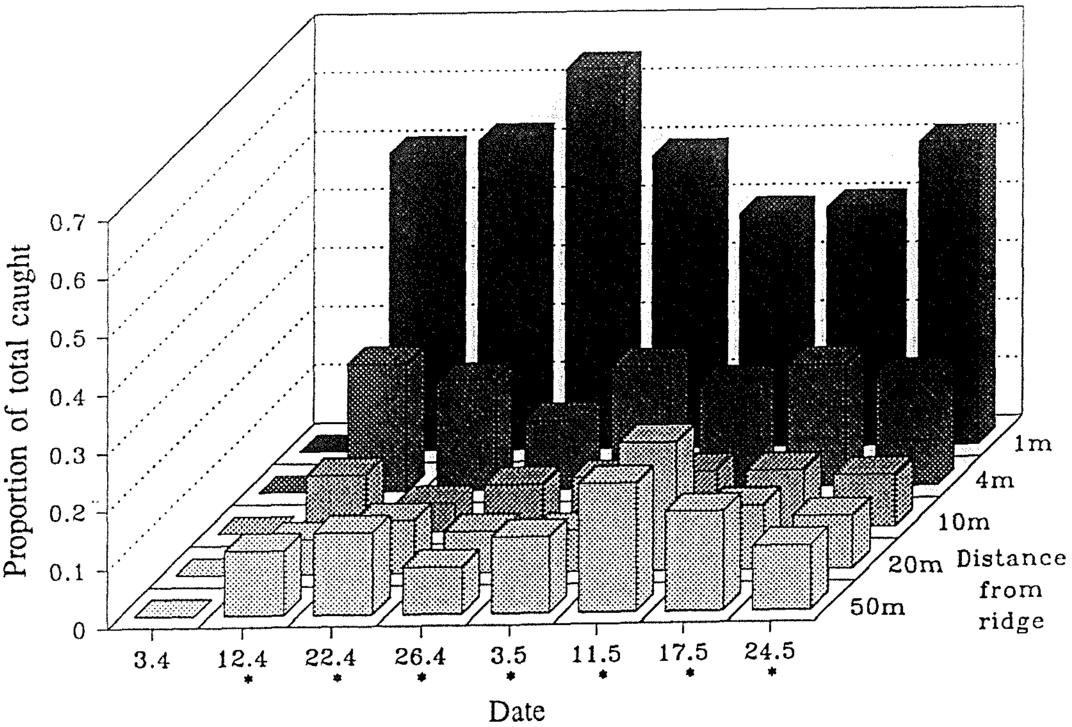


Figure 3.12. Emigration pattern of the carabid Demetrias atricapillus from the spring 1990 vacuum-net study. See Fig.3.3.

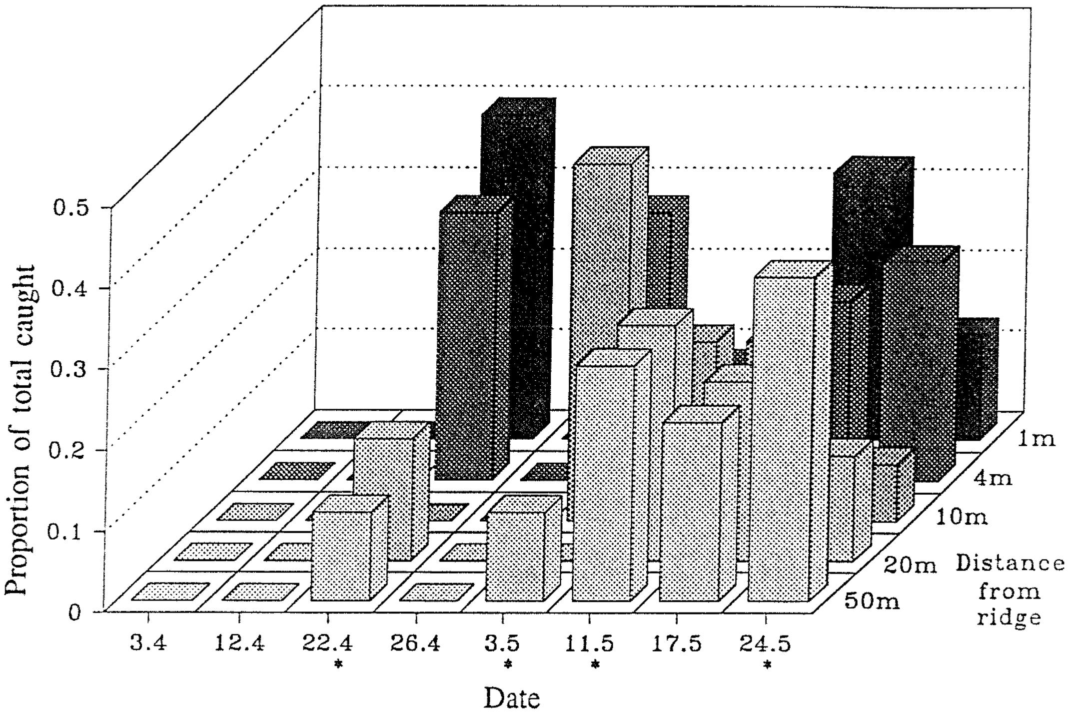
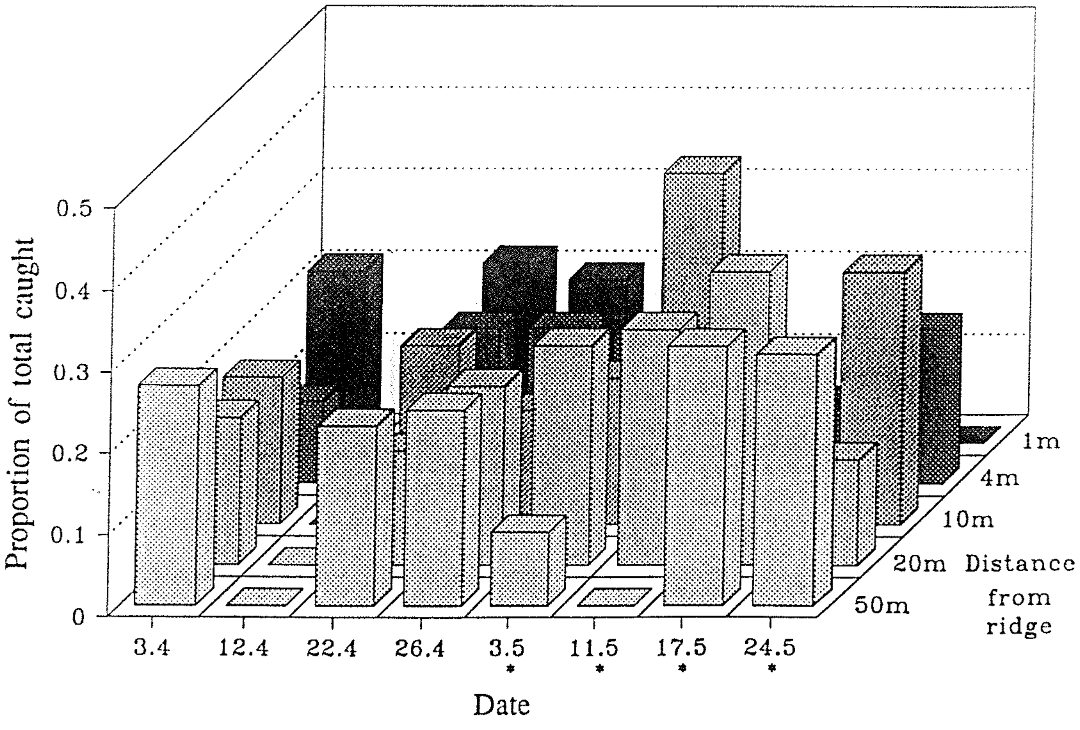


Figure 3.13. Emigration pattern of the staphylinid Tachyporus hypnorum from the spring 1990 vacuum-net study. See Fig.3.3



3.4 DISCUSSION

Predation studies

For the 1988 predation study, it was originally considered that the pattern of activity into the crop through time was associated with a wave of emigration of carabids as recorded by Coombes & Sotherton (1986). With high predator densities in spring 1989, it was expected that previous trends would be confirmed and the influence of the overwintering population detected at greater distances into the surrounding field. Although interpretation was not aided by incomplete data sets on two dates, the results suggested no such trends. Instead, higher levels of predation were recorded on the ridge and its immediate environment suggesting limited invasion. The findings of the 1988 study therefore could be an artifact of the limited distance over which the investigation was carried out, the wave of immigration being no more than localised movements within close proximity to the ridge. Alternatively, the differences in predator population structure between years could account for the different predation patterns observed, with indeed only limited invasion of the crop taking place. This supports findings of Desender & Alderweireldt (1988) where it appeared that boundaries not only acted as overwintering habitats, but provided a more stable environment, even suitable for breeding of some carabid species, until the crop cover provided suitable alternative microhabitats. Persistent association with permanent field edge habitats by certain species of carabid was also recorded by Wallin (1985, 1986).

Spring 1989 predator sampling

Carabidae and Staphylinidae

The results of the 1989 spring sampling study however, suggested that the ridges provided a nucleus predator population at the field centres from which emigration could take place. This was particularly apparent for Demetrias atricapillus, a highly-ranked cereal aphid predator (Sunderland & Vickerman 1980), the emigration of which led to a uniform dispersion through the crop. Three small peaks at 60m from 18 April to 3 May however, suggest that the natural hedgerow population as well as the ridge population, may have contributed to the final spatial distribution. A similar pattern was observed for Tachyporus hypnorum, a species suggested by simulation modelling (Winder 1990) and in population manipulation experiments (Dennis & Wratten (1991a)) to also be one of the most important polyphagous predators of aphids in cereal fields. However, because this species has a more rapid dispersal than D. atricapillus (Coombes & Sotherton 1986) and is thought to disperse by flight rather than by walking, the influence of the natural hedgerow population (105m from the ridge) was probably more apparent. The final densities of both species throughout the crop compared favourably with mean densities of a range of predator species recorded during the aphid population increase phase in a previous study in southern England (Sunderland & Vickerman 1980).

Araneae

In contrast to the coleopteran dispersal patterns described above, the 1989 vacuum net study suggested limited crop invasion by linyphiid spiders from the within-field ridge. The ability to "balloon" allows rapid aerial dispersal of certain species and it is thought that aerial migrations in spring and summer mainly account for colonisation of crops (Duffey 1956). Extensive crop invasion from sources external to the single-field study system, therefore, could have obscured a more subtle invasion from the within-field overwintering habitat. Alternatively, the pooling of several species into the family Linyphiidae may have masked single-species' dispersal patterns. Also, although it is unlikely that many species can remain within the field all year round, requiring alternative habitats for development or overwintering because of disruption of the annual system (Luczak 1979), certain species might be autochthonous within a more permanent "boundary type" habitat. That is, certain species may infact remain within the ridge habitat and have limited interaction with the crop. As the original concept of this project was to create overwintering habitats for polyphagous predatory Coleoptera however (as discussed in Chapter 2), identification of the Linyphiidae to species level was not carried out and so these questions cannot be answered fully.

Spring 1990 predator sampling

Carabidae

Low numbers of individuals necessitated the pooling of several species into one "boundary" carabid group in the barrier-pitfall study. No single species was dominant so although the mechanisms of dispersal were similar, the slight temporal and spatial differences between the carabid species (Coombes & Sotherton 1986) could have obscured individual species patterns. However, it was still possible to see a trend where highest proportions were initially found adjacent to the ridge early in the summer. Similarly, emigration of D. atricapillus in the 1990 vacuum-net study showed higher numbers adjacent to the ridge early on, followed by an increase away from the ridge into the crop through time. Overall therefore, these results broadly followed the findings of Coombes & Sotherton (1986) and the vacuum-net study of the previous spring, i.e. a slow wave-like dispersal of Carabidae from the overwintering habitat into the adjacent field.

In the study of Coombes & Sotherton (1986), the total dispersal period (the period taken to reach the stage of no significant difference between numbers at 5m and 100m from the boundary) for D. atricapillus was approximately 50 days. In the 1990 study however, the analogous total dispersal period (uniform spatial pattern between 1m and 50m) was 25 days, with a similar period for the previous spring. This would be expected, as there were obvious differences between the final dispersal distances in the two studies i.e. 100m in Coombes & Sotherton (1986) but only 50m in this study. It showed however, that the creation of the within-field habitat reduced the time taken for predators to reach the effective field centre i.e. in the absence of the ridge the actual field centre would be c. 100m from a boundary and require a period of c. 50 days for complete dispersal; with the within-field habitat, the effective field centre becomes c. 50m from boundary or ridge and as such, assuming invasion from both sources, would require only c. 25 days for uniform dispersion throughout the crop.

The carabids B. obtusum and N. brevicollis showed no wave like patterns of emigration. As neither of these species have marked aggregations towards boundary overwintering sites however (Sotherton 1985), it is perhaps not surprising that no consistent spatial patterns were observed. However, it is possible to see a shallow gradient of N. brevicollis numbers sloping away from the ridge. This was only significant on one date but might indicate uneven emergence of tenerals across the field. Wallin (1987, 1988) showed that the larvae of Harpalus rufipes (De Geer) accumulated along field edges after harvest, resulting in large numbers of tenerals emerging at this site. It is possible therefore that N. brevicollis also being a larval overwinterer, shows similar temporal and spatial distribution patterns, tending to aggregate along islands of vegetation following the harvest disruption.

Staphylinidae

The results of both spring 1990 studies for Tachyporus spp. revealed no clear spatial patterns during the monitoring period. The results of the 1989 study however, demonstrated a clear influence of the ridge population of T. hypnorum in achieving uniform field cover at this site. It is possible therefore that pooling several Tachyporus species into one group could have masked dispersal patterns of individual species in the present study, in a similar way to that of the boundary carabids discussed above. Alternatively, early emigration may have been encouraged by a mild winter and warm spring (increasing temperature and daylength are reported to be the stimuli for dispersal of

Tachyporus spp. into the cereal crop (Lipkowe 1966)). Thus, no emigration patterns were observed in 1990 because dispersal had already taken place at the onset of the spring study.

Finally, apparent between-year differences in Tachyporus emigration patterns could have been an artifact of the experimental design. Transects in the 1989 spring study started at 0m (i.e. on the ridge itself), whereas in the 1990 spring, transects for both sampling methods started at 1m into the crop. Consequently, the data generated during 1990 were actually a measure of Tachyporus spp. that had, or were dispersing, as opposed to the 1989 study which measured the decline in numbers from the overwintering habitat as dispersal took place. In this way, the results of both years tend to agree with the results of Coombes & Sotherton (1986) from field boundaries who showed higher numbers at 0m prior to emigration, as in 1989, but uniform numbers from 5m onwards once dispersal was underway (i.e. instantaneous invasion), analogous with 1m onwards in spring 1990.

Araneae

In contrast to the 1989 vacuum-net study, the results of barrier-pitfall study for the Linyphiidae appeared to show a shallow wave of emigration away from the ridge through time; the shallowness possibly being a result of invasion from external sources diluting within-field dispersal patterns. The final pattern was higher numbers away from, rather than immediately adjacent to, the ridge habitat. As the barrier-pitfalls could be considered to be directional, low numbers adjacent to the ridge would suggest minimal movement from the ridge into the crop at this time, i.e. no further emigration. However, as the barrier pitfall traps sample individuals actually penetrating the crop (as discussed above), there still remains the possibility of an autochthonous population within the ridge habitat, as suggested by the results 1989 study.

