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Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods

A. J. Haughton[1], G. T. Champion[2], C. Hawes[3], M. S. Heard[4], D. R. Brooks[1],
D. A. Bohan[1*], S. J. Clark[1], A. M. Dewar[2], L. G. Firbank[5], J. L. Osborne[1],
J. N. Perry[1], P. Rothery[4], D. B. Roy[4], R. J. Scott[5], I. P. Woiwod[1], C. Birchall[1],
M. P. Skellern[1], J. H. Walker[1], P. Baker[2], E. L. Browne[1], A. J. G. Dewar[2],
B. H. Garner[2], L. A. Haylock[2], S. L. Horne[1], N. S. Mason[1], R. J. N. Sands[2]
and M. J. Walker[2]

[1]*Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK*
[2]*Broom's Barn Research Station, Higham, Bury St Edmunds, Suffolk IP28 6NP, UK*
[3]*Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK*
[4]*NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK*
[5]*NERC Centre for Ecology and Hydrology, Merlewood, Grange-over-Sands, Cumbria LA11 6JU, UK*

The effects of the management of genetically modified herbicide-tolerant (GMHT) crops on the abundances of aerial and epigeal arthropods were assessed in 66 beet, 68 maize and 67 spring oilseed rape sites as part of the Farm Scale Evaluations of GMHT crops. Most higher taxa were insensitive to differences between GMHT and conventional weed management, but significant effects were found on the abundance of at least one group within each taxon studied. Numbers of butterflies in beet and spring oilseed rape and of Heteroptera and bees in beet were smaller under the relevant GMHT crop management, whereas the abundance of Collembola was consistently greater in all GMHT crops. Generally, these effects were specific to each crop type, reflected the phenology and ecology of the arthropod taxa, were indirect and related to herbicide management. These results apply generally to agriculture across Britain, and could be used in mathematical models to predict the possible long-term effects of the widespread adoption of GMHT technology. The results for bees and butterflies relate to foraging preferences and might or might not translate into effects on population densities, depending on whether adoption leads to forage reductions over large areas. These species, and the detritivore Collembola, may be useful indicator species for future studies of GMHT management.

Keywords: agro-ecology; Farm Scale Evaluations; environmental impact; invertebrate biodiversity; Carabidae; Araneae

1. INTRODUCTION

The management of GMHT crops is known to affect the abundance of within-field arthropods, through the indirect effects of the herbicide management regime on the weed flora (Squire *et al.* 2003; Dewar *et al.* 2003). These within-field arthropods are components of the farmland biodiversity in their own right, and also provide important functions, including pollination and the recycling of detritus. Changes in arthropod abundance and diversity in arable ecosystems are difficult to quantify because of the inherent difficulty of long-term monitoring (Woiwod

1991) and the enormous species diversity within the group (Potts 1991). However, published data suggests that there has been a general decline in many non-pest invertebrate species that are associated with farmland (Robinson & Sutherland 2002) and that particular groups, such as the Lepidoptera (Woiwod & Harrington 1994; Pollard *et al.* 1995) and bumble-bees (Williams 1986), have declined markedly over the past 50 years.

The use of within-field weed vegetation by bees and butterflies is not well documented, but flowering weeds (Fussell & Corbet 1992) and flowering crops, in particular oilseed rape (Williams 1985; Free 1993), provide a considerable supply of nectar and pollen that can attract foraging bees and butterflies, potentially from a range of several kilometres (Osborne *et al.* 2001). In the USA, milkweed (Asclepiadaceae) growing within maize fields has been shown to provide a resource for larvae of the

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monarch butterfly, *Danaus plexippus* (Oberhauser *et al.* 2001). In the UK, within-field weeds are considered to be of little benefit to larvae, particularly in comparison with field-margin vegetation (Feber & Smith 1995). Changes in weed vegetation mediated by the application of herbicides have been shown to reduce the diversities and abundances of epigeal groups, including the Araneae (spiders) (Hassall *et al.* 1992; Feber *et al.* 1998), Heteroptera (true bugs) (Chiverton & Sotherton 1991) and Carabidae (ground beetles) (Raskin *et al.* 1994). Abundances of epigeal Collembola (springtails), such as the Sminthuridae, may also be expected to vary with changes in the availability and quality of their host weed plants (Hopkin 1997).

The results presented here form part of the output from the FSEs that were set up in response to concerns expressed about the possible adverse environmental impacts of the proposed commercial introduction of GMHT crops into the UK (Firbank *et al.* 2003*a*). Of particular concern were the roles of arable weeds and invertebrates as food resources for farmland birds, whose populations have declined widely with recent agricultural intensification (Krebs *et al.* 1999; Chamberlain *et al.* 2000). The FSEs were designed to evaluate the effects that the adoption of GMHT crops would have on farm wildlife abundance and diversity by comparing herbicide management in GMHT crops with current conventional herbicide management (Firbank *et al.* 2003*b*). Crops tolerant to either glyphosate or glufosinate-ammonium were grown from the year 2000 to 2002 on a total of 201 farms around the UK that reflected the current geographical distributions of each non-GMHT crop (Champion *et al.* 2003). Effects are unlikely to be the result of the toxicity and persistence of glyphosate, used in beet, or glufosinate-ammonium, used in maize and spring oilseed rape (Ahrens 1994; Haughton *et al.* 2001*b*), but are more probably the result of the indirect effects outlined above.

Amongst bees, butterflies, Araneae, Collembola, Heteroptera and Carabidae there are indicators of ecological importance that show marked responses to anthropogenic perturbations generally (Kromp 1999) and may be sensitive, in particular, to the changes in herbicide management that might result from the large-scale planting of GMHT crops.

Aerial species, such as bees and butterflies, are present in the cropped area for relatively short periods, from a few minutes to a number of days. In contrast, many epigeal invertebrate species of arable farmland are resident within the cropped area for much of the growing season. In this paper, epigeal is taken to mean those species that spend most of their life on plant and soil surfaces, and aerial species are those whose main activity in the crop involves a substantial proportion of time spent in flight. The more highly mobile species, which tend to be aerially active, move into the crop from surrounding areas, such as margins, in response to flowering of both the crop and the weed vegetation. Counts of these highly mobile species probably relate to foraging preferences, and give an insight into the changing value of cropped habitats over time. The highly mobile species also link the effects of herbicide management that occur within the field to effects that may

be observed in areas adjacent to the crop, as discussed by Roy *et al.* (2003).

