

3.5. QUANTIFYING THE IMPACT OF HABITAT MANIPULATION ON THE ABUNDANCE AND DISTRIBUTION OF GENERALIST PREDATORS AND APHIDS

Certain non-crop habitats are known to encourage beneficial invertebrates leading to subsequent reductions in pest numbers in adjacent crops, as described in section 3.1. On farmland, however, these areas occupy a relatively small proportion of the land while set-aside typically forms 13% of arable land (Defra Statistics). There is therefore potential to manage set-aside land to benefit biocontrol through provision of overwintering sites and floral resources, as investigated for field margins in section 2. The set-aside strips established within the study area were initially sown with a mixture of kale, millet, *Phacelia*, quinoa, triticale, sunflowers and yellow sweet clover, although a weedy understorey also developed during the course of the study. These provided considerable floral resources that could be utilised by hoverflies and parasitoids, and in the latter years the weedy understorey may have provided overwintering sites for beetles and spiders. To test specifically whether the strips were encouraging beneficial insects and whether aphid abundance was being reduced, an experimental design similar to that used in section 2 was established.

3.5.1. Effect of Set-Aside Strips on Aphid and Predatory Invertebrate Abundance in 2002

In 2002, a pilot study was conducted to determine whether the set-aside strips were affecting aphid abundance on winter wheat. To test whether the set-aside strips were affecting the numbers of predatory epigeal invertebrates within the crop a subset of the spatial dataset described in section 3.2 was analysed.

3.5.1.1 Materials and methods.

Four fields of winter wheat were used on the Cranborne Estate, Dorset. Two were large fields that had 24 m wide set-aside strips established along two edges, the third contained a single set-aside strip while the fourth had none. Three sampling transects were established at the same distances (10, 30 & 100 m from the crop edge) as used in section 2. Transects were established next to four set-aside strips and four conventional field margins which acted as controls. The large fields were considered of sufficient size to accommodate transects next to set-aside and conventional margins without interaction between the two, although subsequent results from the hoverfly and parasitoid manipulation studies (section 2) indicate that these insects are capable of dispersing across large fields. Cereal aphids were counted on three occasions (14, 20 & 27 June) *in situ* on 25 tillers chosen at random along each transect. Numbers of each species present on all parts of the plant were recorded along with any natural enemies present and their development stage (e.g. ladybird eggs, larvae, pupae, adults). These included parasitoid mummies and aphids killed by fungal pathogens. The number of rose-grain aphids and grain aphids was analysed after log transformation using regression analysis comparing the effect of distance from the crop edge and treatment (with or without set-aside strip).

A subset of the spatial dataset was analysed to examine whether the numbers of predatory invertebrates was higher next to the margins with, compared to without, the set-aside strips. The mean number of predatory invertebrates for three transects of pitfall traps (7 traps/transect) located in the crop at approximately 10, 30 and 100 m from four standard field boundaries and from four with set-aside strips was calculated. Data were analysed as above for the June and July data separately.

3.5.1.2 Results

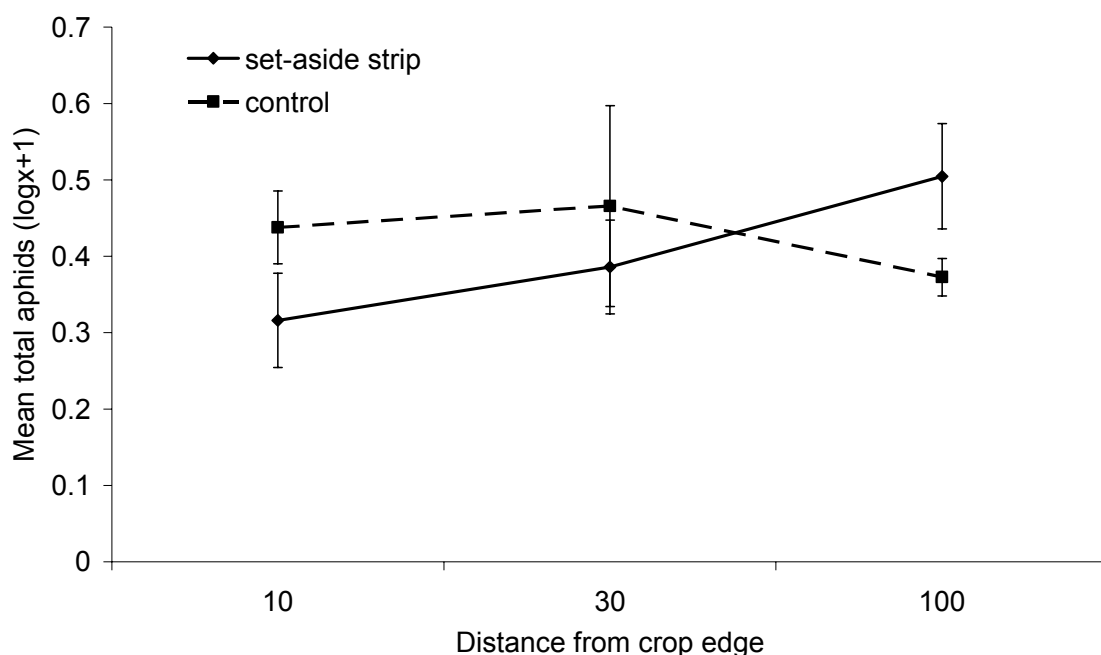
The treatment or distance from the margin had no significant effect on grain aphids (Table 3.31), although the distance from the margin had an almost significant effect on total aphids ($F=1.98$, $p=0.06$). Grain aphids were lower in the fields with the set-aside strips at 10 and 30 m from the crop edge but the reverse occurred at 100 m (Fig. 3.22).

In June there was no significant effect of the set-aside strips on numbers of predatory invertebrates captured by the pitfall traps. However, by July there were significantly more ($F=5.4$, $p=0.04$) in those transects located next to the set-aside strips where there were 1.7 (Mean number transformed $\log x+1$) compared to 1.5 next the field boundaries. The distance of the transect from the crop had no effect.

Table 3.31. Regression analysis for aphid numbers comparing winter wheat fields with and without set-aside strips and at three distances from the boundary. Mean for three sampling occasions. (NS=non-significant)

	Field		Treatment		Distance		TxD	
Rose-grain aphid	NS		NS		NS		NS	
Grain aphid	NS		t=1.8	p=0.08	t=2.0	p=0.06	t=-1.9	p=0.09

Figure 3.22. Effect of set-aside strips on cereal aphids in winter wheat.



3.5.1.3 Conclusions

1. There was some indication that set-aside strips sown with game cover reduced cereal aphid distribution or abundance for up to 30 m into the field.
2. Numbers of predatory invertebrates captured by pitfall trapping were higher in three transects located next to set-aside strips compared to the field boundary.

3.5.2. Effect of Set-Aside Strips on Aphids and Beneficial Invertebrates in 2003

This study had three aims:

1. To confirm whether the set-aside strips increase beneficial insects and decrease cereal and pea aphid infestation levels.
2. To confirm whether previous differences in predatory beetle captures from pea and wheat fields were due to increased survival over winter in the pea fields.
3. To confirm whether predatory beetles were consuming cereal and pea aphids.

3.5.2.1 Materials and methods.

In 2003, the effect of the set-aside strips on cereal and pea aphids was tested. Four pea fields and four winter wheat fields were used that contained set-aside strips. The 24 m wide set-aside strips were established in 2001 but by 2003 they contained a mixture of sown plants that had survived through self seeding and also a wide range of weed species. In 2003, half of each strip was re-sown with the original mixture.

Next to each set-aside strip and on the opposite side of the field next to a normal field boundary three sampling transects at 10, 30 and 100 m from the crop edge were established. At each distance there were five sampling locations 20 m apart. At each sampling location the abundance of beneficial and pest species were measured using a range of sampling techniques.

- a) Three standard pitfall traps (2 m apart arranged in a triangle) containing a mixture of water and detergent. Traps were operated continuously from when aphids started to appear and were emptied weekly.
- b) At 30 m only. One 1m² emergence trap, as described in section 4.3.1. Traps were set up in early April and emptied fortnightly from mid-April.
- c) Three 6 cm diam. empty pitfall traps (wheat fields only). These were used for collecting *Pterostichus melanarius* and *P. madidus* (Carabidae) from which predation on cereal aphids was determined by analysing their gut contents using PCR. Traps were opened overnight and contents immediately frozen after collection. Sampling was conducted once during the aphid population peak. Gut contents were extracted, weighed and refrozen. Project partners at SAC conducted PCR analysis to determine the proportion that had consumed aphids (section 4).

- d) Two D-vac suction net samples, each of 10 sucks of 10 seconds each (area sampled = 1 m²/location). Samples were taken at weekly intervals.
- e) For wheat fields, cereal aphids were counted on 20 tillers/sampling location in a designated aphid counting area. Counts were carried out weekly (9/10 June, 16/17 June), from when aphids first appeared.
- f) For pea fields, pea aphids were counted on 12 plants/sampling location in a designated aphid counting area. Counts were carried out weekly from when aphids first appeared.

In the pitfall trap samples, all relevant arthropods were identified to species, along with wolf spiders (Lycosidae). In the D-vac suction samples, all beetles (Coleoptera) were identified to species, spiders (Araneae) and predatory flies (Diptera) to family and aphids (Aphididae) to species.

To test whether the set-aside strips affected invertebrates within the crop, some predatory invertebrate taxa, those important as bird food and aphids, were analysed from the Dvac suction sampling (Table 3.29). The predatory invertebrates included the total number of spiders and the money spiders (Linyphiidae), the predatory flies from the families Empididae and Dolichopodidae, total predators and number of predatory species. Those invertebrates important for farmland birds included total invertebrates important as food, Heteroptera and Homoptera. From the pitfall traps the following groups were analysed: Boundary overwintering Carabidae, Carabidae, number of carabid species, Staphylinidae, number of staphylinid species, total invertebrates, total predators and number of predatory species. Data were analysed using a repeated measures ANOVA comparing treatment and sampling distance with field as a blocking factor in Genstat.

The number of individuals in each taxon captured using the emergence traps was summed over the whole trapping period and the effect of the set-aside strips compared using one-way ANOVA field as a blocking factor in Genstat. To determine whether invertebrate emergence was greater in wheat compared to pea fields, the results for fields with and without set-aside were tested separately as initial analysis indicated there was a significant interaction effect between cropping and the margin type for all groups tested.

3.5.2.2. Results

The aphid counting revealed that the abundance of cereal aphids on the wheat ears and the total number were significantly higher in the transects next to the set-aside strips (Table 3.32). The aphid counting revealed that there were no significant differences in the numbers of pea aphids between transects with and without the set-aside strips. Pea aphids reached very high numbers in all fields, with almost 100% of plants infested.

All of the taxa or groups tested varied significantly over time as expected. Other significant results are shown in Table 3.31. The abundance of pea aphids sampled by D-vac suction sampling varied with distance and

was highest at 30 m from the field boundary (Table 3.32). Numbers of *Sitobion avenae* collected by suction sampling were significantly higher in the transects next to the set-aside strips.

The pitfall trapping revealed that there were fewer staphylinid beetles in the transects next to the set-aside strips compared to the control areas in the pea fields (Table 3.32). The number of carabid and staphylinid species declined with distance from the crop edge in the pea fields. In the wheat fields the total numbers of invertebrates and predators increased with distance from the crop edge.

The emergence traps showed that the set-aside strips in the wheat fields were decreasing the number of some predatory taxa and overall abundance of predatory invertebrates at 30 m into the field (Table 3.33). In contrast, in the peas the reverse trend was found with greater numbers of some taxa occurring where there were set-aside strips.

More invertebrates of all taxa tested emerged in wheat compared to pea control fields (Table 3.34). However, in the fields with the set-aside strips only higher numbers of *P. cognatus* emerged in the wheat fields.

Table 3.32. ANOVA results and means examining effect of set-aside strips on invertebrates within fields. Means are $\log(x+1)$. (C=control, S=set-aside strip, ** $p < 0.01$, * $p < 0.05$)

Group	Factor	F value and significance	Means			SE of mean
APHIDS-Wheat						
Total aphids	Treatment	4.9 *	C=0.36	S=0.52		0.05
APHIDS-Peas						
Pea aphid	Distance	3.9 *	10m=0.57	30m=0.62	100m=0.51	0.03
DVAC-Wheat						
<i>S. avenae</i>	Treatment	4.5 *	C=1.15	S=1.39		0.14
DVAC-Peas						
Heteroptera	Distance	5.0 *	10m=0.04	30m=0.01	100m=0.01	0.006
Pea aphid	Distance	4.5 *	10m=1.39	30m=1.37	100m=1.24	0.04
PITFALL-Wheat						
Total insects	Distance	3.9 *	10m=1.11	30m=1.23	100m=1.27	0.12
Predators	Distance	6.2 **	10m=1.05	30m=1.19	100m=1.22	0.04
PITFALL-Peas						
No. carabid spp.	Distance	4.7 *	10m=0.80	30m=0.73	100m=0.71	0.02
No. carabid & staphylinid spp.	Distance	4.2 *	10m=0.89	30m=0.84	100m=0.81	0.03
Staphylinidae	Treatment	8.02 **	C=0.55	S=0.41		0.04

Table 3.33. ANOVA results and means examining effect of set-aside strips on invertebrate emergence within fields. Means are log(x+1). (NS=non-significant, ***=p<0.001, **p<0.01, *p<0.05)

Wheat	F value and significance	Control	Set-aside strips	SE of mean
<i>Pterostichus</i> spp.	6.59 *	1.18	0.90	0.08
<i>Harpalus</i> spp.	3.09 NS	1.12	1.0	0.05
Carabidae	2.13 NS	1.80	1.70	0.05
No. carabid species	0.7 NS	1.08	1.06	0.02
<i>P. cognatus</i>	0.90 NS	0.40	0.48	0.06
Staphylinidae	13.3 ***	1.37	1.16	0.04
No. staphylinid spp.	14.5 ***	1.09	0.95	0.03
Field overwintering	5.15 *	1.62	1.44	0.06
Predators	13.3 ***	2.10	1.88	0.03
Peas				
<i>Pterostichus</i> spp.	3.0 NS	0.55	0.78	0.09
<i>Harpalus</i> spp.	13.7 ***	0.84	1.09	0.05
Carabidae	14.4 ***	1.34	1.57	0.04
No. carabid species	10.4 **	0.92	1.02	0.02
<i>P. cognatus</i>	1.36 NS	0.14	0.08	0.04
Staphylinidae	1.25 NS	1.01	1.1	0.05
No. staphylinid spp.	0.6 NS	0.93	0.97	0.04
Field overwintering	13.1 ***	1.14	1.40	0.05
Predators	9.08 **	1.59	1.75	0.04

