

Reduced numbers of generalist arthropod predators after crop management

P. THORBEK*† and T. BILDE†‡

*National Environmental Research Institute of Denmark, Department of Wildlife, Ecology and Biodiversity, Grenaavej 14, Kalo, DK-8410 Ronde, Denmark; †Department of Zoology, University of Aarhus, Building 135, DK-8000 Aarhus C, Denmark; and ‡Department of Ecology and Genetics, University of Aarhus, Ny Munkegade Building 540, DK-8000 Aarhus C, Denmark

Summary

1. Generalist arthropod predators act as natural enemies of insect pests in agroecosystems. Crop management activities may cause a reduction in arthropod densities, either directly through mortality and emigration, or indirectly through habitat disruption. Our aim was to quantify direct mortality caused by mechanical crop treatments. For some treatments, we also quantified emigration and other indirect effects, such as population declines caused by the impact of habitat deterioration on reproduction and survival.

2. Direct mortality was determined by measuring predator densities simultaneously in control and treatment plots using closed emergence traps immediately following a mechanical treatment. Treatments consisted of the following crop management activities: ploughing, non-inversion tillage, superficial soil loosening, mechanical weed control and grass cutting. Predator densities were measured a second time 5–26 days after treatment to quantify emigration and indirect effects.

3. All treatments had a negative influence on one or more arthropod taxa. Direct mortality caused a 25–60% reduction in arthropod densities. Overall, spiders were more vulnerable to mechanical crop treatment than carabid and staphylinid beetles. Intensive soil cultivation, such as ploughing and soil loosening, did not kill more arthropods than weed harrowing and grass cutting.

4. We estimated the cumulative effects of mortality, emigration and indirect effects 3 weeks following treatment. The cumulative effect was greater than direct arthropod mortality, suggesting delayed effects of habitat disruption.

5. Grass cutting caused spiders and staphylinid beetles to move out of the crop, except in one case when the grass was left to dry, suggesting an important role of organic material or structural elements for arthropod persistence. Our results also suggest that arthropod predators aggregate in undisturbed or less disrupted habitats.

6. *Synthesis and applications.* Mechanical operations in arable crops and grass cutting cause mortality and emigration of generalist arthropod predators, especially spiders. Effects can be species-specific and are likely to be affected by the timing of management. In grassland, cutting and removal have greater adverse impacts than leaving cuttings that contribute to habitat structure. Adjacent, less-disturbed refuge areas are colonized by predators following husbandry events, demonstrating significant spatial dynamics among farmland arthropods. The negative effects of crop husbandry operations might be mitigated by the provision of refuge areas within and adjacent to fields and by maintaining crop and landscape diversity.

Key-words: mechanical weed control, non-inversion tillage, ploughing, recolonization, refuge, superficial soil loosening

Journal of Applied Ecology (2004) **41**, 526–538

Introduction

In recent decades there has been a growing awareness of the role of generalist arthropod predators acting as natural enemies of insect pests in agro-ecosystems. Spiders, carabid beetles and staphylinid beetles constitute a major and ecologically important group of generalist arthropod predators, consuming a wide range of prey species, some of which are herbivorous pests of crops. Comprehensive studies have shown that arthropod predators in arable fields reduce pest numbers and may prevent economically important outbreaks (reviewed in Symondson, Sunderland & Greenstone 2002).

Crop management activities, including soil cultivation and pesticide application, present a serious threat to beneficial generalist predators in fields. So far, the main focus of research has been directed at estimating mortality caused by insecticide applications, and few studies have estimated the mortality caused by mechanical crop management practices (Topping & Sunderland 1994; Halley, Thomas & Jepson 1996; Thomas & Jepson 1997; Kromp 1999; Lee, Menalled & Landis 2001). Common crop husbandry practices are soil cultivation, sowing and harvest and also, in Europe in particular, integrated mechanical systems that aim to reduce chemical input (Sunderland *et al.* 1995; Kromp 1999). These activities may have profound effects on the survival and population dynamics of generalist arthropod predators. Populations may have to recover several times a year after mechanical disturbance (Topping & Sunderland 1994; Halley, Thomas & Jepson 1996; Thomas & Jepson 1997; Hossain *et al.* 2002). The direct mortality caused by mechanical management is, however, difficult to measure and therefore a potentially important aspect of the population dynamics of beneficial predators remains largely unquantified.

In Europe, attempts are made through organic and integrated farming to increase the sustainability of agriculture by reducing chemical inputs. Mechanical weed control is an alternative to herbicide treatment, and superficial soil loosening that releases soil-bound nutrients may replace artificial fertilizers. If, however, these management practices reduce populations of generalist arthropod predators and cause a release of pest insects, the overall benefit may be questionable.

Mechanical crop management practices may reduce the population of beneficial arthropods in different ways. First, arthropods can be killed directly by mechanical damage or by burying, defined here as 'direct mortality'. Secondly, habitat disturbance may cause arthropods to disperse from the field shortly after cultivation, defined here as 'immediate emigration'. Thirdly, cultivation may cause 'indirect effects' through habitat deterioration, by altering microhabitats, removing essential microhabitats for reproduction or other life-history processes, removing plant cover and thereby increasing predation risk, or reducing prey densities.

Such effects would cause predator populations to decline because they disperse, reproduce less or die. These indirect effects are expected to occur at a slower rate than direct mortality and immediate emigration.

Previous studies have addressed the long-term effects of crop management practices on populations of generalist predators, comparing arthropod densities in fields of conventional vs. reduced tillage management (Stinner & House 1990; Symondson *et al.* 1996; Baguette & Hance 1997; Krooss & Schaefer 1998). Positive effects of reduced management practices on predator populations could be identified, but specific effects on direct mortality, emigration and indirect effects could not be distinguished. Other studies have investigated the effects of crop management practices on beneficial arthropods by sampling the field before and after management events (Symondson *et al.* 1996; Thomas & Jepson 1997; Topping & Sunderland 1998). These studies revealed decreases in numbers of arthropods after cultivation; but immediate emigration or direct mortality could not be distinguished. If arthropods emigrate to the surrounding habitats following crop management they will still be present in the landscape pool of potential natural enemies (Lee, Menalled & Landis 2001; Hossain *et al.* 2002). We will refer to the potential relocation of arthropods to surrounding undisturbed areas as the 'refuge effect'. Support for the refuge effect is provided if arthropods accumulate in untreated (control) areas following soil cultivation.

We conducted field experiments with the aim of quantifying and separating direct and delayed effects of some common mechanical crop management activities on generalist arthropod predators. We estimated direct mortality by comparing arthropod densities sampled in control plots and treatment plots simultaneously. In addition, we measured delayed effects, such as immediate emigration and indirect effects (see above). The indirect effects were measured as delayed changes in population densities caused by cultivation-induced disruptions of the soil structure or microhabitat affecting population growth or population persistence.

We summarized the overall cultivation effects to (i) cumulative treatment effects, the sum of direct mortality, immediate emigration from treatment plots, immigration into control plots and indirect effects, and (ii) secondary treatment effects, the sum of immediate emigration and indirect effects (Table 1).