Chavin (1960) reported that the numbers of ground dwelling spiders along alfalfa margins was 33% higher than in the centre. Also, in a study by Boiteau (1983), total spider catches in potato fields were higher at the edge than in the centre. In a similar way, the results from the barrier-pitfall catches in the present study showed significantly higher numbers of Lycosidae at 1m on all dates, although they were represented at all distances into the crop. This spatial pattern was characertistic of an edge effect resulting from limited between-habitat interaction at the interface of adjacent habitats (Lewis 1969; Mader et al. 1986) e.g. between hedgerow and field populations. Once again, this could suggest the presence of an autochthonous population resident within the ridge habitat, and as such, provides evidence of the ridge to be undergoing successional changes towards representing a "permanent" environmental feature.

Conclusion

From the results of the predation studies, the influence of the ridges on spring predator distribution remained unclear. This was possibly because high variation in the number of prey taken per bait dish could have swamped spatial patterns which may have existed. Linked to this the artificial prey used may have been unattractive relative to other prey items available in the field, consequently masking potential differences in predation pressure.

From the predator sampling studies however, it appeared that the ridges provided a nucleus population of predators which could influence subsequent spring dispersal patterns in the field. The 1989 vacuum-net study showed this to be most apparent for two important boundary overwintering predators, with evidence for a wider range of species provided by the 1990 studies. Moreover, the dispersal studies indicated that the within-field ridge enhanced field colonisation of the Coleoptera, especially the Carabidae, during the spring invasion period, thus enhancing the biocontrol potential of this predatory group. The results of the 1990 studies also suggested more subtle effects of the ridges; influencing the distribution of one species of larval overwintering carabid, and possibly acting as a permanent habitat for Lycosidae and to a lesser extent Linyphiidae.

CHAPTER 4. ABIOTIC AND BIOTIC FACTORS INFLUENCING THE WINTER DISTRIBUTION OF PREDATORY INSECTS ON FARMLAND.

SUMMARY

(1) A variety of environmental factors were investigated to analyse the mechanisms involved in successful overwintering and possibly overwintering site selection, for Tachyporus hypnorum and Demetrias atricapillus, both important coleopteran predators of cereal aphids.

(2) Structural and vegetational surveys of natural boundary habitats revealed a positive correlation between D. atricapillus distribution and the presence of Cock's- foot tussocks.

(3) Enclosure experiments showed that although differential mortality occurred between different overwintering habitats for both species, it was unlikely that this alone was sufficient to account for the variable patterns of distribution observed in the field in winter.

(4) Laboratory experiments and dissection of field caught specimens indicated food supply to be important for both predator species during the winter period, although the role of biotic factors in site selection in the autumn could not be clearly demonstrated.

(5) The winter distribution of the two species however, could be explained well in terms of abiotic factors.

(6) It is suggested that these and other similar predator species have well-defined overwintering requirements and that appropriate management or creation of field boundary habitats should be encouraged.

4.1 INTRODUCTION

Chapter 2 reported the results of a habitat creation scheme which attempted to enhance the densities of beetle and spider predators of cereal aphids by providing new overwintering habitats in arable land. Destructive sampling of the new habitats during the second and third winters following their establishment revealed high predator densities. In particular, the most abundant carabid beetle (Demetrias atricapillus) and the most abundant staphylinid (Tachyporus hypnorum), both highly ranked predators of cereal aphids (Sunderland & Vickerman 1980; Winder 1990; Dennis & Wratten 1991a) were found at the highest densities in tussock-forming grass species compared with mat-forming species.

The results of this habitat creation scheme therefore showed that the arable environment could be manipulated to create suitable overwintering refugia for certain species of polyphagous predator. Similarly, Desender (1982), Chiverton (1989) and Riedel (1990) suggested the possibility of improving overwintering conditions for polyphagous predators on farmland via habitat manipulation. Little is known however about the mechanisms governing successful overwintering or influencing site selection. In order to identify individual factors which might influence these processes, the complex of environmental factors has to be analysed via its constituents (Thiele 1977). The aim of this chapter therefore is to identify and quantify the more important abiotic and biotic factors that determine the distribution of overwintering predators, especially D. atricapillus and T. hypnorum, between different boundaries (recorded by Sotherton (1985)) and different habitat types (as observed on the within-field ridges).

4.2 STRUCTURAL AND VEGETATIONAL SURVEYS OF NATURAL FIELD BOUNDARIES

4.2.1 MATERIALS AND METHODS

Study Areas

The investigations were carried out during two winters on two separate farms. Data generated during winter 1982/83 were collected as part of an intensive survey of field boundary habitats carried out by Sotherton (presented in part in Sotherton 1984, 1985) on a 627 ha mixed farm on chalk downland near the Hampshire-Dorset border (South Allenford Farm, Damerham, Hampshire). The majority of the land was in cereals, mostly winter wheat. The field boundaries chosen for the study all bordered fields with a recent cropping history of cereals, and were chosen so as to include the major types of boundary commonly found in such farmland, as defined by Sotherton (1985) i.e. grass bank, hedge bank, grass strip, and shelterbelt.

The second study site, during winter 1988/89, was the principal study farm described in Chapter 2. Once again, the field boundaries chosen all bordered fields with a recent cropping history of cereals and were typical of those found on such farmland.

Field boundary surveys

Winter 1982/83

During the winter months of 1982/83, 24 field boundaries (three north facing (north-east to north-west) and three south facing (south-east to south-west) of each of the four boundary types) were classified according to their structural and vegetational characteristics using six quantitative variables:

1. Aspect
2. Mean height of underbank (cm)
3. Mean percentage cover: grass
4. Mean percentage cover: deciduous leaf litter
5. Mean percentage cover: dicotyledons (mostly stinging nettle Urtica dioica L.)
6. Mean number of tussocks of Cocksfoot (Dactylis glomerata) per m of boundary.

Subjective estimates of mean percentage cover were made in 16 x 0.1 m^2 quadrats per boundary.

To determine the distribution and overwintering density of polyphagous predatory arthropods, twelve soil samples, each 0.04m^2 in surface area and 35cm deep (or to bedrock) were taken between December and February from each of the boundaries surveyed. Samples were taken at regular intervals along the boundaries' length, sampling both tussock and non-tussock areas. Invertebrate fauna were extracted by a flotation technique (Sotherton 1984) and a mean density of each of six predator species calculated for each site. The species chosen for study comprised three species of Carabidae (including D. atricapillus), two species of Staphylinidae (including T. hypnorum) and the common earwig Forficula auricularia. These were selected because they were known to overwinter in field boundaries in high numbers (Sotherton 1984) and because when assessed as polyphagous predators of cereal aphids, these species all appeared near the top of the ranking list (Sunderland & Vickerman 1980).

Winter 1989/90

During winter 1989/90, a further 19 boundaries were surveyed at the second study site (north and south facing examples of three of the four boundary types, shelterbelts being virtually absent at this site). A representative 50m section of each boundary was selected, and classified according to the six quantitative variables described above (subjective estimates of percentage cover from 10 x $0.1m^2$ quadrats at 5m intervals in this case). Ten soil samples ($0.04m^2$ x 10cm deep, at 5m intervals) were taken from each 50m section of each the 19 boundaries. The invertebrate fauna was extracted from the soil samples using the method described in Chapter 2 (soil samples were placed in polythene bags, thoroughly broken up in white photographic trays in the laboratory, and their fauna hand sorted), and densities of the six predator species described above were recorded.

The mean density ($0.04m^{-2}$) of each species was calculated for each field boundary. Densities of each species (log(n+1 no./$0.04m^2$) transformation) were compared between field boundaries grouped according to type (one-way analysis of variance).

Data from the structural and vegetational surveys of both years were combined. Pairs of variables were correlated against each other in a correlation matrix, and stepwise multiple regressions carried out between each of the six predator species and the six quantitative variables.

4.2.2 RESULTS

Although densities of the predators varied between individual boundaries (Table 4.1), analysis of variance of the 1989/90 data revealed no significant differences in densities of any of the predator species between the field boundaries grouped according to type.

Similar analysis of the 1982/83 data (carried out by Sotherton and presented in full in Sotherton (1985)) however, revealed significantly more D. atricapillus and Bembidion lampros along hedge banks than along any other boundary type. There were fewer D. atricapillus in the grass strips than in any of the other three habitats, whereas Tachyporus spp. were consistently more densely distributed beneath shelterbelts than in any other boundary type. The grass strips harboured significantly fewer T. chrysomelinus than did the other boundary types. Agonum dorsale was least abundant in grass strips but did not vary in numbers between the other three habitats.

The correlation matrix revealed three significant correlations between predator numbers and the structural and vegetational boundary variables. D. atricapillus was significantly positively correlated with cocksfoot ($r_{41} = 0.47$, $P < 0.01$) and southerly aspect ($r_{41} = 0.31$, $P < 0.05$), and F. auricularia was significantly positively correlated with deciduous leaf litter ($r_{41} = 0.39$, $P < 0.01$). The stepwise multiple regressions however produced only two significant positive relationships; D. atricapillus on Cock's-foot ($y = 0.59 + 0.56x$, $r_{41} = 0.48$, $P < 0.05$), and F. auricularia on leaf litter (when year effect was taken into account in the analysis) ($y = 0.51 + 1.48x$, $r_{41} = 0.51$. $P < 0.05$). The effect of aspect was not selected in the regression procedure for D. atricapillus, suggesting that cocksfoot and aspect were themselves correlated, and that any correlation between aspect and D. atricapillus was contained within that between cocksfoot and D. atricapillus.

Table 4.1. Abundance of six species of polyphagous predators obtained by destructive sampling from 19 field boundaries during winter 1989/90. GB = grass bank, HB = hedge bank, GS = grass strip, N = northerly aspect, S = southerly aspect.

	Mean densities ($0.04m^{-2}$) (log n+1) ± 95% C.L.					
Boundary type	Agonum dorsale	Bembidion lampros	Demetrias atricapillus	Tachyporus hypnorum	Tachyporus chrysomelinus	Forficula auricularia
HB S	0.00	0.00	0.60 ± 0.024	0.51 ± 0.094	0.00	0.12 ± 0.157
GB N	0.05 ± 0.092	1.05 ± 0.192	0.06 ± 0.117	0.70 ± 0.185	0.00	0.00
GS N	0.00	0.99 ± 0.243	0.00	0.37 ± 0.207	0.03 ± 0.059	0.00
HB S	0.09 ± 0.176	1.04 ± 0.137	0.19 ± 0.232	0.80 ± 0.236	0.03 ± 0.059	0.00
HB S	0.00	0.59 ± 0.214	0.06 ± 0.078	0.72 ± 0.237	0.00	0.00
HB N	0.03 ± 0.059	0.00	0.20 ± 0.141	0.68 ± 0.253	0.00	0.00
HB S	0.00	0.00	0.22 ± 0.139	0.65 ± 0.259	0.00	0.00
HB S	0.06 ± 0.079	0.06 ± 0.078	0.54 ± 0.219	0.61 ± 0.238	0.00	0.00
GB S	0.09 ± 0.089	0.06 ± 0.078	0.52 ± 0.222	0.49 ± 0.249	0.03 ± 0.059	0.06 ± 0.078
GS N	0.08 ± 0.104	0.03 ± 0.059	0.03 ± 0.059	0.33 ± 0.237	0.03 ± 0.059	0.08 ± 0.105
HB N	0.13 ± 0.146	0.19 ± 0.127	0.03 ± 0.059	0.68 ± 0.321	0.06 ± 0.079	0.00
GB N	0.03 ± 0.059	0.09 ± 0.089	0.03 ± 0.059	0.57 ± 0.204	0.00	0.03 ± 0.059
HB N	0.11 ± 0.111	0.06 ± 0.078	0.50 ± 0.174	0.17 ± 0.114	0.03 ± 0.059	0.03 ± 0.059
GB N	0.00	0.00	0.26 ± 1.177	0.72 ± 0.227	0.00	0.00
GS S	0.00	0.00	1.21 ± 0.432	0.97 ± 0.177	0.00	0.00
HB S	0.00	0.16 ± 0.129	0.29 ± 0.217	0.72 ± 0.286	0.07 ± 0.105	0.05 ± 0.093
GB S	0.07 ± 0.136	0.09 ± 0.089	0.09 ± 0.126	0.62 ± 0.206	0.06 ± 0.079	0.09 ± 0.089
HB S	0.00	0.06 ± 0.078	0.03 ± 0.058	0.40 ± 0.215	0.03 ± 0.059	0.03 ± 0.059
GS S	0.00	0.46 ± 0.133	0.53 ± 0.318	0.86 ± 0.196	0.05 ± 0.093	0.08 ± 0.105

4.3 INVESTIGATIONS INTO OVERWINTERING SURVIVAL OF Tachyporus hypnorum AND Demetrias atricapillus.

4.3.1 MATERIALS AND METHODS

Tachyporus hypnorum

Ten turves ($0.04m^2$ x 0.05m deep) each of the grass species Dactylis glomerata, Lolium perenne and Festuca ovina L., together with twenty bare earth soil-sections, were removed from natural field boundary sites on the principal study farm during late October 1987. These were warmed in the laboratory (c. 20°C) for one week to allow removal of existing predatory arthropods by hand searching.

Small flints were added to half of the bare earth samples, creating five treatment types with a gradient of structural complexity ranging from simple bare earth to complex D. glomerata tussocks (bare earth was considered the simplest structural component of a boundary habitat; flints added some structural heterogeneity; F. ovina represented a densely tufted grass structure with no compressed vegetative shoots or tussock form (Hubbard 1984); L. perenne represented a loosely to densely tufted grass, which unlike F. ovina, produced foliage to a height of 90cm, but again lacked the compressed vegetative shoots and tussock form of D. glomerata (Hubbard 1984)).

Each of the turves and soil-sections was then surrounded by 0.5m-diameter pieces of 0.2 x 0.3mm mesh size Terylene netting and "re-planted" at 1m intervals in a randomised design along an existing post and wire-fence boundary with a slight underbank, so that the soil-surfaces of the enclosed soil samples were flush with the soil-surface of the adjacent boundary. Each enclosed sample was therefore exposed to the same boundary characteristics of drainage and aspect, and differed only in treatment type.

Twenty-two adult T. hypnorum, collected from adjacent field margins at the study site, were introduced into each enclosed turf and soil-section on 2 November. This density/enclosed sample ($550m^{-2}$) was within the density range occurring naturally for this species in field boundaries (Dennis 1989) and on the within-field ridges (Chapter 2) in winter. Half of the enclosed samples (five of each treatment) were removed on 20 January. The remaining soil samples were left in place until 9 March. At the end of each period, the number of live T. hypnorum in each enclosed sample was recorded.

Demetrias atricapillus

During winter 1988/89, a similar experiment to the one described above was carried out for Demetrias atricapillus. This time however, rather than just manipulating abiotic factors by providing a gradient of structural complexity, an attempt was made to investigate biotic factors by varying the amount of food available during the winter period.