Table 3.34. Comparison of invertebrate emergence in peas and winter wheat for with and without the set-aside strips. Means are log(x+1). (NS=non-significant, ***=p<0.001, **p<0.01, *p<0.05)

Control fields	t-test	Peas		Winter wheat	
		Mean	SE	Mean	SE
<i>Pterostichus</i> spp.	-3.6 ***	0.55	0.08	1.18	0.15
<i>Harpalus</i> spp.	-2.1 *	0.84	0.07	1.12	0.12
Carabidae	-4.2 ***	1.34	0.06	1.8	0.09
No. carabid species	-3.3 **	0.92	0.03	1.08	0.03
<i>P. cognatus</i>	-3.1 **	0.14	0.04	0.39	0.07
Staphylinidae	-5.1 ***	1.0	0.06	1.4	0.04
No. staphylinid spp.	-2.9 **	0.92	0.05	1.09	0.03
Field overwintering	-3.8 ***	1.14	0.06	1.16	0.11
Predators	-6.4 ***	1.59	0.06	2.05	0.05
Set-aside fields					
<i>Pterostichus</i> spp.	-0.7 NS	0.78	0.1	0.90	0.14
<i>Harpalus</i> spp.	0.7 NS	1.1	0.07	1.0	0.09
Carabidae	-1.5 NS	1.57	0.05	1.71	0.07
No. carabid species	-1.1 NS	1.02	0.02	1.06	1.03
<i>P. cognatus</i>	-4.5 ***	0.07	0.04	0.48	0.08
Staphylinidae	-1.4 NS	1.1	0.04	1.2	0.04
No. staphylinid spp.	0.34 NS	1.0	0.03	1.0	0.03
Field overwintering	-0.3 NS	1.4	0.05	1.44	0.1
Predators	-1.7 NS	1.75	0.05	1.88	0.06

The PCR technique was successfully used to confirm aphid predation in two carabid species (see Section 4). Of the 233 beetles tested for the presence of aphid remains, 21% were found to have consumed aphids. For males and females the percentage that had consumed aphids was 23 and 19% respectively. In the fields without and with set-aside strips 18 and 23% respectively had consumed aphids (Table 3.35). At 10m from the set-aside strip, 10% more of beetles had fed on aphids compared to where there was no set-aside strip.

Table 3.35. Number and percentage of *Pterostichus madidus* and *P. melanarius* that tested positive or negative for aphids in fields with and without the set-aside strips.

		10m		30m		100m		Total	
		+ve	-ve	+ve	-ve	+ve	-ve	+ve	-ve
Control	No.	5	30	8	28	7	33	20	91
	%	14	86	22	78	18	82	18	72
Set-aside strip	No.	9	29	11	33	8	32	28	94
	%	24	76	25	75	20	80	23	77

3.5.2.3. Conclusions

1. The set-aside strips sown with game cover had no affect on the distribution or abundance of pea aphids in peas but increased cereal aphids on winter wheat.
2. The set-aside strips had no affect on the distribution or abundance of most predatory invertebrates within the adjacent crop measured by suction sampling and pitfall traps.
3. The set-aside strips had a negative affect on invertebrate emergence in wheat but a positive affect in pea fields.
4. Invertebrate emergence was higher in wheat compared to peas where there were no set-aside strips.
5. Aphid consumption by the carabids, *P. madidus* and *P. melanarius* was confirmed using the PCR technique and 21% on average were found to have consumed aphids.

3.5.3. Effect of Weed Cover on Beneficial Invertebrates.

A positive association between beneficial invertebrates and weed cover was found from analysis of their spatial correlation. To confirm this relationship an experiment was established in which weed cover was manipulated through a reduction in herbicide inputs and the impact on beneficial invertebrates measured. Weed levels within fields of spring barley were increased by omitting/reducing the spring herbicide application.

3.5.3.1 Materials and methods.

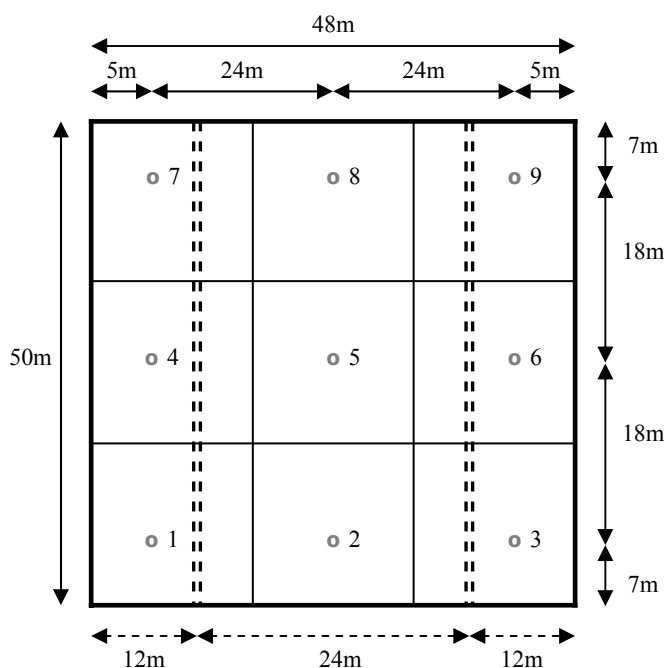
Two fields of spring barley were used on the Cranborne Estate, one located at Cranborne farm and the other at Woodyates farm, both in North-East Dorset. Within each field there were eight 0.5 ha plots (48 m wide x 50 m long) each arranged in a row with 50 m between each plot. The two treatments were randomly

allocated, providing four fully sprayed and four selectively sprayed plots. On Cranborne farm the fully sprayed field received an application of bromoxynil, ioxynil and mecoprop-p on 7/5/03 and tralkoxydim on 29/5/03. The fully sprayed and control plots were treated with metsulfuron-methyl and fluroxypyr on 12/6/03 to control weed growth, particularly of charlock (*Sinapis arvensis*). On Woodyates farm the fully sprayed plots received an application of tralkoxydim on 28/5/03 and metsulfuron-methyl on 12/6/03. The control plots received no herbicide.

Within each plot, beneficial invertebrates were assessed at 9 sampling locations/plot arranged in a 3 x 3 grid with a grid spacing of 18 m (Fig. 3.23). At each sampling location, epigeal invertebrates were measured using a single pitfall trap (6 cm diam.). The pitfall traps were first opened on 28th May 2003 and collected after a week and replaced with closed, clean pitfalls. These were again opened a week later. This was repeated for a total of four times. Crop and ground active invertebrates were collected by taking three D-vac suction net samples per plot. Whilst the pitfall traps were open, D-vac suction samples were taken at sample points 1, 5 and 9. At each point the D-vac was placed over the ground for 5x ten second intervals, thereby sampling an area of approximately 0.5m² at each post. Due to the weather, D-vac samples were not taken at exactly two week intervals but were sampled on the following dates: 30th May, 13th June, 1st July and 15th July, here on referred to as Dates 1, 2, 3 and 4.

Figure 3.23. Pitfall layout in each plot.

(○ represents a single pitfall trap, parallel dashed lines indicate location of the tramlines)



Invertebrates collected by the pitfall traps and D-vac suction sampling were counted and placed in the following groups:

Ground dwelling Invertebrates (obtained by pitfall trapping): Total number of carabid beetles (excluding larvae); Total number of staphylinid beetles (excluding larvae); All Other Coleoptera (consisting of click beetles (Elateridae), weevils (Curculionidae), ladybird adults and larvae (Coccinellidae) and leaf beetles (Chrysomelidae)); wolf spiders (Lycosidae); Total invertebrates (adults); Species richness (number of different species found); Carabid larvae; Staphylinid larvae; Other Coleoptera larvae.

Crop dwelling Invertebrate groups (obtained by the D-vac suction sampler): Aphid adults and nymphs (Aphididae); Carabid adults and larvae; Predatory Invertebrates (consisting of spiders (Araneae), lacewing larvae (Neuroptera), Carabid adults and larvae, Staphylinid adults and larvae, ladybirds (Coccinellidae), predatory flies (Dolichopodidae & Empidae and soldier beetles (Cantharidae)); Species Richness (number of different species found); Total Invertebrates and Total Predatory Invertebrates.

A chick food index (CFI) was determined by grouping invertebrates from the D-vac samples according to the following list:

Carabidae (adults) and Elateridae

Symphyta (sawflies), Lepidoptera (adults and larvae) and Neuroptera

Chrysomelidae (adults and larvae) and Curculionidae

Non-aphid Hemiptera (adults and nymphs)

Aphididae (adults and nymphs)

The CFI was then calculated using the following formula:

$$0.1411*(\text{Carabidae} \ \& \ \text{Elateridae}) \ + \ 0.1199*(\text{Symphyta}, \ \text{Lepidoptera} \ \& \ \text{Neuroptera}) \ + \\ 0.0832*(\text{Chrysomelidae} \ \& \ \text{Curculionidae}) \ + \ 0.00614*(\text{Non-aphid Hemiptera}) \ + \ 0.000368*(\text{Aphididae})$$

Weed cover and diversity was determined at each sampling point within each plot on 28 May 2003. At each point the weed cover for each species was estimated in four 0.5m² quadrats located randomly within 1m of the marker cane.

3.5.3.2 Data analysis

The results for invertebrates and weeds were analysed separately due to the proliferation of weeds at the Cranbourne site that were not present at the Woodyates site. For the invertebrates, a Repeated Measures ANOVA was used to test for treatment effects. Where there was a statistically significant interaction between date and treatment, ANOVA's were carried out to determine when treatment was having a

statistically significant effect for each of the four dates. The percentage cover for each weed species, total percentage cover and total number of weed species was analysed using a one-way ANOVA.

3.5.3.3 Results

The weed cover only varied significantly between the control (fully sprayed) and selectively sprayed plots at the Cranborne site (Table 3.36). This was caused by an increased survival of *Sinapis arvensis* (charlock) which accounted for the majority of the weed cover. Very little weed cover developed at the Woodyates site (Table 3.37). Historically this farm has always been less weedy but the dry spring also inhibited weed germination.

Table 3.36. Mean percentage cover (± 1 SE) and ANOVA results for treatment effect at the Cranborne Site, (*= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$)

Variate	Treatment		F- value	Significance
	Control	Selectively sprayed		
	mean ± 1 se			
Percentage weed cover	12.3 \pm 0.55	97.2 \pm 5.45	739	***
Number of weed species	5.5 \pm 0.29	6.0 \pm 0.41	3.0	NS
<i>Fallopia convolvulus</i>	0.3 \pm 0.25	2.2 \pm 1.44	2.8	NS
<i>Sinapis arvensis</i>	0.5 \pm 0.13	82.3 \pm 5.81	1237	***
<i>Galium aparine</i>	1.0 \pm 0.33	1.25 \pm 0.78	0	NS
<i>Viola arvensis</i>	4.0 \pm 1.65	4.3 \pm 1.31	0.2	NS
<i>Fumaria officinale</i>	5.0 \pm 2.07	5.4 \pm 3.04	0.03	NS
<i>Polygonium aviculare</i>	1.5 \pm 0.58	0.5 \pm 0.21	4.1	NS
<i>Papaver rhoeas</i>	0.2 \pm 0.05	1.5 \pm 0.69	4.1	NS

Table 3.37. Mean percentage cover (± 1 SE) and ANOVA results for treatment effect at the Woodyates Site. (*= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$)

Variate	Treatment		F- value	Significance
	Control	Selectively sprayed		
	mean ± 1 se			
Percentage weed cover	7.1 \pm 1.07	5.5 \pm 0.53	1.0	NS
Number of weed species	5.0 \pm 0.58	5.5 \pm 0.65	0.02	NS
<i>Fallopia convolvulus</i>	0.4 \pm 0.17	0.4 \pm 0.21	0	NS
<i>Sinapis arvensis</i>	0 \pm 0	0.1 \pm 0.05	1.0	NS
<i>Galium aparine</i>	0 \pm 0	0 \pm 0	-	N/A
<i>Viola arvensis</i>	3.5 \pm 1.54	2.6 \pm 0.54	0.1	NS
<i>Fumaria officinale</i>	0 \pm 0	0.1 \pm 0.05	1.0	NS
<i>Polygonium aviculare</i>	1.3 \pm 0.47	0.8 \pm 0.14	0.9	NS
<i>Papaver rhoeas</i>	0.1 \pm 0.05	0 \pm 0	1.0	NS

At the Cranborne site, of the ground dwelling invertebrates captured by pitfall trapping, only the total number differed between the control and selectively sprayed plots (Table 3.38). No significant differences

were found at the Woodyates site (Table 3.39). Of the crop active invertebrates collected by suction sampling the two bug groups (Homoptera & Heteroptera) and money spiders (Linyphiidae) were all significantly lower in the selectively sprayed plots (Table 3.40). In contrast the predatory Diptera, species richness, staphylinid beetles, total invertebrates and total predators were all higher where the plots had been selectively sprayed (Table 3.40). There was, however, a time.treatment interaction effect and thus for the predatory Diptera, staphylinid beetles, total invertebrates and total predators the differences were only found on certain dates. At the Woodyates site, there were no significant effects on the ground or crop active invertebrates (Table 3.41).