Materials and methods

We quantified the effects of mechanical crop treatments on arthropod predators in experimental fields, where arthropod densities were determined simultaneously in control and treatment plots. We determined direct mortality of the following crop management activities: (i) superficial soil loosening, (ii) mouldboard ploughing, (iii) non-inversion tillage (NINV), (iv) mechanical weed control and (v) grass cutting. Treatments

Table 1. Experimental design details for all treatments. Row numbers refer to Fig. 1. Effects: 1, direct mortality (row A minus row B); 2, cumulative effects (row C minus row D); 3, secondary effects (row B minus row D); 4, immediate emigration (row B minus row E); 5, combined effect of mortality and migration (row A minus row E)

Treatment	Crop	Sampling design (Fig. 1)	Treatment date	Effects measured	Interval from treatment until next row(s) set up	Treatment area (control area)	Numbers of blocks and traps
Soil loosening	Winter wheat	Design 1	Rows A–B: 20 May 1999	1,2,3	Rows C–D: 18 days	3840 m ² (200 m ²)	8 blocks of 6 traps (3 in row A and 3 in row B)
Mouldboard ploughing	Spring barley	Design 1	Rows A–B: 21 April 2000	1,2,3	Rows C–D: 26 days	3840 m ² (200 m ²)	4 blocks of 9 traps: 3 in row A, 6 in row B
Non-inversion tillage	Spring barley	Design 1	Rows A–B: 21 April 2000	1,2,3	Rows C–D: 26 days	3840 m ² (200 m ²)	(3 plough and 3 NINV)
Weed harrowing	Winter wheat	Design 2	Rows A–B: 4 May 2001	1,4,5	Row E: 6 days	Whole field (3 times 1 × 20 m ²)	3 blocks of 18 traps (6 in row A, 6 in row B, 6 in row E)
Grass cutting	Oat	Design 2	Rows A–B: 25 May 2001	1,4,5	Row E: 6 days	Whole field (3 times 1 × 20 m ²)	3 blocks of 18 traps (6 in row A, 6 in row B, 6 in row E)
	Clover–grass	Design 2	Rows A–B: 4 July 2000	1,4,5	Row E: 5 days	Whole field (4 times 1 × 20 m ²)	4 blocks of 15 traps (5 in row A, 5 in row B, 5 in row E)

(i), (iii) and (v) were conducted in separate experiments in separate fields, whereas treatments (ii) and (iii) were performed in the same field but in different plots (Table 1). In addition, we estimated the secondary effects (immediate emigration and indirect effects) and cumulative effects (direct mortality, emigration and indirect effects) in treatments (i), (ii) and (iii), and the immediate emigration following treatments (iv) and (v) (Table 1).

All experiments were carried out at Rugballegaard, an experimental organic farm belonging to The Danish Institute of Agricultural Sciences, situated near Horsens, Denmark. The farm is 140 ha, with both animal and plant production. The fields were managed according to modern organic farming practices.

SAMPLING METHODOLOGY

We collected spiders (Araneae), ground beetles (Carabidae: Coleoptera) and rove beetles (Staphylinidae: Coleoptera) in emergence traps. We used emergence traps (photoelectors) because they seal off the trapping area, thus preventing both emigration and immigration, and such traps have been used successfully for density estimates of arthropods (reviewed in Sunderland *et al.* 1995). The emergence traps consisted of a plastic ring (diameter 39.5 cm, = 0.1225 m², height 30 cm), on which a lobsterpot-type trap filled with preservative trapping fluid on top. The plastic ring was buried 5–10 cm into the ground and a pitfall trap was placed inside the plastic ring of the emergence trap. The trapping fluid was a mixture of half water, half ethylene glycol plus one drop of unperfumed detergent. Spiders were identified to species following Roberts (1987), carabids were identified to species following Lindroth (1985, 1986), whereas staphylinid beetles were not identified further. Both adult and juveniles spiders were counted, but only adult beetles were included, thus we only measured mortality of adult beetles.

SAMPLING DESIGN

Emergence traps were placed within replicate blocks following two different block designs, design 1 and design 2 (Fig. 1). The specific details of treatments, number of experimental blocks and replications are described in separate sections for each type of treatment below and in Table 1. Design 1 was used to determine direct mortality following soil loosening, mouldboard ploughing and NINV, and to estimate the secondary and the cumulative effects 18 days after treatment (soil loosening) and 26 days after treatment (ploughing and NINV). One row of emergence traps was established in untreated (control) plots immediately before the treatment was implemented (row A, design 1; Fig. 1) to avoid potential immigration from adjacent treatment plots. Within 5 min of cultivation a second row of emergence traps was established in the treated area (treatment

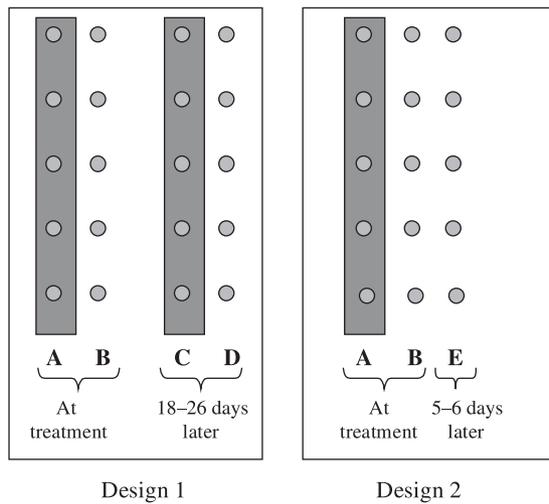


Fig. 1. Layout of a single block from design 1 and one block from design 2. The dark strips are control plots, the white area shows where crop management was carried out, and the grey circles are emergence traps. Design 1 was used to estimate direct mortality, secondary effects and cumulative effects caused by superficial soil loosening, ploughing and non-inversion deep soil loosening (NINV). Design 2 was used to estimate direct mortality and immediate migration caused by weed harrowing and grass cutting. The number of traps per row varied between experiments.

plots; row B, design 1; Fig. 1). The traps were emptied after 6 days and the soil surface inside the trap was searched for any remaining arthropod predators. After 18 days (soil loosening) and 26 days (ploughing and NINV), a second set of rows was set up; row C in the control area (an uncultivated strip) and row D in the cultivated area (design 2; Fig. 1). Direct mortality was calculated as the difference between rows A and B. The secondary effects were calculated as the difference between rows B and D. Cumulative effects were measured as the difference between rows C and D. Population changes can be due to husbandry-induced changes or natural changes such as eclosion and natural mortality. By sampling control and treatment plots simultaneously, we intended to control for phenological changes in population densities.

Design 2 was used to quantify direct mortality and immediate emigration following two treatments: grass cutting and mechanical weed control. Rows A (control) and B (treatment) (Fig. 1) were established in a similar way as for design 1. An additional new row of emergence traps (row E; Fig. 1) was set up in the treatment plots 5–6 days after crop management activities had been carried out. The traps were then emptied after a further 5–6 days. Direct mortality was calculated as the difference between rows A and B, and immediate emigration was calculated as the difference between rows B and E. The combined effect of direct mortality and immediate emigration was calculated as the difference between rows A and E, which corresponds to comparing a sample taken before treatment with a sample taken after treatment. Each set of rows A, B and E was one block.

TREATMENTS

Superficial soil loosening

Soil loosening is applied to release nutrients for plant growth and was performed between plant rows in a field of winter wheat. Soil was loosened 8 cm below the surface with a single pass of a Kress hoe with tines mounted (Kress & Co. GmbH, Vaihingen, Germany). The treatments were applied to 12 × 40-m plots in a randomized block design with eight replicates (Table 1).

Ploughing and non-inversion deep soil loosening

The ploughing treatment consisted of conventional mouldboard ploughing followed by compact harrowing and sowing. The conservation tillage treatment was a NINV deep soil loosening (0–35 cm) tillage system; soil tillage was carried out using a combined tillage and sowing implement, which consisted of a 3-m wide non-inversion rigid tine subsoiler with four 65-cm wide shares mounted ahead of a rotavator (working depth 5 cm) and a seed drill (for details of ploughing and NINV treatments see Munkholm, Schjonning & Rasmussen 2001). The treatments were applied to 12 × 40-m plots in a randomized block design with four replicates (Table 1).

Weed harrowing

Weed harrowing was carried out in an oat and a winter wheat field with a 12-m Straw Tined Weeder (Einböck GmbH & Co. KG, Dorf an der Pram, Austria). Weed harrowing disturbed the top 1–2 cm of the soil. Both crop fields had previously been weed harrowed once within the growth season (Table 1).

Grass cutting

Grass cutting was carried out in three blocks with a Forage Plot Harvester (Haldrup a/s, Løgstør, Denmark). In these three blocks, the grass was removed at harvest. In a fourth block, grass was cut with a disc mover with conditioner (TAARUP, Kverneland Group, Kverneland, Norway) and left to dry (Table 1).