Two extremes of structural complexity were provided with forty enclosed bare earth and forty enclosed D. glomerata soil samples, the same as those described above.

After warming in the laboratory (c. 20°C.) for one week, the fauna were removed from half of the turves and soil-sections as thoroughly as possible by vacuum-netting (Thornhill 1978) and hand-searching. The remaining soil samples however, had only the predatory arthropods removed. There were therefore twenty replicates of each of four treatments (bare earth + potential prey items, D. glomerata + potential prey items, bare earth + no prey, D. glomerata + no prey). These were "re-planted" in a randomised design, along the same post and wire-fence boundary used in the previous study.

Ten adult Demetrias atricapillus collected from adjacent field margins were added to each enclosed turf and soil-section on 17 November. As with T. hypnorum, this density/enclosed sample (250m^{-2}) was within the range occurring naturally for this species in field boundaries (Coombes 1987) and on the within-field ridges (Chapter 2) in winter. Following this, five replicates of each treatment type were removed at intervals of approximately five weeks and the number of live Demetrias atricapillus within each enclosed sample recorded. An attempt was made to maintain between treatment differences in prey availability, by monthly "re-seeding" the appropriate treatments with prey items (such as Collembola, Diptera, Thysanoptera, Homoptera) obtained by vacuum-net sampling from field boundaries adjacent to the study site.

Microclimate

Throughout the D. atricapillus overwintering trial, hourly temperature recordings were taken automatically using Grant "Squirrel" microclimate recorders. Thermistor probes were inserted within one replicate of each of the enclosed treatment types (at soil-surface or base of vegetation level, where appropriate) and in equivalent physical and vegetative types in the adjacent open boundary i.e. within a single D. glomerata tussock and at soil-surface level of an area of exposed bare earth. Air temperature (0.3m above ground) was also recorded. Daily temperature means together with daily temperature variances (treating variance as a variate indicating temperature fluctuation, with log (variance+1) transformation for parametric statistics) were compared between positions.

4.3.2 RESULTS

One-way analysis of variance on the numbers of live individuals (expressed as a proportion of the initial population/enclosed sample (√arcsine transformation)) at the end of the various experimental time intervals, followed by Tukey's test, was used to investigate survival rates of the test species between treatments.

Tachyporus hypnorum

The mean percentage of live individuals in the various treatments during the 1987/88 trial are presented in Table 4.2. Analysis of variance for the first winter period revealed significant between-treatment effects, with D. glomerata turves supporting populations with significantly higher survival than did the bare earth soil-sections ($F_{4,20}$ = 3.91, $P < 0.05$).

By the end of the second period greater and more variable mortality had occurred, enhancing between-treatment effects. Populations within turves of D. glomerata and L. perenne had significantly higher survival rates than populations within either bare earth or bare earth + flint treatments. Survival rate of populations within F. ovina treatments fell between these maximum and minimum levels ($F_{4,20}$ = 8.46, $P < 0.001$). Mean percentage mortality overall increased from 21.4% in the first period to 49.6% by the end of the second.

Demetrias atricapillus

Results of the 1988/89 survival trial are presented in Table 4.3. Significant between-treatment differences in survival rate were observed only for the third trial period. At this time, bare earth + prey, D. glomerata + prey and D. glomerata + no prey treatments supported populations with significantly higher survival than did treatments of bare earth + no prey ($F_{3,16}$ = 5.70, $P < 0.01$).

During assessment of survival at the end of the various trial periods, it became apparent that removal of prey at the beginning of the experiment had not been complete and all treatments contained elements of a prey population. There was, however, a trend for all trial periods, implicating some between-treatment differences in prey availability i.e. those treatments with prey populations maintained by introduction tended to provide improved conditions for survival compared with like treatments with prey populations depleted at the onset of the trial.

Microclimate

Faults with the microclimate recorder and associated software, meant that temperature recordings were available only for seventy days of the 1988/89 survival experiment.

Comparison between the daily temperature means ± 95% C.L. in the treatments and the various natural boundary recording positions revealed no significant differences. The transformed variances for the temperatures at each position however, showed a gradient in temperature variability from the enclosed tussock treatment (the least variable) to the exposed bare earth soil-surface (the most variable) (Table 4.4). The terylene netting provided some degree of protection against temperature fluctuation, the enclosed treatments having lower mean daily temperature variances than their matched exposed areas.

Table 4.2. Mean percentage survival of Tachyporus hypnorum during two trial periods in the 1987/88 overwintering survival trial. Different letters indicate significant between-treatment differences at the 5% level for each trial interval (one-way analysis of variance (√arcsine transformation) followed by Tukey's test).

Period	Treatment	Mean percentage	
2 Nov - 20 Jan	Bare earth	57.3	(b)
	Bare earth + flints	80.9	(ab)
	Festuca ovina	72.7	(ab)
	Lolium perenne	76.4	(ab)
	Dactylis glomerata	83.6	(a)
2 Nov - 9 March	Bare earth	30.9	(b)
	Bare earth + flints	33.6	(b)
	Festuca ovina	51.8	(ab)
	Lolium perenne	60.0	(a)
	Dactylis glomerata	73.6	(a)

Table 4.3. Mean percentage live Demetrias atricapillus at the end of the various trial periods in the 1988/89 overwintering survival trial. See Table 4.2.

Period	Treatment	Mean percentage	
17 Nov - 21 Dec	Bare earth	82.0	(a)
	Dactylis glomerata	92.0	(a)
	Bare + food	90.0	(a)
	Dactylis glomerata + food	98.0	(a)
17 Nov - 25 Jan	Bare earth	82.5	(a)
	Dactylis glomerata	85.0	(a)
	Bare + food	90.0	(a)
	Dactylis glomerata + food	97.5	(a)
17 Nov - 2 March	Bare earth	62.0	(b)
	Dactylis glomerata	92.0	(a)
	Bare + food	90.0	(a)
	Dactylis glomerata + food	97.5	(a)
17 Nov - 6 March	Bare earth	20.0	(a)
	Dactylis glomerata	50.0	(a)
	Bare + food	22.0	(a)
	Dactylis glomerata + food	58.0	(a)

Table 4.4. Mean daily transformed temperature variances (log n+1) ± 95% C.L., recorded at various positions in the 1988/89 Demetrias atricapillus survival trial.

Position of temperature probe.	Mean daily variance ± 95% C.L.	
Enclosed tussock	0.39	± 0.011
Exposed tussock	0.47	± 0.022
Enclosed soil surface	0.88	± 0.042
Exposed soil surface	1.45	± 0.082
Air	1.39	± 0.047

4.4 ASSESSMENT OF MICROCLIMATE

4.4.1 MATERIALS AND METHODS

Winter 1987/88

Throughout the mid-winter period (mid-December to end of February), hourly temperature recordings were taken automatically on ridge 1 and in the field using Grant "Squirrel" microclimate recorders. Temperature probes were positioned to monitor temperature in six specific areas. These were: on the crest of the ridge 5cm below the soil-surface; the soil-surface on the centre and both sides of the ridge; field soil-surface temperature and the temperature within a single plant tussock of L. perenne (one of the most uniformly established grass treatments at this time). Daily temperature means together with transformed daily temperature variances (log (variance+1) transformation) were compared between positions.

Winter 1988/89

Hourly temperature recordings were taken from ridge 1 during January and February. Probes were positioned at the base of each grass type to monitor any differences that might exist between the grass species. Ridge bare earth soil-surface and air temperatures (0.3m above ground) were also recorded. Daily means and transformed daily variances were compared.

Winter 1989/90

As with the previous winter, probes were positioned to investigate whether any differences existed between grass species. Rather than monitoring during the mid-winter period however, this investigation focused on the early winter period (from late September to end October), which is around the time when selection of overwintering sites by polyphagous predators takes place (Wallin 1985). Hourly temperature recordings were taken from three thermistor probes placed at the vegetation base of each of the grass types (three probes for each grass species) on one within-field ridge. These were then averaged to provide a single temperature measure per hour for each grass type. Air temperature (0.3m above ground) and ridge bare earth soil-surface temperatures were also recorded. Once again, daily temperature means and transformed daily variances for the different recording positions were compared.

4.4.2 RESULTS

The results of the temperature studies for all three winters are presented in Table 4.5. There were no significant differences between the mean temperatures recorded in the six positions in 1987/89. The transformed variances for the temperatures at each site however, showed that the within-soil and within-grass refuges provided habitats with the least variable temperatures.

For the 1988/89 and 1989/90 temperature studies which compared grass species, there were no significant differences between the temperature means. The transformed variances of temperature records for each position however, revealed a similar gradient in temperature variability for both years; *D. glomerata* and *H. lanatus* had the least variable temperature environments, air and bare earth soil surface had the most variable, and *L. perenne* and *A. stolonifera* were intermediate.

Table 4.5. Mean daily transformed temperature variances (log n+1) ± 95% C.L., recorded at various positions on within-field ridge 1 during 1987/88, 1988/89 and 1989/90 winters.

Winter 1987/88	Position of temperature probe.	Mean daily variance ± 95% C.L.
	Field	0.60 ± 0.088
	Ridge	
	Northerly aspect	0.48 ± 0.067
	Southerly aspect	0.62 ± 0.076
	Centre	0.50 ± 0.063
	Within soil	0.39 ± 0.059
	Within grass (*L. perenne*)	0.25 ± 0.043
Winter 1988/89	*A. stolonifera*	0.45 ± 0.065
	D. glomerata	0.24 ± 0.043
	H. lanatus	0.27 ± 0.049
	L. perenne	0.38 ± 0.061
	Bare ground	0.81 ± 0.099
	Air	0.79 ± 0.112
Winter 1989/90	*A. stolonifera*	1.02 ± 0.045
	D. glomerata	0.83 ± 0.029
	H. lanatus	0.88 ± 0.034
	L. perenne	0.91 ± 0.034
	Bare ground	1.51 ± 0.110
	Air	1.48 ± 0.103

4.5 RIDGE VEGETATION STRUCTURE AND PREY AVAILABILITY

4.5.1 MATERIALS AND METHODS

Vegetation structure

Turves removed as part of the predator sampling regime during winter 1988/89 (see Chapter 2) were used to investigate structural differences between the four grass species on within-field ridges 1 & 2. Six turves (one from each block) of each grass species were analysed from each ridge. Grass from individual turves was cut into three height categories: 0-5cm (0cm being at the soil surface), 5-15cm and 15+cm. Grass belonging to each height category was then divided into live and dead material, dried at c. 80°C for 48h (or until constant weight) and then weighed.

Assessment of prey density

Accompanying the predator sampling in the winter 1989/90, densities of potential prey in the four single-grass species treatments on ridge 1 were assessed. A salt flotation technique adapted from Sotherton (1984) was used to extract the prey; predators were removed by hand sorting and the soil and grass debris of each turf immersed in saturated saline solution. Samples were left for 1h for soil particles to settle and the floating organic matter then poured off into a series of sieves. The initial sieve (aperture 2mm) separated large particles of grass from the smaller organic particles, including the prey items, which were collected in a second much finer sieve (aperture size 250 microns). The fine organic debris was then transferred to 70% alcohol for storage. Prey were identified, using a binocular microscope, into six broad taxa: Homoptera, Collembola, Hymenoptera, Diptera, Chrysomelidae, and others. Nine turves of each grass species were assessed (three turves from each of three blocks per grass species).

To quantify the efficiency of the flotation method, ten of the turf samples were each "seeded" with 100 freeze-killed Drosophila melanogaster (Meigen) pupae, obtained from a laboratory culture. Pupae were added to the soil of each sample after the turf had been broken up and the predators had been removed by hand sorting. The number of pupae counted during sorting and identification of the prey was then used to calculate percentage efficiency which was applied to all prey types.

4.5.2 RESULTS

Vegetation structure

The mean biomass of the grass species for each of the plant height and live/dead categories is presented in Table 4.6. Two-way analysis of variance (grass species by ridge) followed by the Tukey (1949) multiple range test for each grass category, revealed no significant differences for each grass species between the two ridges. Significant differences between grass species were, however, observed for all grass components (0-5cm live $F_{1,40} = 32.74$, $P < 0.001$; 0-5cm dead $F_{1,40} = 8.19$, $P < 0.001$; 5-15cm live $F_{1,40} = 9.40$, $P < 0.001$; 5-15cm dead $F_{1,40} = 8.33$, $P < 0.001$; 15+cm live $F_{1,40} = 23.54$, $P < 0.001$; 15+cm dead $F_{1,40} = 46.14$, $P < 0.001$; total live $F_{1,40} = 8.98$, $P < 0.001$; total dead $F_{1,40} = 19.38$, $P < 0.001$; total biomass $F_{1,40} = 20.42$, $P < 0.001$). Overall, D. glomerata tended to have the highest biomass for each of the different categories (except 0-5cm live), with a decline in biomass in the order of H. lanatus > L. perenne > A. stolonifera.

To investigate the relative importance of plant biomass in predator distribution, regressions of densities of Demetrias atricapillus and Tachyporus hypnorum (log (n+1 no./$0.04m^2$)) on each measure of grass weight were carried out for individual turves i.e. grass species were not treated individually. Predator numbers were also regressed against the ratios of live:dead grass for each grass height, and also against the total live:dead ratios for each sample. Ridges 1 & 2 were tested independently because of significant between-ridge differences in predator numbers. For ridge 1, numbers of Demetrias atricapillus were significantly positively correlated with all measures of dead biomass (0-5cm $r_{22}^2 = 0.75$, $P < 0.001$; 5-15cm $r_{22}^2 = 0.64$, $P < 0.001$; 15+cm $r_{22}^2 = 0.42$, $P < 0.001$). There was also a significant positive relationship with the 5-15cm and 15+cm measures of live biomass ($r_{22}^2 = 0.79$, $P < 0.001$ and $r_{22}^2 = 0.74$, $P < 0.001$, respectively). Forward stepwise multiple regression, including each of these factors (variables entering the regression at $P = 0.05$), selected 0-5cm dead and 5-15cm live to be the most important, these two factors combined accounting for 86% of the variability in Demetrias atricapillus density (i.e. $r^2 = 0.86$). The remaining measures were not selected in the regression procedure, suggesting strong intercorrelation between these factors and the two selected in the stepwise regression (i.e. several variables interdependent on one another). Total live biomass, total dead biomass and total biomass also produced significant positive relationships (total live $r_{22}^2 = 0.53$, $P < 0.001$; total dead $r_{22}^2 = 0.68$, $P < 0.001$; total $r_{22}^2 = 0.71$, P

< 0.001), with no other significant relationships revealed.

Regression of Tachyporus hypnorum numbers on all measures of biomass for ridge 1 produced only one significant relationship; this was a positive correlation with 5-15cm dead biomass ($r_{22}^2 = 0.25$, $P < 0.05$).

Unlike ridge 1, when data for ridge 2 were used to calculate a regression of Demetrias atricapillus numbers on the individual biomass variables, significant relationships occurred only with 0-5cm and 5-15cm dead ($r_{22}^2 = 0.18$, $P < 0.05$ and $r_{22}^2 = 0.22$, $P < 0.01$, respectively). Similarly, Tachyporus hypnorum produced only two significant relationships (5-15cm live $r_{22}^2 = 0.22$, $P < 0.05$ and 5-15cm dead $r_{22}^2 = 0.18$, $P < 0.05$).