This paper describes the indirect effects of the management of GMHT crops on within-field epigeal and aerially active arthropods, using sampling approaches that reflect the differences in behaviours and abundances of these groups. This paper complements the studies of the effects of GMHT management on within-field soil-surface-active invertebrates (Brooks *et al.* 2003), within-field invertebrate trophic groups (Hawes *et al.* 2003) and field-margin invertebrates (Roy *et al.* 2003). This paper and the paper by Brooks *et al.* (2003) consider the potential effects of treatments on Araneae, Collembola and Carabidae, but adopt different sampling methods. While Brooks *et al.* (2003) use pitfall trapping to sample the activity densities of these taxa, we adopt a suction-sampling approach to sample the arthropods that inhabit the plant surface, litter and soil surface (Stewart & Wright 1995). Suction sampling is a long-established method of directly estimating the densities of epigeal arthropods in grassland and arable crops (see, for example, Dietrick 1961; Thornhill 1978; Southwood & Henderson 2000). It is recognized, however, that, whereas smaller arthropods, such as Linyphiidae (Araneae), are sampled efficiently (Stewart & Wright 1995), larger arthropods, such as the larger Lycosidae (Araneae) (Mommertz *et al.* 1996) and Carabidae, may be undersampled. This leads to differences between the compositions of the taxa common to this paper and Brooks *et al.* (2003).

The overall objective of this paper is to examine the effects of the management of GMHT varieties, relative to non-GMHT crops, on key groups of epigeal and aerially active arthropods within each of three crops, with particular reference to the weed vegetation that supports them. Specifically, we aim first to test the null hypothesis that there is no difference between the management of GMHT varieties of sugar and fodder beet, fodder maize and spring oilseed rape and that of comparable conventional varieties in their effects on the abundances of bees, butterflies, Araneae, Collembola, Heteroptera and Carabidae; second, to estimate the magnitudes of any observed differences in abundances and diversities; third, to evaluate the importances of farmland and crop whole-field covariates, including environmental zone, initial seedbank as a measure of farming intensity (Heard *et al.* 2003*a*; Squire *et al.* 2003) and a comparison between sugar and fodder beet, half-field covariates such as weed biomass and variates such as year and distance from the crop edge into the crop; fourth, to discuss how any observed differences may result from herbicide effects on the weed vegetation; and, fifth, to consider the likely implications for these invertebrate groups if GMHT crops were planted on a large scale.

2. METHODS

The methods described here are specific to arthropod sampling; for methods generic to the FSEs, the rationale behind the invertebrates chosen as indicator groups and an overview of the overall experimental approaches, refer to Firbank *et al.* (2003*a*) and Squire *et al.* (2003). The background to the experimental design, experimental power and statistical analysis are given in Perry *et al.* (2003).
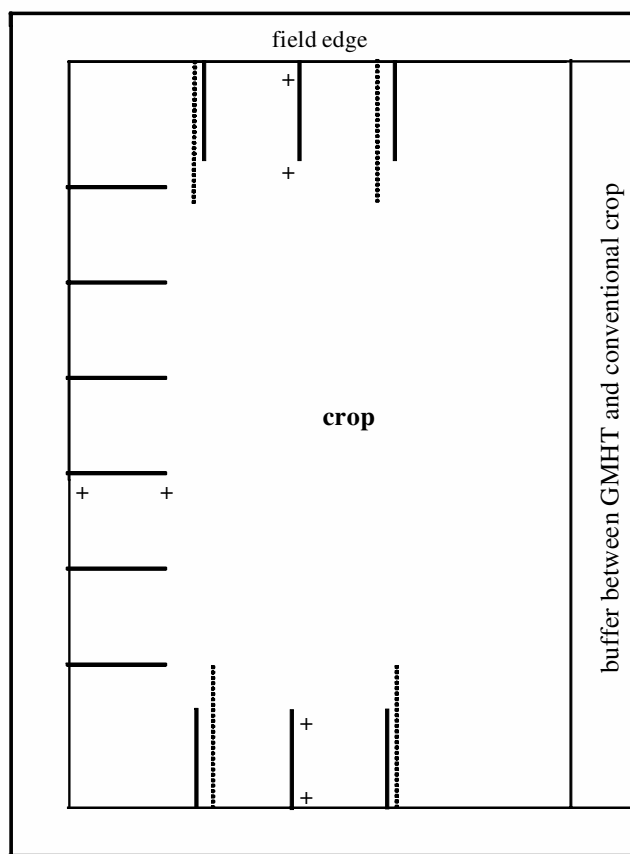
Figure 1. Locations of sample points in a standard half-field. Solid lines, transects; +, Vortis sampling; dotted lines, bee and butterfly transects.

(a) *Aerial arthropods*

Aerial arthropods (bees and butterflies) were counted using a modified version of the line-transect method developed for the BMS (Pollard & Yates 1993) and used as a standard method for bee surveys (Banaszak 1980). Transects were each walked once in June, July and August for all crops, with an additional record in May for beet to take account of the timing of herbicide application (see Perry *et al.* 2003). Where possible, counts were recorded for maize and spring oilseed rape sites when the crop was in flower. The two halves of the field were walked on the same day, with the order being chosen at random because time of day affects flight activity. Walks took place between 10.00 and 17.30 when the weather conformed to BMS standards (temperature above 13 °C with at least 60% clear sky or above 17 °C in any sky conditions apart from heavy rain; Beaufort wind speed of less than 5). Four well-spaced 100 m sections were walked into the crop parallel to four of the transects used to sample vegetation (figure 1). Standard transect walks were impracticable in flowering maize owing to the height of the crop. On these occasions, four well-spaced 5 m × 5 m areas of flowering crop were sampled by watching from a stepladder (3 m above ground level) for 10 min (Kearns & Inouye 1993).