DATA ANALYSIS AND STATISTICAL TESTS

The effects of soil loosening, weed harrowing and grass cutting were tested by two-way ANOVAs with treatment, block and the interaction term included in the model (Sokal & Rohlf 1995). Direct mortality, cumulative effects, secondary effects, immediate emigration and combined effect of direct mortality and immediate emigration effects were tested separately (for details on effects and treatment see Table 1). The effects of ploughing and NINV were tested with a two-way ANOVA where treatment, block and the interaction term were included in the model. Differences between ploughing, NINV and

the control were tested with a Tukey–Kramer pairwise comparison (Sokal & Rohlf 1995). Direct mortality, secondary effects and cumulative effects were tested separately.

When necessary, variance and residuals were homogenized with $\ln(x + 1)$ or square-root transformations (Table 3). Standard errors were calculated as the standard error of the least-square mean. Analyses were performed with the SAS system (SAS Institute Inc. 1999–2001). The sample unit was the total catch for a trap.

Results

In total, 1541 spiders, 1242 carabid beetles and 5477 staphylinid beetles were caught during the sampling. We found 31 carabid and 40 spider species, of which the 10 most common are listed in Table 2.

SUPERFICIAL SOIL LOOSENING

Soil loosening caused significant direct mortality of spiders, reducing densities by 25% (Fig. 2a and Table 3a). Soil loosening also caused a cumulative effect: 18 days following treatment, spider densities remained significantly lower in the soil-loosened plots compared with the control plots. A significant proportion of the cumulative effect was caused by secondary effects, although densities had also decreased in the control area. This pattern was the same for the three dominant species: *Erigone atra* Blackwall, *Oedothorax apicatus* Blackwall, and *Pachygnata degeeri* Sundewall (Table 4a).

We found strong direct mortality and cumulative effects on carabid beetle densities. Direct mortality was 51% (Fig. 2b and Table 3b), and this effect persisted 18 days after soil loosening, when the difference in beetle density between the control area and soil-loosened plots (i.e. cumulative effect) was 41%. In contrast to the spiders, the secondary effects did not contribute to the cumulative effects, as the densities of carabid beetles were higher both in the control area and the soil-loosened plots 18 days after soil loosening. Despite the overall increase in carabid beetle density for both treated and untreated plots, a strong treatment effect was nevertheless detected by a second sampling of the control area.

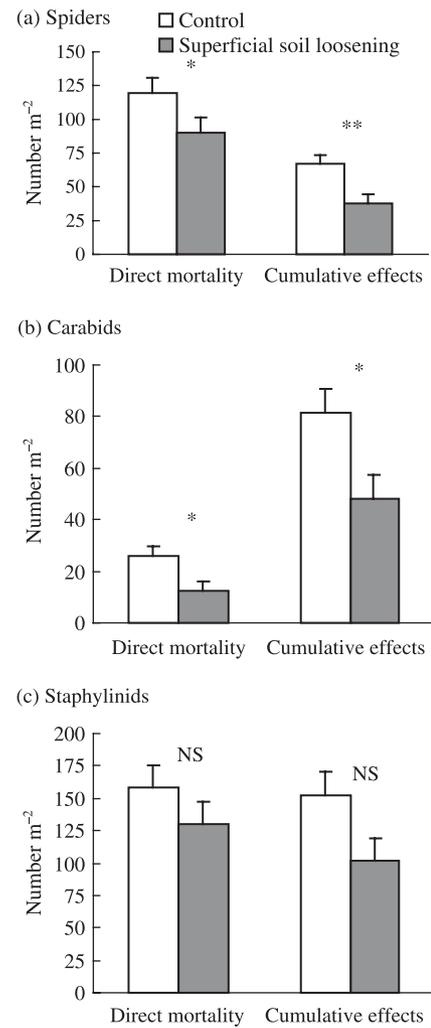


Fig. 2. Direct mortality and cumulative effects caused by superficial soil loosening. Densities of (a) spiders, (b) carabids and (c) staphylinids at treatment (direct mortality) and 18 days after treatment (cumulative effects). Secondary effects: difference between treatment plots at the time of treatment and 18 days later. * $P < 0.05$, ** $P < 0.01$, NS $P > 0.05$.

The increase in carabid density 18 days after soil loosening stemmed mostly from an increase in the densities of *Pterostichus melanarius* Illiger and *Trechus quadristriatus* Schrank, which were only present in very low

Table 2. The most common spider and carabid species caught in Danish agricultural fields during 1999–2001. Spiders and carabids were caught in emergence traps

Carabids	Number	Spiders	Number
<i>Amara familiaris</i>	241	<i>Erigone atra</i>	625
<i>Bembidion lampros</i>	222	<i>Oedothorax apicatus</i>	258
<i>Pterostichus melanarius</i>	178	<i>Bathyphantes gracilis</i>	148
<i>Agonum dorsale</i>	142	<i>Pachygnatha degeeri</i>	118
<i>Trechus quadristriatus</i>	105	<i>Porrhomma microphthalmum</i>	74
<i>Clivina fossor</i>	91	<i>Erigone dentipalpis</i>	26
<i>Bembidion tetracolum</i>	47	<i>Meioneta rurestris</i>	13
<i>Bembidion obtusum</i>	31	<i>Araeoncus humilis</i>	11
<i>Nebria brevicollis</i>	17	<i>Savignya frontata</i>	11
<i>Harpalus affinis</i>	15	<i>Pardosa prativaga</i>	9

Table 3. Results of statistical tests of the effect of ploughing, non-inversion tilling (NINV), superficial soil loosening, weed harrowing and grass cut on (a) spider, (b) carabid and (c) staphylinid densities, as direct mortality, cumulative and secondary effects, and migration (see text)