Table 3.38. Mean ground active invertebrates (± 1 SE) and Repeated Measures ANOVA results for treatment effect at Cranborne site. (*= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$)

Variate	Treatment		F- value	Significance
	Control	Selectively sprayed		
	mean ± 1 se			
Carabidae	26.4 \pm 6.39	20.7 \pm 2.79	0.16	NS
Staphylinidae	12.9 \pm 3.62	11.4 \pm 3.42	0.36	NS
All other Coleoptera	0.7 \pm 0.20	0.6 \pm 0.12	0.02	NS
Lycosidae	0.7 \pm 0.18	0.8 \pm 0.20	0.17	NS
Total invertebrates	42.2 \pm 8.85	34.9 \pm 4.29	7.86	*
Species richness	8.4 \pm 0.48	7.7 \pm 0.45	1.60	NS
Carabid larvae	0.1 \pm 0.12	0.5 \pm 0.28	1.47	NS
Staphylinid larvae	0.8 \pm 0.49	0.1 \pm 0.10	2.20	NS
Other Coleopteran larvae	0.7 \pm 0.58	0.5 \pm 0.37	0.62	NS

Table 3.39. Mean ground active invertebrates (± 1 SE) and Repeated Measures ANOVA results for treatment effect at Woodyates site. (*= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$)

Variate	Treatment		F-value	Significance
	Control	Selectively sprayed		
	mean ± 1 se			
Carabidae	1.9 \pm 0.45	2.9 \pm 0.66	3.6	NS
Staphylinidae	2.9 \pm 0.59	1.9 \pm 0.35	1.2	NS
All other Coleoptera	0.6 \pm 0.11	0.9 \pm 0.11	2.1	NS
Lycosidae	1.8 \pm 0.51	0.1 \pm 0.60	0.9	NS
Total invertebrates	7.4 \pm 0.92	7.6 \pm 0.87	0	NS
Species richness	3.1 \pm 0.22	3.3 \pm 0.15	1.3	NS
Carabid larvae	0.1 \pm 0.06	0.1 \pm 0.04	0.01	NS
Staphylinid larvae	0.2 \pm 0.08	0.5 \pm 0.21	1.8	NS
Other Coleopteran larvae	0.1 \pm 0.06	0.1 \pm 0.06	0.2	NS

Table 3.40. Mean crop active invertebrates (± 1 SE) and Repeated Measures ANOVA results for treatment effect at Cranborne site. (*= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$)

Variate	Treatment		F-value	Significance
	Control	Selectively sprayed		
	Mean ± 1 se			
Aphidae	62.3 \pm 4.47	81.5 \pm 13.8	0.7	ns
CFI	0.6 \pm 0.15	0.9 \pm 0.16	4.8	ns
Carabidae	0.5 \pm 0.14	0.3 \pm 0.09	1.1	ns
Heteroptera	0.5 \pm 0.17	0.2 \pm 0.36	12.8	*
Homoptera	3.8 \pm 0.75	2.3 \pm 0.45	14.3	**
Linyphiidae	5.1 \pm 0.69	2.7 \pm 0.52	12.0	*
Predator species richness	4.0 \pm 0.30	3.8 \pm 0.31	0.6	ns
Predatory Diptera	7.2 \pm 1.61	11.4 \pm 1.85	5.7	*
Species Richness	7.9 \pm 0.34	9.8 \pm 0.26	42.8	***
Staphylinidae	5.4 \pm 1.3	9.5 \pm 1.78	8.9	*
Total invertebrates	94.4 \pm 6.74	255 \pm 47.9	74.0	***
Total Predators	20.0 \pm 2.77	25.8 \pm 3.47	6.2	*

Table 3.41. Mean crop active invertebrates (± 1 SE) and Repeated Measures ANOVA results for treatment effect at Woodyates site(*= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$)

Variate	Treatment		F-value	Significance
	Control	Selectively sprayed		
	Mean ± 1 se			
Aphidae	34.8 \pm 2.49	33.4 \pm 2.38	0.1	ns
CFI	0.39 \pm 0.07	0.3 \pm 0.06	3.5	ns
Carabidae	0.38 \pm 0.2	0.3 \pm 0.09	0.6	ns
Heteroptera	0.44 \pm 0.18	0.5 \pm 0.20	0.03	ns
Homoptera	5.7 \pm 0.80	6.5 \pm 0.79	1.1	ns
Linyphiidae	3.8 \pm 0.53	3.9 \pm 0.54	0.1	ns
Predator species richness	3.1 \pm 0.29	3.2 \pm 0.38	0.1	ns
Predatory Diptera	9.6 \pm 2.53	11.8 \pm 3.50	1.9	ns
Species Richness	6.5 \pm 0.32	6.9 \pm 0.51	0.3	ns
Staphylinidae	1.8 \pm 0.36	1.8 \pm 0.43	0.01	ns
Total invertebrates	61.1 \pm 4.79	62.1 \pm 5.88	0.01	ns
Total Predators	17.4 \pm 3.31	19.5 \pm 4.30	0.6	ns

3.5.3.4. Conclusions

1. The reduced herbicide inputs did not increase weeds at one site because dry weather inhibited weed germination.
2. Where weed cover was higher, this did not increase numbers of ground dwelling invertebrates but increased densities of predatory Diptera, Staphylinidae, total invertebrates, total predators and species richness on some occasions.
3. The higher weed cover reduced the density of some of the invertebrates groups important as bird food.

3.6 SPATIAL DISTRIBUTION OF PEA APHIDS AND THEIR PREDATORS

The spatial distribution of cereal aphids has been much studied recently (Winder et al., 1999) and this revealed that cereal aphids had an ephemeral distribution within cereal fields with patches appearing and disappearing through the summer. Examination of the spatio-temporal association between the carabid beetle *P. melanarius* and two aphid species revealed a strong correlation (Winder et al., 2001). These spatially coupled dynamics were sufficiently strong for this beetle predator to have a negative effect on the intrinsic rate of aphid increase. This was the first time that generalist predators were confirmed as impacting on aphid population dynamics. Research on the dynamics of cereal aphids and their prey has continued with BBSRC funding and therefore was not investigated here; instead the spatial relationships between pea aphids and generalist predators were examined. Pea aphids exhibit a similar behavioural response to cereal aphids in the presence of predators; to escape predation they drop to the ground (Clegg & Barlow, 1982). This also makes them vulnerable to ground active predators. In alfalfa, ground active predators worked synergistically with foliage active ones to make a significant contribution to aphid suppression (Losey & Denno, 1998a). The value of ground active predators for pea aphid control in pea crops has not been investigated.

3.6.1 Materials and Methods.

In 2001, the distribution of pea aphids and epigeal invertebrates was monitored within one of the study fields (L1) during the period of pea aphid infestation. Pea aphid abundance was measured at each sampling point within the field by counting the number of aphids on 10 plants on 18, 21, 25 and 29 June and 3 July. The number of epigeal predators was measured using the grid of pitfall traps as described in section 3.2.1.2., and data was collected on three sampling occasions (Table 3.1).

The distribution of pea aphids and the total number of invertebrate predators collected in the pitfall traps was analysed using the Sadie red/blue method. The spatial association between pea aphids on five sample dates and total number of aphid predators on four occasions, giving 20 possible combinations over the five lagged sample occasions, was calculated as described in section 3.2.1.5.. The spatial correlation value X was plotted in two dimensions, as carried out in Winder et. al. (2001).

3.6.2. Results

Pea aphid numbers showed an initial increase followed by a decrease then built further towards the last sample date (Fig. 3.24). They exhibited evidence of significant clustering into patches with gaps between on the 2-5 sampling occasions (Table 3.42), but the location of the patches and gaps was ephemeral (Fig. 3.25). The size of the patches and gaps also varied during the infestation.

The number of predators peaked between 25 and 29 June, but was relatively consistent over the pea aphid infestation period (Fig 3.24). The predator numbers were highest in the bottom corner of the field, with a small patch mid-field (Fig. 3.26).

Table 3.42. Degree of clustering into 'patches' using overall index \bar{v}_i and associated probability P_i , or of 'gaps' using overall index \bar{v}_j and associated probability P_j for pea aphids and the total number of predatory arthropods in field L1 in 2001. (***=P<0.001, **= P<0.01, *= P<0.05).

	Sample dates	Pea aphids	Sample dates	Total predators
\bar{v}_j	18/06/01	-1.05	18-21/6/2001	-1.86
\bar{v}_i		0.99		1.85
P_j		NS		***
P_i		NS		***
\bar{v}_j	21/06/01	-1.25	21-25/6/2001	-2.23
\bar{v}_i		1.28		2.32
P_j		NS		***
P_i		NS		***
\bar{v}_j	25/06/01	-1.62	25-29/6/2001	-1.63
\bar{v}_i		1.74		1.78
P_j		***		***
P_i		***		***
\bar{v}_j	29/06/01	-2.72	29/6-3/7/2001	-2.85
\bar{v}_i		2.72		2.82
P_j		***		***
P_i		***		***
\bar{v}_j	03/07/01	-1.47		
\bar{v}_i		1.45		
P_j		*		
P_i		*		

Figure 3.24. Abundance of pea aphids and predatory invertebrates.

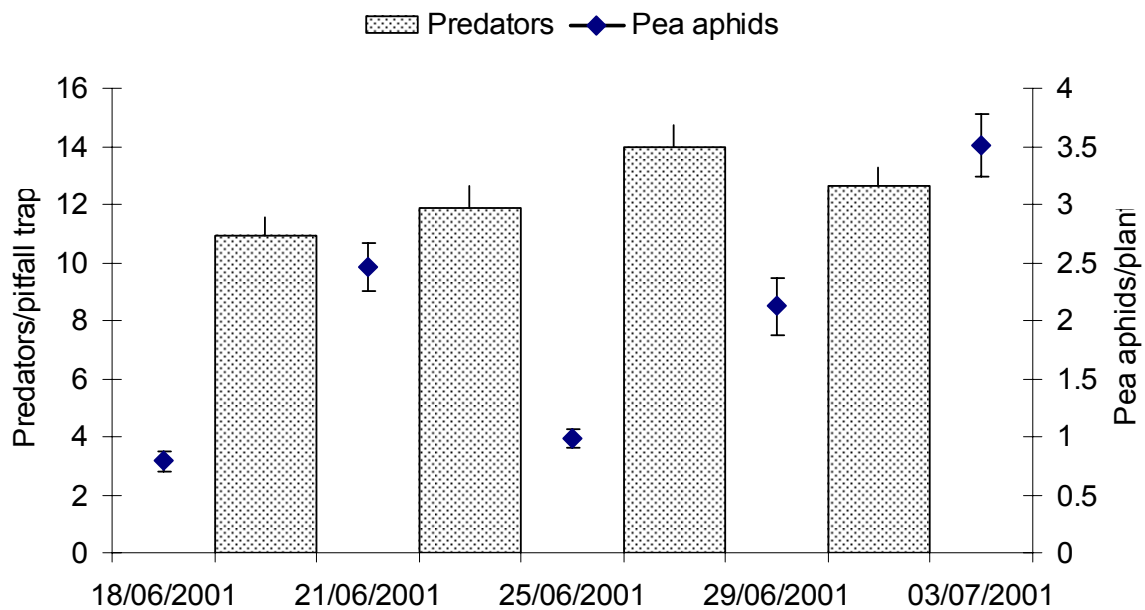


Figure 3.25. Spatial clustering for pea aphids on a) 21/6, b) 25/6, c) 29/6 and d) 3/7/2001. The maps indicate clusters of relatively high counts ($v_i > 1.5$) and small counts ($v_i < -1.5$).

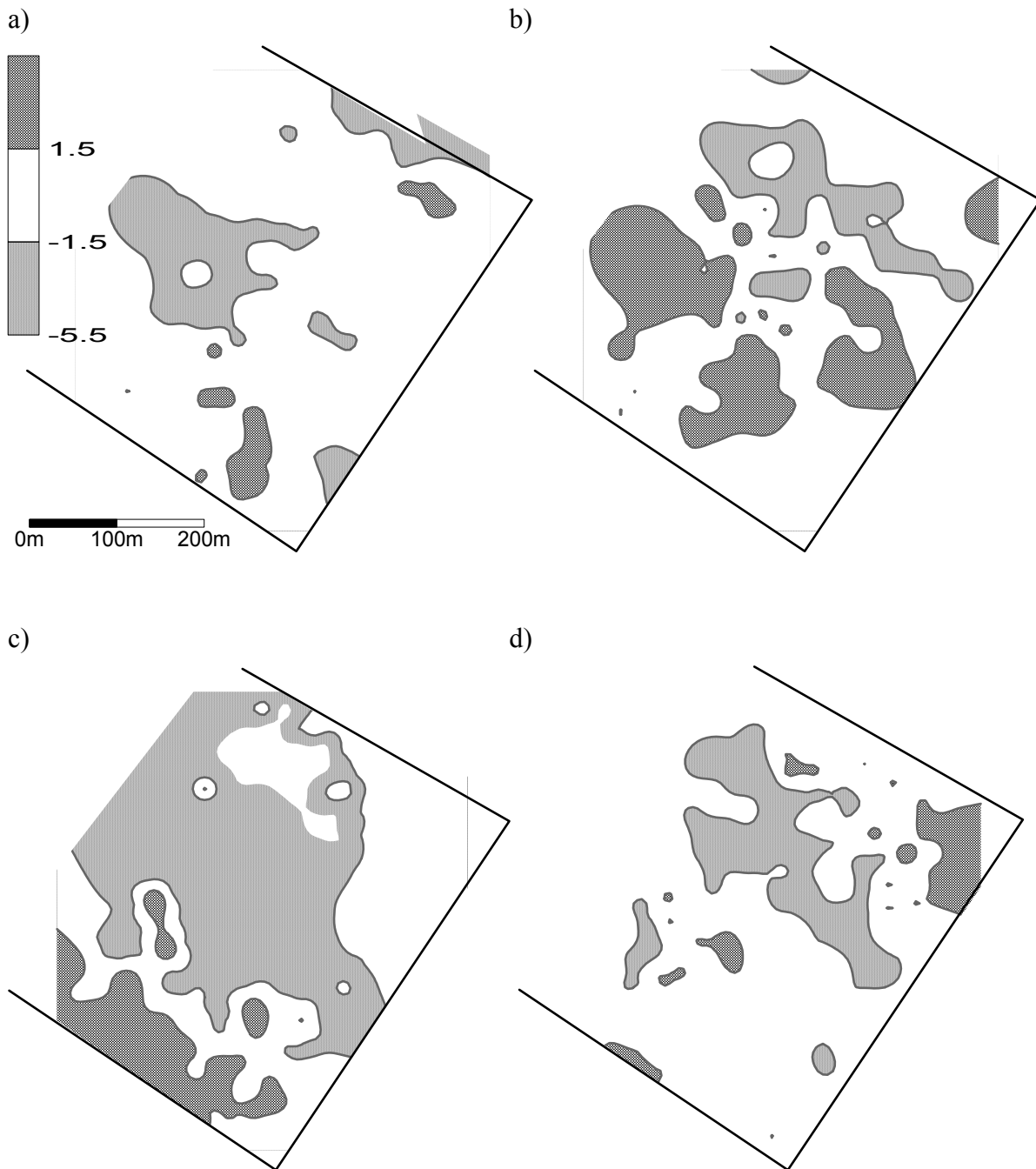


Figure 3.26. Spatial clustering for predatory invertebrates in pitfall traps on a) 25-29/6 and b) 29/6-3/7/2001. The maps indicate clusters of relatively high counts ($v_i > 1.5$) and small counts ($v_i < -1.5$).