During transect walks, bees were counted within 2 m and butterflies within 5 m of the transect line. Given the need to identify the bees in flight, counts were made for groups of *Bombus* (bumble-bee) species based on colour type, according to Prŷs-Jones & Corbet (1991). Separate counts were also made for honeybees (*Apis mellifera*), cuckoo bees (*Psithyrus* spp.) and solitary bees. In all cases, only actively foraging individuals or nest-

searching queens were counted. The flowering species on which the bees were foraging were listed. Counts were made separately for all butterfly species, except for *Pieris* species that were not identifiable in flight, which were assigned to a 'mixed white' category.

(b) *Epigeal arthropods*

Epigeal arthropods were sampled using a Vortis suction sampler (Arnold 1994). This suction-sampling technique is comparable with the conventional D-vac suction sampler and has been used widely in similar entomological field studies (e.g. Moreby *et al.* 1997). Although extraction efficiency is always less than 100%, suction samples represent a constant proportion of the population density, thus allowing valid statistical comparisons to be made between treatments for the same habitat.

Samples consisted of five 10 second Vortis 'sucks' taken 1 m apart at 2 m and 32 m from the crop edge at each of three locations around each half of the field in June and August (figure 1), giving an area over which each set of bulked samples was taken of 0.09 m². Samples were taken when both soil and vegetation were dry to the touch, and sampling was completed for the whole field within 4 h on each occasion.

Arthropod samples were placed in labelled polythene bags in a cool box containing frozen blocks during transit from the field, and then stored in a freezer in the laboratory. The arthropods were separated from other organic matter and soil particles by repeated flotation prior to being counted and identified to the appropriate taxonomic level under a microscope. Nomenclature followed Roberts (1993) for Araneae, Fjellberg (1980) for Collembola, Southwood & Leston (1959) for Heteroptera and Lindroth (1974) and Forsythe (2000) for Carabidae.

(c) *Response variables*

Total bee and butterfly (aerial arthropods) counts were analysed. Also, counts of honeybees (*A. mellifera*), bumble-bees (*Bombus* spp. and *Psithyrus* spp.) and a subgroup of long-tongued bumble-bees (*B. hortorum*, *B. pascuorum* and bees in the same colour groups) were analysed separately. Long-tongued bumble-bees were chosen because they are selective about the plants they feed on, and may be particularly sensitive to any reduction in farmland floral resources. Owing to their higher abundance in spring oilseed rape crops, the butterfly groups *Pieris* (whites) and non-*Pieris* were analysed separately. Total counts of epigeal arthropods were analysed for the following taxonomic groups: Araneae (order and selected species); Collembola (order and families); Heteroptera (suborder, herbivores and predators); and Carabidae (family, *Bembidion* spp. and selected species). Indicator epigeal taxa were selected for analysis on the basis of overall abundance (Firbank *et al.* 2003a).

(d) *Statistical analysis*

A description of the experimental design has been given in detail elsewhere (Perry *et al.* 2003) and is only summarized here. Records for each variate analysed were obtained from systematic samples within each of $2n$ half-fields of three spring crops in a randomized block experimental design in which the blocks were paired treatments (half-fields). Most analyses were based on total counts per treatment, c_{ij}, for treatment i at site j, transformed to $l_{ij} = \log(c_{ij} + 1)$. Sites, j, for which the whole-field total count, $c_{1j} + c_{2j}$, was zero or unity were removed from the analyses. The number of sites remaining for each analysis is reported as n, and the number of sites not sampled or removed from the analyses may be calculated by subtracting n from the total

number of fields for that crop. To give an approximate indication of abundance, geometric means for each treatment, i, were calculated from back-transformed values of arithmetic means of l_{ij}. The standard analysis of abundance was performed using a randomized-block ANOVA of the transformed values, l_{ij}, termed the lognormal model by Perry *et al.* (2003). The null hypothesis was tested with a paired randomization test, using $d = \Sigma_j[l_{2j} - l_{1j}]/n$, the mean of the differences between the GMHT and conventional treatments on the logarithmic scale, as a test statistic. The treatment effect was measured as R, the multiplicative ratio of the GMHT treatment divided by the conventional treatment, calculated as $R = 10^d$; confidence limits about R were obtained by back-transformation of the confidence interval of d on the logarithmic scale, derived from the standard error of d and $t_{0.05}$. Response variables were analysed separately for each occasion and for all occasions totalled over the entire season (see § 3). Where appropriate, differences in the responses to GMHT and conventional treatments between occasions within a season were studied by forming a new response variable, $q_{ij} = l_{ijv} - l_{iju}$, to represent the change in response from occasion u to occasion v; q_{ij} was then analysed by the standard methods used for l_{ij}, as described above. The response variables are appropriate for analysing treatment effects in both single- and multi-generation species; for the latter, it was assumed that individuals of the same species that were recorded on the same sampling occasion were at the same growth stage on both halves of each field.

Covariate analyses were conducted to establish whether certain of the larger measured treatment effects on invertebrates could be explained either by the treatment effect on the abundance of vegetation, or, for predators, by the treatment effect on the abundance of their prey. Four specific half-field covariates were used. For bees, the covariate used was the total annual count of those weed species observed to be visited by bees. For butterflies, it was the total annual count of Asteraceae. For predators of aphids, such as the predatory Heteroptera, it was the annual count of aphids determined from the recorded herbivores on crop plants (Hawes *et al.* 2003). For all other taxa it was the total weed biomass sampled shortly before harvest (Heard *et al.* 2003*a*). If the treatment effect reported for the simple test of the null hypothesis was reduced in magnitude and significance by the inclusion of such a half-field covariate, and the covariate itself had an important effect, then the primary effect was probably on the covariate, and the reported treatment effect was probably indirect. For such analyses the estimate of the multiplicative treatment ratio adjusted for the covariate, R_{adj}, is given together with its associated probability level, p_{adj}, and the probability level, p_{cov}, for the covariate; R_{adj} and p_{adj} may be compared with the corresponding values for the simple analyses without covariates, reported in the relevant tables. This approach is similar to that taken by Hawes *et al.* (2003) to study interactions at several trophic levels between consumers and resources.