Assessment of prey

No significant relationships were revealed in regressions between the numbers (log(n+1 no./0.04m^2)) of D. atricapillus and T. hypnorum and any individual prey group (log(n+1 no./0.04m^2)) or pooled total prey items (log(n+1 no./0.04m^2)) in the individual soil samples. From the counts in the ten soil samples to which Drosophila pupae were added, the mean efficiency of the salt flotation technique was 73%.

Table 4.6. Mean biomass (g) at different height categories (see text) of four species of grass from within-field ridges 1 & 2, winter 1988/89. Different letters within a row indicate significant between-treatment differences at the 5% level (two-way analysis of variance followed by Tukey's test).

Biomass category (g)	Agrostis stolonifera	Dactylis glomerata	Holcus lanatus	Lolium perenne
0-5cm live	5.63 (a)	3.56 (b)	1.47 (c)	0.79 (c)
0-5cm dead	9.94 (b)	20.93 (a)	20.02 (a)	14.23 (ab)
5-15cm live	3.74 (c)	7.47 (a)	6.77 (ab)	4.32 (bc)
5-15cm dead	16.05 (b)	28.92 (a)	28.48 (a)	16.83 (b)
15+cm live	0.83 (b)	4.92 (a)	2.27 (b)	1.40 (b)
15+cm dead	5.77 (b)	34.49 (a)	9.65 (b)	6.79 (b)
Total live	10.20 (b)	15.95 (a)	9.83 (b)	7.19 (b)
Total dead	31.77 (c)	84.33 (a)	58.15 (b)	37.84 (bc)
Total biomass	41.97 (c)	100.28 (a)	67.98 (b)	45.04 (bc)

4.6 LABORATORY AND EXPERIMENTAL INVESTIGATIONS INTO THE IMPORTANCE OF FOOD.

4.6.1 MATERIALS AND METHODS

Starvation experiment

To investigate the potential importance of food during the winter period an experiment was carried out to study the effects of starvation on mortality in a test population of D. atricapillus. It was intended to carry out a parallel experiment on T. hypnorum but high mortality in the field-collected population meant that sufficient numbers were not available.

Approximately 400 adult D. atricapillus were collected from natural field boundaries during late December 1989. These were maintained in the laboratory (c. 15°C, 10h day length) with food (small amounts of fish paste) for approximately one week before the experiment began.

At the onset of the experiment, all beetles were starved at c.20°C for 60h to ensure that their guts were completely empty (Coombes 1987). Eight beetles were then placed in each of forty-two, 10cm diameter ventilated polystyrene Petri dishes, each containing a 0.5cm depth of sterile soil (Levington's F2) and three strips (15cm x 1cm) of moistened tissue paper to maintain humidity and provide refuges. This density/dish (c. $1000m^{-2}$), although very high, was within the range of that occurring for this species on ridge 1 in winter 1988/89. An excess of food (fish paste) was then introduced into half of the dishes and all dishes were placed outdoors in a shaded position, in a large ventilated clear plastic container (0.7mx0.6m x 0.3m deep) so that they were exposed to the ambient temperature, but protected from the direct effects of rainfall.

Dishes were assessed at weekly intervals, when three dishes from each of the two treatments were randomly selected and the number of live beetles in each dish recorded. These beetles were starved as before (60h at 20°C) and then freeze killed. The remaining dishes were re-set (tissue paper moistened and food replenished) and replaced outdoors in the container. In addition, all dishes were checked twice during each weekly period and any dead beetles removed to reduce the potential for cannibalism, potentially most likely in the treatments with no food. These overall assessments were carried out for seven weeks from 10 January 1990.

Hourly temperature recordings inside one Petri dish (identical to the test dishes but without D. atricapillus) and at soil level adjacent to the experimental container were monitored throughout the trial period using a Grant "Squirrel" microclimate recorder.

Freeze killed beetles were sexed (examination of the underside of the abdomen at x30 magnification revealed a pair of sclerotised coxites visible through the basal sternites for females, and a single sclerotised aedeagus for males (Coombes, 1987)) and individual fresh weights recorded. The combined length of head and pronotum were also recorded. This measure provided an indication of size independent of abdomen length; the latter could be influenced by physiological condition (factors such as size of fat body can influence the degree of abdomen distention in this species (Coombes, 1987)).

Gut dissection of field caught specimens

Field caught individuals of T. hypnorum and D. atricapillus were dissected to look for prey fragments in the gut. This was in order to determine whether any feeding was taking place during the winter period. Individuals were collected from field boundaries on various dates throughout winter 1989/90, although more intensively (approximately weekly) during the late winter period. Daily shade temperature data were available throughout the collection period from meteorological records taken near to the study site.

Beetles were killed immediately following collection by placing in 70% alcohol. Guts were removed under a binocular microscope and placed on a slide with 50% glycerol. For D. atricapillus it was possible reliably to remove only the fore-gut, so assessments of food content were confined to this section. For T. hypnorum, the mid- and hind-gut were the most easily identified gut sections. For both species the amount of food present in the gut sections was estimated using a scale of 0 to 3, similar to that of Coombes (1987), where: 0 = no food, 1 = few food particles, 2 = many food particles, and 3 = full.

4.6.2 RESULTS

Starvation experiment

Two-way analysis of variance was carried out to compare between-week percentage mortality (√arcsine transformation) in the starved and fed D. atricapillus populations. The results indicated significantly higher percentage mortality in the population without food than in the population with food provided ($F_{1,30} = 25.88$, $P < 0.001$) (Fig.4.1). This was reflected in the overall mean percentage mortality of the two populations (19.6% in the fed population, 49.4% in the starved population). No significant differences were revealed for percentage mortality between weeks. However, when the two populations were tested individually (one-way analysis of variance), significant between-week differences in percentage mortality (√arcsine transformation) were observed for the starved population; greatest mortality occurred in the final two weeks ($F_{6,14} = 2.94$, $P < 0.05$). No significant between-week mortality differences were revealed for the population with food.

Starvation-induced mortality was calculated by subtracting the number of dead individuals (out of the initial twenty-four) in the control population from the number of dead individuals in the starved population for each week. Regression analysis revealed no significant relationships between these values and values for mean weekly temperature, weekly maximum and minimum temperatures or weekly mean temperature variance. However, a significant positive relationship existed between starvation induced-mortality and cumulative mean temperature (calculated by adding one week's mean temperature to all the preceding weeks' and dividing by week number (e.g. the value for week 3 was a product of weeks 1, 2 and 3) ($y = -35.4 + 5.7x$, $r_5 = 0.81$, $P < 0.05$). No significant differences were observed between temperature means and temperature variances inside the experimental container and the equivalent ambient temperature measures.

The sex ratio of the live individuals at the end of each week did not differ between the control and the starved populations (Mann-Whitney U test, $U = 0.06$ $P = 0.95$, $n = 14$).

To investigate weight loss through time it was necessary to correct for size variation between individuals (females larger than males, for instance). Weights of individual beetles were therefore divided by the combined length of their head and pronotum. One-way analysis of variance revealed significant between-date differences for the corrected weights of the starved population, with the lowest values tending to occur towards the end of the experiment ($F_{6,59}$ = 12.1, P < 0.001). For the fed population however, no significant between-date differences were observed for the corrected weights i.e. no significant weight loss occurred during the experiment (Fig.4.2).

Gut dissection of field-caught animals

Few of the T. hypnorum dissected contained any solid food in their guts (Fig. 4.3). Kruskall-Wallis one-way analysis by ranks revealed no significant differences in gut index between dates or sexes.

A high proportion of D. atricapillus individuals however, had food in their guts, and this species had higher overall gut indices than those recorded for T. hypnorum (Fig. 4.4). As for T. hypnorum, Kruskall-Wallis analysis revealed no significant differences in gut index between sexes. There were however significant differences between dates (H = 22.8, n = 10, P = 0.007). The lowest overall values were observed on 4 December and 11 January, with the highest on 8 February and 8 March. An attempt was made to explain this between-date variation in terms of temperature using Spearman rank correlation. Although higher temperature appeared to be associated with higher overall gut index levels (Fig.4.4), no significant correlations existed between mean gut index or proportion of individuals with zero gut index and the mean temperature for the week prior to collection (the mean air temperatures for the weeks prior to each sample date were calculated from the meteorological recordings described above; temperature prior to sampling was considered to have a more important influence on gut content than that on the sampling date itself, as suggested by Coombes (1987)).

Figure 4.1. Mean weekly percentage mortality (√arcsine transformation) ± 95% C.L. of Demetrias atricapillus populations with (▓) and without (░) food (see text).

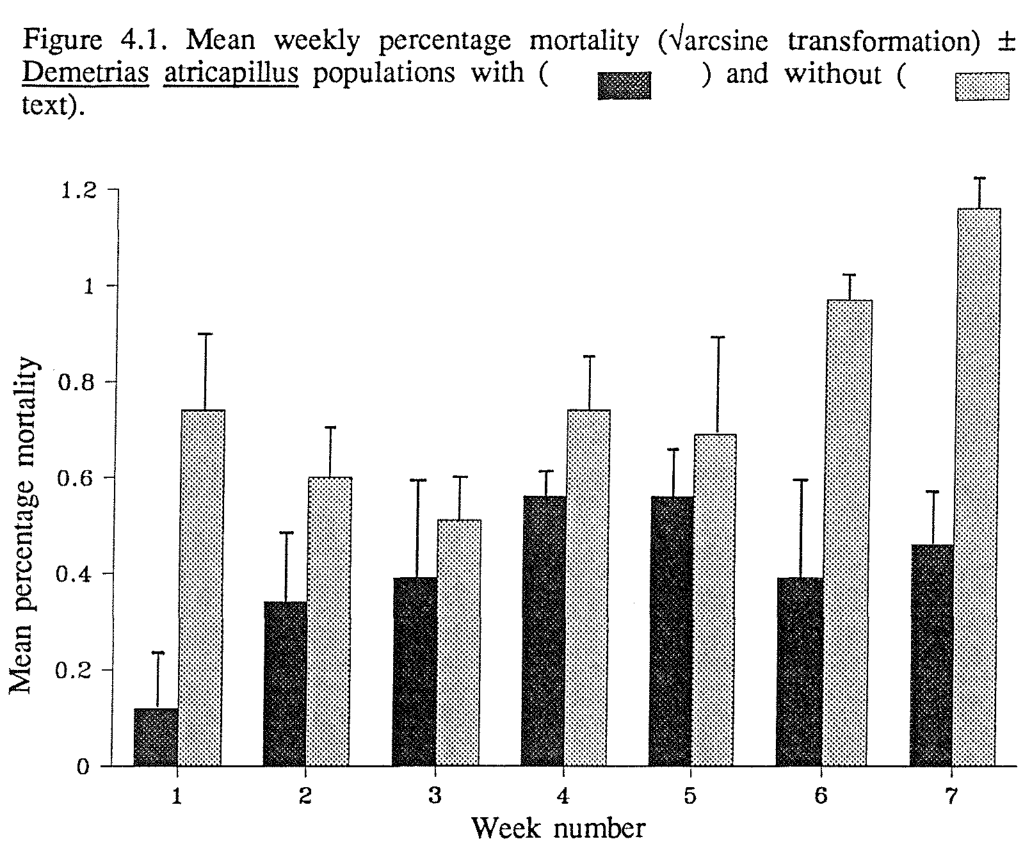


Figure 4.2. Mean weekly corrected weight ± 95% C.L. of Demetrias atricapillus populations with (▓) and without (░) food.

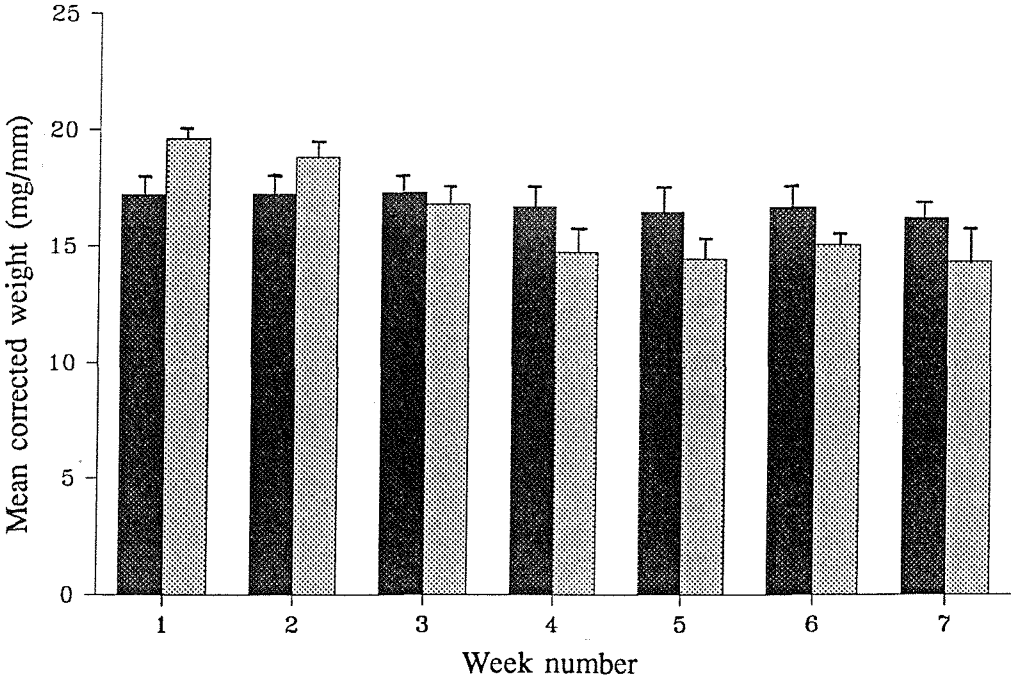


Figure 4.3. Gut content indices for Tachporus hypnorum sampled during winter 1989/90. Indices expressed as proportion of individuals in each class per date. (Gut classes 0 = ▩ 1 = ▨ 2 = ░ 3 = ☐).