Treatment	Effect	Test statistics	P	Transformation	Density change (%)
(a) Spiders					
Superficial soil loosening	Direct mortality	$F_{1,32} = 4.29$	0.0465	Square root	-25
	Cumulative effects	$F_{1,32} = 8.11$	0.0076	Square root	-44
	Secondary effects	$F_{1,32} = 25.51$	< 0.0001	Square root	-58
Ploughing and NINV	Direct mortality	$F_{2,35} = 2.18$	0.1221	Square root	
	Cumulative effects	$F_{2,35} = 11.38$	0.0002	Square root	
Ploughing (pairwise comparison with control)	Direct mortality	Tukey-Kramer _{3,35}	NS	Square root	-38
	Cumulative effects	Tukey-Kramer _{3,35}	< 0.05	Square root	-93
	Secondary effects	$F_{1,24} = 4.07$	0.0549	Square root	-63
NINV (pairwise comparison with control)	Direct mortality	Tukey-Kramer _{3,35}	NS	Square root	-63
	Cumulative effects	Tukey-Kramer _{3,35}	< 0.05	Square root	-80
Weed harrowing	Secondary effects	$F_{1,24} = 0.07$	0.7883	Square root	+66
	Direct mortality	$F_{1,60} = 4.13$	0.0466	Square root	-37
	Immediate migration	$F_{1,60} = 2.99$	0.0887	Square root	+58
Grass cutting	Mortality + migration	$F_{1,60} = 0.06$	0.8148	Square root	0
	Direct mortality	$F_{1,31} = 1.61$	0.2143	Square root	-24
	Immediate migration	$F_{1,31} = 3.89$	0.0575	Square root	-32
	Mortality + migration	$F_{1,31} = 10.52$	0.0028	Square root	-50
(b) Carabid beetles					
Superficial soil loosening	Direct mortality	$F_{1,32} = 5.05$	0.0316	Square root	-51
	Indirect effects	$F_{1,32} = 5.29$	0.0282	Square root	-41
	Secondary effects	$F_{1,32} = 20.00$	0.0001	ln(x + 1)	+280
Ploughing and NINV	Direct mortality	$F_{2,35} = 4.34$	0.0207	ln(x + 1)	
	Cumulative effects	$F_{2,35} = 27.27$	< 0.0001	ln(x + 1)	
Ploughing (pairwise comparison with control)	Direct mortality	Tukey-Kramer _{3,35}	< 0.05	ln(x + 1)	-27
	Cumulative effects	Tukey-Kramer _{3,35}	< 0.05	ln(x + 1)	-92
	Secondary effects	$F_{1,24} = 0.33$	0.5683	Square root	-23
NINV (pairwise comparison with control)	Direct mortality	Tukey-Kramer _{3,35}	NS	ln(x + 1)	+26
	Cumulative effects	Tukey-Kramer _{3,35}	< 0.05	ln(x + 1)	-85
Weed harrowing	Secondary effects	$F_{1,24} = 0.00$	0.9986	Square root	-11
	Direct mortality	$F_{1,60} = 0.27$	0.6069	ln(x + 1)	-25
	Immediate migration	$F_{1,60} = 1.03$	0.3139	Square root	+25
Grass cutting	Mortality + migration	$F_{1,60} = 0.35$	0.5536	Square root	-8
	Direct mortality	$F_{1,31} = 0.30$	0.5885	Square root	-29
	Immediate migration	$F_{1,31} = 0.31$	0.5803	Square root	0
	Mortality + migration	$F_{1,31} = 1.19$	0.2844	Square root	-36
(c) Staphylinids					
Superficial soil loosening	Direct mortality	$F_{1,32} = 1.18$	0.2848	ln(x + 1)	-18
	Cumulative effects	$F_{1,32} = 3.08$	0.0891	ln(x + 1)	-34
	Secondary effects	$F_{1,32} = 2.98$	0.0938	Square root	-22
Ploughing and NINV	Direct mortality	$F_{2,35} = 2.66$	0.0841	Square root	
	Cumulative effects	$F_{2,35} = 3.37$	0.0458	Square root	
Ploughing (pairwise comparison with control)	Direct mortality	Tukey-Kramer _{3,35}	NS	Square root	+46
	Cumulative effects	Tukey-Kramer _{3,35}	NS	Square root	-31
	Secondary effects	$F_{1,24} = 3.47$	0.0746	Square root	-51
NINV (pairwise comparison with control)	Direct mortality	Tukey-Kramer _{3,35}	NS	Square root	-14
	Indirect effects	Tukey-Kramer _{3,35}	< 0.05	Square root	-57
Weed harrowing	Secondary effects	$F_{1,24} = 5.54$	0.0271	Square root	-49
	Direct mortality	$F_{1,60} = 1.43$	0.6069	ln(x + 1)	-10
	Immediate migration	$F_{1,60} = 1.62$	0.2077	ln(x + 1)	+22
Grass cutting	Mortality + migration	$F_{1,60} = 0.22$	0.643	ln(x + 1)	+9
	Direct mortality	$F_{1,31} = 0.66$	0.5151	ln(x + 1)	-15
	Immediate migration	$F_{1,31} = 2.64$	0.1145	ln(x + 1)	-18
	Mortality + migration	$F_{1,31} = 5.84$	0.0251	ln(x + 1)	-30

densities prior to treatment, and from an increase of *Agonum dorsale* Pontoppidan (Table 4b).

Soil loosening caused a reduction in staphylinid beetle densities by direct mortality, secondary effects and cumulative effects. However, these effects were not statistically significant (Fig. 2c and Table 3c).

PLOUGHING AND NON-INVERSION DEEP SOIL LOOSENING

Although the direct mortality of spiders caused by ploughing and NINV deep soil loosening was high, with 38% fewer spiders caught in the ploughed area compared

Table 4. Results of statistical tests of the effects of crop management activities on direct mortality, cumulative effects and immediate migration in (a) spiders and (b) carabid beetles. Sampling dates: the difference between total numbers caught at time of treatment and total numbers caught 18–26 days after treatment. *n*, numbers caught. Too few *A. familiaris*, *P. melanarius*, and *T. quadristriatus* were caught to test for direct mortality

Crop management	Species (<i>n</i>)	Effect	Density change (%)	Test statistics	<i>P</i>	
(a) Spiders						
Superficial soil loosening	<i>Erigone atra</i> (424)	Direct mortality	-12	$F_{1,32} = 0.70\ddagger$	0.4075	
		Cumulative effects	-37	$F_{1,32} = 2.60\ddagger$	0.1169	
		Sampling dates	-47	$F_{1,79} = 13.78\ddagger$	0.0004	
	<i>Oedothorax apicatus</i> (176)	Direct mortality	-36	$F_{1,32} = 3.26\ddagger$	0.0803	
		Cumulative effects	-46	$F_{1,32} = 1.63\ddagger$	0.2103	
		Sampling dates	-70	$F_{1,79} = 33.32\ddagger$	< 0.0001	
	<i>Pachygnatha degeeri</i> (104)	Direct mortality	-36	$F_{1,32} = 0.85\ddagger$	0.3635	
		Cumulative effects	-71	$F_{1,32} = 3.23\ddagger$	0.0818	
		Sampling dates	-91	$F_{1,79} = 57.41\ddagger$	< 0.0001	
Grass cutting	<i>Bathypantes gracilis</i> (86)	Direct mortality	-21	$F_{1,30} = 1.63\ddagger$	0.2121	
		Immediate migration	-74	$F_{1,30} = 10.61\ddagger$	0.0028	
	<i>Erigone atra</i> (161)	Direct mortality	-42	$F_{1,30} = 1.13\ddagger$	0.2958	
		Immediate migration	-16	$F_{1,30} = 1.57\ddagger$	0.2195	
	<i>Oedothorax apicatus</i> (58)	Direct mortality	+24	$F_{1,30} = 0.01\ddagger$	0.9214	
		Immediate migration	-5	$F_{1,30} = 0.23\ddagger$	0.6332	
(b) Carabids						
Superficial soil loosening	<i>Agonum dorsale</i> (129)	Direct mortality	-68	$F_{1,32} = 8.20\ddagger$	0.0073	
		Cumulative effects	-51	$F_{1,32} = 4.12\ddagger$	0.0509	
		Sampling dates	+43	$F_{1,79} = 2.08\ddagger$	0.1531	
	<i>Pterostichus melanarius</i> (163)	Cumulative effects	-40	$F_{1,32} = 1.67\ddagger$	0.2061	
		Sampling dates	+1282	$F_{1,79} = 65.13\ddagger$	< 0.0001	
		<i>Trechus quadristriatus</i> (91)	Cumulative effects	-40	$F_{1,32} = 0.91\ddagger$	0.3474
	Ploughing and NINV	<i>Amara familiaris</i> (208)	Sampling dates	+5000	$F_{1,83} = 25.92\ddagger$	< 0.0001
			Plough cumulative effects*	-100	Tukey†	< 0.05
			NINV cumulative effects*	-98	Tukey†	< 0.05
Ploughing and NINV	<i>Bembidion lampros</i> (86)	Sampling dates	-28	$F_{1,83} = 0.47\ddagger$	0.4930	
		Plough direct mortality*	-95	Tukey†	< 0.05	
		Plough cumulative effects*	-40	Tukey†	NS	
		NINV direct mortality*	+58	Tukey†	NS	
		NINV cumulative effects*	-20	Tukey†	NS	
		Weed harrowing	<i>Bembidion lampros</i> (101)	Direct mortality	-37	$F_{1,60} = 1.81\ddagger$
Immediate migration	+31			$F_{1,60} = 1.19\ddagger$	0.2793	

*Pairwise comparison with control.

†Data square root transformed; ‡data $\ln(x + 1)$ transformed.

with the control and 63% fewer spiders found in the NINV area compared with the control, this reduction was not significant (Fig. 3a and Table 3a). However, spider densities were low and variance was high, therefore the lack of significance may have been caused by low sample size. In contrast, we found strong cumulative effects of ploughing and NINV on spider populations. Thus, 26 days after tillage, 93% fewer spiders were caught in the ploughed plots than the control plots, and 80% fewer spiders were found in the NINV plots compared with the control plots. The differences in spider densities between the control and both ploughed and NINV plots were highly significant (Table 3a). The large differences between ploughed and NINV and the control plots were mostly caused by an increasing spider density in the control plots, and to a much smaller degree by secondary effects decreasing densities in the ploughed and the NINV plots. None of the species was caught in sufficient numbers for individual analysis.