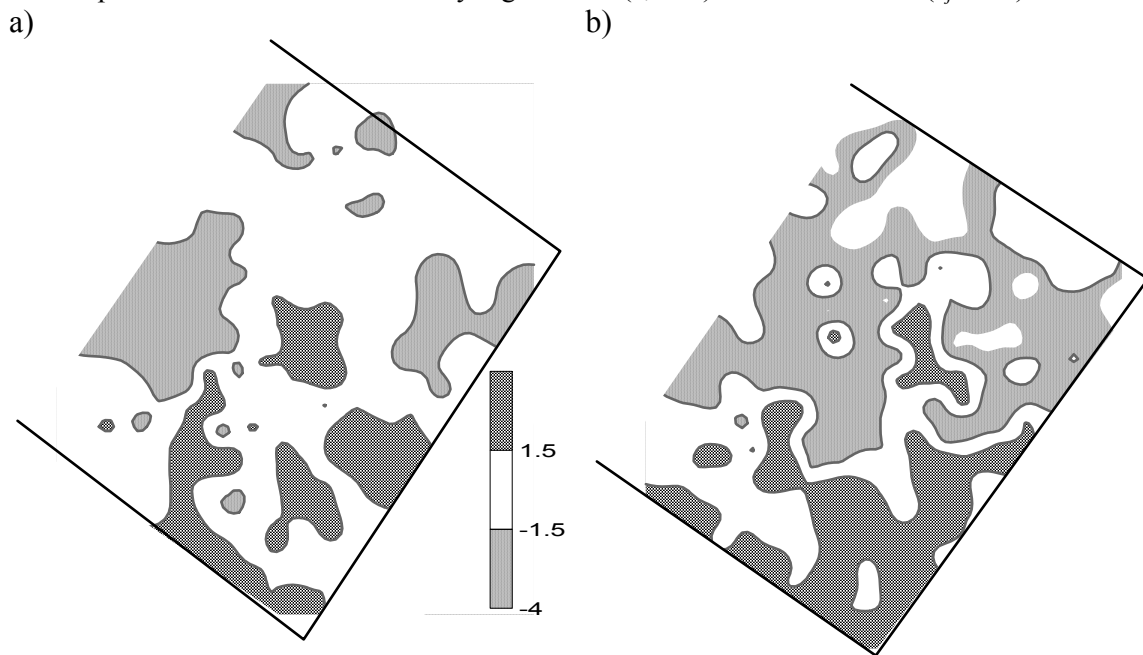
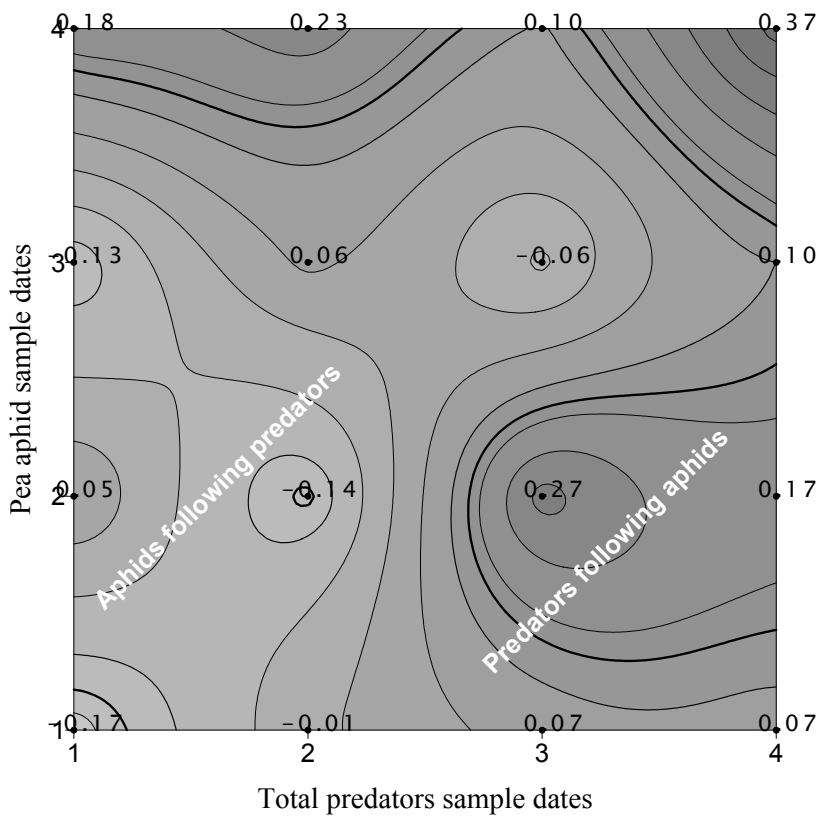


Figure 3.27. Spatio-temporal association between predator and prey. Interpolated surface of unlagged (main diagonal) and lagged (above and below main diagonal) associations between pea aphids (y -axes) and predatory invertebrates (x -axis).



The contour map depicting the spatio-temporal correlation between predators and pea aphids for all possible sampling combinations indicates that for those samples taken simultaneously there was negative then positive association (Fig. 3.27). The lagged associations revealed that the predators were positively correlated with the preceding aphid spatial pattern while the aphids were negatively correlated with the preceding predator spatial pattern. Much of this relationship was likely to be driven by what occurred in the bottom corner of the field, where a large predator patch developed, in which pea aphids were largely absent.

3.6.3. Conclusions

1. Pea aphids were highly aggregated with patches of high density, but the location of these varied through the infestation period.
2. The location of the patches containing the highest number of predators was consistent through the pea aphid infestation period.
3. There was evidence that the ground active predators were influencing the abundance and distribution of pea aphids.

3.7 THE INFLUENCE OF FIELD MARGINS ON INVERTEBRATES WITHIN FIELDS

Many species of beneficial invertebrate overwinter either in the hedgebase or in the hedge vegetation. In addition, the field margins provide food resources such as pollen, nectar, vegetation and seeds, along with prey for predatory and parasitic species. As a consequence, they are a rich source of beneficial invertebrates, some of which colonise the cropped areas. The field margins also act as a refuge from otherwise damaging crop production practices such as cultivation and insecticide spraying. Field margins, however, vary enormously in terms of their structure and species composition. Around the six fields in which the spatial studies were conducted there was a range of different field margin types including hedges with a hedge base, grassy strips and farm tracks that varied in the diversity of their vegetation and structure. This may have influenced the abundance and diversity of invertebrates within the nearby field area. To assess whether there was any such impact, the structure and vegetational diversity of each field margin was surveyed in 2000 and 2002 and relationships sought to the within-field invertebrate community.

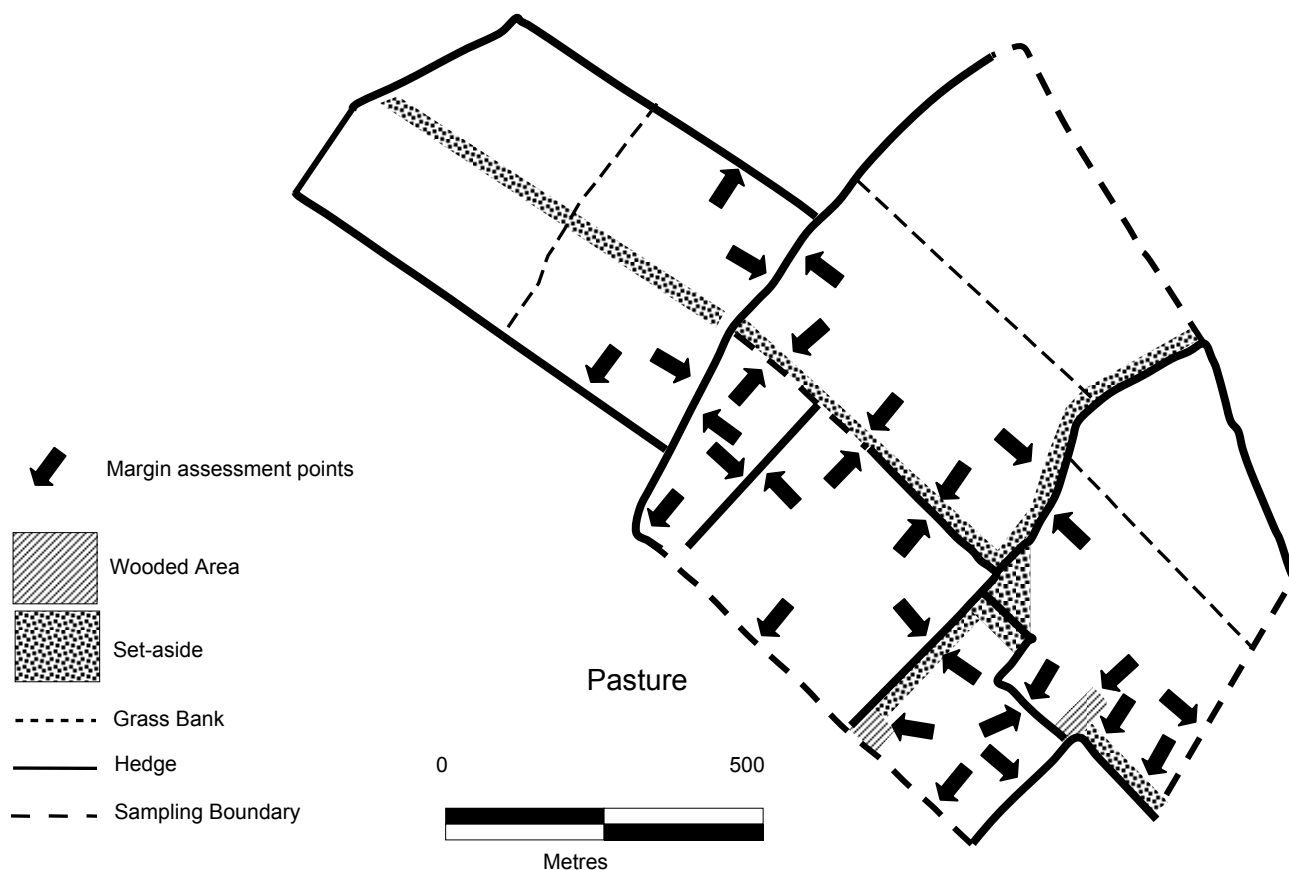
3.7.1 Materials and Methods.

The field boundary vegetation was assessed in 30 field boundary lengths from the six study fields (Fig. 3.28). Boundary lengths were separated on the basis of aspect and major change in boundary structure, e.g. post and wire fences were split from hedgerow lengths along the same field edge. The higher plant species present in each field boundary length were recorded as part of the ground flora (0-1m), the shrub layer (1-4m) or the tree layer (>4m) in June 2000 and 2002. Each species present was given a score (0-9), based on a modified Braun-Blanquet cover-abundance score (Table 3.43) (Westhoff & Maarel, 1973).

Table 3.43. Cover-abundance scores (0-9) used to assess the flora of Cranbourne field boundaries, based on modified dominance scores (Westhoff & Maarel, 1973).

Score	Description; % ground cover by eye	% cover used for formal analyses
1	Rare; 1 or 2 plants	0.25
2	Sparse; 3 – 10 small plants	0.5
3	Frequent, <4% cover	1
4	Abundant, 5% cover	2
5	5 - 12.5%	5
6	12.5 - 25%	12.5
7	25 - 50%	25
8	51 - 75%	50
9	76 - 100%	75

Figure 3.28. Location of field margin assessment points across study area.



To determine whether there was any relationship between the field boundary characteristics and the invertebrates, a subset of the spatial distribution data for June 2000 and 2002 was used. Data was summed from a block of eight pitfall sampling locations (3 in the first row, 2 in the second and 3 in the third row in from the boundary) adjacent to each boundary monitoring position. This gave a figure that was matched with the data point provided in the vegetation survey data sets. Regression analyses were run to establish if there was a linear relationship between species richness of the herb layer and species richness or abundance of the invertebrates adjacent to each boundary position in June. Invertebrate data were log transformed and the analysis was run in GENSTAT 7. There was no significant relationship in either 2000 or 2002.

An RDA analysis was used to: 1) establish whether characteristics of the shrub layer in hedges were related to the composition of the invertebrate community and 2) to establish whether species richness of the herb layer was related to the composition of the invertebrate community. The RDA was run in CANOCO; invertebrate data were used as the species data (response variable) and were log transformed before analysis. The shrub and herb data were used as environmental (predictive) variables as follows: hedge width, hedge height, percentage gaps in hedge, abundance of grass in the herb layer, number of grass species in the herb layer, abundance of forbs in the herb layer, number of forb species in the herb layer and total species richness of the herb layer. Data from 2000 and 2002 was analysed separately.

The extent to which the vegetation composition of the hedge base influenced the invertebrate community composition sampled using the pitfall traps was examined by matching the similarity matrices for invertebrate and ground flora data using RELATE in PRIMER.

3.7.2. Results

In 2000 canonical axes 1 and 2 were significant (Fig. 3.29). The results suggest that swards dominated by grass supported a different community than that supported by forbs. Grasses were associated with *Bembidion* spp. and *Carabus* spp. (carabid beetles), *Tachinus* spp. (staphylinid beetles) and both staphylinid and carabid larvae. In contrast, forb species richness was associated with ladybirds (Coccinellidae) and weevils (Curculionidae). The carabid *P. madidus* was associated with forb abundance. Species such as the carabids *P. melanarius* and *Poecilus cupreus* were associated with gaps in the hedge. In general, grass abundance was more influential than grass species richness.

General species richness was associated with the same species as forb species richness, probably because this amounts to the same thing (i.e. where there is increased species richness it is due to an increase in the numbers of forbs, not grasses). *Demetrias* spp., and *Notiophilus biguttatus* (carabid beetles) and *Paederus* spp. (staphylinid beetles) were associated with taller, thicker hedges.

In 2002, canonical axis was significant (Fig. 3.30). However, the relationships were not quite so clear in 2002. Much of the community composition was not influenced by the environmental variables and it is likely that there was some other factor that was important in determining species distribution. There was less differentiation in the community composition according to the species richness of grass and forbs, only forb abundance was separated on the graph (Fig. 3.28). However, some of the associations hold true. *Bembidion* spp., total carabid beetles and elaterid beetles were found in grassy areas and ladybirds were associated with forb species richness.

The similarity matrices for invertebrate and herb layer data were matched using RELATE in PRIMER, but no relationship was established in either 2000 or 2002.

Figure 3.27. Ordination plot showing the relationship between vegetation characteristics and invertebrate communities in June 2000. Key: hedgewid = hedge width, Hedgeheg = hedge height, gaps = percentage of gaps in hedge, Gras_abu = grass abundance, Gras_spr = grass species richness, Forb_spr = forb species richness, Forb_abu = forb abundance, , Sp_rich = herb layer species richness.