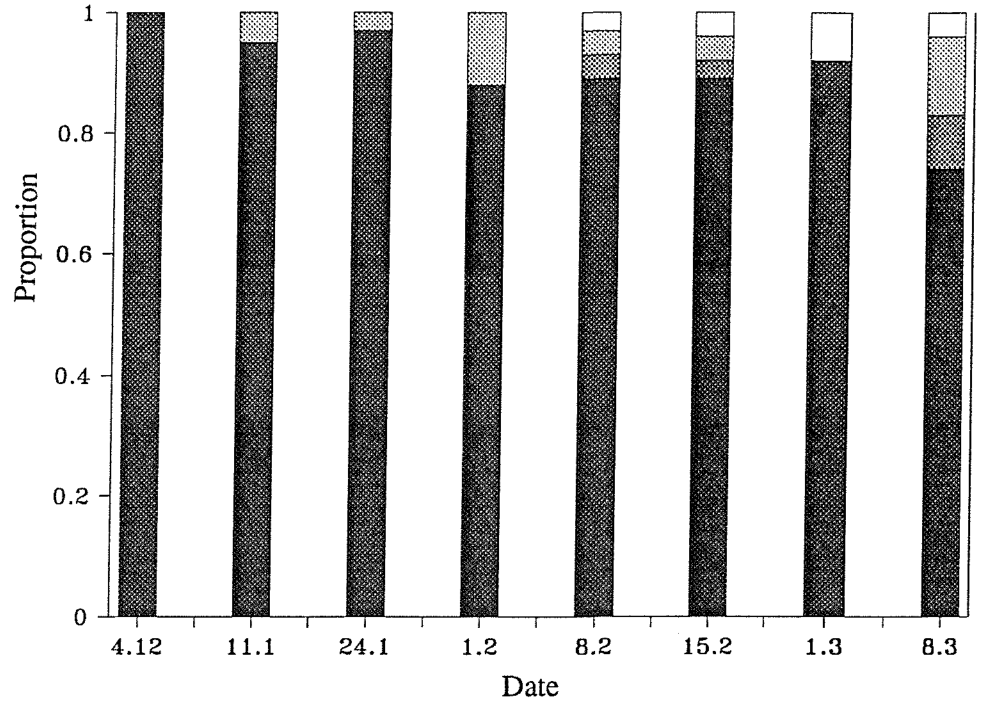
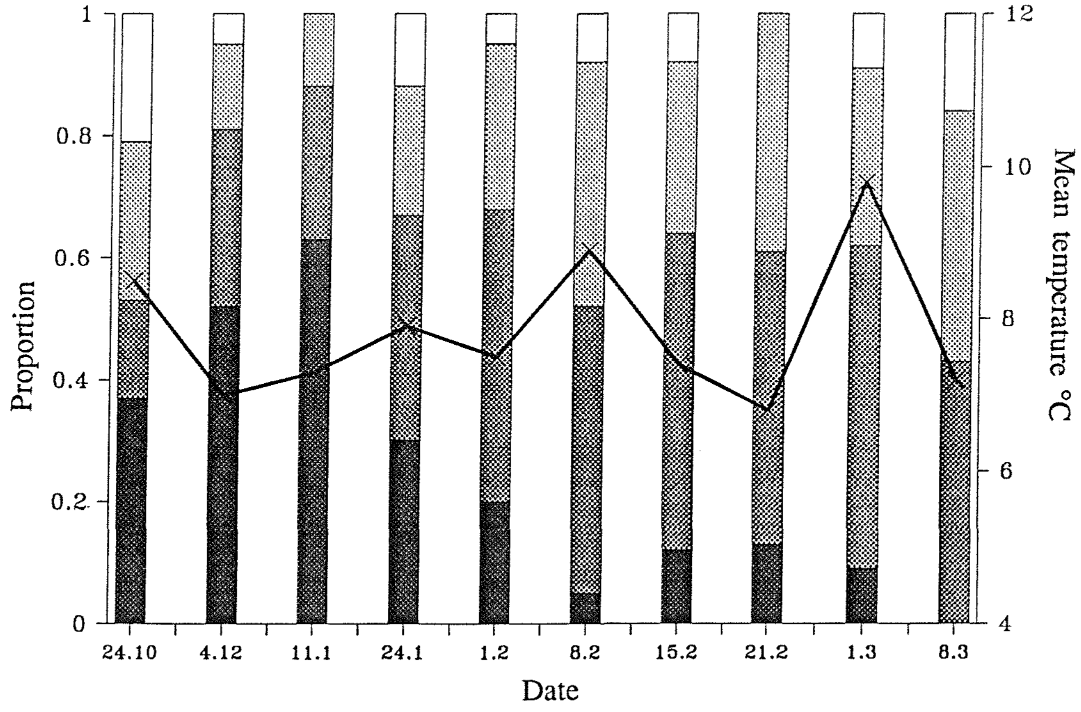


Figure 4.4. Gut content indices for Demetrias atricapillus sampled during winter 1989/90 (see Fig.4.3). Also shown is the mean temperature for the week prior to collection.



4.7 DISCUSSION

Boundary surveys

The results of the 1982/83 predator distribution study showed that predator numbers could vary significantly between particular types of field boundary (Sotherton 1985). In the 1989/90 study, although numbers were observed to vary between individual boundaries (which could indicate differences in boundary quality), there were no clear distribution patterns between boundaries grouped according to type. However, as composition and relative abundance of carabid (Thiele 1977; Wallin 1985) and Tachyporus species (Dennis 1989) have been shown to vary considerably between fields, it is possible that localised differences in abundance could have masked underlying trends in selection of favourable habitats i.e. overwintering predator densities, even in the most suitable habitats, are likely to reflect local abundance. Similarly, local differences in abundance could explain the poor relationships revealed in the regression analysis when the two seasons' data were combined (only one factor correlated with D. atricapillus distribution (namely the presence of Dactylis glomerata) and no factors correlated with the distribution of Tachyporus spp.). These results suggest therefore, that in order to understand the mechanisms of overwintering survival and site selection, it is necessary to examine species at the within-field population level, or even at the level of individual predators.

Overwintering survival experiments

By designing an enclosed manipulation experiment on a single field boundary, the problems of between-boundary physical and biotic heterogeneity discussed above were removed. The results of the 1987/88 and 1988/89 trials indicated differential mortality between overwintering refugia for both predator species. For T. hypnorum, mortality varied with the gradient of structural complexity; greatest mortality in the bare earth treatments and lowest mortality within tussocks of Dactylis glomerata. For D. atricapillus, a similar trend in mortality was observed, with food availability also implicated as an important factor for survival. The microclimate studies in both experiments indicated that temperature fluctuation could be an influence in overwintering survival (a factor discussed in detail below). However, even in the treatments with greatest mortality (the bare earth), 30% of T. hypnorum and 20% of D. atricapillus survived to the end of the experiment. In the ridge predator sampling studies of winters 1988/89 and 1989/90, T. hypnorum and D. atricapillus were found at higher overwintering densities in the tussock-forming grass species than in adjacent mat-forming species. As these differences were obtained from data collected throughout the mid-winter period (suggesting that maximum overwintering mortality levels had not been reached) and the grass treatments with even the lowest predator densities provided more suitable refugia than bare earth, it would suggest that the marked between-treatment distribution patterns on the within-field ridges could not be attributed to differential mortality alone, indicating some degree of active habitat selection.

Investigations into microclimate and vegetation structure

In winter 1987/88 the grass mat/tussock refuge provided a less variable temperature environment than the other five profiles recorded; this buffering capacity by grass tussocks and leaf litter of temperature variation has been highlighted previously for naturally occurring tussocks (Luff 1965; Edgar & Loenen 1974; Bossenbroek et al. 1977a). A positive correlation has been shown to exist between high overwintering predator densities and a less variable temperature environment, and such an environment may have the effect of reducing insect mortality (Desender 1982). It is of interest therefore that such microclimate characteristics could be created within the first year of within-field grass ridge establishment. With improved grass establishment during the 1988/89 winter, this feature was enhanced, with the between-species temperature study showing that certain grass species, namely the tussock forming Dactylis glomerata and Holcus lanatus, provided less variable temperatures in overwintering refugia than did the two mat forming grass species Agrostis stolonifera and Lolium perenne. These between-grass differences were also apparent in the 1989/90 study, with the tussock forming grasses again providing less variable temperature environments. The results of the 1988/89 study however showed this temperature stabilising effect during the mid-winter period, whereas the results of the 1989/90 study also indicated that such differences were detectable during early winter.

Grum (1971) suggested there could be considerable spatial differentiation in abiotic factors, providing a mosaic of microhabitats within a particular site. These in turn were thought by Grum to be responsible for the level of aggregation of individuals of some carabid species. In this way, the temperature buffering properties of the tussock forming grasses could be an abiotic cue in overwintering site selection for both T. hypnorum and D. atricapillus.

The vegetation biomass study indicated that physical structure differed between grass species. Strong positive correlations existed between the distribution of D. atricapillus and several measures of grass biomass for ridge 1. However, equivalent statistical examination of ridge 2 revealed only two, much weaker, relationships. This was attributed to much lower densities of D. atricapillus on ridge 2 at this time (Chapter 2), as between-ridge differences with respect to the various measures of grass biomass were not apparent.

Andersen (1985) concluded that structure of vegetation and substrate provided important stimuli in the process of site selection for certain Bembidion spp.. Similarly, Bossenbroek et al. (1977a) suggested that the numbers of animals (insects and spiders taken together) within tussocks were not limited by abiotic factors only, but also influenced by the biomass of living and dead grass leaves. From the results of the present study, using biomass as an indicator of structure, it was unlikely that vegetation structure alone influenced the distribution of T. hypnorum, as only poor correlations with the various measures of biomass were obtained from both ridges. For D. atricapillus however, strong positive relationships with various biomass categories implicated vegetation structure as an influence on winter distribution, at least at the higher densities observed on ridge 1.

Laboratory and experimental investigations

Dissection of field caught D. atricapillus showed a high proportion containing food. From laboratory feeding and gut dissection studies, Coombes (1987) obtained results suggesting that not all D. atricapillus individuals known to have fed contained solid remains in their guts. It was predicted that at 10°C only 71% of those beetles known to have fed within the previous 48 hours would show gut contents on dissection. Although these data were obtained during the summer, they suggest that the proportion of individuals feeding, and hence the importance of food over the winter period, was underestimated by gut dissection. The results of the starvation experiment however, confirmed the importance of food for this species during the winter. Test populations without food suffered significantly higher weight loss and mortality than populations with food provided.

Temperature affects digestion rate (Chapman 1969) and feeding rate (Coombes 1987) in insects. The influence of temperature on D. atricapillus was revealed in the starvation experiment, with a strong positive correlation existing between cumulative weekly mean temperature and starvation induced mortality. However, no simple relationship was revealed between feeding and temperature in the dissection study, although the amount of feeding in terms of the gut index and percentage of individuals containing food varied between dates. Coombes (1987) reported that D. atricapillus did not enter an obligative diapause, but was subject to variable periods of reduced activity induced directly by environmental factors (i.e. a quiescent period induced directly by environmental factors, rather than a true diapause which is a cessation of growth, of a specific developmental stage, induced by internal factors (Crowson 1981)). It is possible therefore that feeding is influenced by a complex of environmental factors rather than just temperature alone.

Gut dissection results for T. hypnorum suggested that less feeding took place during the winter in this species than in D. atricapillus. These results are similar to those obtained by Sunderland in winter 1974/5 (in Dennis 1989) which showed that only 5-10% of T. hypnorum overwintering in pasture contained food in their guts during the period of December to February. Lipkowe (1966) demonstrated that overwintering adults undergo an obligative diapause before sexual maturation. The reduced activity during this development phase could therefore account for the observed rate of feeding. However, in laboratory feeding experiments followed by gut dissection, Sunderland et al. (1987) showed that only 42% of individuals of Tachyporus spp contained solid fragments following an aphid meal (the low proportion being attributed to their fluid feeding ability). Gut dissection of field-caught individuals therefore, as with D. atricapillus discussed above, will tend to underestimate the actual level of feeding activity. Furthermore, mycophagous activity in cereals in spring and summer (Dennis & Wratten 1991b) might suggest fungi to be an important component of their winter diet, a factor likely to have been missed during assessment of gut contents (spores being less apparent on dissection than solid fragments of arthropod prey (Vickerman pers. comm.)).

Overall therefore, the presence of a suitable food source appeared to be an important requirement for successful overwintering for both species, although perhaps more markedly for D. atricapillus. Whether the presence of prey and saprophytic fungal food provide biotic stimuli in habitat selection is unclear. Bryan & Wratten (1984) demonstrated that many polyphagous predators including T. hypnorum could detect and respond to prey aggregations in summer. However, in the present study, no relationships were observed between predator numbers and potential prey numbers. If T. hypnorum was responding to abundance of fungal food rather than to arthropod prey, then this might be expected; Webster (1959) reported Dactylis glomerata to support a range of fungal species. For D. atricapillus however, it suggests that factors other than food are likely to influence site selection, although there remains the possibility that differential prey densities may have existed early in the season and influenced subsequent predator distribution accordingly.

One factor so far ignored is humidity. However, although its importance as a factor governing choice of habitat has been highlighted previously (Thiele 1977), the inability to monitor humidity accurately in the field excluded this factor from the present investigation.

Conclusion

In the present study, a complex of biotic and abiotic variables were implicated as important factors in the overwintering process. It was unclear however, whether distribution and survival were governed by one, some, or the combined action of all. For example, the physical characteristics which provided the highest correlations with Demetrias atricapillus distribution were associated with the two tussock forming grass species D. glomerata and H. lanatus. These tussock-forming grasses however, also provided the most stable temperature environments. It is not possible therefore to separate physical structure from temperature microclimate as a selection stimulus, as both factors are likely to be highly intercorrelated. Similarly, the degree of temperature fluctuation and the importance of food can also be linked. In many Coleoptera for example, regular daily fluctuations of temperature lead to improved survival and faster development rates than equivalent constant temperatures (Crowson 1981); a factor illustrated for D. atricapillus by Coombes (1987), who showed in laboratory-based experiments, that consumption rates were higher in populations subject to variable temperature and humidity than in populations maintained under constant conditions. A stable temperature environment therefore may reduce the demands for food over the winter period, thus reducing the levels of starvation induced mortality (a potentially important factor if, as suggested by Coombes (1987) for D. atricapillus, food supply might be limited). Furthermore, other factors such as drainage (shown to be enhanced by D. glomerata (Beddows 1959)), shelter from wind (provided by tussock structures (Bossenbroek et al. (1977b)) and humidity (shown to be high within tussocks in the winter (Webster 1956)) could all influence habitat selection and are all likely to be intercorrelated to some extent (Thiele 1977). However, the observed distribution patterns of D. atricapillus and T. hypnorum suggest that the overwintering requirements of these species are quite specific. As other species belonging to such eurytopic groups would be expected to have similar, average characteristic microhabitat requirements

(Thiele 1977), appropriate management or creation of suitable field boundary habitats should be encouraged, in order that these requirements are satisfied, and populations of such beneficial insects maintained or enhanced in farmland.

CHAPTER 5. SPATIAL DISTRIBUTION OF POLYPHAGOUS PREDATORS IN CEREAL FIELDS AND ADJACENT HABITATS IN SUMMER

SUMMARY

(1) Data are presented from a descriptive study which investigated the distribution of polyphagous predators in arable land in summer.

(2) The results of the study indicated that even the most forest-like boundary habitats contained few forest-specific species; most predator species interacted between field and boundary habitats to some extent.

(3) The results also showed that several important boundary overwintering predator species maintained some association with certain boundary types during summer, providing further evidence of the importance of boundary habitats in the arable environment.

5.1 INTRODUCTION

The distribution of carabid beetles in arable land has been the subject of many investigations. The importance of boundary habitats as overwintering sites for certain species has been established (Desender 1982; Sotherton 1984, 1985; Wallin 1985). Gorny (1970) and Bonkowska (1970) both identified shelterbelts as important permanent features of the agricultural environment, providing alternative habitats for several species of predatory carabids. Other authors however, suggest that other than some seasonal migration between habitats typical of a few eurytopic species, many carabid species are confined to either field or boundary habitats i.e. interaction between habitats occurs only to a minor extent (Thiele 1964; Pollard 1968b). The main objective of this chapter is to evaluate the importance of surrounding habitats for the densities and distribution of polyphagous predator populations (including predator groups other than Carabidae) in arable fields in the summer and to investigate, for example, whether boundary habitats may have a role to play beyond that of providing overwintering sites for certain predator species.