Ploughing caused significant direct mortality of carabids (27%) (Fig. 3b and Table 3b), whereas no direct mortality from NINV was detected. In contrast, 26% more carabids were found in the NINV treatment compared with the control plots. A pairwise comparison showed that significantly more carabid beetles were found in the NINV plots compared with ploughed plots (Tukey-Kramer 3,35 $P < 0.05$). We found significant cumulative effects of ploughing and NINV compared with the control plot, whereas the difference between the NINV and ploughed treatments had disappeared after 26 days (Tukey-Kramer 3,35 $P < 0.05$). The difference between cultivated and control plots was primarily caused by an increase in carabid densities in the control plots 26 days after treatment, and only to a much smaller degree by secondary effects decreasing numbers in the tilled plots. The marked increase in the control plots was largely due to a dramatic increase in the density of *Amara familiaris* Duftschmid (Table 4b). However, excluding *A. familiaris* from the analysis did

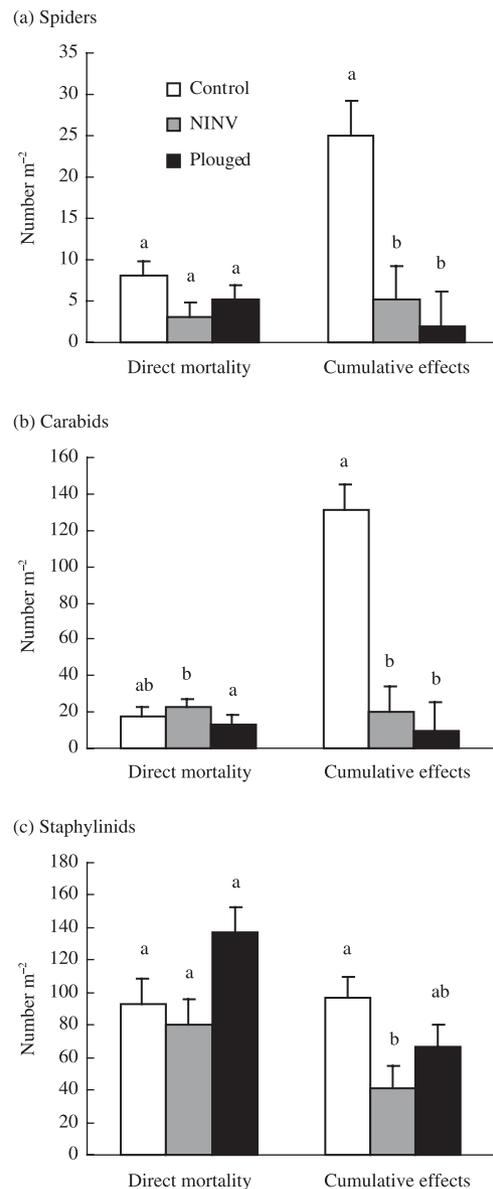


Fig. 3. Direct mortality and cumulative effects caused by non-inversion tilling (NINV) and mouldboard ploughing (ploughed). Densities of (a) spiders, (b) carabids and (c) staphylinids at treatment (direct mortality) and 26 days after treatment (cumulative effects). Letters above columns: difference between control, ploughed and NINV, different letters indicate significance at $P < 0.05$.

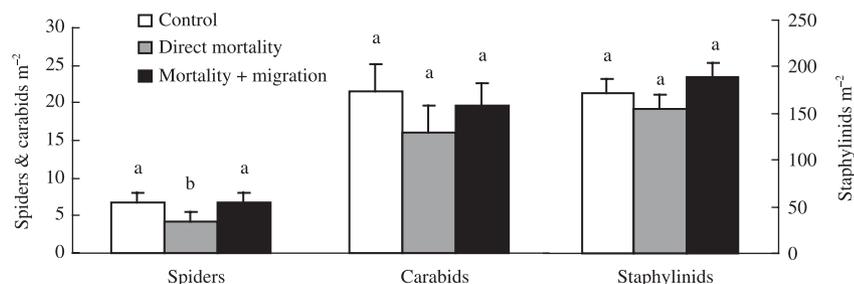


Fig. 4. Direct mortality and immediate migration caused by weed harrowing (mechanical weed control). Densities of spiders, carabids and staphylinids in controls, weed-harrowed plots (direct mortality) and plots that had been weed harrowed and left for 6 days to allow the arthropods to migrate (mortality + migration). Different letters denote significant differences in densities at $P < 0.05$.

not change this pattern; 26 days following cultivation carabid densities were higher in the control plots ($F_{2,36} = 5.73$, $P = 0.0069$).

No direct mortality of staphylinid beetles through ploughing or NINV was detected (Fig. 3c and Table 3c). The cumulative effects on staphylinids were lower than was the case for spiders and carabids, but secondary effects were higher. Only NINV caused significant secondary and cumulative effects. In contrast to the spiders and carabid beetles, the difference between the control area and the NINV plots was caused mainly by secondary effects leading to a reduction in the numbers in the tilled plots, and not by an increase in the control plots. To summarize, spiders and carabid beetles seemed to aggregate in the control area, while staphylinid beetles suffered an overall decline in the treatment plots. Generally, NINV caused smaller secondary and cumulative effects than ploughing.

WEED HARROWING

Weed harrowing caused significant direct mortality of spiders (Fig. 4a and Table 3a), reducing spider density by 37%. Apparently, spiders recolonized the fields within 7 days of weed harrowing; spider density increased by 58% over this period. Consequently, the effects of mortality and immigration cancelled each other out. None of the spider species was caught in sufficient numbers for individual analysis.

Weed harrowing caused substantial direct mortality of carabid beetles, although this was not statistically significant. We did not detect an effect on immediate emigration (Fig. 4 and Tables 3b and 4b) nor any clear effect on staphylinid beetles (Fig. 4c and Table 3c).

GRASS CUTTING

Direct mortality and immediate migration led to a reduction in spider densities (Fig. 5a), but only the effect of immediate emigration bordered on statistical significance (Table 3a). However, a strong combined effect of direct mortality and immediate emigration resulted in a significant 50% reduction in spider density 1 week after grass cutting. The dispersal pattern of the

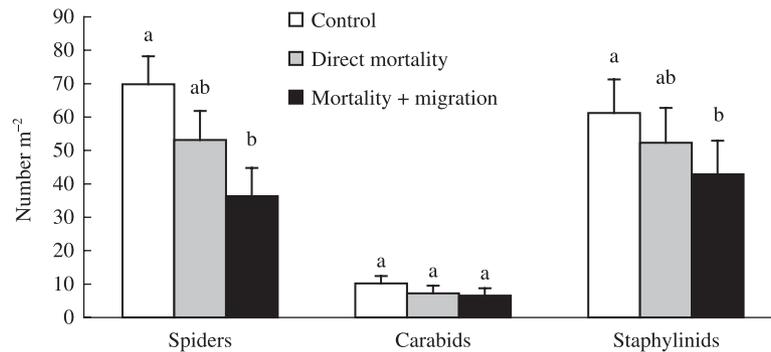


Fig. 5. Direct mortality and immediate emigration caused by grass cutting. Densities of spiders, carabids and staphylinids in controls (plots where the grass was not cut), plots where the grass was cut (direct mortality) and plots where the grass was cut and left for 1 week for the arthropods to migrate (mortality + migration). Different letters denote significant differences in densities at $P < 0.05$.

spiders was not the same in the four blocks, as there was a significant interaction between block and treatment ($F_{3,31} = 2.97$, $P = 0.0472$). The interaction was caused by an increase in spider density in the block where grass was left to dry for hay, whereas spider densities declined in the three blocks where grass was removed at harvest. The three dominant spider species were affected differently by grass cutting: *E. atra* suffered the highest mortality, *Bathyphanes gracilis* showed the highest immediate emigration whereas *O. apicatus* was least affected overall (Table 4a).

Carabid beetles were not strongly affected by grass cutting. The combined effect of direct mortality and immediate emigration led to a 36% reduction in carabid density, which was not statistically significant (Fig. 5b and Table 3b). None of the species was caught in numbers sufficient for individual analysis.