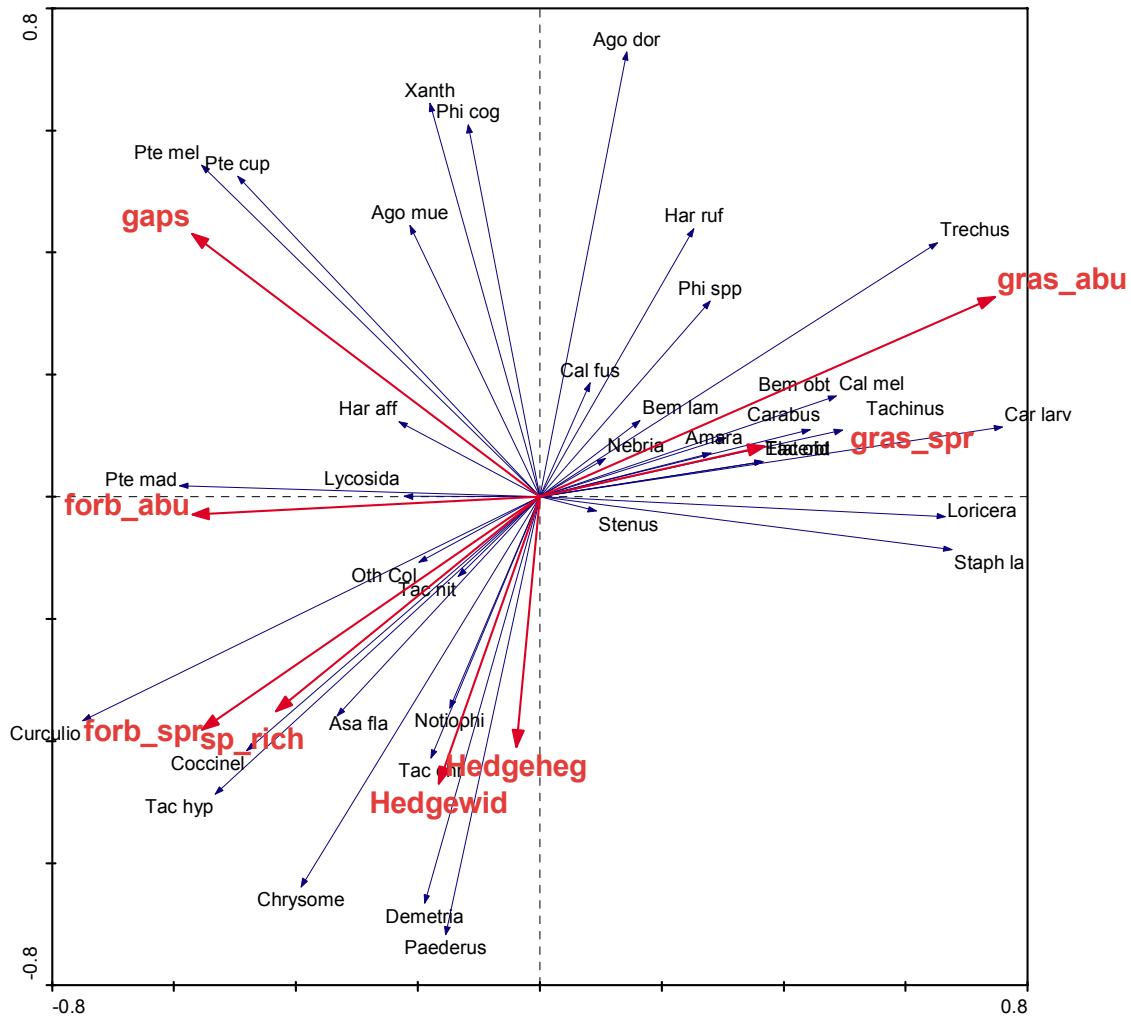
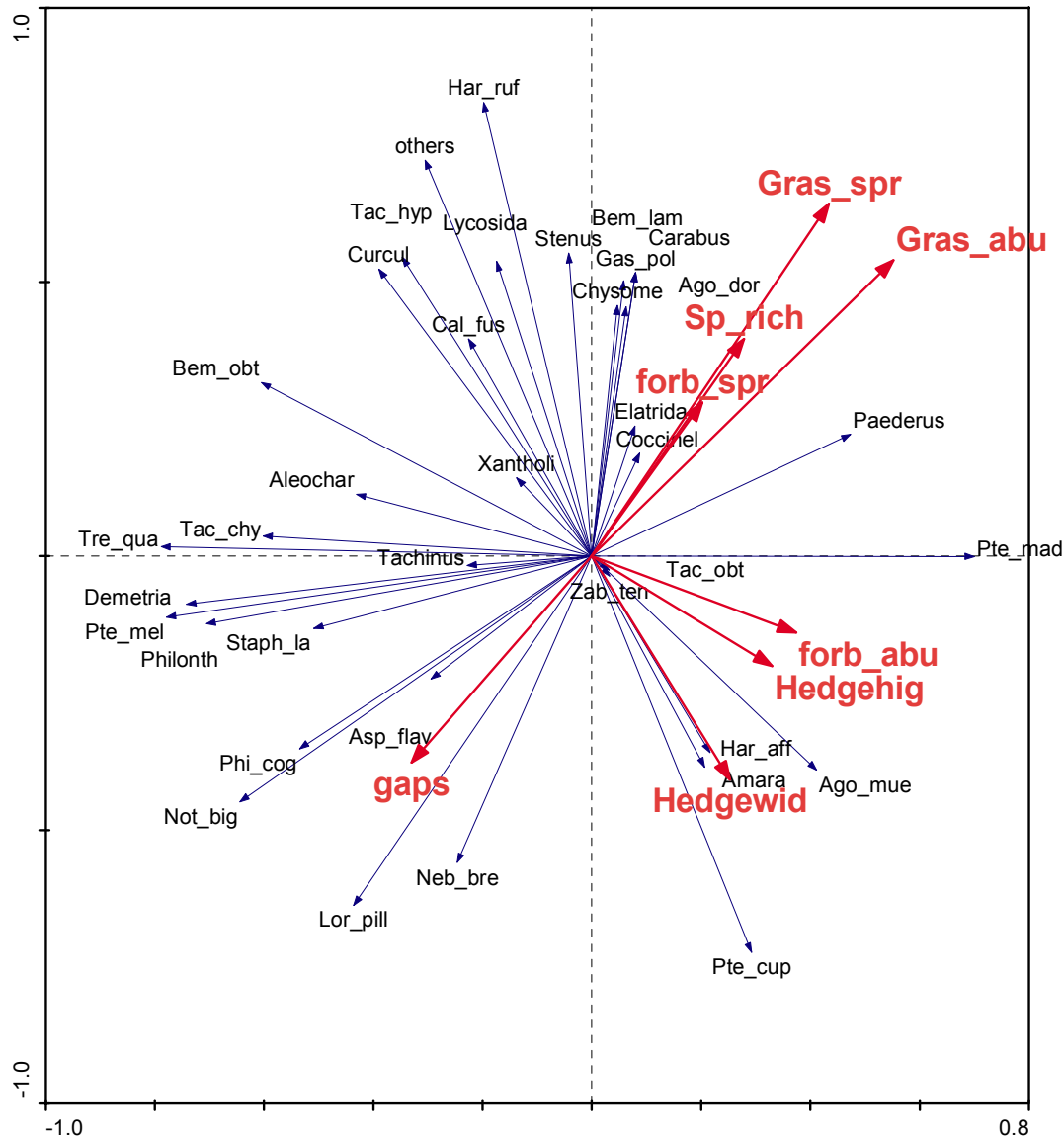


Figure 3.28. Ordination plot showing the relationship between vegetation characteristics and invertebrate communities in June 2002. Key: hedgewid = hedge width, Hedgehig = hedge height, gaps = percentage of gaps in hedge, Gras_abu = grass abundance, Gras_spr = grass species richness, Forb_spr = forb species richness, Forb_abu = forb abundance, , Sp_rich = herb layer species richness.



3.7.3 Determining the cost of establishing flower-rich field margins

One of the outcomes of the knowledge transfer meeting held in the last year of the 3DF project was a decision to find a way to communicate to farmers the costs and benefits of introducing margins on to farms. It was decided that this would be best presented as a 'margin calculator'. The aim of the margin calculator was to provide a user-friendly system for farmers to compare income generated on their own farm both with and without margins. **A prototype of the calculator has been developed. Using the 'margin calculator' a farmer will be able compare potential income from incentive schemes with current income based upon only a few essential facts about farm income.**

Calculations, based on the current Countryside Stewardship and ESA agreements, are embedded in the spreadsheet. The user has a choice of whether to use imperial, metric or a screen that allows one to enter in imperial and have the calculations converted into metric. These calculations can be easily updated when the Entry Level and Higher Tier Scheme is in place.

Information on how margins will benefit wildlife has been added on separate sheets within the workbook. It is envisaged that the information on wildlife benefits is enlarged but kept straightforward. Links to more detailed information can be added. The aim is to refine the calculations, adding an option to put in margins tailored inline with the findings of the 3D Farming project. This is dependent on the final costings being passed on.

It is possible to put this spreadsheet on the web, however the front end is not immediately attractive. **It is recommended that a small sum is invested in employing a software designer to produce a simple clean system to present the calculator as user friendly.**

3.7.4 Conclusions

1. The margin structure and vegetation influenced the invertebrate species composition in the adjacent crop.
2. More associations were found for 2000 than for 2002, but there were some consistent trends. Carabids were more strongly associated with grassy margins and Coccinellidae with the forbs.

3.8 DISCUSSION

3.8.1 Investigation of the Large-Scale, Spatio-Temporal Dynamics of Predatory Epigeal Invertebrates in Arable Farmland.

The spatial dynamics of predatory invertebrates was examined across a contiguous block of six fields through a cereal-cereal-pea rotation. **The spatial scale and extent of the trapping grid used in this study surpassed all previous investigations of this type anywhere in the world.** Previous studies have focussed on either parts of fields, whole single fields or pairs of neighbouring fields. In addition, no previous study has ever examined the spatial dynamics of predatory invertebrates between years. As a consequence it has been possible to answer some key questions regarding the spatio-temporal dynamics of predatory invertebrates and thus to understand their ecology better and be able to inform farmers and agronomists on how best to encourage the natural biocontrol provided by these generalist predators. Some of the key questions were:

1. To what extent are predatory invertebrate distributions aggregated across a contiguous block of fields?
2. How stable are predatory invertebrate aggregations within and between years?
3. What is the scale of the predatory invertebrate distribution patterns across the study area?
4. What factors (biotic and abiotic) influence predatory invertebrate distribution patterns in the field?
5. How important are different field boundary types to invertebrate abundance, distribution and diversity within the fields?

The answers to these questioned are addressed below.

The discussion is focussed towards the findings that are likely to be of most relevance to agricultural advisors, scientists and policy makers, however, there is also a wealth of key ecological information that has not been discussed. Moreover, in order to keep the text as short and accessible as possible the results have not been fully discussed with respect to the published scientific literature. This will be achieved when the findings are compiled for scientific journals.

1. To what extent are predatory invertebrate distributions aggregated across a contiguous block of fields?

In other words are patches of higher than average density isolated within fields or do they extend across field boundaries? This is important because it can affect the potential for population recovery following adverse agricultural practices, such as an insecticide application; invertebrates reinvade treated areas from adjacent unsprayed crops and habitats. In addition, this information will allow us to determine to what extent field boundaries act as sources of invertebrates or as barriers to their distributions. Species with populations that are isolated within single fields are more at risk of becoming locally extinct within that field compared to species with more widely dispersed populations. The level and size of population aggregations will also influence the extent of pest control. If the total predatory effort is relatively evenly distributed across arable fields then likewise pest control may be similarly even. However, if there is an uneven distribution, for

example, a higher predatory effort near to field margins, then management plans are needed to encourage a more even distribution.

In this study, pitfall trapping was used and therefore the invertebrates collected were predominantly ground-active, generalist predators. **Early in the year (May and June) the predatory fauna was more diverse being largely composed of those species that had overwintered in the margins as adults. In July, those species that had overwintered as larvae within the field started to emerge as adults and these then dominated the species composition, while also being very numerous. The boundary overwintering species remained close to the field margins (<100 m) throughout the summer in 2000**, as found previously in studies of single fields (Holland et al., 1999). Only in the smallest field did they penetrate to the field centre, where the distance to the centre was only 60 m. In 2001 and 2002 the boundary overwintering species penetrated further into the larger fields. Why this occurred in these years and fields cannot be ascertained from the data yet analysed. Set-aside strips and a beetle bank were established around these fields in the autumn of 2000 and may have contributed to the more widespread dispersal of field boundary species, although this was not apparent from the detailed investigations in which the impact of the set-aside strips on within field invertebrate abundance was examined (section 3.5.2). In 2002, cereal aphids were very abundant in the winter wheat fields L1 and L2, where the boundary overwintering species were highest and this may have encouraged a more widespread dispersal across the fields. Previous studies employing transects of pitfall traps also found that boundary overwintering species moved rapidly across fields in the spring and were fully dispersed across the fields in late May-June (Coombes & Sotherton, 1986; Jensen et al., 1989; Kromp & Nitzlander, 1995; Thomas et al., 2000), although some species remained associated with the field boundaries (Kromp & Nitzlander, 1995).

The mid-field overwintering species were, as expected, found spread across fields. For some species the patches extended across several fields, while for others they were more restricted and were found only in certain fields or parts thereof. Thus it would appear that **the spatial extent of a species' local population patch is species specific but they can extend across field boundaries.** Likewise, a study examining the distribution of six carabid species in parts of two adjacent fields revealed that each species restricted its distribution to certain parts of the fields (Thomas et al., 1998; Fernández García *et al.*, 2000; Thomas et al., 2001). A further study comparing invertebrate distributions in two fields of 4 and 16 ha also confirmed that many of the species present had heterogeneous distributions, although some of the more mobile species showed no evidence of spatial pattern (Holland et al., 1999). Consequently, if maximum biodiversity is to be maintained then broad-scale management treatments (eg. cropping and insecticide applications) should be avoided across groups of fields, otherwise there is a risk of reducing species diversity within individual fields. Reinvasion from untreated fields is also likely to be faster if these are in close proximity to the treated ones.

Data from these spatial studies could be used to design sampling strategies that are more accurate at predicting the within field numbers of beneficial invertebrates while also reducing the labour inputs needed to make such measurements. This would be of benefit when designing protocols to estimate the effects of plant protection products for registration purposes or when introducing changes in crop management such as the use of GM crops. Likewise, more efficient sampling protocols can improve the value of ecological studies. Such an approach was tried using data on the spatial distribution of cereal aphids and revealed considerable differences in the accuracy of the various sampling regimes currently in use (Alexander et al. submitted).