Differences between the treatment effects for samples recorded at different distances into the crop were tested using a repeated-measures ANOVA (Greenhouse & Geisser 1959) with a term for the treatment × distance interaction. For each distance into the field, the half-field total for that distance was deemed to be missing if over half of the samples were missing. If half or fewer of the samples were missing, the missing samples were estimated proportionately, relative to the sum of the non-missing values for that distance. If the half-field total for a particular distance was missing, then the overall half-field total was also deemed to be missing and that site contributed no infor-

mation to the estimated treatment effect or to the test of the null hypothesis. Before the exclusion of missing values from the analyses, the percentage of data values that were missing in the entire database did not exceed 1% for any variable sampled by Vortis.

Separate covariate analyses were used to detect whether the measured treatment effects differed with the whole-field covariates initial seedbank (Heard *et al.* 2003*a*), environmental zone and crop type (sugar or fodder) for beet. The whole-field total initial seedbank count was taken as a measure of the overall weed status of each site (Heard *et al.* 2003*a*). The six environmental zones (Haines-Young *et al.* 2000) of the Institute of Terrestrial Ecology Land Classification of Great Britain (Bunce *et al.* 1996) were used to group sites with similar topography and climate.

A large number of hypothesis tests are reported in this paper. Bonferroni procedures could be used to adjust the significance level of each, but this is made unnecessary by the provision in the tables of estimates of treatment effects with measures of variability, and the presentation of exact randomization probabilities in addition to significance levels. The misuse of such adjustments was highlighted by Perry (1986).

The power to detect significance depends on the magnitude of the estimated treatment effect and the variability of that estimate, which depends on the sampling scheme. The results for the Araneae, Collembola and Carabidae sampled by Vortis were compared with the pitfall-sampled results presented in Brooks *et al.* (2003). The estimated treatment effects ($d = \log R$) and their confidence intervals for the Araneae, Collembola and Carabidae common to both papers were compared for the two sampling methods, using ANOVA.

3. RESULTS

In this paper, the geometric-mean counts for GMHT half-fields are usually expressed as percentages of the corresponding means for conventional half-fields. The tables include the effects for higher-order taxa and species by year total and individual date. Response variables are presented separately for each occasion, unless differences in R between occasions were less than 0.3, in which case the results are given only for the entire year. Where R differed by more than 0.3 or was significant on one sampling date, the results are presented in the text. Only significant covariate whole-field analyses are presented.

(a) *Bees*

The relative densities of bees over the sampling period on the conventional crops were highest in the spring oilseed rape crop, and were much lower in the beet- and maize-cropped areas (table 1). However, it should be noted that the maize estimates during flowering are not always directly comparable with the other crops, because a different method of observation was used. The majority of bees in all crops were bumble-bees (*Bombus* spp. and *Psithyrus* spp.): 64% in beet, 85% in maize and 59% in spring oilseed rape. The majority of the bumble-bees were of the *B. terrestris–B. lucorum* colour group, although *B. lapidarius* and *Psithyrus* spp. also occurred frequently in spring oilseed rape. The remaining bees were mainly honeybees, with approximately 5% being solitary bees or unidentified individuals. The relative proportions of each group were similar in conventional and GMHT treatments for all crops.

Table 1. *Geometric-mean densities of taxonomic groups in conventional beet, maize and spring oilseed rape.*

(Values are combined totals over the sampling season. For bees and butterflies, units are per kilometre; for other taxa, units are per square metre.)

	beet	maize	spring oilseed rape
bees	2.26	0.95	36.90
butterflies	3.53	2.73	13.50
Araneae	15.31	11.46	14.99
Collembola	104.06	133.70	208.64
Carabidae	7.51	5.78	6.17
Heteroptera	9.14	6.23	8.91

Table 2. *Half-field whole-season mean counts of bees in conventional (C) and GMHT beet, maize and spring oilseed rape, and their respective treatment effects.*

(Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

crop and taxa	period	n	geometric mean		R (95% CI)	p-value
			C	GMHT		
beet						
total bees	year	20	3.62	1.55	0.55 (0.31–0.99)	0.05*
Apis mellifera	year	7	4.73	0.55	0.27 (0.20–0.36)	0.03*
bumble-bees	year	18	2.58	1.07	0.58 (0.31–1.07)	0.09
long-tongued bees	year	5	1.71	0.00	0.37 (0.31–0.44)	0.10
maize						
total bees	year	15	1.14	2.09	1.44 (0.58–3.57)	0.41
A. mellifera	year	3	0.71	4.24	3.07 (0.01–1136.41)	0.49
bumble-bees	year	14	1.02	2.12	1.55 (0.65–3.65)	0.32
spring oilseed rape						
total bees	year	62	44.28	36.52	0.83 (0.66–1.05)	0.13
A. mellifera	year	51	10.95	9.16	0.85 (0.57–1.28)	0.44
bumble-bees	year	62	27.38	21.58	0.80 (0.63–1.00)	0.06
long-tongued bees	year	38	2.68	2.02	0.82 (0.61–1.10)	0.16

* $p < 0.05$.

The multiplicative ratios of treatment effects, R, for seasonal counts of all bees, of honeybees and of bumble-bees were smaller in GMHT beet than in conventional beet: abundances in GMHT crops were 55%, 27% and 58%, respectively, of those in the conventional crops (table 2). The differences were significant for all bees and for honeybees (where the sample size, n, was only seven because many fields had too few bees for analysis). In maize and spring oilseed rape, there were no differences in seasonal bee counts (table 2), although R was consistently greater than one in maize and consistently less than one in spring oilseed rape. Results were consistent across occasions.

(b) *Butterflies*

The relative densities of total butterflies over the sampling period were greatest in spring oilseed rape crops and consistently low in the beet- and maize-cropped areas (table 1). *Pieris rapae* was the most abundant species recorded for all three crops, comprising 60%, 54% and 46% of all individuals found in spring oilseed rape, beet and maize crops, respectively. The other *Pieris* species, *P. brassicae* and *P. napi*, were the next most abundant species, comprising on average 23% and 6%, respectively, of individuals found for each crop. The most consistent treatment effects on butterfly numbers were found for

spring oilseed rape crops (table 3), for which R never exceeded unity. Counts in GMHT halves of the fields over the whole season were only 78% of those in conventional half-fields, and effects of very similar magnitude were found for both *Pieris* and non-*Pieris* species. The treatment effect on non-*Pieris* butterfly numbers was large in July, after the peak time of crop flowering. Butterfly numbers in beet crops were also lower in the GMHT treatment, with a similar magnitude of treatment effect over the whole year; the greatest difference was in August when the abundance in GMHT half-fields was 68% of that in conventional half-fields. In maize, numbers were 75% greater in GMHT half-fields in July, but not in the other months sampled or overall.