Similarly, grass cutting did not cause significant degrees of direct mortality or immediate emigration in staphylinid beetles. However, the combined effects of direct mortality and emigration caused a significant 30% reduction in staphylinid beetle densities (Fig. 5c and Table 3c). The staphylinid beetles emigrated from the blocks where the grass was removed but increased in the block where the grass was left to dry (interaction between treatment and block: $F_{3,30} = 2.84$, $P = 0.0537$).

Discussion

All the crop management practices that were tested caused reductions in at least one arthropod taxon. The relative importance of direct mortality, immediate emigration and cumulative effects varied with the management type and affected the three arthropod taxa differently. Spiders were generally more affected by management practices than carabid beetles, and staphylinid beetles appeared to be the most robust group. Direct mortality contributed less to population declines (25–60%) than we had expected. The cumulative effects measured 3–4 weeks after soil cultivation were quite substantial (40–90%) in comparison with direct mortality. This was due to an aggregation of arthropods in

the control areas (refuge) following cultivation. However, it is possible that damage to beetle larvae and pupae reduced the eclosion rate in the cultivated areas. These results suggest that indirect effects (i.e. habitat deterioration) of crop management practices may have a stronger overall impact on arthropod population dynamics than direct mortality. A reduction in habitat quality could be linked to alterations in soil structure. This may influence the density of soil-dwelling linyphiid spiders by limiting the number of suitable spots available for web construction (Alderweireldt 1994a; Samu *et al.* 1996). Furthermore, habitat disruption following soil cultivation could lead to changes in prey availability, for example tillage was shown to decrease densities of detritivores such as Collembola (Hendrix *et al.* 1986). Petersen (2002) compared effects of NINV tillage and ploughing on collembolan populations in the same field system as this study. A 66% reduction of collembolans was recorded immediately after cultivation and this effect was still evident the following spring (Petersen 2002). Ploughing had a greater effect on the upper soil layer compared with NINV, thus affecting epigeic collembolan species, which are important prey for generalist arthropod predators (Marcussen, Axelsen & Toft 1999; Bilde, Axelsen & Toft 2000; Petersen 2002). It appears that less disruption of the upper soil layer may be beneficial for several trophic levels in the soil food web. For example, Symondson *et al.* (1996) found that carabid beetles *P. melanarius* contained more food when caught in directly drilled and therefore less disrupted plots than those caught in conventional and reduced tillage plots.

Whereas the overall effect of ploughing and NINV was a reduction in generalist predator densities, the difference between NINV and mouldboard ploughing was not conclusive. Our results indicated that simultaneous deep soil loosening, rotary cultivation, harrowing and sowing (NINV) caused direct mortality in the same range as sequential ploughing, harrowing and sowing. The finding that NINV is less harmful to epigeic collembola than ploughing (Petersen 2002), in combination with our results (that NINV caused smaller

secondary effects than mouldboard ploughing), suggests that reduced tillage methods are less detrimental to soil-inhabiting arthropods than inversion cultivation methods. Less habitat disruption is expected when non-inversion methods are applied, reducing the likelihood of arthropod emigration.

Population decline following grass cutting was caused both by direct mortality and immediate emigration. Emigration by spiders and staphylinid beetles indicated that cutting rendered grass fields unfavourable habitats, perhaps due to the removal of plant structure when grass was removed from the treated plots. Indeed, when grass was left to dry in one of our experimental plots, no immediate emigration of spiders was observed; spider and staphylinid densities increased under such circumstances. Baines *et al.* (1998) found that leaving cut plant material in field margins increased spider densities, and Hossain, Gurr & Wratten (2000) and Hossain *et al.* (2002) found that unharvested strips accumulated insect predators during harvest of hay lucerne. In our study, the three dominant spider species responded differently to grass cutting, with *B. gracilis* emigrating in greater numbers. This may be due to differences in their biology; *B. gracilis* builds its webs on the plants, *E. atra* builds its web on the soil and *O. apicatus* often hunts without the use of a web (Alderweireldt 1994b).

In contrast to grass cutting, we did not observe immediate emigration in response to weed harrowing. All three groups decreased slightly in numbers due to direct mortality but only spiders were significantly affected. This was followed by a complete recovery, apparently as a result of immigration. This is in accordance with Krooss & Schaefer (1998), who found no long-term effects of mechanical weed control on staphylinid beetles, and Lorenz (1995) who, in semi-field trials, observed that carabid beetles were not affected by weed harrowing. Although habitat quality was not immediately affected by weed harrowing, the removal (or prevention) of weeds is likely to alter the microhabitat for arthropods, including potential prey for generalist predators. In addition, loss of protective plant cover may lead to increased predation by birds or other insect predators on beneficial arthropods. Several studies have shown positive relationships between high weed cover and densities of spiders, beetles and their prey (Bommarco 1998, 1999; Krooss & Schaefer 1998; Harwood, Sunderland & Symondson 2001; Lemke & Poehling 2002; K.D. Sunderland, personal communication). Therefore, a long-term effect of mechanical weed removal may appear later in the season. Our results showed that spider populations had recovered from direct mortality 1 week after weed harrowing. However, recolonization implies an available source habitat from which spiders can re-invade (Bishop 1990; Weyman 1993).

Comparisons of traditional and reduced-tillage cultivation methods have often been inconclusive with respect to their effects on generalist arthropod predators (Rice & Wilde 1991; Carcamo, Niemala & Spence

1995; Symondson *et al.* 1996; Baguette & Hance 1997; Langmaack, Land & Buchs 2001). One of the major constraints in the interpretation of results has been the frequent use of open pitfall traps, which may provide information about arthropod activity density but not about absolute densities (reviewed in Sunderland *et al.* 1995). In this study, we explicitly chose closed traps in an attempt to quantify densities accurately, although this method may underestimate densities of large and very active predators (Sunderland *et al.* 1995).

The timing of cultivation treatments could have a strong influence on the degree of damage imposed on insect predators, and subsequently on the results of comparative sampling between treated and non-treated areas. In temperate agro-ecosystems there is much focus on predatory beetles that hibernate in field margins and disperse into arable fields to reproduce in spring (Holland 2002). Larvae are present from April to June and eclosion of teneral beetles occurs in June–August (e.g. *A. dorsale*, *Bembidion lampros*, *P. melanarius*, *T. quadristriatus* (Carabidae); *Tachyporus hypnorum* (Staphylinidae); Mitchell 1963; Jones 1979; Sotherton 1984; Pedersen, Pedersen & Abildgaard 1990). Therefore, late spring cultivation is detrimental compared with summer or autumn tillage, and spring cultivation should occur prior to the onset of reproduction. For those species reproducing in autumn and producing winter larvae, such as *P. melanarius* and *T. quadristriatus*, additional effects may occur. Thus, *P. melanarius* larvae were more sensitive to tillage in spring than in autumn, because the third instar larvae and pupae are more vulnerable to soil disruption than the small first instar larvae in autumn (Fadl, Purvis & Towey 1996).

Many species of linyphiid spiders reproduce in the fields from early spring until late summer (Topping & Sunderland 1998; Thorbek, Sunderland & Topping 2003). A flexible reproductive behaviour and ballooning dispersal of all life-history stages may allow recolonization following post-cultivation declines (Blandenier & Fürst 1998). Some linyphiids migrate to undisturbed habitats following harvest and hibernate in arable fields (Alderweireldt 1989; Dinter 1997; Thorbek, Sunderland & Topping 2004). As a consequence, recovery may be delayed after autumn or winter cultivation of such habitats.