5.2 MATERIALS AND METHODS

To investigate the distribution of polyphagous predators during the summer months, pitfall trap catches, providing a measure of "effective abundance" (den Boer 1977), were taken between 14 June and 5 August 1988 from the same mixed arable farm (South Allenford Farm, Damheram, Hampshire) used in the 1982/83 winter boundary study (described in Chapter 4). Five pitfall traps (diameter 9cm, depth 13cm) filled to 1/3 with water containing detergent were placed in a line 10m apart at the centres of each of three winter wheat fields (varying in size from 32 to 39 ha). Five pitfall traps were also placed along a representative 50m portion (one trap every 10m) of eight of the field boundaries adjacent to these cereal fields. The field boundaries were chosen so as to include north- and south-facing examples of the three most common boundary types at this study site i.e. three hedge banks, three grass banks, and two shelterbelts. Pitfall traps were emptied and re-set at weekly intervals throughout the study period (eight weekly catches in total). The most abundant polyphagous predatory arthropods, specifically species of Carabidae and Staphylinidae considered to have some predatory potential (after a variety of sources including Speight & Lawton (1976), Thiele (1977), Hengeveld (1980) and Sunderland & Vickerman (1980)), but excluding the Araneae, were identified to species or genus.

5.3 RESULTS

The mean number/trap (± 95% C.L.) of the most abundant species of polyphagous predators recorded in the various habitats throughout the sampling period are given in Table 5.1. Comparison of the means and 95% C.L. indicated that many species were caught evenly throughout the various habitats. *Loricera pilicornis*, *Pterostichus madidus*, *P. melanarius* and to a lesser extent *Tachyporus hypnorum* however, were all caught in higher numbers in the open field areas. Conversely, *Agonum dorsale*, *Paederus littoralis*, *Philonthus* spp. (excluding *P. cognatus*) and *Forficula auricularia*, all tended to show lower numbers at the field centres. *Bembidion obtusum*, *Harpalus affinis* and *H. rufipes* although represented throughout, showed highest numbers in the grass bank habitats and lowest numbers in the shelterbelts.

Table 5.1. Pitfall trap catches (mean number per trap ± 95% C.L.) of predatory arthropods in three cereal fields and adjacent boundary habitats between 14 June and 5 August 1988. Those species marked with a * show some significant differences in distribution between habitats. Species without an authority have been listed in previous chapters.

Species	Cereal field	Grass bank	Hedge bank	Shelterbelt
Carabidae				
Agonum dorsale*	1.4 ± 0.66	4.5 ± 1.80	6.6 ± 4.34	1.6 ± 1.57
Agonum muelleri Herbst	0.4 ± 0.31	0.2 ± 0.22	0.1 ± 0.13	0.8 ± 0.82
Amara spp.	1.4 ± 1.43	6.5 ± 4.33	1.1 ± 0.86	1.2 ± 1.03
Badister bipustulatus Fab.	0.1 ± 0.17	0.7 ± 0.51	0.5 ± 0.83	0.8 ± 0.52
Bembidion lampros	4.4 ± 2.54	12.4 ± 6.85	8.7 ± 2.93	8.0 ± 5.79
Bembidion obtusum*	4.1 ± 2.22	5.2 ± 4.75	3.1 ± 2.46	0.8 ± 0.82
Calathus spp.	0.6 ± 0.55	0.7 ± 0.56	0.1 ± 0.14	3.8 ± 3.12
Carabus monilis Fab.	0.5 ± 0.71	0.1 ± 0.19	0.3 ± 0.32	0.2 ± 0.28
Carabus nemoralis Mull.	0.1 ± 0.18	0.1 ± 0.28	0.3 ± 0.43	0.0
Carabus violaceus L.	0.2 ± 0.28	0.1 ± 0.65	0.3 ± 0.24	1.0 ± 0.63
Demetrias atricapillus	0.6 ± 0.66	0.4 ± 0.39	0.1 ± 0.28	0.2 ± 0.28
Harpalus affinis Schrank*	1.1 ± 1.01	4.1 ± 2.14	1.2 ± 0.86	1.0 ± 0.63
Harpalus rufipes*	5.9 ± 2.27	13.7 ± 3.37	5.5 ± 3.33	2.0 ± 0.99
Leistus spinibarbis Fab.	0.5 ± 0.49	1.0 ± 0.78	0.5 ± 0.45	0.8 ± 0.53
Loricera pilicornis Fab.*	7.1 ± 2.99	1.7 ± 0.82	2.6 ± 1.41	3.0 ± 1.17
Nebria brevicollis	3.1 ± 2.48	8.1 ± 5.19	3.3 ± 1.61	3.6 ± 2.11
Notiophillus biguttatus	0.8 ± 0.43	1.7 ± 0.82	1.5 ± 1.04	1.6 ± 1.14
Pterostichus madidus Fab.*	37.4 ± 20.28	7.0 ± 4.28	5.5 ± 3.14	10.2 ± 5.96
Pterostichus melanarius Ill.*	386.0 ± 135.45	190.4 ± 49.99	133.0 ± 36.47	140.0 ± 44.78
Synuchus nivalis Panz.	0.3 ± 0.38	1.0 ± 0.99	2.2 ± 2.83	1.8 ± 1.21
Trechus qaudristriatus	8.3 ± 4.08	3.1 ± 1.40	3.3 ± 1.61	4.0 ± 0.88
Staphylinidae				
Paederus littoralis Grav.*	0.2 ± 0.35	1.4 ± 0.75	0.7 ± 0.74	0.8 ± 0.52
Philonthus cognatus Stephens	8.4 ± 7.23	3.0 ± 1.4	0.7 ± 0.71	3.2 ± 0.82
Other Philonthus spp.*	3.3 ± 3.28	24.0 ± 11.76	8.6 ± 3.69	20.8 ± 7.17
Stenus spp.	1.0 ± 1.10	2.6 ± 1.63	2.1 ± 1.23	2.6 ± 1.22
Tachyporus chrysomelinus	6.3 ± 5.33	1.7 ± 1.39	0.9 ± 0.99	0.8 ± 0.82
Tachyporus hypnorum*	12.4 ± 9.10	2.5 ± 1.52	2.5 ± 1.83	0.4 ± 0.34
Tachyporus nitidulus Fab.	6.1 ± 5.28	5.0 ± 2.55	5.5 ± 2.94	1.2 ± 1.12
Tachyporus obtusus*	2.1 ± 1.88	0.5 ± 0.56	0.5 ± 0.44	0.0
Xantholinus spp.	1.4 ± 1.63	1.6 ± 1.67	0.9 ± 0.96	1.2 ± 0.69
Other groups				
Forficula auricularia*	0.0	0.5 ± 0.53	0.1 ± 0.18	1.2 ± 0.28
Opiliones	1.2 ± 1.34	6.3 ± 5.11	3.9 ± 1.77	2.8 ± 1.74

5.4 DISCUSSION

In a similar pitfall study (carried out in west Germany) to the one presented here, Thiele (1964) reported that none of the carabid species most commonly caught was equally distributed between hedge and field and it was concluded that: "the dominant carabids of the hedgerow, being forest species, scarcely penetrate at all into the fields, which are climatically unsuitable for them." In the present study however, although certain species of carabid and staphylinid were caught in high numbers in boundary habitats and others in high numbers at the field centres, the same conclusion can not be drawn, as several species were evenly distributed and even those which were not, appeared to interact with their adjacent habitat to some extent. The exceptions are the common earwig Forficula auricularia which was the only species which did not occur in the field centre, and Tachyporus obtusus and Carabus nemoralis which were the only species absent from a boundary habitat (namely the shelterbelt which represented the most forest-like habitat). Thiele (1977) however, suggested that in the British Isles, where forests are not so common, the forest species element in both fields and hedges is less well developed. It is possible therefore that because of an impoverished fauna, the absence of true forest species (such as Abax ater Villers, Trechus obtusus Erichson and Leistus ferrugineus L., reported in a study in England by Pollard (1968b) to be present in hedgerows but absent from field centres) from the present study site may have reduced the marked between-habitat effect described by Thiele (1964).

Of the species which were present, it is of interest to note that the boundary-overwintering (Sotherton 1985) Agonum dorsale, Bembidion lampros, Demetrias atricapillus and the Tachyporus spp. all showed high levels of interaction with some of the boundary habitats, even at a time when dispersal into the crop is supposed to have taken place (see Chapter 3). Of these, only Tachyporus hypnorum was found at highest numbers at the field centre, and this was significant only from the numbers recorded in the forest-like shelterbelt.

A similar study was carried out in Sweden by Wallin (1988). Of the species common to both studies, the distributions of the autumn breeding Pterostichus melanarius and Harpalus rufipes related well to those presented here. Wallin showed that P. melanarius was caught in field, boundary, and adjacent non-crop habitats; however the central parts of the fields were favoured for reproduction and larval development, indicated by the largest number of teneral adults caught in this area. Similarly P. melanarius was most abundant at the field centres in the present study, with a high proportion of teneral adults caught (personal observation). Wallin also observed that H. rufipes larvae accumulated along field edges after harvest, resulting in large numbers of teneral adults emerging at this site. This compares well with the observed distribution of H. rufipes in the present study and may explain the greater abundance in the grass banks than in the other habitats, since these grassy edges are essentially islands of vegetation vital to the survival of the seed-eating larvae of this species (Luff 1980).

Conclusion

The results of this distribution study showed that at this study site at least, even the most forest-like boundary habitats contained few forest-specific species; most predator species interacted between field and boundary habitats to some extent. Furthermore, the high abundance of certain predator species in some field boundary types (especially the grass banks and hedge banks) indicates that as well as providing overwintering refugia, field boundaries may play an important role during the summer months, perhaps by providing alternative stable habitats for food or reproduction; such "risk spreading" (den Boer 1982) tactics ensure survival of at least some offspring in the event of a severe habitat disturbance.

From a pest management perspective, the high level of population interaction with boundary habitats might indicate the need for some intra-crop manipulation such as under-sowing or mulching (shown to encourage spring field predator colonisation by Vickerman (1977) and Dennis (1989) respectively) so that field colonisation can be enhanced and the biocontrol potential of these predators maximised.

CHAPTER 6. GENERAL DISCUSSION

Economics of ridge production

The costs of establishing the within-field ridges described in the previous chapters were outlined in Wratten (1988b). Updated to 1990 prices, the combination of labour costs for bank establishment (1-2 man days) with the yield loss due to the land taken out of production (c. £30 assuming average yield = 6t/ha at £110/t), together with the cost of grass seed (ridge sown with just D. glomerata = £5), would amount to c. £85 in the first year for a 20ha winter wheat field. Subsequent costs would comprise gross yield loss at only £30 per year. However, an aphid population kept below a spray threshold by enhanced natural enemy populations could save £300 per annum in labour and pesticide costs for a 20ha field; alternatively, prevention of an aphid-induced yield loss of 5% could save £660 for a 20ha field.

Once such ridges are established, the competitive nature of the grass species chosen should exclude most noxious weeds; in the summers of 1988 and 1989, such species as Galium aparine L. (cleavers) and Alopecurus myosuroides Huds. (black grass) were occasional on the ridges and occurred only in areas of poor grass establishment. Such areas however were a consequence of hand sowing small areas. In a similar study in Sweden it has been possible to establish equivalent new habitats by machine drilling, thus minimising low percentage grass cover (Chiverton, 1989). Another potential problem is that autumn or spring applications of grass herbicide to adjacent crops could damage the grass cover; a bare rotovated or residual herbicide-treated strip between ridge and crop would minimise this, although obviously this would increase the area of land taken out of production. However, no such damage to the grasses on the ridges in the present study occurred during three commercial cropping seasons, in the absence of such a strip. Furthermore, with respect to herbicide drift/management, Festuca spp are not affected by many graminicides (M. Nowakowski, Willmots Ltd., pers. comm.) and therefore are a possible idea for the future with respect to the creation of overwintering habitats (although the role of such grasses as overwintering refuge sites has not been quantified).

Beyond the potential for enhancing biocontrol in arable land (potentially allowing a reduction in chemical control measures as a consequence), the creation of within-field ridges may also have economic and environmental benefits with respect to soil erosion. Although wind erosion is less likely to cause great problems in the U.K., Evans & Cook (1987) concluded that water erosion occurred widely throughout England, was more prevalent than was previously thought and documented evidence that it was currently on the increase. Evans (1985) estimated that some 40% of arable land in England & Wales was now at risk. Soil erosion on slopes however, is undoubtedly reduced with hedgerows along contours; the hedge underbanks (equivalent to the within-field ridges) being of particular importance in reducing surface run-off (Forman & Baudry 1984). Similarly, from a study in the Californian prairies, Anderson (in Bugg 1990) suggested restoration of native perennial bunch grasses, even along road side verges, could help to control soil erosion. Moreover, the distance between hedgerows is an important factor in inhibiting soil erosion, and Pihan (1976) estimated 40% more erosion with a doubling in distance between hedgerows. Similar patterns of mineral nutrient run-off may be expected (Forman & Baudry 1984). However, soil erosion is not the only factor governing field size, and therefore, from a management perspective, the number of ridges per field. Several other biological and agronomic factors need to be considered when designing a field system and these will be discussed in detail below.

Biological considerations relating to arable land management

The replicated experimental system described in the previous chapters is not a working management strategy and some questions remain unanswered. For example, it is not known from the present study whether the introduction of within-field ridges actually contributed to a reduction in aphid numbers. As there can be large variation in aphid numbers between fields (in some cases between adjacent fields on the same farm) (Wratten et al. 1990), no attempt was made to compare aphid populations between control fields and the three fields containing ridges. Dennis & Wratten (1991a) however, showed, using small inclusion barriers, that enhanced predator densities resulted in reduced aphid numbers. In an analogous fashion therefore, enhanced predator densities resulting from the introduction of a ridge could be expected to provide an increase in predator pressure and a subsequent reduction in aphid numbers.

Furthermore, it is not known at this time whether the ridges have an optimum "life-span" and whether a point may be reached where further successional changes might prove less favourable for agricultural purposes (as suggested in a study on habitat creation by Nentwig (1988)). Similarly, it is unclear whether the creation of predator populations at the field centres was simply a consequence of redistributing existing populations within the field or whether it has implications for long term population enhancement (i.e. is inadequate provision of overwintering site a "key factor" (Varley & Gradwell 1960) in the between-generation changes in predator populations and, therefore, does the creation of ridges reduce this effect ?). Also, although the predator population of one ridge could be seen to influence predator dispersal patterns in the spring, the question of optimum distance between ridges still needs to be answered, as mentioned previously. Linked to these points, further work needs to investigate whether field-scale manipulations such as those described here have an influence on the ecology only at the field scale, or whether the processes driving overall population dynamics are at a larger, landscape or metapopulation (Opdam 1990) level.

Succession

As discussed in Chapter 2, the successional changes observed on the ridges during the course of the study indicated a shift from pioneer r-selected species towards more specialist K-selected species (in the Araneae at least). Similarly, in a study of secondary succession based on a range of experimental field sites of different ages which were allowed to recolonize and develop naturally, Brown & Southwood (1987) showed that early successional stages ("young fields" of 0-2 years) were exploited by opportunist organisms (both plants and insects) representing r-strategists. The organisms of an "old field" (6-8 years) exhibited very different traits; predacious insects had become an important and diverse component of the fauna and in general, displayed more features of the K-strategy.