(c) *Bees, butterflies and flowering plants*

In beet fields, bees and butterflies were recorded visiting weeds from 19 plant genera in the conventional treatment and nine plant genera in the GMHT treatment. Overall, 55% of foraging records in the conventional treatment were to Asteraceae flowers (mainly to *Carduus* spp., *Cirsium* spp. and *Sonchus* spp.) and 22% of records were to *Brassica napus*, occurring as volunteers at two beet sites in particular. There were far fewer foraging records on the GMHT beet treatment, where 37% were to *B. napus* and

Table 3. Half-field whole-season and monthly mean counts of butterflies in conventional (C) and GMHT beet, maize and spring oilseed rape, and their respective treatment effects.
(Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

			geometric mean			
crop and taxa	period	n	C	GMHT	R (95% CI)	p-value
beet						
total butterflies	year	58	5.65	3.88	0.73 (0.59–0.91)	0.003**
	May	5	1.09	1.05	0.98 (0.24–4.02)	1.00
	June	11	1.55	2.09	1.21 (0.66–2.24)	0.48
	July	32	2.62	2.07	0.85 (0.60–1.19)	0.33
	August	51	3.93	2.33	0.68 (0.52–0.87)	0.004**
maize						
total butterflies	year	35	3.28	3.74	1.11 (0.81–1.51)	0.50
	June	6	1.57	0.78	0.69 (0.31–1.56)	0.37
	July	15	1.63	3.61	1.75 (1.39–2.22)	< 0.001***
	August	28	2.61	2.50	0.97 (0.64–1.48)	0.86
spring oilseed rape						
total butterflies	year	65	16.17	12.41	0.78 (0.67–0.91)	0.002**
	June	34	4.39	3.12	0.76 (0.56–1.04)	0.098
	July	49	4.63	3.50	0.80 (0.60–1.07)	0.11
	August	54	9.96	8.13	0.83 (0.67–1.03)	0.099
Pieris	year	65	13.82	11.15	0.82 (0.70–0.97)	0.023*
	June	34	4.04	2.97	0.79 (0.56–1.10)	0.17
	July	44	3.77	3.28	0.90 (0.65–1.23)	0.52
	August	52	10.02	8.04	0.82 (0.66–1.02)	0.069
non-*Pieris*	year	42	2.37	1.39	0.71 (0.52–0.96)	0.024*
	June	3	4.60	0.26	0.23 (0.03–1.89)	0.41
	July	25	2.46	1.19	0.63 (0.44–0.91)	0.013*
	August	15	1.93	1.55	0.87 (0.45–1.69)	0.67

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

the only member of the Asteraceae visited was *Cirsium vulgare* (16% of records). The covariate of annual counts of weeds visited by bees was ineffective in explaining the treatment effect for honeybees ($R_{adj} = 0.27$, $p_{adj} < 0.001$, $p_{cov} = 0.005$), but moderately important for bumblebees ($R_{adj} = 0.65$, $p_{adj} = 0.17$, $p_{cov} = 0.074$) and total bees ($R_{adj} = 0.61$, $p_{adj} = 0.11$, $p_{cov} = 0.096$) in beet.

Bees and butterflies were recorded visiting maize in both treatments but they were also recorded visiting four weed genera in the conventional treatment and eight weed genera in the GMHT treatment. In the conventional maize, 70% of records were to maize itself and 15% were to *Cirsium arvense*. There were almost twice as many foraging records in the GMHT maize, 32% of which were to maize itself, 32% were to *Lamium* spp. and 9% were to Asteraceae (*C. vulgare* and *Centaurea scabiosa*).

In spring oilseed rape fields, most foraging records for bees and butterflies were to *B. napus* itself (81% in the conventional treatment and 93% in the GMHT treatment). There were three times as many foraging records to weeds in the conventional treatment (to 11 genera) as in the GMHT treatment (to 10 genera). Again, in both half-fields, the majority of visits were to Asteraceae: 62% in the conventional treatment (comprising *Cirsium* spp., *Sonchus* spp., *Matricaria recutita* and *Tripleurospermum inodorum*) and 30% in the GMHT treatment (comprising *Cirsium* spp. and *Sonchus* spp.). The covariate of annual Asteraceae abundance explained much of the treatment effect for all butterflies ($R_{adj} = 0.85$, $p_{adj} = 0.10$, $p_{cov} = 0.001$) and all *Pieris* species ($R_{adj} = 0.88$, $p_{adj} = 0.24$, $p_{cov} = 0.005$), but had little explanatory power for the non-*Pieris* species ($R_{adj} = 0.75$, $p_{adj} = 0.13$, $p_{cov} = 0.25$).

(d) *Araneae*

The relative densities of total Araneae over the sampling period were similar in each of the crops (table 1). The abundance of total Araneae was lower in GMHT than in conventional spring oilseed rape in August (table 4), but did not differ between treatments in either beet or maize. The covariate of total weed biomass explained most of the treatment effect for Araneae in spring oilseed rape in August ($R_{adj} = 0.88$, $p_{adj} = 0.38$, $p_{cov} = 0.035$). Linyphiidae represented 44%, 49% and 50% of the spiders caught in beet, maize and spring oilseed rape, respectively. The estimated treatment effects for the Linyphiidae indicated that abundances were greater in GMHT than in conventional treatments in June, but greater in conventional than in GMHT treatments in August in both beet and spring oilseed rape, and abundance in GMHT treatments was only 75% of that in conventional treatments in spring oilseed rape in August. For Linyphiidae in spring oilseed rape in August, the covariate of total weed biomass explained a moderate part of the treatment effect ($R_{adj} = 0.77$, $p_{adj} = 0.12$, $p_{cov} = 0.044$), although, in a similar result to that of Brooks *et al* (2003), covariates representing collembolan-prey abundance were ineffective in explaining this result. There were no treatment effects for

Table 4. *Half-field whole-season and monthly mean counts of Araneae in conventional (C) and GMHT beet, maize and spring oilseed rape, and their respective treatment effects.*

(Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

			geometric mean			
crop and taxa	period	n	C	GMHT	R (95% CI)	p-value
beet						
total Araneae	year	64	8.68	8.73	1.01 (0.83–1.24)	0.96
Linyphiidae	year	59	3.98	3.93	0.97 (0.80–1.18)	0.77
	June	23	1.54	2.32	1.31 (0.82–2.09)	0.28
	August	57	3.52	2.90	0.86 (0.71–1.04)	0.13
L. tenuis	year	26	1.98	1.30	0.77 (0.55–1.09)	0.15
maize						
total Araneae	year	55	6.50	6.11	0.95 (0.75–1.20)	0.67
Linyphiidae	year	41	3.29	2.83	0.89 (0.64–1.25)	0.49
L. tenuis	year	10	1.77	1.82	1.02 (0.39–2.64)	0.98
spring oilseed rape						
total Araneae	year	64	8.50	6.93	0.84 (0.69–1.01)	0.06
	June	44	2.29	2.47	1.06 (0.80–1.39)	0.73
	August	59	7.09	5.53	0.81 (0.65–1.00)	0.05*
Linyphiidae	year	62	4.35	3.34	0.81 (0.64–1.03)	0.08
	June	30	1.97	2.23	1.09 (0.75–1.57)	0.66
	August	56	3.79	2.60	0.75 (0.58–0.97)	0.024*
L. tenuis	year	32	2.03	1.29	0.76 (0.56–1.03)	0.08

* $p < 0.05$.

the Linyphiidae in either beet or maize (table 4). The abundance of the important beneficial predator *Lepthyphantes tenuis* did not differ between treatments in any of the three crops.

(e) *Collembola*

Relative densities of total Collembola over the sampling period were greatest in spring oilseed rape, in which they were twice those in beet, where abundance was lowest (table 1). Over 98% of the Collembola recorded consisted of Entomobryidae, Isotomidae and Sminthuridae, with these families accounting for 40%, 35% and 24%, respectively, of the total Collembola in beet, 33%, 39% and 26%, respectively, in maize and 43%, 40% and 16%, respectively, in spring oilseed rape.

The treatment effect for total Collembola was consistent, with $R > 1$, but only moderate over each sampling occasion in beet and spring oilseed rape. In maize, the abundance in June in the GMHT crop was almost double that in the conventional treatment, although this effect had reduced to a 45% increase by August (table 5). For total Collembola ($R_{adj} = 1.53$, $p_{adj} = 0.019$, $p_{cov} < 0.001$) and Isotomidae ($R_{adj} = 1.57$, $p_{adj} = 0.043$, $p_{cov} < 0.001$), total weed biomass was an important explanatory covariate of the treatment effect in maize. There was a general trend for the abundances of families of Collembola to be greater in GMHT beet and, especially, in maize: 14 out of 18 entries for these crops in table 5 had $R > 1$. In beet, the year effect on Isotomidae was explained well by the covariate of total weed biomass ($R_{adj} = 1.38$, $p_{adj} = 0.19$, $p_{cov} = 0.003$). The estimated values of R varied by more than 0.3 for the Isotomidae and Sminthuridae between sampling occasions in maize (table 5).

(i) *Influence of distance on treatment effects for Collembola*

The abundance of Entomobryidae in maize crops decreased with increasing distance into the field in both treatments, but did so more rapidly in the conventional treatment ($F_{1,52} = 6.00$, $p = 0.018$). Analyses at each distance showed that abundance was significantly greater in the GMHT treatment at 32 m ($F_{1,54} = 17.30$, $p < 0.001$), but not at 2 m ($F_{1,54} = 0.80$, $p = 0.374$).

(f) *Heteroptera*

The relative densities of Heteroptera over the sampling period were similar in each of the three crops (table 1). Heteroptera samples were dominated by nymphs, which are extremely difficult to identify at the species level. The resulting small number of species and the low abundance of individuals prevented species-abundance and further diversity analyses (as done for Carabidae by Brooks *et al.* (2003)). Sample sizes for herbivorous Heteroptera were also very small, and the abundances of herbivorous and predatory Heteroptera did not differ between treatments, although there were notably fewer predatory Heteroptera in GMHT beet than in conventional beet (table 6). The lower abundance of total Heteroptera across the year in GMHT beet was well explained by the covariate of total weed biomass ($R_{adj} = 0.71$, $p_{adj} = 0.20$, $p_{cov} = 0.015$). The covariate of total aphid numbers across the year explained most of the treatment effect for the predatory Heteroptera ($R_{adj} = 0.83$, $p_{adj} = 0.41$, $p_{cov} = 0.059$).

(g) *Carabidae*

The relative densities of Carabidae over the sampling period were broadly similar in each of the three crops (table 1). Total counts of Carabidae were low and

Table 5. Half-field whole-season and monthly mean counts of Collembola in conventional (C) and GMHT beet, maize and spring oilseed rape, and their respective treatment effects.
(Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