Evaluation of the impact of crop management on arthropod predators is influenced by their phenology. Husbandry-induced changes may coincide with natural population changes, such as immigration or eclosion, while emigration and natural mortality due to age may cause population declines (Thiele 1977; Toft 1989). For example, the coincidence between harvest-induced dispersal and natural dispersal makes it very difficult to assess the relative contributions to the observed post-harvest decline of spiders, if the sampling area is not sealed off (Dinter 1996; Thomas & Jepson 1999). Symondson *et al.* (1996) found that carabid beetle densities declined following harvest, but as they sampled the field for a longer period than we did in this study,

the effect of harvest may not be separable from natural declines in population densities, for example caused by migration to winter hibernation habitats (Thiele 1977; Alderweireldt 1989; Dinter 1997). In our study, we attempted to separate treatment effects from phenological changes in population densities by separating post-cultivation effects into direct mortality, immediate emigration and (short-term) secondary effects. Nevertheless, we did not completely avoid the influence of phenology; in the soil-loosening treatment we found more carabid beetles 18 days after soil loosening compared with numbers before treatment, a result that could have been misinterpreted as a positive treatment effect if the sampling of control plots had not been included. Indeed, we found a strong post-treatment effect but simultaneously there had been an overall increase of carabid beetles across all plots, which could be caused by the refuge effect, natural immigration or juvenile mortality of beetle larvae causing lower eclosion (Fadl, Purvis & Towey 1996). The density of *P. melanarius* and *T. quadristriatus* in particular increased after soil loosening, an increase likely to be caused by emergence of a new generation (Mitchell 1963; Jones 1979; Sotherton 1984). The opposite effect was observed in the spiders. We found a negative treatment effect and an overall population decline, which apparently coincided with naturally occurring declines of field-living linyphiid spiders (De Keer & Maelfait 1987, 1988; Toft 1989; Dinter 1996, 1997).

We conclude that the contribution of numerically important species should be taken into account when analysing treatment effects on communities of generalist arthropod predators. However, different species or groups show different responses to the type and timing of mechanical treatment. Therefore, a composite and diverse community of arthropod predators should be most robust to intensive agricultural management, because variation among species in sensitivity to different treatments buffers the effect on the overall community.

In summary, emigration and indirect effects inflicted by crop management practices had a strong influence on the spatial dynamics of generalist arthropod predators. Direct mortality was not as severe as expected, whereas cumulative effects indicated that arthropods emigrate either as a consequence of direct disturbance or as a result of habitat disruption. Such indirect effects may result in aggregations of arthropods in refuges of less disturbed habitat. The movement of animals between habitat types in the agricultural landscape can be viewed in the light of source-sink population dynamics (Pulliam 1988; Ekbom, Irwin & Robert 2000). Permanent and undisturbed habitats, such as permanent pasture, field margins and hedgerows, serve as refuge and source habitats from which arthropods could recolonize crop fields following management practices (Gravesen & Toft 1987; reviewed in Ekbom, Irwin & Robert 2000; Landis, Wratten & Gurr 2000; Sunderland & Samu 2000; Giulio, Edwards & Meister 2001; Thomas

et al. 2001). Crops cultivated out of phase, for example winter crops, spring crops and grass in rotation, may also serve as transient refuges. A diverse agricultural landscape consisting of crop fields and refuges may reduce the catastrophic effects of cultivation events on arthropod population densities. Spatial and temporal variation in timing of cultivation events may further reduce the negative impacts of treatment. With changing roles over time, the different landscape components can thus contribute to buffering the effect of intensive crop management on the spatial dynamics of generalist arthropod predators.

Acknowledgements

We thank Frank W. Oudshoorn, Erling Olesen and staff on The Organic Research Station Rugballegaard (The Danish Institute of Agricultural Sciences) for tremendous assistance with the experiments. Thomas Larsen, Mette Møller and Bente Marcussen assisted with field work. Keith D. Sunderland, Søren Toft and three anonymous referees provided invaluable suggestions for improving earlier drafts. Funding was provided by Danish Research Agency, Danish Research Centre for Organic Farming and the National Environmental Research Institute of Denmark.

References

- Alderweireldt, M. (1989) Seasonal migration and the importance of edge zones for the survival of *Bathyphanes gracilis* (Blackwall, 1841) (Araneae: Linyphiidae) on high input crop fields. *Medelingen van de Fakulteit Landbouwwetenschappen Rijksuniversiteit Gent*, **54/3a**, 835–844.
- Alderweireldt, M. (1994a) Habitat manipulations increasing spider densities in agroecosystems: possibilities for biological control. *Journal of Applied Entomology-Zeitschrift für Angewandte Entomologie*, **118**, 10–16.
- Alderweireldt, M. (1994b) Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields. *The Bulletin of the British Arachnological Society*, **9**, 300–308.
- Baguette, M. & Hance, T. (1997) Carabid beetles and agricultural practices: influence of soil ploughing. *Entomological Research in Organic Agriculture* (eds B. Kromp & P. Meindl). *Biological Agriculture and Horticulture*, **15**, 185–190.
- Baines, M., Hamblen, C., Johnson, P.J., Macdonald, D.W. & Smith, H. (1998) The effect of arable field margin management on the abundance and species richness of Araneae (spiders). *Ecography*, **21**, 74–86.
- Bilde, T., Axelsen, J.A. & Toft, S. (2000) The value of *Collembola* from agricultural soils as food for a generalist predator. *Journal of Applied Ecology*, **37**, 672–683.
- Bishop, L. (1990) Meteorological aspects of spider ballooning. *Environmental Entomology*, **19**, 1381–1387.
- Blandenier, G. & Fürst, P.-A. (1998) Ballooning spiders caught by a suction trap in an agricultural landscape in Switzerland. *Proceedings of the 17th European Colloquium of Arachnology* (ed. P.A. Selden), pp. 177–186. British Arachnological Society, Burnham Beeches, Bucks.
- Bommarco, R. (1998) Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity. *Ecological Applications*, **8**, 846–853.
- Bommarco, R. (1999) Feeding, reproduction and community impact of a predatory carabid in two agricultural habitats. *Oikos*, **87**, 89–96.