Forman & Baudry (1984), describing natural hedgerow development, suggested that species diversity increases, at least for a time, as birds and wind bring in new species. In early stages these will be largely field and forest-edge species but as trees develop and the shrub layer becomes more dense, some invasion of forest interior species is expected. They go on to suggest that in proximity to woods this process takes place more rapidly. Furthermore, indirect evidence that species colonise a hedgerow from an attached wood is available from wrens (Williamson 1969), butterflies (Pollard et al. 1974), snails (Cameron et al. 1980) and shrubs (Helliwell 1975), and interaction between forest, hedgerow and field habitats has been recorded by Wallin (1985, 1988) for several species of carabid. Forman & Baudry (1984) conclude from the evidence available that hedgerows function as corridors for movement across a landscape by many species (both plants and animals). This introduces the concept of connectivity in the arable landscape (connectivity in a structural sense: interpatch distance, density of stepping stones and corridors, permeability of landscape matrix for dispersers i.e. the landscape characteristics governing the dispersal flow (Opdam 1990)) and implicates field size, shape, and position relative to other habitats, as important factors in determining the speed and direction of ridge succession. A single ridge placed in the centre of a very large field for example (i.e. a large distance from any source populations), might be expected to undergo successional change at a slower rate than a ridge placed within a similar but smaller field with greater connectivity allowing rapid colonisation in the latter case. In the field, this difference in connectivity could be expressed in two ways: first, adoption of the new habitats as overwintering sites by predatory arthropods would be expected to be slower in the large field than in the small field (not only because the predators themselves might be slow to establish but also because suitable prey items (Chapter 4) could be equally slow to colonise); and second, if the ridges do indeed reach an optimum successional stage (as discussed above), then the ridge in the small field would be expected to have a shorter life than ridge in the large. There is a situation therefore where an optimum field size could be reached at which succession was rapid enough to be beneficial from a pest control viewpoint, but slow enough such that dominance by boundary-specific and forest species was postponed as long as possible (although new ridges could of course be re-created very simply). In the present study, the effects of field size could have influenced the densities of the carabid communities on the three ridges (overwintering carabid densities tended to reduce as field size increased) although variability in density between fields, irrespective of size, can be considerable (Thiele 1977; Wallin 1985). Furthermore, a few seedlings of hawthorn (Crataegus spp.) and oak (Quercus spp.) were apparent on ridges 1 & 2 by the third year indicating further stages of secondary succession.

Dispersal

Superimposed on, or contained within, the successional balance described above are the agronomic requirements for field size and the dispersal abilities of the predator species.

With respect to the agronomic considerations, it has been concluded that as small fields take proportionally longer to cultivate than large fields (proportionally greater time spent turning coupled with smaller farm machinery), 4ha is the minimum field size from an economic perspective (Le Clezio 1976). It has also been reported that 20ha is an economically viable field size and the reasons for larger fields are tenuous (Anon 1991). A guideline could be suggested therefore, such that within-field ridges are used to reduce the effective size of very large fields to 20ha or less. However, Forman & Baudry (1984) introduced the theory of mesh size as an important property of the hedgerow network. They suggest that mesh size (the area of landscape elements enclosed by the lines) is important in relation to grain size (the distance or area a species is sensitive to in carrying out its functions such as feeding and reproduction) of a species. Thus in a Brittany (France) landscape, the predatory ground beetle Poecilus cupreus L., which is a fine-grained species (i.e. requiring a small mesh size), disappeared where the average mesh size of fields was greater than 4ha (Deveaux 1976). Although there is no evidence suggesting that predator species have been lost from fields considerably larger than this in the present study (i.e. similar species were found in all fields), it is possible that with large field sizes, certain species may be operating at sub-optimum population levels. Furthermore, from a pest management perspective it is important that predatory species not only persist within the arable landscape, but penetrate to the field centres in significant numbers.

The results of the present study and the study of Coombes & Sotherton (1986) indicated that the Carabidae were the predatory group most influenced by field size during the spring emigration period (Staphylinidae and Linyphiidae having aerial powers of dispersal). In terms of potential management guidelines therefore, field size should be adjusted to allow this predator group time to complete field penetration during the aphid build up phase (the time when their potential for biocontrol is at its highest (Edwards et al. 1979; Chambers et al. 1982)) and prior to the time when application of aphicides might be considered necessary (the current ADAS threshold for aphicide application against S. avenae is 75% stem infestation at flowering; flowering occurring between mid to end June at the principal study farm during the three years of this study). Coombes & Sotherton (1986) showed that of the carabid species studied, all were evenly dispersed (no difference between numbers at 5m and 100m from the boundary ($P > 0.05$)) by late May to early June; a suitable time relative to the optimum predator activity window suggested above. If it is assumed that both field and ridge populations contribute to field colonisation (see Chapter 3) then a distance of 200m between ridge and boundary would result in even field cover at the appropriate time. With this in mind, it is estimated that a square 20ha field (c. 450m x 450m) would require one centrally positioned ridge to achieve uniform predator cover early in the season, the ridge design allowing the field still to be worked as a 20ha unit.

Predator population dynamics

As discussed above it is unclear whether the creation of the within-field habitats was responsible for any predator population enhancement. Although the experimental design of the present study was not best suited to answering this question, an indication of whether predator populations were enhanced or simply redistributed can be provided by comparing overwintering data from several field boundary habitats with data from the experimental field systems. For example, an estimate of the existing population range of a particular predator group can be calculated (using 95% C.L.) for field system 1 (ridge + boundary populations). Similarly, an estimate of the population range for field 1 if the ridge was absent (the predicted population range) can be calculated using data from other typical arable boundaries. If the predicted and estimated population ranges for a particular group do not overlap, then the populations can be considered different; a higher mean value in the existing population indicating enhancement.

The results of such a comparison for fields 1 & 2, for a range of predator groups, are presented in Figs. 6.1 & 6.2 respectively (the methods used to calculate the range values are presented in Appendix II). These results show that although the means of the existing populations (the mid-point of the population ranges) exceed those of the predicted populations for most predatory groups, no population enhancement is indicated as the predicted and existing population ranges overlap within each group. It should be pointed out however that the crude assumptions contained within the calculations make such conclusions rather tentative. Furthermore, even if the ridge predator populations are a product of redistribution alone, the enhanced field penetration which results in the spring is still beneficial from a pest management perspective. With respect to population dynamics however, it may be that factors other than inadequate provision of overwintering habitat influence predator numbers. Larval mortality during the summer period may certainly be important for spring breeding Staphylinidae and Carabidae; the vulnerability of this developmental stage was indicated in field experiments on the carabid Pterostichus oblongopunctatus Fab. by Brunsting et al. (1986) who reported combined larval and pupal mortality of c. 96%. Beyond this, there remains the possibility that the processes driving overall population dynamics act at a larger scale than that of the single field system.

Figure 6.1. Estimated existing (E) and predicted (P) population ranges (95% C.L.) for various predatory groups in field system 1, winter 1989/90.

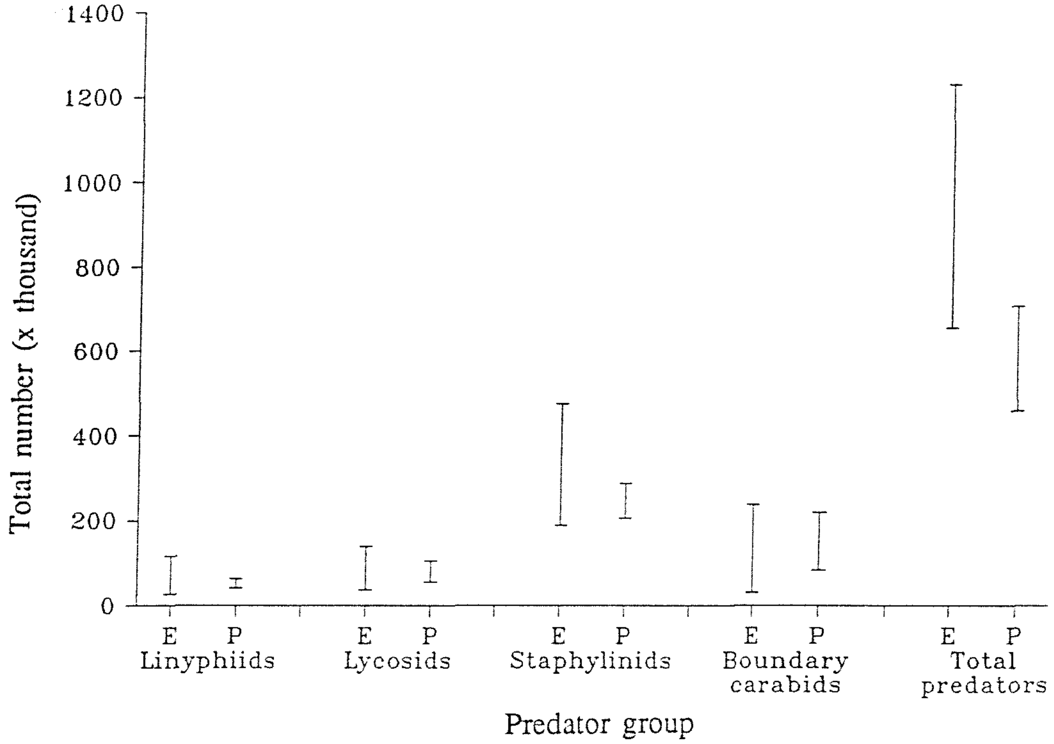
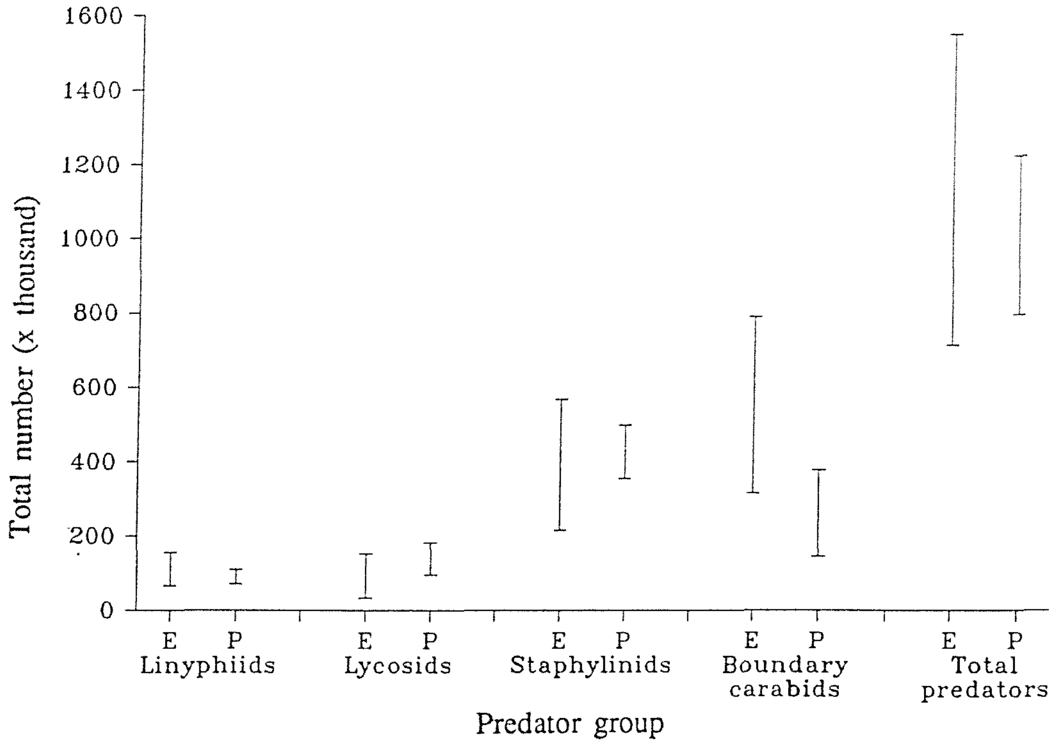


Figure 6.2. Estimated existing (E) and predicted (P) population ranges (95% C.L.) for various predatory groups in field system 2, winter 1989/90.



Opdam (1990) suggested that because the dynamic behaviour of populations has a stochastic component, any completely isolated population will become extinct sooner or later. The smaller the population, the greater the risk of extinction. For this reason, dispersal was suggested to be the key to survival in the landscape, particularly in such fragmented systems as agricultural landscapes. The term metapopulation was used to describe a set of populations in such a fragmented landscape, as long as the subunits (subpopulations) are interconnected by dispersing animals. "Between-patch dispersal is then the landscape process linking the subpopulations in each patch, thus forming a population on a higher level of organisation: the "metapopulation" (Opdam 1990). This concept agrees well with the findings of den Boer (1981) who, studying a number of carabid populations from various habitats over several years, suggested that fluctuation within subpopulations is an important factor for survival of the population as a whole; the "risk of extinction" is importantly "spread" over a number of differently fluctuating sub populations. He concluded that populations that are composed of large numbers of highly interconnected "interaction groups" (subpopulations) may show an impressive survival time, if the risk of extinction is "sufficiently spread over a great part of these subpopulations".

The dynamics and survival of such a population as a whole, is theoretically determined by the dynamics of the subpopulations, i.e. the size of the patches and habitat quality (extinction rate); the connectivity between patches, i.e. the dispersal rate (functional connectivity) and landscape characteristics (structural connectivity) (recolonisation rate); and the spatial and temporal variation in habitat quality among patches in combination with dispersal, i.e. spreading of risk, dampening of fluctuations in the size of the metapopulation (after Opdam (1990)).

It is suggested therefore that as populations of certain species of polyphagous predators (especially the Carabidae with limited powers of dispersal) can be considered to exist as interacting subpopulations (e.g. as subpopulations between fields under different cropping regimes, different boundary habitats during winter, or even as subpopulations between field and boundary during summer (see Chapter 5)), then the landscape processes described above could determine the overall population densities.

Mader (1988) described the agroecosystem as a multiple series of fields within a matrix of landscape elements such as road verges and hedgerows. Although there is a considerable amount of discontinuity within different compartments (i.e. within the individual fields) a degree of stability was suggested within the system as a whole (stability in this case defined as the ability of a system to withstand disturbance or to regain its former state or function after disturbance). The internal discontinuity is a factor to which the majority of species have adapted perfectly (Mader 1988). However, as modern agriculture, with high impact mechanical and agrochemical practices, can be seen to have an adverse influence on the metapopulation processes described above, increasing intensity beyond a threshold could well result in a breakdown of internal control features and stability of the agroecosystem as a whole (a process seemingly taking place already in certain parts of the New World (Mader 1988)). Habitat creation schemes such as those described here, could be seen as methods to increase stability of modern agroecosystems, enhancing the internal control features of the system and making external control less important (Mader 1988).

Conclusions and future research

Overall, from a pest management perspective, this study has gone some way to showing the possibility of beneficially manipulating the arable environment in an ecologically short time.