2. How stable are predatory invertebrate aggregations within and between years?

The species and groups analysed had a consistent distribution pattern within each year, the patches and gaps remaining in the same parts of the study area. This is in agreement with most other studies that have examined within-year distribution (Thomas et al., 1998; Holland et al., 1999; Fernández García *et al.*, 2000; Thomas et al., 2001), although one of the species, *P. melanarius* has been shown in another study to be more mobile within the year, moving in response to the distribution of aphids (Winder et al., 2001) and slugs (Bohan et al., 2000). Redistribution of carabids from June to August was likewise found using a grid sampling approach that encompassed two pairs of fields (Brown, 2000; Thomas et al., 2002). The difference in cropping was considered to be important, with a preference being shown for a bean compared to a wheat field. **In this study the total predatory effort as indicated by their numbers was stable within years but not between years.** There were exceptions for some species, for example *P. melanarius*, which remained in the same location over the three years, and some other species and groups that persisted in broadly the same place for two years. Thus, for some species, notably one of the most common and widespread predatory carabids, a great deal of affinity is shown for particular locations. This is likely to be due to microclimatic, edaphic and hydrological factors which, if determined, may make excellent predictors of parts of farmland where care should be taken to preserve the area from damage. Such locations are likely to act as sources for seeding population spread across wider areas of a farm when optimum conditions prevail. For other species whose population distributions appear less stable between years, these findings suggest that either: a) population patches are continually being destroyed and created, giving the appearance of a dynamic redistribution; or b) that the invertebrates are moving around the landscape and re-aggregating in different areas in response to changing conditions; or c) that both these mechanisms are to some extent responsible to various degrees for different species. Consequently, **the level of bio-control within each field may be expected to vary between years.** Understanding why these changes occur is critical if we are to better manipulate generalist predators for biocontrol.

3. What is the scale of the predatory invertebrate distribution patterns across the study area?

All of the species studied showed heterogeneous distribution patterns across the study area indicating that certain areas provided more attractive conditions and they were dispersing to congregate in these

areas or the areas favoured their population growth. The importance of movement is considered in section 3.8.2. **The size of patch within each field and across the site varied between species.** Some species appeared to be restricted to particular areas of the study site, for example the patches of *P. melanarius* covered approximately 10 ha, whereas those of *P. madidus* extended across several fields and covered 23 ha in July 2000. This is much larger than previously found for these species (Thomas et al., 1998; Holland et al., 1999; Brown, 2000), but reflects the scale of this study compared to previous ones. For some of the smaller species the patches were also much smaller. The heterogeneous distributions patterns, especially early in the year, indicate that for invertebrates arable fields are far from uniform in their suitability for colonisation, despite our attempts to create homogeneous monocultures. When considering the potential for biological control it is the total number of predatory invertebrates that is important but this also varied spatially, with some fields having relatively even coverage across the whole field, while others had much less. **The extent of coverage varied most between May and June, the extent of the patches being relatively consistent between June and July each year. The between year differences showed that the number of predators was inconsistent within a field between years.** To some extent this may have been a result of changes in cropping as discussed below. However, there is potential to manipulate the environment to reduce such variation and ensure more consistent, predictable and dependable levels of biological control.

4. What factors (biotic and abiotic) are influencing predatory invertebrate distribution patterns in the field?

The distribution of invertebrates within farmland will be governed by historical and current management, along with abiotic and biotic factors that will be influenced to some extent by the management. Thus factors such as previous methods of tillage, agrochemical inputs and cropping will have influenced soil structure and the weed seedbank. The subsequent weed and crop growth will then determine cover and humidity, which will, in turn, affect which invertebrate species find the environment most suitable. Current management will likewise be influential and it is likely that this may change through the year and between years. For invertebrates, the factors that are already known to determine the suitability of a particular area include: a) presence of food, which includes pest species, b) microclimatic conditions, most importantly humidity and c) the physical structure of habitat. The ability of a species to locate and colonise suitable areas will depend on their life strategy: those with good dispersal abilities and high reproductive rates being the most able. For most predatory species found in arable fields we know little about their movement, fecundity and factors controlling this; neither do we know much about survival rates.

In this study we examined whether the crop, weed cover or soil moisture influenced the predatory invertebrate distribution patterns. The importance of these and other factors on the spatial distribution of Carabidae was reviewed by Thomas et al. (2002). The importance of abiotic and biotic factors for Carabidae was reviewed by Holland & Luff (2000) but little information exists for Staphylinidae.

Crop type

The type of crop will influence many factors that are important to beneficial invertebrates including: the type and timing of cultivations; extent and timing of vegetation cover; abundance of prey; environmental conditions; agrochemical inputs and time of harvest. It is therefore likely that particular crops will favour particular species according to their phenology, environmental requirements and diet. This will determine the species composition and dominance ratios as found previously (Holland, 2000; Hance, 2002: reviewed for Carabidae). Overall, root crops were found to have a negative impact on ground-active invertebrates whilst there was little difference between cereals and legumes. In this study the species composition varied between winter wheat and peas, probably because of marked differences in their physical characteristics, management and sowing dates. As conditions change within a crop this may also affect its suitability and encourage immigration or emigration. The invertebrate distribution patterns were relatively stable within-years suggesting that there was little movement between crop types prior to harvest, as confirmed in the mark-release-recapture studies. In contrast, the distribution of *P. melanarius* has been shown to shift between bean and wheat fields during summer (Brown, 2000; Thomas et al., 2002). The large differences in the location of patches between the years indicated that either movement was occurring or survival was different between fields.

High numbers of predators were captured in the pea fields in 2000 and 2001 indicating that this crop may have favoured the survival of some species, especially *P. madidus* which was the numerically dominant species. The comparison of community composition between the crops showed that there were only differences between winter wheat and spring-sown peas. It was often just a few species that were responsible for most of the differences, notably the large species that overwintered within the fields as larvae, e.g. *P. melanarius*, *P. madidus* and *P. cognatus*. There were also some differences between the results for June and July. In June *P. madidus* was more abundant in wheat than peas but the reverse was found in July, but this can be explained by examining the age of the captured beetles. In June the adults that had survived the winter dominated the catch, whereas by July most of the beetles caught were teneral. This may have also held true for *P. cognatus*. The pitfall traps also only provide a snapshot measurement of the invertebrate community whereas the emergence traps provided season-long activity. When they were used in these two crops, the emergence of Carabidae (including *Pterostichus* species) and Staphylinidae was higher from winter wheat compared to the spring-sown peas. The difference in the timing of the soil cultivations could have affected beetle survival. The species found here were autumn breeding species that have large larvae, and these were considered to be more susceptible to spring than autumn cultivations (Fadl et al. 1996; Purvis & Fadl, 1996).

Diversity declined as the crop matured and the fauna became dominated by just a few species. This is typical for arable fields and the decline of other species may occur for a range of reasons. Many of these species are active early in the year and activity naturally declines through the summer following breeding. The conditions within the crop may become unsuitable, they may be predated by, for example, the larger species

that emerge later, prey may become less abundant or they may succumb to disease and parasitism. A more diverse fauna is considered to improve biological control because the pests are controlled through a variety of mechanisms. Nevertheless, the large carabid beetles that dominated the ground fauna in July were shown to actively focus on cereal aphid patches and contribute to their demise (Winder et al., 2001). Further studies on these species using marked beetles are currently underway, funded through BBSRC.

Long-term investigations of invertebrates, in which the same fields were repeatedly sampled, showed that particular fields can consistently have high numbers of an individual species, but densities of other species were highly variable between years (Thomas et al., 2002). There was, however, always some variation between years. In this study, high numbers of predators were always captured in field L3, despite the changes in cropping. The community composition analysis also revealed that differences between the fields were always greater than between the crops. **These results and those from studies of dispersal suggest that it is changes in invertebrate reproduction, survival and mortality that are driving population change rather than mass dispersal.** Moreover, the impact of cropping and the associated management were less influential than those factors that make a particular field most suitable, e.g. soil type and moisture levels. There will always be species specific response to management inputs because each species differs in its susceptibility to change. For example, the impact of deep cultivation will depend on the species phenology and lifecycle. However, we know very little about the comparative impact of management inputs. Partly this is because many of the factors that influence invertebrate populations interact with each other, as depicted for Carabidae in Holland (2002).

In 2000 and 2001 the insecticide 'pirimicarb' was applied for pea aphid control in mid-June. Pirimicarb is considered to be a selective insecticide with a low toxicity to beneficial invertebrates. The toxicity to ground and crop-active predators has been examined in a number of laboratory (Çilgi et al., 1996), semi-field (Kennedy et al., 2001) and field trials (Vickerman et al., 1987). In the laboratory trials the full application rate of pirimicarb (as used in the peas) caused between 5-26% mortality of four carabid species, although lower mortality would be expected in the crop because only a proportion of the spray penetrates to ground level. The semi-field trials were a rigorous test of mortality because enclosures were used to prevent immigration or emigration, yet under field-like conditions. In these trials, pirimicarb had no impact on Carabidae or Staphylinidae. In full field trials, the reductions in the density of Carabidae and Staphylinidae were 27% and 26% respectively, possibly due to emigration. There were, however, differences between species; the crop-active species were more susceptible than those at ground level. The abundance of some species may have been reduced by the pirimicarb applications in 2000 and 2001, but as there was only one untreated pea field, the effect cannot be statistically tested. The total predatory effort was unlikely to be much effected because the most abundant species were the large, predominantly ground-active Carabidae and Staphylinidae, as found in the semi-field trials.

Crop and weed cover

Analysis of the spatial association between vegetation cover and invertebrates captured in the pitfall traps revealed many significant findings. **Weed cover was more strongly associated with the invertebrates than total vegetation cover that included crop cover.** The proportion of ground covered by vegetation can influence humidity, shading, soil moisture and architectural complexity at ground level, and these are known to be important in habitat selection for a number of taxa (Tutin et al., 1991; Rypstra et al., 1999). Hydrophilic species will choose dense crops or areas of high weed cover whereas hydrophobic species will choose those with a more open canopy and less weed cover. It is likely that the low growing weeds would have a larger impact on humidity than the taller crop which has most of the leaves well above the ground. Indeed, the application of a herbicide reduced the numbers of carabid larvae (Powell et al., 1985) possibly because the weedy areas had a higher humidity that was attractive to gravid females. In addition, the weeds may support a variety of phytophagous invertebrates that could attract the generalist predators (Speight & Lawton, 1976) and provide seed for spermophagous and generalist species (Tooley & Brust, 2002). Generalist predators were also found to be better fed in areas of higher weed density and this may lead to higher populations through improvements in their fecundity and survival (Chiverton & Sotherton, 1991). **Whatever, the mechanism the results show that weed cover could be manipulated to encourage predatory invertebrates.** The attractiveness of weedy crops for generalist predators has been shown previously (Speight & Lawton, 1976; Purvis & Curry, 1984; Powell et al., 1985; Kromp, 1989; Pavuk et al., 1997) but no attempt was made to determine what percentage of weed cover is needed to maximise usage by invertebrates. **In this study between 10 and 14% was optimal when the total number of predators was considered, however, this could vary according to the species composition.** The patchy distribution of weeds may also be beneficial as greater habitat diversity may occur. The weedy areas create a dense humid environment in contrast to the more open, drier areas where no weeds are present. Indeed, invertebrate species richness was also found to be higher where weeds were allowed to develop (Pavuk et al., 1997).

Soil moisture

The soil moisture levels within a field are governed by the soil type and drainage, along with the type and amount of vegetation and can be expected to change considerably within the year. Consequently, a wet area in winter may not necessarily persist through the summer. Previous studies examining carabid distributions within cereal fields showed that for some carabid species soil moisture was a key factor (Hengeveld, 1979). Adults may seek out particular humidity conditions, but the location of the preferred soil moisture requirements are likely to be more important to the less mobile, soil-bound larval stages as this may affect survival and development (Thomas et al., 2002). This was confirmed in this study. **The soil moisture levels in summer were less important to the distribution of active adults than their emergence densities earlier in the season. Indeed, there appeared to be a particular range of soil moisture conditions that were optimal for several carabid and one staphylinid species.** The measurements provided by the Magnascan cannot be converted to a soil moisture content so further work would be needed to identify the

optimal conditions. There exists the possibility that certain soil types could best provide these optimal conditions which could lead to management advice on the preservation of predatory invertebrates in such areas, but again would require more detailed investigations.

5. How important are different field boundary types to invertebrate abundance, distribution and diversity within the fields?

For cereal aphids, natural enemy impact early in the infestation period is considered important if an outbreak is to be prevented (Ekbohm et al., 1992 & see section 2 of this report), and the evidence collected here and in other studies (Chiverton, 1986; Coombes & Sotherton, 1986) indicated that the boundary overwintering species of ground-dwelling predators are more likely to provide aphid control at this time. Having suitable off-crop overwintering habitats has been identified as one key factor influencing invertebrate survival through the winter (eg. Desender, 1982; Sotherton, 1984; Andersen, 1997), the type of habitat controlling the species present and their abundance (Griffiths et al., 2000) and subsequently numbers reinvading the crop in the spring (Thomas et al., 2000). The margins also provide a different habitat to that of the crop and so support additional species, some of which may also move into the crop. In addition, the field edges are often weedier, providing better foraging resources. Indeed, practical ways of encouraging predatory arthropods for pest control through the provision of additional non-crop habitat have been developed. These techniques include the reintroduction of hedges, beetle banks, weedy strips and wildflower margins and various headland management schemes. In addition, practices that help prevent damage to boundaries by cultivation and misapplication of fertilisers, herbicides and insecticides should also be beneficial e.g. buffer zones and Conservation Headlands. Although, it has been demonstrated that margin habitats support high densities of beneficial insects *per se*, the benefits for pest control in the adjacent crop remain, on the whole, to be demonstrated. There is some evidence that beetle banks, a technique that improves overwintering conditions, can help reduce cereal aphid infestations (Collins *et al.*, 2002) but other overwintering habitats have not been investigated. Landscape evaluations have also revealed that invertebrate reproduction and diversity can be higher in areas with greater complexity and a larger proportion of non-crop areas (Bommarco, 1999). Landscapes with more abundant field margins and perennial crops were also associated with lower aphid establishment and population growth (Östman et al. (2001). **We would therefore recommend that management practices that improve, increase and protect the boundaries and allow the tussock forming grasses that provide the most suitable overwintering habitat for the survival of these ground-dwelling predators should be encouraged.**

3.8.2. Invertebrate Emergence Patterns within Arable Fields

Entomological field experiments using pitfall traps are often criticised, sometimes justifiably, on the grounds that activity-density can be difficult to interpret (Thomas et al., 1998). This can be true, particularly in cases where sampling is conducted in small, within-field plots, such as are often employed in pesticide trials, when

treatments under comparison may have sub-lethal effects including direct and variable effects on activity. However, in this study we have used a grid of pitfall traps to take repeated ‘snapshots’ of invertebrate activity-density at an extremely large spatial scale. Since locomotory activity in natural populations is influenced principally by temperature (Honek, 1997), pitfall trap data from our experimental design describe very well the relative variation in absolute density over a wide area. It is still not possible, however, to state from these data the absolute population density at any particular location; although the mark-recapture data does give an overall measure of population density. **Our deployment of emergence traps over two of the fields had four main functions. First, to allay the type of criticisms mentioned above, it allowed a correlate of activity-density to be taken and a direct comparison of the two sampling methods to be made. Second, it allowed an absolute measure of population density to be made over part of the farm. Third, it allowed the timing of the appearance in the field of adults of different species to be made. Fourth, from the spatial distribution of adult emergence it allowed us to infer the locations that were optimal or preferred by different species for oviposition or larval development and survival.** These latter data were also spatially correlated with environmental factors, notably soil moisture.