- Carcamo, H.A., Niemala, J.K. & Spence, J.R. (1995) Farming and ground beetles: effects of agronomic practice on populations and community structure. *Canadian Entomologist*, **127**, 123–140.
- De Keer, R. & Maelfait, J.-P. (1987) Life history of *Oedothorax fuscus* (Blackwall, 1834) (Araneae, Linyphiidae) in a heavily grazed pasture. *Revue D'Écologie et de Biologie du Sology*, **24**, 171–185.
- De Keer, R. & Maelfait, J.-P. (1988) Observations on the life cycle of *Erigone atra* (Araneae, Erigoninae) in a heavily grazed pasture. *Pedobiologia*, **32**, 201–212.
- Dinter, A. (1996) Population dynamics and egg sac parasitism of *Erigone atra* (Blackwall) in winter wheat. *Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3–8-IX.1995* (ed. V. Mahnert), pp. 153–164. Volume Hors. Série. Revue Suisse de Zoologie, Geneva.
- Dinter, A. (1997) Density and activity density fluctuation of *Oedothorax apicatus* (Blackwall) in winter wheat in northern Germany. *Arthropod Natural Enemies in Arable Land III: The Individual, the Population and the Community* (ed. W. Powell), pp. 87–99. Aarhus University Press, Aarhus, Denmark.
- Ekbom, B., Irwin, W.E. & Robert, Y. (2000) *Interchanges of Insects between Agricultural and Surrounding Landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Fadl, A., Purvis, G. & Towey, K. (1996) The effect of time of soil cultivation on the incidence of *Pterostichus melanarius* (Illig.) (Coleoptera: Carabidae) in arable land in Ireland. *Annales Entomologici Fennici*, **33**, 207–214.
- Giulio, M.D., Edwards, P.J. & Meister, E. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology*, **38**, 310–319.
- Gravesen, E. & Toft, S. (1987) Grass fields as reservoirs for polyphagous predators (Arthropoda) of aphids (Homopt., Aphididae). *Journal of Applied Entomology*, **104**, 461–473.
- Halley, J.M., Thomas, C.F.G. & Jepson, P.C. (1996) A model for the spatial dynamics of linyphiid spiders in farmland. *Journal of Applied Ecology*, **33**, 471–492.
- Harwood, J.D., Sunderland, K.D. & Symondson, W.O.C. (2001) Living where the food is: web location in relation to prey availability in winter wheat. *Journal of Applied Biology*, **38**, 88–99.
- Hendrix, P.F., Parmalee, R.W., Crossley, D.A. Jr, Coleman, D.C., Odum, E.P. & Groffman, P.M. (1986) Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience*, **36**, 374–380.
- Holland, J.M. (2002) *The Agroecology of Carabid Beetles*. Intercept, Andover.
- Hossain, Z., Gurr, G.M. & Wratten, S.D. (2000) Effects of harvest on survival and dispersal of insect predators in hay lucerne. *Biological Agriculture and Horticulture*, **17**, 339–348.
- Hossain, Z., Gurr, G.M., Wratten, S.D. & Raman, A. (2002) Habitat manipulation in lucerne *Medico sativa*: arthropod population dynamics in harvested and 'refuge' crop strips. *Journal of Applied Ecology*, **39**, 445–454.
- Jones, M.G. (1979) The abundance and reproductive activity of common Carabidae in a winter wheat crop. *Ecological Entomology*, **4**, 31–43.
- Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment*, **74**, 187–228.
- Krooss, S. & Schaefer, M. (1998) The effect of different farming systems on epigeic arthropods: a five-year study on the rove beetle fauna (Coleoptera: Staphylinidae) of winter wheat. *Agriculture, Ecosystems and Environment*, **69**, 121–133.
- Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.
- Langmaack, M., Land, S. & Buchs, W. (2001) Effects of different field management systems on the carabid coenosis in oil seed rape with special respect to ecology and nutritional status of predaceous *Poecilus cupreus* L. (Col., Carabidae). *Journal of Applied Entomology*, **125**, 313–320.
- Lee, J.C., Menalled, F.D. & Landis, D.A. (2001) Refuge habitats modify insecticide disturbance on carabid beetle communities. *Journal of Applied Ecology*, **38**, 472–483.
- Lemke, A. & Poehling, H.M. (2002) Sown weed strips in cereal fields: overwintering site and 'source' habitat for *Oedothorax apicatus* (Blackwall) and *Erigone atra* (Blackwall) (Araneae: Erigonidae). *Agriculture Ecosystems and Environment*, **90**, 67–80.
- Lindroth, C.H. (1985) *The Carabidae (Coleoptera) of Fennoscandia and Denmark. I. Fauna Entomologica Scandinavica*, Vol. 15, Part 1. E. J. Brill/Scandinavian Science Press Ltd, Leiden and Copenhagen.
- Lindroth, C.H. (1986) *The Carabidae (Coleoptera) of Fennoscandia and Denmark. II. Fauna Entomologica Scandinavica*, Vol. 15, Part 2. E. J. Brill/Scandinavian Science Press Ltd, Leiden and Copenhagen.
- Lorenz, E. (1995) *Mechanische Unkrautbekämpfungsverfahren in Zuckerrübenkulturen und ihre Nebenwirkungen auf Laufkäfer (Coleoptera, Carabidae) und andere epigäische Arthropoden*. PhD Thesis. University of Göttingen, Göttingen, Germany.
- Marcussen, B.M., Axelsen, J.A. & Toft, S. (1999) The value of two Collembola species as food for a linyphiid spider. *Entomologia Experimentalis et Applicata*, **92**, 29–36.
- Mitchell, B. (1963) Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). I. Life cycles and feeding behaviour. *Journal of Animal Ecology*, **32**, 289–299.
- Munkholm, L.J., Schjonning, P. & Rasmussen, K.J. (2001) Non-inversion tillage effects on soil mechanical properties of a humid sandy loam. *Soil and Tillage Research*, **62**, 1–14.
- Pedersen, M., Pedersen, L.T. & Abildgaard, K. (1990) Annual and diurnal activity of some *Tachyporus* species (Coleoptera: Staphylinidae) in two spring barley fields and a hedge. *Pedobiologia*, **34**, 367–375.
- Petersen, H. (2002) Effects of non-inverting deep tillage vs. conventional ploughing on collembolan populations in an organic wheat field. *European Journal of Soil Biology*, **38**, 177–180.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- Rice, M.E. & Wilde, G.E. (1991) Aphid predators associated with conventional- and conservation-tillage winter wheat. *Journal of the Kansas Entomological Society*, **64**, 245–250.
- Roberts, M.J. (1987) *The Spiders of Great Britain and Ireland*, Vol. 2. *Linyphiidae*. Harley Books, Colchester, UK.
- Samu, F., Sunderland, K.D., Topping, C.J. & Fenlon, J.S. (1996) A spider population in flux. Selection and abandonment of artificial web-sites and the importance of intraspecific interactions in *Lepthyphantes tenuis* (Araneae: Linyphiidae) in wheat. *Oecologia*, **106**, 228–239.
- SAS Institute Inc. (1999–2001) *The SAS System for Windows*. SAS Institute Inc., Cary, NC.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. Freeman, New York, NY.
- Sotherton, N.W. (1984) The distribution and abundance of predatory arthropods overwintering on farmland. *Annals of Applied Biology*, **105**, 423–429.
- Stinner, B.R. & House, G.J. (1990) Arthropods and other invertebrates in conservation-tillage agriculture. *Annual Review of Entomology*, **35**, 299–318.
- Sunderland, K.D. & Samu, F. (2000) Effects of agricultural diversification on the abundance, distribution, and pest control

- potential of spiders: a review. *Entomologia Experimentalis et Applicata*, **95**, 1–13.
- Sunderland, K.D., De Snoo, G.R., Dinter, A., Hance, T., Helenius, J., Jepson, P., Kromp, B., Lys, J.-A., Samu, F., Sotherton, N.W., Toft, S. & Ulber, B. (1995) Density estimation for invertebrate predators in agroecosystems. *Arthropod Natural Enemies in Arable Land I. Density, Spatial Heterogeneity and Dispersal* (eds S. Toft & W. Riedel), pp. 133–162. Aarhus University Press, Aarhus, Denmark.
- Symondson, W.O.C., Glen, D.M., Wiltshire, C.W., Langdon, C.J. & Liddell, J.E. (1996) Effects of cultivation techniques and methods of straw disposal on predation by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable field. *Journal of Applied Ecology*, **33**, 741–753.
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, **47**, 561–594.
- Thiele, H.-U. (1977) *Carabid Beetles in Their Environments*. Springer, Berlin, Germany.
- Thomas, C.F.G. & Jepson, P.C. (1997) Field-scale effects of farming practices on linyphiid spider populations in grass and cereals. *Entomologia Experimentalis et Applicata*, **84**, 59–69.
- Thomas, C.F.G. & Jepson, P.C. (1999) Differential aerial dispersal of linyphiid spiders from a grass and a cereal field. *Journal of Arachnology*, **27**, 294–300.
- Thomas, C.F.G., Parkinson, L., Griffiths, G.J.K., Garcia, A.F. & Marshall, E.J.P. (2001) Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. *Journal of Applied Ecology*, **38**, 100–116.
- Thorbek, P., Sunderland, K.D. & Topping, C.J. (2003) Egg sac development rates and phenology of agrobiont spiders in relation to temperature. *Entomologia Experimentalis et Applicata*, **109**, 89–100.
- Thorbek, P., Sunderland, K.D. & Topping, C.J. (2004) Reproductive biology of agrobiont linyphiid spiders in relation to habitat, season and biocontrol potential. *Biological Control*, **30**, 193–202.
- Toft, S. (1989) Aspects of the ground-living spider fauna of two barley fields in Denmark: species richness and phenological synchronization. *Entomologiske Meddelelser*, **57**, 157–168.
- Topping, C.J. & Sunderland, K.D. (1994) A spatial population dynamics model for *Lepthyphantes tenuis* (Araneae: Linyphiidae) with some simulations of the spatial and temporal effects of farming operations and land use. *Agriculture, Ecosystems and Environment*, **48**, 203–217.
- Topping, C.J. & Sunderland, K.D. (1998) Population dynamics and dispersal of *Lepthyphantes tenuis* in an ephemeral habitat. *Entomologia Experimentalis et Applicata*, **87**, 29–41.
- Weyman, G.S. (1993) A review of the possible causative factors and significance of ballooning in spiders. *Ethology, Ecology and Evolution*, **5**, 279–291.

Received 29 April 2003; final copy received 9 February 2004