| crop and taxa | period | n | geometric mean | | R (95% CI) | p-value |
			C	GMHT		
beet						
total Collembola	year	64	59.00	66.75	1.13 (0.91–1.40)	0.29
	June	54	17.23	18.30	1.06 (0.78–1.45)	0.72
	August	62	38.28	47.56	1.24 (0.97–1.58)	0.08
Entomobryidae	year	64	19.29	21.00	1.08 (0.82–1.43)	0.56
	June	47	5.15	4.76	0.94 (0.65–1.35)	0.73
	August	61	14.59	17.97	1.22 (0.90–1.65)	0.21
Isotomidae	year	58	9.61	15.54	1.56 (1.17–2.08)	0.004**
Sminthuridae	year	55	15.75	13.75	0.88 (0.67–1.16)	0.36
	June	45	8.44	7.70	0.92 (0.61–1.39)	0.68
	August	48	7.23	6.52	0.91 (0.69–1.21)	0.53
maize						
total Collembola	year	57	75.81	119.01	1.56 (1.17–2.09)	0.002**
	June	52	23.33	46.99	1.97 (1.39–2.81)	0.001***
	August	53	42.09	61.47	1.45 (1.02–2.06)	0.05*
Entomobryidae	year	55	23.24	34.44	1.46 (1.09–1.96)	0.014*
	June	49	6.09	8.79	1.38 (0.95–2.01)	0.10
	August	51	15.76	23.09	1.44 (0.98–2.11)	0.05*
Isotomidae	year	54	18.55	33.80	1.78 (1.21–2.62)	0.005**
	June	43	5.84	14.50	2.27 (1.43–3.60)	0.002**
	August	49	12.23	19.96	1.58 (1.01–2.48)	0.043*
Sminthuridae	year	53	12.29	19.42	1.54 (1.04–2.27)	0.03*
	June	47	8.61	15.45	1.71 (1.13–2.59)	0.007**
	August	41	6.31	6.56	1.03 (0.69–1.55)	0.86
spring oilseed rape						
total Collembola	year	64	118.30	125.36	1.06 (0.84–1.34)	0.60
	June	55	31.91	31.90	1.00 (0.71–1.41)	0.99
	August	60	79.98	94.79	1.18 (0.97–1.44)	0.11
Entomobryidae	year	61	37.64	36.10	0.96 (0.77–1.20)	0.75
	June	44	6.73	6.63	0.99 (0.69–1.41)	0.94
	August	56	37.11	37.77	1.02 (0.80–1.30)	0.90
Isotomidae	year	60	36.29	38.00	1.05 (0.79–1.39)	0.77
	June	45	15.44	15.05	0.98 (0.67–1.43)	0.89
	August	55	24.74	27.01	1.09 (0.80–1.49)	0.60
Sminthuridae	year	57	16.31	18.82	1.15 (0.78–1.68)	0.46
	June	48	13.08	12.92	0.99 (0.63–1.56)	0.97
	August	46	5.82	7.67	1.27 (0.85–1.91)	0.28

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

variable. In beet and maize, the estimates of R differed between occasions by more than 0.3 (table 7). In maize, in August, counts were greater in the GMHT crop than in the conventional crop (table 7) but this effect was not explained by the covariate of total weed biomass ($R_{adj} = 1.47$, $p_{adj} = 0.044$, $p_{cov} = 0.86$). *Bembidion lampros*, *B. obtusum* and *Trechus quadristriatus* were the most dominant species in the three crops, representing 22%, 16% and 14%, respectively, of the total Carabidae in beet, 21%, 17% and 9%, respectively, in maize and 23%, 13% and 14%, respectively, in spring oilseed rape. The counts of all of these species and the total count of *Bembidion* spp. did not differ between the conventional and GMHT treatments in any of the three crops (table 7).

(h) *Whole-field covariates*

There were no interactions of treatment with the covariates describing year, beet-crop type, environmental zone

or initial abundance of weed seed in the soil for any of the results described in § 3.

(i) *Comparing pitfall trapping with Vortis sampling*

The analyses showed that the values of d achieved were similar for pitfall trapping and Vortis sampling for the Carabidae and the Collembola ($F_{1,52} = 0.83$, $p = 0.37$; and $F_{1,70} = 0.87$, $p = 0.35$, respectively) (figure 2a). For the Araneae, the values of d were different ($F_{1,62} = 17.4$, $p < 0.001$), with the pitfall traps yielding larger estimates. The variability of the sampling methods used in the FSEs differed significantly, with Vortis sampling being systematically more variable than pitfall trapping for each taxon ($p < 0.001$) (figure 2b). Similar results were obtained when the analyses were repeated with variability expressed as standard deviations rather than confidence intervals.

Table 6. *Half-field whole-season mean counts of Heteroptera in conventional (C) and GMHT beet, maize and spring oilseed rape, and their respective treatment effects.*
(Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

| crop and taxa | period | n | geometric mean | | R (95% CI) | p-value |
			C	GMHT		
beet						
total Heteroptera	year	48	5.18	2.80	0.62 (0.44–0.87)	0.011*
herbivores	year	11	2.01	1.21	0.73 (0.38–1.41)	0.29
predators	year	26	2.56	1.35	0.66 (0.42–1.04)	0.07
maize						
total Heteroptera	year	42	3.53	3.14	0.92 (0.61–1.38)	0.68
herbivores	year	7	1.25	1.07	0.92 (0.41–2.07)	0.93
predators	year	35	1.95	1.98	1.01 (0.70–1.47)	0.95
spring oilseed rape						
total Heteroptera	year	41	5.05	3.82	0.80 (0.58–1.09)	0.15
herbivores	year	9	1.51	1.01	0.80 (0.39–1.66)	0.63
predators	year	31	3.51	2.22	0.71 (0.49–1.04)	0.10

* $p < 0.05$.

Table 7. *Half-field whole-season and monthly mean counts of Carabidae in conventional (C) and GMHT beet, maize and spring oilseed rape, and their respective treatment effects.*
(Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

| crop and taxa | period | n | geometric mean | | R (95% CI) | p-value |
			C	GMHT		
beet						
total Carabidae	year	57	4.26	3.84	0.92 (0.73–1.16)	0.47
	June	25	1.49	2.72	1.49 (1.00–2.23)	0.07
	August	52	3.85	2.97	0.82 (0.64–1.04)	0.09
Bembidion lampros	year	34	1.54	1.52	0.99 (0.70–1.40)	0.96
Bembidion obtusum	year	20	2.30	1.58	0.78 (0.51–1.20)	0.33
Trechus quadristriatus	year	22	1.53	1.53	1.00 (0.65–1.55)	0.99
maize						
total Carabidae	year	43	3.28	4.13	1.20 (0.95–1.52)	0.11
	June	19	1.63	1.41	0.92 (0.55–1.52)	0.73
	August	38	2.56	3.98	1.40 (1.07–1.84)	0.019*
B. lampros	year	21	1.37	1.82	1.19 (0.73–1.95)	0.46
B. obtusum	year	11	1.92	2.83	1.31 (0.68–2.53)	0.37
T. quadristriatus	year	11	1.27	1.29	1.01 (0.50–2.06)	0.99
spring oilseed rape						
total Carabidae	year	54	3.50	3.55	1.01 (0.81–1.26)	0.65
B. lampros	year	23	1.59	2.48	1.35 (0.94–1.94)	0.11
B. obtusum	year	17	1.81	1.15	0.77 (0.42–1.41)	0.40
T. quadristriatus	year	21	1.19	1.46	1.13 (0.70–1.81)	0.64

* $p < 0.05$.