Little need be said about the correlation between pitfall trap data and emergence trap data, other than it was good and highly significant on most dates. There were insufficient data on *Nebria brevicollis* and *P. melanarius* in field L2 for SADIE analyses and in June the regressions between emergence and pitfall trap data were not significant. This is probably due to the progressive disappearance of *N. brevicollis* into aestivation sites at this time, and simply too low numbers of *P. melanarius* in an unfavoured field. In field S2, *N. brevicollis* and *Philonthus cognatus* showed no spatial patterning into significant aggregations. Generally, the emergence trap data give good justification of the use of pitfall traps for this type of study.

The absolute measures of population density are given in the results section for 15 taxa. Few data on absolute population density exist elsewhere in the literature for most of these taxa. Where data do exist they have been derived from mark-release-recapture data on the active population of the large and frequently most abundant carabid *P. melanarius*. These types of study have generally determined population density of that species to be of the order of 1 m⁻², occasionally a little higher (Ericson, 1978; Hance et al., 1990; Thomas et al., 1998; section 3.5). Our emergence trap data show the accumulated population density of emerging beetles of all species to be at least 1 m⁻², while *P. melanarius* and *P. madidus* emerged at densities of nearly 30 m⁻² in field S2. In L2, *P. madidus* emerged at over 40 m⁻² with *P. melanarius* at very low density. **Overall, carabids together with staphylinids emerged at population densities of 86 m⁻² in L2 and almost double that density at a massive 157 m⁻² in S2. These results highlight the important productivity of arable soils for these invertebrates.** Considering that population persistence, in its simplest terms, only requires the survival of two individuals m⁻² to maintain a population at that density and that the females of many of these species produce several hundred eggs, clearly **the greater biomass of these invertebrates serves not only to contribute to pest population suppression but also represents a major food resource for farmland**

birds and small mammals, and in some cases each other. Indeed, the Carabidae, which were the most abundant taxa emerging from the soil, were identified as one of the most important families of invertebrates in the diet of farmland birds (Wilson et al., 1999). Their contribution to ecosystem function is thus critical and these data emphasise the importance of maintaining invertebrate diversity in farmland. Of all the farming practices, intensive soil cultivations and inversion tillage are probably the most damaging to invertebrates overwintering within the soil (Fadl et al. 1996; Purvis & Fadl, 1996; Holland & Reynolds, 2003). However, alternatives to these are now available e.g. non-inversion tillage and direct drilling, and offer a means by which invertebrate survival can be improved while also providing additional environmental benefits (Holland, 2004).

Further emphasis on the importance of invertebrate diversity for ecosystem function can be seen in the data of the timing of emergence. Although these are given for only a few selected species it can be seen that the timing of peak emergence and the breadth of the emergence curve, varies among the different species. **Thus, a diversity of species helps to provide a continuous supply of predators for pest control throughout the season, and a reliable and reasonable duration of potential food items for farmland birds.**

One of the most interesting observations revealed by the emergence trap data was the spatial association of emergence with soil moisture. Soil with good moisture retention properties has often been considered to be a key factor in determining the distribution of epigeal invertebrates, though rarely observed (Hengeveld, 1979). Initially, our results seemed contradictory, as emergence was highest in the wettest area of S2 and in the driest area of L2. However, further analysis showed that the soils of the two fields were generally different in moisture content. Closer analysis showed that highest carabid emergence in both fields was associated with areas where soil moisture levels were in the range between -750 and -800 EMI units. Not only does this confirm our hypothesis that soil moisture is probably a key factor for oviposition and larval development but the observation offers important potential for management and manipulation of populations. **Soil moisture is a factor that can be measured, and may be done so as routine in precision agriculture. Areas of a farm important for sustaining populations of epigeal invertebrates could therefore be identified and protected.** Furthermore, soil moisture is a factor that could be manipulated by drainage and the addition of organic material such as farm yard manure. Further experimental work would be required to refine the detail of our knowledge of invertebrate moisture requirements and test the ease with which this factor could be economically manipulated by simple management procedures at the field and farm scale.

3.8.3 The Spatial Dynamics and Movement of Carabid Beetles between and within Arable Fields

The extensive spatial scale at which this study was conducted, involving nearly 2000 traps in a grid covering nearly 70 ha, has allowed, for the first time, the spatial dynamics of carabid populations to be studied in detail at a scale approaching that of the whole farm. This is the most natural unit of management since it is

generally under the control of a single farmer. It is the spatial scale at which various agri-environment schemes are implemented in which both crop and non-crop features are considered. It is also the relevant scale at which to study processes in spatially dynamic populations. Previous studies by Thomas et al. (1998), Holland et al. (1999), Winder et al. (2001) and others, although limited to single or paired fields, have determined the vagility of some of the dominant *Pterostichus* carabid species with either mean daily dispersal rates or diffusion coefficients. Some of these studies and others in small experimental plots (e.g. Mauremooto et al., 1995) have also demonstrated that field boundaries (such as hedgerows) are not impenetrable barriers to movement. Taken together these studies have conclusively demonstrated the potential for some individuals in populations of these key species to disperse across areas as large as a whole farm within a single season or generation. However, none has demonstrated the actual extent of this movement at the farm-scale.

The snapshot views of species' spatial distributions across the grid, within and between years were discussed in detail in the previous section and more fully in other papers published elsewhere (reviewed by Thomas et al., 2002). The temporal stability of these distributions gives some indication of the dynamics of population distributions and has shown that there are fairly consistent differences between the two dominant *Pterostichus* species. *P. melanarius* existed as a highly stable patch in S1 and the lower half of S2. This stability was apparent both within and between years. *P. madidus* was more varied in its behaviour. In the first year (2000) its distribution appeared quite unstable with populations aggregating successively in different fields. However, between July 2001 and July 2002 the population was consistently aggregated in a large patch spread across the majority of L2 and L3 with a further, smaller, stable patch in L1. The snapshot views of population distributions also showed that *P. melanarius* existed in a much smaller sized patch than *P. madidus*.

These results suggested *P. madidus* to be a more vagile species than *P. melanarius*. However, snapshot views of population distributions do not reveal whether aggregations appearing and disappearing in different fields are a result of mass movement of individuals between fields or of differences in the timing of emergence of populations in different fields. The execution of the two large-scale mark-release-recapture experiments within the extensive trapping grid in 2000 and 2001 did, however, enable some questions concerning movement of individuals within populations to be addressed.

The first experiment was conducted over the whole 66 ha grid. Sex was noted during marking and for analysis, but no significant differences between the dispersal behaviour of males and females were found. Previous smaller scale studies at finer levels of resolution have found small differences in the activity of male and female carabids but these are probably irrelevant at the spatial and temporal scale of the present study. Males and females were therefore combined for most analyses here. The overall recapture rate of 11.4% and 7.4% for *P. melanarius* and *P. madidus* respectively were similar to other comparable studies

(Brown, 2000; Thomas & Brown, unpublished). Although the recapture rate for *P. madidus* was lower than that for *P. melanarius*, suggesting lower dispersal power, this may have been due to more *P. madidus* emigrating from the system, since other results (see below) clearly show higher dispersal power for that species. The results confirmed that *P. madidus* was the more mobile of the two *Pterostichus* species. 67% of recaptured *P. madidus* had moved to a different block from their original release area compared with only 20% of *P. melanarius*. In some fields, the populations of *P. madidus* were small at the time of marking (e.g. L1 and L2) and it is difficult to draw firm conclusions about the dispersal behaviour of this species since in L1 100% of recaptured beetles were found in other fields, while in L2 none were. Both these fields were winter cereals. In field L3, however, there appears to have been a mass emigration of *P. madidus*. Of over 40 recaptured individuals originally marked in that field only one was recaptured there. The greater majority of the others had migrated to fields S1, S2 and S3. This must have been unrelated to crop type as all these fields were planted to peas in 2000. A similar process occurred with *P. melanarius*.

Analysis of (mean) release and (actual) recapture positions showed the daily displacement distances of *P. madidus* in 2000 to be approximately twice that of *P. melanarius* with mean daily displacement distances of 12 and 5 m per day, respectively, and maxima of 43 and 29 m per day, respectively. This provides further evidence confirming the greater dispersal power of *P. madidus* compared with *P. melanarius*. Previous studies on the dispersal power of *P. melanarius* conducted at smaller spatial scales also gave values of approximately 5 m per day (Thomas et al., 1998; Brown, 2000). In the following year, 2001, there were too few *P. melanarius* for mark-recapture and the experimental work focussed on *P. madidus*. Conducted at a smaller spatial scale, the three small fields S1, S2 and S3 were divided into more and smaller blocks. As in 2000, more beetles moved between blocks than remained where they were. However, more beetles stayed within their original field than moved to another. This is also reflected in an overall lower mean daily dispersal rate for *P. madidus* in 2001 compared with 2000 at 4 m per day compared with 12 m per day. When viewed at the larger scale, *P. madidus* population aggregations were also more stable in 2001 than 2000 as noted above. These results together with data from other studies suggest that *P. madidus* is generally more mobile than *P. melanarius* but that its dispersal rates are also more variable between years. It is difficult to state why this should be so. We found no evidence of density dependent dispersal, although further analysis of our data and meteorological records may reveal new insights into the environmental cues that drive movement behaviour in these species.

Two further observations of interest were firstly, that in the fields and blocks where *P. melanarius* were most abundant, emigration was least; and vice versa – emigration was highest from fields where abundance was lowest. This indicates that, at least at the population densities found here, crowded neighbourhoods are not an incentive to disperse and corroborates the lack of density dependent dispersal observed. It further suggests that populations actively aggregate in high density patches where conditions are most favourable for them, either in terms of food availability, microclimate, or soil conditions for oviposition. The fact that the

optimum environmental parameter values for each of these are likely to differ, and the associated behaviour is likely to be exhibited at different seasons, and all of these are likely to vary among species, may go some way to explaining why some species' aggregations appear more or less static whilst others change as the optimum conditions are sought. The other observation of interest was that all the *P. melanarius*, and virtually all the *P. madidus*, that were marked in pea fields and that moved between fields, only moved to another pea field. This may indicate an important behaviour that could be used to manage population distribution and spread at the farm scale – for example by using strips of favoured vegetation as corridors linking areas where natural pest control was most required. However, these results may be an artefact as the numbers of beetles involved were small. The disposition of the crop types and field boundaries may have made all the pea fields most accessible to each other. Further manipulative studies would be required in a geometrically symmetrical layout of crop types in an otherwise uniform environment to eliminate the potential biases from the natural farm situation used in the present study.

Movement between blocks within fields appeared to occur with no pattern, indicating free mixing at that spatial scale; although there were some areas of S2 in 2001 within which *P. madidus* remained after marking. In the same year, approximately 80% of recaptures were made in the same field. Thus, **the field boundaries certainly function as barriers retaining the majority of individuals within a field. However, they are not impenetrable and a certain amount of population exchange between fields does occur.** As mentioned in the introduction, there is likely to be an optimum level of boundary permeability for survival of carabid metapopulations at the farm-scale where local populations within fields are exposed to lethal insecticide sprays at different times and frequencies throughout a season. So far, such scenarios have only been addressed in theoretical models (Sherratt & Jepson, 1993) as the field data at an appropriate spatial scale required to parameterise such models have been wanting. Our study for the first time goes some way to providing such data.

Where recaptured beetles were found to have moved between fields there was, as expected, a declining percentage of migrants with distance to the field in which they were recaptured. For *P. madidus* 74%, 21% and 7% must have crossed at least one, two or three hedgerows, respectively, to reach their destination. Similarly, although less dispersive, 78% and 22% *P. melanarius* must have moved through one or two hedgerows, respectively. Thus, migration reduces by a factor in the order of approximately two thirds with each hedgerow crossed into an adjacent field. Although derived from the most extensive field experiment yet conducted, these data still represent movement over a fairly small scale and the numbers of beetles involved are necessarily small. Nevertheless, these data provide the most extensive direct field evidence of carabid movements at the farm scale. Their value and importance will be enhanced in future modelling work. It will now be possible to build a simulation model of the farm system at Cranborne including the fields and field boundaries. Beetle movements within the system would then be parameterised with speed of movement, turning angle and frequency etc. These parameters would then be manipulated to simulate accurately the

dispersal of *P. melanarius* and *P. madidus* observed within fields in this and other studies. Boundary permeabilities (probability of a beetle passing through a hedgerow when encountered), can then be varied to simulate the between field movements observed in this study. More generalised farm-scale (and larger) metapopulation models could then be constructed using the parameter values so determined. **These models could then ultimately be used to test the outcome of various farm-scale and landscape-scale management scenarios including the effects of corridors for movement, crop types and cropping patterns, pesticide regimes, organic or low input areas, cultivations, beetle banks and other non-crop areas as refugia and agri-environment schemes.**

3.8.3.1. Summary and Conclusions

The mark-release-recapture experiments investigating carabid movements at the field- and farm-scale focussed on two *Pterostichus* species: *P. melanarius* and *P. madidus*. Despite their similarity in size, general morphology, habits and habitat, they have been shown to differ in their behaviour, with *P. madidus* being generally more dispersive than *P. melanarius*, although its higher mobility is probably not consistent between years. Both species move freely within fields yet exist in discrete aggregations, with those of *P. melanarius* being more spatially stable both within and between years. Both species are also capable of longer distance movements between adjacent fields and further involving the crossing of one or more hedgerows or other potential barriers to movement. Approximately 20% of *P. madidus* emigrate from their original 'home' field. Because *P. melanarius* appears to remain in more localised and stable population aggregations it may be more vulnerable to the detrimental effects of intensive farming. Such an instance may have been observed on a farm in Hampshire (Thomas et al., 2002) where over a large extent of farmland *P. melanarius* appears to have been replaced by *P. madidus* over a period of approximately 15 years. These differences between species mean that it is unlikely that all species can be managed together under one general management plan.