At a time when there is over-production of cereals in western Europe, new ideas for manipulating the arable environment could prove important; the approach outlined here could lend a role to set-aside and other surplus land, to enhance its biocontrol potential. Beyond this, Van Emden & Wratten (1991) suggest that the potential and current economic climate in Western Europe make the application of I.P.M. ideas in cereals a real prospect for the first time. The fact that within-field ridges (sown with just D. glomerata, or D. glomerata and H. lanatus combined) have already been created voluntarily by farmers in Hampshire, Oxfordshire and Cambridgeshire, would suggest this to be true. However, Van Emden & Wratten also suggest that successful biocontrol within an I.P.M. framework depends on the combined action of a range of natural enemies. With this in mind, current work at Southampton University is drilling metre-wide field-margin strips around winter wheat fields with two species of flowering plant (to provide pollen and nectar) and assessing the consequences for hoverfly (Syrphidae) foraging, oviposition and predation rate. Other work at Southampton University, in collaboration with Willmot Industries, is examining the ability to create herb-rich grassland at field margins. Preliminary results have shown that by the correct timing of selective herbicides, aggressive weeds can be removed and a variety of insects (including butterflies and beneficials) and small mammals found within the new habitats. Beyond this, research is under way to combine flowering plants (for hoverflies) and grass-sown raised banks (for overwintering polyphagous predators) to develop a working management prescription as part of an integrated system for pest control. Regarding the present study, a colour leaflet is being produced with sponsorship/collaboration from the Farming and Wildlife Advisory Group (FWAG), The

Game Conservancy Trust, independent crop consultants and pesticide companies, with the aim of extending knowledge within the farming community and publicising the within-field ridge as a potential management tool towards the goal of integrated pest management.

On a wider scale, the concepts of the present goal-orientated study can be applied to a range of agricultural systems; cereals are not the only crops to potentially gain from dynamic land management strategies. This points out the need for future research in the area of "balanced habitat management" (Van Emden 1988) in agroecosystems as a whole. Indeed, Altieri & Whitcomb (1979) suggested that understanding basic crop-weed-insect interactions occurring in a geographical area might provide important clues on how agroecosystems should be structured to minimize pest incidence. They suggested an approach directed not only at the cultivated field, but also the surrounding matrix of uncultivated land which constitutes a vital part in the life systems of many entomophagous arthropods.

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APPENDICES

APPENDIX I.

Diagramatic representation of the randomised block design of within-field ridges 1, 2 & 3. Blocks A,B,C,D,E, & F were arranged sequentially in a linear design in the field. A.s. = Agrostis stolonifera, D.g. = Dactylis glomerata, H.l. = Holcus lanatus, L.p. = Lolium perenne, 25% = mix of the four grass species, 33% = mixture of three grass species (A. stolonifera excluded), B.G. = bare ground, F.P. = flowering plants to provide pollen and nectar.

Ridge 1

A	B	C	D	E	F
A.s.	F.P.	B.G.	D.g.	B.G.	L.p.
D.g.	H.l.	H.l.	L.p.	H.l.	H.l.
25%	A.s.	25%	33%	L.p.	33%
B.G.	B.G.	L.p.	A.s.	33%	D.g.
33%	L.p.	A.s.	F.P.	25%	A.s.
F.P.	D.g.	F.P.	H.l.	D.g.	F.P.
L.p.	33%	D.g.	25%	A.s.	B.G.
H.l.	25%	33%	B.G.	F.P.	25%

Ridge 2

A	B	C	D	E	F
L.p.	33%	B.G.	F.P.	B.G.	25%
B.G.	H.l.	33%	25%	F.P.	F.P.
H.l.	B.G.	L.p.	33%	L.p.	L.p.
F.P.	A.s.	A.s.	D.g.	D.g.	H.l.
25%	25%	D.g.	H.l.	A.s.	D.g.
33%	L.p.	25%	L.p.	25%	B.G.
D.g.	F.P.	F.P.	A.s.	33%	33%
A.s.	D.g.	H.l.	B.G.	H.l.	A.s.

APPENDIX I (cont.)

Ridge 3

A	B	C	D	E	F
H.l.	F.P.	F.P.	F.P.	A.s.	B.G.
25%	33%	33%	L.p.	33%	A.s.
D.g.	H.l.	B.G.	33%	25%	25%
L.p.	D.g.	A.s.	B.G.	D.g.	33%
B.G.	25%	25%	H.l.	F.P.	F.P.
33%	L.p.	D.g.	D.g.	H.l.	L.p.
F.P.	A.s.	L.p.	A.s.	L.p.	D.g.
A.s.	B.G.	H.l.	25%	B.G.	H.l.

APPENDIX II

Calculation of estimated existing and predicted predator populations in field systems 1 & 2.

Chapter 4 presented predator density data from 19 field boundaries collected during winter 1989/90. Of these 19 boundaries, eight were immediately adjacent to the fields containing within-field ridges 1 & 2 (i.e. the boundaries of fields 1 & 2). The mean density (m^{-2}) (± 95% C.L.) of a range of predator groups was calculated for each of these eight boundaries. A single mean density for each of these groups (± 95% C.L.) was also calculated for the remaining eleven boundaries grouped together. The 95% C.L. of the means were used as upper and lower density estimates in the population calculations.

Upper and lower density estimates of a predator group (e.g. boundary carabids) in each of the four boundaries surrounding a particular field (e.g. field 1) were mutliplied by the area of the boundaries (the average width of a boundary approximated to 1m and so the densities were infact multiplied by boundary length). This gave an estimate of maximum and minimum values of the total number of boundary overwintering carabids within the boundaries. These values were then added to the equivalent upper and lower estimates of the total number of individuals belonging to this group on the corresponding ridge (calculated from max. and min. density for each treatment x total treatment area), giving an upper and lower estimate of the total number of boundary carabids within the field system (i.e. boundaries + ridge). For example:

Field system 1 - estimated population of boundary carabids

boundary 1 max density (m^{-2}) x length (m) = 105 x 365 = 38325
boundary 2 max density (m^{-2}) x length (m) = 108 x 170 = 18360
boundary 3 max density (m^{-2}) x length (m) = 23 x 355 = 8165
boundary 4 max density (m^{-2}) x length (m) = 704 x 200 = 140800
Total max = 205650

Using the same procedure with minimum densities
Total min = 24435

The total area of each ridge treatment = 1.5m x 6m x 6 (blocks) = $54m^2$. Therefore, total boundary carabid numbers for each single-species grass treatment = [max density x 54] and [min density x 54]. These upper and lower values were then used to calculate maximum and minimum population estimates for the grass-mixture treatments (each grass species present in the mixture was considered to contribute equally to the total population i.e. the appropriate single grass species totals were averaged for the three- and four-species mixtures).

From this, the maximum total ridge population = 31773
the minimum total ridge population = 6588

Therefore, the total maximum boundary carabid population = 205650 + 31773
= 237423

the total minimum boundary carabid population = 24435 + 6588
= 31023

This procedure was repeated for a range of predator groups in field systems 1 & 2.

Using data from the remaining eleven field boundaries, an average upper and lower predator density estimate was calculated for each of the predator groups described above. This provided an average density range for a typical boundary habitat at the study site. Upper and lower values were then multiplied by total boundary length to produce a predicted population range for field systems 1 & 2 i.e. the population range expected in the absence of the ridges. For example:

Field system 1 - predicted population of boundary carabids
Average maximum density of typical boundary = 201
Average minimum density of typical boundary = 77

Total boundary length = 1090m

Therefore, maximum predicted population = 201 x 1090 = 219090
minimum predicted population = 77 x 1090 = 83930

The results of this investigation for field systems 1 & 2 are presented in Table II.1.

Table II.1. Estimated existing and predicted population ranges for a range of predatory groups from field systems 1 & 2.

	Existing population		Predicted population	
Field 1	Max.	Min.	Max.	Min.
Linyphiids	115658	26422	63220	42510
Lycosids	139456	37514	104640	55590
Staphylinids	476109	189212	287760	204920
Boundary carabids	237423	31023	219090	83930
Total predators	1233591	654584	705230	458890
Field 2				
Linyphiids	155928	64933	109620	71820
Lycosids	152927	33143	181440	96390
Staphylinids	567997	215625	498960	355320
Boundary carabids	790629	315738	379890	145530
Total predators	1549245	712436	1222830	795690

APPENDIX III

Publications and reports produced during the tenure of the MAFF research contract:

Thomas, M.B. (1988). Causes of variation in the numbers of predators of cereal aphids overwintering in field boundaries. The Game Conservancy Review of 1988, **20**, 71-72.

Thomas, M.B. (1989). Diversification of the arable ecosystem to control natural enemies of cereal aphids. The Game Conservancy Review of 1989, **21**, 68-69.

Thomas, M.B. (1989). The creation of island habitats to enhance populations of beneficial insects. Brighton Crop Protection Conference- Weeds 1989, **3**, 1097-1102.

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Thomas, M.B., Wratten, S.D. & Sotherton, N.W. (1991). Creation of island habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. Journal of Applied Ecology (in press).

Thomas, M.B., Wratten, S.D. & Sotherton, N.W. (submitted). Creation of island habitats in farmland to manipulate populations of beneficial arthropods: successional changes in predator community structure. Journal of Applied Ecology.

Thomas, M.B., Mitchell, H.J. & Wratten, S.D. (submitted). Abiotic and biotic factors influencing the winter distribution of predatory insects. Oecologia.

Boatman, N., Dover, J., Wilson, P., Thomas, M. & Cowgill, S. (1989). Modification of farming practice at field margins to encourage wildlife and to promote pest control. Biological Habitat Construction (Ed. by G.P. Buckley). pp 299-311. Belhaven Press.

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APPENDIX X

Data used to calculate the "proportions of total caught/date" used to illustrate spring dispersal patterns in Chapter 3 (Figs. 3.3 - 3.13). "-" indicates where numbers were too low for analysis.

Demetrias atricapillus (Fig 3.3)

		Mean number per sample (no./1.5m^2) for each date						
		14/4	18/4	26/4	3/5	8/5	16/5	22/5
Distance	0m	14.0	8.8	3.6	3.8	0.2	2.0	4.0
	3m	1.0	0.0	0.0	0.8	0.0	2.0	0.0
	10m	0.0	0.0	0.0	0.0	0.4	0.0	2.0
	30m	0.0	0.0	0.0	0.0	0.2	1.0	4.0
	60m	0.0	0.3	0.4	0.3	0.4	3.0	4.0

Tachyporus hypnorum (Fig 3.4)

		Mean number per sample (no./1.5m^2) for each date						
		14/4	18/4	26/4	3/5	8/5	16/5	22/5
Distance	0m	13.5	6.5	4.0	1.7	0.3	1.8	1.5
	3m	2.0	0.8	3.0	5.6	2.0	2.5	5.5
	10m	1.5	0.5	1.0	6.5	2.8	2.0	5.0
	30m	1.0	1.0	3.0	10.0	3.3	1.3	11.5
	60m	8.0	4.3	6.0	9.3	4.0	2.0	12.5

Linyphiidae (Fig 3.5)

		Mean number per sample (no./1.5m^2) for each date						
		14/4	18/4	26/4	3/5	8/5	16/5	22/5
Distance	0m	20.0	17.0	24.0	14.5	8.0	14.0	8.5
	3m	4.0	3.0	4.5	3.3	5.0	2.0	2.0
	10m	4.0	1.5	4.5	5.0	5.0	4.0	1.0
	30m	1.0	1.5	2.0	3.3	4.0	4.0	3.2
	60m	1.0	2.0	3.0	6.0	5.0	3.3	3.2

Boundary carabids (Fig 3.6)

		Mean number per sample (no./trap) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	-	-	2.4	1.9	2.1	-	2.4	1.1
	4m	-	-	2.7	1.6	2.3	-	2.7	1.9
	10m	-	-	1.9	1.6	2.3	-	2.0	1.6
	20m	-	-	1.6	1.4	0.9	-	1.4	1.8
	50m	-	-	1.4	1.5	1.4	-	1.2	1.6

Tachyporus spp (Fig 3.7)

		Mean number per sample (no./trap) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	9.4	1.3	4.5	-	-	1.3	3.5	2.5
	4m	3.1	1.4	4.0	-	-	1.3	10.5	4.8
	10m	10.1	1.3	5.0	-	-	1.9	3.5	4.6
	20m	7.0	1.4	7.3	-	-	2.3	16.0	4.5
	50m	9.4	0.9	4.3	-	-	2.9	16.0	3.4

Bembidion obtusum (Fig 3.8)

		Mean number per sample (no./trap) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	3.4	4.0	6.0	1.5	0.8	0.6	2.0	3.1
	4m	4.2	6.0	6.6	1.8	1.9	2.3	2.8	1.2
	10m	3.8	3.2	4.8	2.2	2.2	2.1	1.5	1.9
	20m	1.2	4.6	4.8	1.8	2.4	1.2	1.5	1.4
	50m	7.4	2.2	7.8	2.6	2.7	1.8	2.1	2.4

Nebria brevicollis (Fig 3.9)

		Mean number per sample (no./trap) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	-	-	1.3	1.1	1.2	3.3	2.3	1.8
	4m	-	-	1.5	1.1	1.7	2.6	1.0	2.6
	10m	-	-	1.5	1.2	2.1	1.4	1.6	2.2
	20m	-	-	1.6	0.8	2.5	1.9	2.3	1.5
	50m	-	-	1.2	0.8	2.5	0.8	0.8	1.9

Linyphiidae (Fig 3.10)

		Mean number per sample (no./trap) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	2.8	2.3	3.1	2.8	1.4	0.8	1.8	0.9
	4m	1.6	2.5	2.8	4.6	1.8	2.6	4.4	2.3
	10m	1.5	1.6	1.9	4.0	2.8	1.8	5.4	2.4
	20m	1.5	1.7	2.3	4.8	1.8	2.9	6.2	2.4
	50m	2.6	1.9	1.8	3.8	2.2	1.9	3.8	2.0

Lycosidae (Fig 3.11)

		Mean number per sample (no./trap) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	-	3.4	5.3	6.5	5.0	4.0	3.8	5.0
	4m	-	1.5	1.9	1.2	2.1	1.8	2.1	1.9
	10m	-	0.7	0.5	0.8	0.9	1.0	1.0	0.9
	20m	-	0.4	0.9	0.7	0.7	1.0	1.1	0.9
	50m	-	0.8	1.4	0.8	1.3	2.2	1.7	1.1

Demetrias atricapillus (Fig 3.12)

		Mean number per sample (no./1.5m^2) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	-	-	1.9	-	0.3	1.0	1.6	0.6
	4m	-	-	1.2	-	0.6	1.0	1.1	1.2
	10m	-	-	0.0	-	1.2	0.8	1.0	0.4
	20m	-	-	0.6	-	0.0	0.6	1.0	0.6
	50m	-	-	0.5	-	0.3	0.3	1.0	1.8

Tachyporus hypnorum (Fig 3.13)

		Mean number per sample (no./1.5m^2) for each date							
		3/4	12/4	22/4	26/4	3/5	11/5	17/5	24/5
Distance	1m	1.0	-	1.2	1.2	0.8	0.0	1.2	0.0
	4m	0.4	-	1.0	1.1	0.8	1.2	1.2	1.1
	10m	0.8	-	1.2	0.8	0.8	2.0	1.0	2.0
	20m	0.8	-	0.8	1.2	1.2	1.3	3.0	0.6
	50m	1.3	-	1.2	1.2	0.4	0.0	2.7	2.0