3.8.4 Quantifying the Impact of Habitat Manipulation on the Abundance and Distribution of Generalist Predators and Aphids

3.8.4.1 Effect of set-aside strips on aphid abundance in 2002

Grain aphids on wheat were higher at 10 and 30 m from the set-aside strips compared to the field boundary indicating that set-aside strips were encouraging biological control. The set-aside strips contained a high proportion of flowering plants at this time, including sown species such as *Phacelia tanacetifolia* and flowering weeds, and thus may have boosted numbers of hoverflies and parasitic wasps leading to higher levels of aphid predation or parasitism. There was some evidence that predatory invertebrates were encouraged by the set-aside strips, possibly through a diversification of food resources and overwinter cover. This was not apparent from the distribution maps (section 3.2.2), but a more detailed analysis may be needed to identify such differences.

3.8.4.2 Effect of set-aside strips on aphids and beneficial invertebrates in 2003

The set-aside strips had the reverse effect on cereal aphids from that in 2002, with higher numbers occurring in the transects adjacent to them. This indicated that levels of biological control were lower in the areas adjacent to the strips. There was no evidence that this occurred from the suction and pitfall sampling, but not all predatory species are collected using these techniques. Hoverfly and lacewing larvae were not sampled, and parasitoids were not identified in the suction samples. Alternatively, the set-aside strips may have acted as a sink habitat, attracting these invertebrates from the adjacent crop. There was some evidence from the emergence traps that this was occurring for Staphylinidae because emergence at 30 m from the strips was lower compared to those traps next to the field boundaries. Further analysis of the spatial dataset is needed to determine to what extent the set-aside strips were acting as a sink habitat.

There was some change in the vegetation within the strips between 2002 and 2003 that may have accounted for the changes observed. In 2002, the floral diversity was greater, and the vegetation was overall much shorter compared to 2003. In 2003, the yellow sweet clover was more abundant and the ground cover was much denser. In addition, half of some strips had been resown with the original mixture, but because of the dry weather establishment and growth was poor. Consequently, the overall abundance of floral resources was lower in 2003 compared to the previous year.

The PCR studies confirmed that aphid predation could be successfully evaluated using this approach, thus providing us with an accurate tool for the extensive evaluation of cereal aphid predation (see section 4). In this study, the average proportion of *P. melanarius* and *P. madidus* that had consumed aphids was 21%. This was very similar to the levels found by gut dissection for *P. melanarius* but a higher proportion of *P. madidus* (34%) had consumed aphids (Holland & Thomas, 1996). A higher proportion of these beetles contained aphid remains at 10 m from the set-aside strip and as aphid numbers were also higher at this distance from the crop edge, this would suggest a density-dependent feeding response was occurring. Although these two species are generalist predators feeding on a wide range of prey, *P. melanarius* has been shown to respond spatially to aphid patches and this subsequently had an impact on the aphid's intrinsic rate of increase (Winder et al., 2001).

In the pea fields the set-aside strips had no effect on the abundance of pea aphids. Numbers of pea aphids were very high, reaching spray threshold levels in all fields. When aphid populations increase rapidly, biological control is often insufficient to prevent outbreaks occurring, especially if natural enemy impact doesn't occur early enough in the aphid population development, and this may explain why no difference was detected. Alternatively, the set-aside strips may not have increased predator abundance or could have acted as a sink habitat. The number of staphylinid beetles sampled by pitfall trapping was lower next to the strips. Many of the most abundant staphylinid beetle species typically found in arable crops (eg. *Tachyporus*

species) overwinter in tussocky grasses before flying into the crop in the spring, therefore it is unlikely that the set-aside strips acted as a barrier to dispersal. The density of several taxa emerging at 30 m from the strips was also lower compared to those emerging near to the field boundaries. This could occur if the adults in the previous year had chosen to oviposit in the strips rather than the crop, thus the set-aside strips could have acted as a sink habitat for oviposition.

Fewer field overwintering invertebrates emerged in the pea compared to winter wheat fields, but only in the fields without the set-aside strips, with the exception of *P. cognatus* which was also lower in the pea fields with set-aside strips. Differences in emergence between the crops are discussed above. The absence of any difference where the set-aside strips were present may have been because the set-aside strips increased the number of adults in the previous crop and subsequent oviposition was higher, increasing the chance of survival in the pea crop and reducing the difference compared to the wheat field.

The contrasting results for 2002 and 2003 indicate that there is potential for set-aside strips to increase levels of biological control within the adjacent crop, but the composition of plants needs to be carefully chosen if the habitat is not to act as a sink or to have no affect.

3.8.4.3. Effect of weed cover on beneficial invertebrates.

The trials to manipulate weed cover were disrupted by the dry weather. This inhibited weed emergence and as a consequence at the Woodyates site there was no difference between the fully sprayed and unsprayed plots. At the other site, the weed cover was dominated by charlock, but because this is a relatively tall species, the differences in cover and humidity at ground level may have been relatively small. Nevertheless, some differences were detected, with **higher numbers of predators occurring where there was higher weed cover**. This confirms what was found from the spatial associations, namely that weed cover effects the distribution of predatory invertebrates. The possible mechanisms behind this are discussed in section 3.8.1.

To enable us to investigate the impact of higher weed cover on aphids this study was repeated in a field of spring oats in 2004 by The Game Conservancy Trust and will be reported elsewhere.

3.8.5. Spatial Distribution of Pea Aphids and their Predators

The distribution of pea aphids was highly aggregated but also extremely ephemeral with patches appearing and disappearing between the four day sampling intervals. Consequently, if crop scouting is to be accurate a large proportion of the field needs to be walked to measure the extent of an infestation. The highly ephemeral nature of their infestation, with little relationship to field boundaries, also precludes the use of patch spraying because an infestation could appear anywhere across the field.

Ground-active predators were exerting a noticeable level of control, with fewer pea aphids occurring where they were present. In the USA, pea aphids are known to be predated by a wide range of generalist and aphid-specific species (Frazer et al., 1981), with the foliage active species causing the release of an alarm pheromone that induces dropping behaviour (Clegg & Barlow, 1981). Once on the ground they will be predated by ground active predators such as beetles and spiders. A similar range of predators are present in the UK and likewise pea aphid control would be expected. The ground-active predators were more effective at reducing pea aphid numbers when foliage active predators, such as ladybirds were present (Losey & Denno, 1998a), thus a strategy to improve pea aphid control should aim to improve the abundance of ground- and crop-active predators. This may be achieved by ensuring that crop management causes the minimum disruption, for example, avoidance of broad-spectrum insecticides and a switch to reduced cultivations. In this study adequate pea aphid control was achieved through the use of a full rate of the selective aphicide 'pirimicarb' instead of a full rate of a broad-spectrum pyrethroid. This would be expected to be less damaging to the beneficial invertebrates. Augmentation of non-crop habitats, through the establishment of beetle banks and wildflower strips would increase numbers of ground- and crop-active predators and parasitoids.

3.8.6. The Influence of Field Margins on Invertebrates within Fields

In 2000 and to a lesser extent in 2002, the type of field margin influenced the ground-active invertebrate community in the adjacent crop. The grasses encouraged the beetle species that had used the margin as an overwintering habitat, along with beetle larvae. Presumably, the undisturbed nature of the margins increased larval survival. The herbaceous forbs increased numbers of ladybirds and weevils. Overall, the presence of grass was more important for the ground-dwelling predatory invertebrates and further supports the evidence that beetle banks are an appropriate way to encourage biological control. Indeed, numbers of predators emerging from grass margins was higher compared to mature hedgerows (Griffiths et al., 2000). Moreover, the different boundary types had their own unique invertebrate fauna and therefore a subset of all field boundary types is required for complete species representation at the farm-scale. Ladybirds were associated with the forbs here because the most abundant forb within the margins was stinging nettle and this supports large numbers of aphids on which ladybird adults and larvae specialise. Two carabid species were associated with gaps in the hedge. They may have been using gaps to cross through the field boundary or the absence of a hedge and thereby shading, may have created more suitable environmental conditions within the crop.

3.8.7. General Discussion

Wratten and Thomas (1990) list five main spatially dynamic processes of relevance to developing integrated control programmes. These are:

- seasonal movements between crops and non-crop habitats;
- movement between phenologically asynchronous crops;

- colonisation of new habitats;
- recolonisation of areas previously depopulated by insecticides;
- aggregative movement to areas of high prey density.

The detection of spatially dynamic processes is a difficult feat to accomplish in the field (Thomas et al., 2002) but the results from this study have greatly improved our knowledge of invertebrate distribution and have provided insights into the spatial dynamic processes that occur across farmland. **We have demonstrated that seasonal movement occurs from non-crop habitats but the extent of this can vary between fields and years. The reluctance of the boundary overwintering, generalist predator species to disperse across fields has implications for the extent and reliability of their contribution to pest control within fields.** Species that appear early have a greater impact on aphid population regulation than those that appear later (Ekbohm et al., 1992). Dispersal across fields may not occur if for example the environmental conditions within the crop are unsuitable or if insufficient prey is present. The density overwintering within the surrounding margins may also be too low to ensure sufficient coverage. Large fields with a low margin:field ratio would be expected to have lower densities of boundary overwintering species and further analysis of the data will be conducted to test for this. There are ways in which the early dispersal of predatory invertebrates could be encouraged and densities increased. Crops could be manipulated to provide more favourable environmental conditions and in this study weed cover was identified as one key factor. Alternative prey can be increased through the application of organic manures (Purvis & Curry, 1984). Field margins may be improved and the margin:field ratio increased. Avoiding intensive soil cultivations may also increase the survival of field overwintering species.

Movement between phenologically asynchronous crops is only likely for the more mobile species, eg. hoverflies and parasitoids, but few studies have investigated the extent of this, partly because of the difficulties in marking and recapturing highly dispersive species. However, data from this project has provided good evidence that both hoverflies and parasitoids are capable of spreading into and across large fields very rapidly (see section 2). Many generalist predators are also capable of flight and dispersal but the extent to which this occurs has not been investigated. In this study, one carabid species, *P. madidus*, that disperses primarily by walking was shown to move between fields, although the proportion that moved between fields was relatively low and declined according to the number of boundaries that had to be crossed. Overall, the invertebrate distribution patterns were relatively stable within each year indicating that little between-field movement was occurring. Consequently, reinvasion following disruptive agricultural practices is always going to be limited and dependent on recolonisation from the margins, as has been shown to occur (Holland et al., 2000) or from unsprayed refuges within the crop including emergence from the soil.

The colonisation of new habitats and recolonisation of areas previously depopulated by insecticides was not investigated in this study. Recolonisation following insecticide application has been the subject of a number of studies (Duffield & Aebischer, 1994; Thomas et al., 1990; Thomas & Jepson, 1997; Holland et al., 2000).

The occurrence of aggregative movement by predators to areas of high cereal aphid density has been the subject of two BBSRC funded projects and further studies on other pests have been completed or are underway. In this study we demonstrated that ground-active predators were regulating pea aphids, but this was not as a consequence of aggregative movement. Instead, pea aphids were regulated where a relatively stable patch of predators occurred. **This indicates that adequate pest control may therefore be achieved by ensuring sufficient predators are present across fields rather than relying on them to respond to the ephemeral prey patches.**

This study has enabled us to further understand some of the factors influencing the spatial dynamics of generalist predators and some recommendations are made based upon the results. We have also contributed to the evidence supporting the benefits of generalist predators for pest control. In this study we showed that the predators were very abundant, originating early in the season from boundaries and later emerging from the soil, ensuring continuity in the overall predator abundance. This ability to rapidly colonise fields in the spring is one of the key abilities required if a natural enemy is to be effective (Symondson et al., 2002). There were however, gaps in their distribution within some fields, especially the larger ones, indicating that some form of enhancement is needed. Moreover, the relative stability of the patches indicated that movement was not as dynamic as shown in some previous studies of individual species (Winder et al., 2001). The persistence of patches through the season would, however, ensure continuity of control, another important attribute for natural enemies to possess (Symondson et al., 2002). Overall, the findings further support the evidence that generalist predators can contribute to pest control whether acting alone or synergistically with specialists as has been shown to occur (Losey & Denno, 1998b). There remains uncertainty regarding the numbers of invertebrates needed to ensure adequate levels of control and this will vary with both crop and target pest. This may not be achievable for some pest situations given the diversity of species and the interactions that can occur between them. However, it may be possible to identify the proportion of the landscape needed to ensure pest levels remain below damage thresholds and this will form part of a new RELU funded project, involving some of the contributors to this Link project.

The value of set-aside strips sown with a range of plants that provide floral and seed resources for pest control was evaluated. These impacted cereal aphids in the adjacent crop in one of the study years but not the other. Moreover, they had few effects on numbers of ground-active predators. Other plant mixtures, specifically designed for this purpose, as studied in section 2, were able to contribute to pest control through the encouragement of beneficial invertebrates. Such mixtures, however, can be costly to establish and only suitable for non-rotational set-aside or margins established in agri-environment schemes. Further studies are

needed if mixtures for non-rotational set-aside are to be developed. In particular, annual mixtures need to be examined as these could be rotated around the farm according to the cropping so concentrating the biocontrol effort where it is most needed. There may also be potential benefits from mixing permanent and temporary habitats. The spatial arrangement of such habitats is also important if maximum field coverage is to be achieved. The concentration of ground-active predators around the field margins found here indicate that non-crop habitats should split the larger fields ensuring that distance to the nearest habitat is 100 m or less.

Only the key data relevant to the end user is presented here, however, a more extensive dataset was compiled containing information on a larger number of species. Moreover, we accept that there are many other ways in which the data could be analysed and interpreted, not only for applied studies relevant to pest control and farming systems, but also to answer key ecological questions. For example, the data could be used to greatly enhance our knowledge of individual species and how they interact with farming practices, but also to explore the factors driving their tempo-spatial dynamics. Every effort will therefore be made to fully utilise this most valuable resource and ensure that the full findings from the study are published in scientific journals and the popular press.

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