4. DISCUSSION

The management of GMHT beet, maize and spring oilseed rape had varying effects on the arthropod taxa reported in this paper. Most taxa were insensitive to the management regime. However, at least one group within each taxon was affected, showing either increased abundance ($R > 1$) or decreased abundance ($R < 1$) in GMHT crops.

Covariate analyses suggested that most differences in abundance were probably indirect effects of variation in

the weed flora mediated by the herbicide management regimes used in the GMHT and conventional crops (see also Hawes *et al.* 2003 and Heard *et al.* 2003*a*). Out of the 106 analyses presented here, 99 had sample sizes of at least eight (tables 2–7), and, out of these, five had estimates of the multiplicative ratio, the mean abundance in GMHT crops relative to that in conventional crops, of less than 0.67 and 10 had estimates of greater than 1.5.

The majority of instances of greater abundance ($R > 1$) in the GMHT crops were in the Collembola. The smaller GMHT abundances ($R < 1$) occurred primarily in the
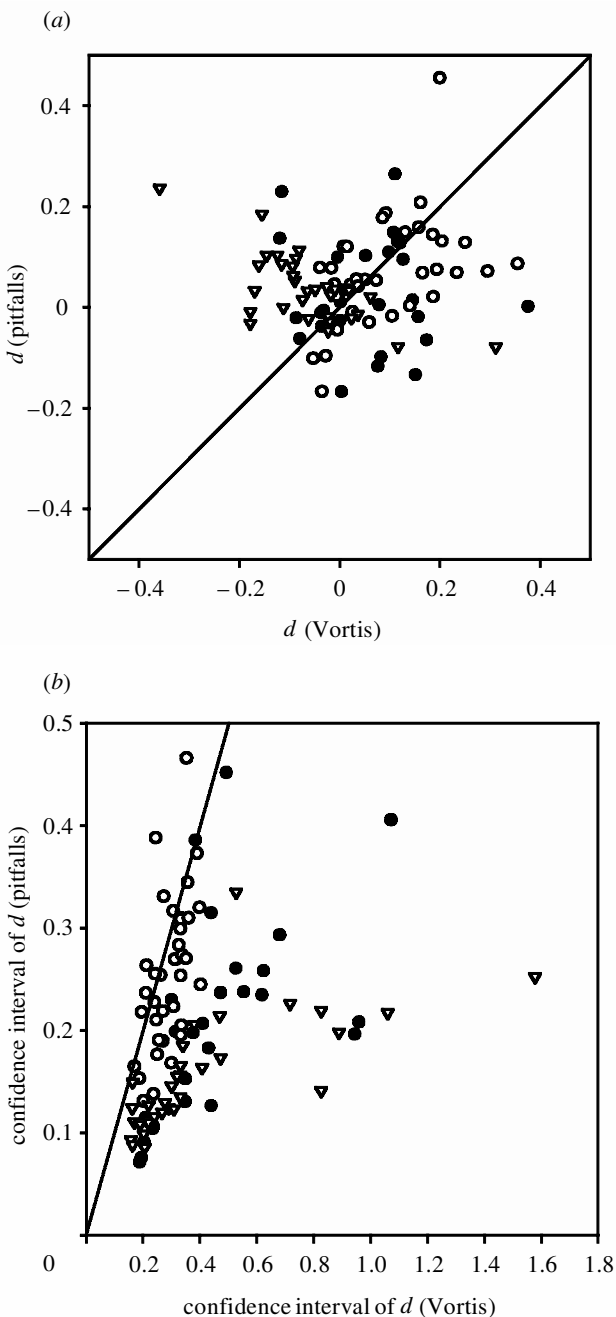
(a)

(b)

Figure 2. Comparison of the magnitudes and variabilities of treatment effects measured by pitfall trapping and Vortis sampling. Points represent species common to this paper (*x*-axes, Vortis sampling) and Brooks *et al.* (2003) (*y*-axes, pitfall trapping): triangles, Araneae; open circles, Collembola; filled circles, Carabidae. (*a*) Mean differences of estimated treatment effects, *d*, between the GMHT and conventional treatments on a logarithmic scale, for 32 Araneae, 36 Collembola and 27 Carabidae analyses. Equality line is shown for reference. (*b*) Variability for each analysis, expressed as the width of the confidence interval for the estimated *d*. Equality line is shown for reference.

bees and the Heteroptera and, to a lesser extent, in the butterflies. Few large treatment effects, where $R < 0.67$ or $R > 1.5$, were found for butterflies, and no such effects were found for the Carabidae or the Araneae. Effects of treatment were not consistent between the three crops. The frequencies of treatment effects where $R < 0.67$ and

$R > 1.5$ in each of the crops were zero and nine, respectively, for maize, four and two, respectively, for beet and one and zero, respectively, for spring oilseed rape.

These findings are consistent with those of the paper analysing the vegetation, where most of the treatment effects with $R > 1.5$ occurred in maize, while $R < 0.67$ was more common in beet and spring oilseed rape (Heard *et al.* 2003*a*). The results emphasize that the adoption of GMHT management may have markedly different effects on different arthropod taxa and in different crops.

(a) *Taxa showing treatment effects*
(i) *Responders showing reduced abundance in GMHT treatments (R < 1)*

The taxa that tended to be less abundant in GMHT beet and spring oilseed rape crops than in their conventional equivalents were dominated by the more mobile actively foraging groups: butterflies (including both *Pieris* and non-*Pieris* butterflies) and bees (including honeybees and bumble-bees). These effects could be the result of differences in the availabilities of weed flowering plants, crop phenology or, in the case of spring oilseed rape, the attractiveness of the crop itself. Beet crops did not provide nectar or pollen since they were not permitted to flower (Champion *et al.* 2003), and covariate analysis confirmed that the treatment effect was most probably related to differences in weed vegetation. Growing GMHT beet allowed more efficient weed control, which resulted in fewer mature and flowering weed plants in the GMHT treatments (Heard *et al.* 2003*b*), a consequent reduction in the available nectar and pollen resources, and less total foraging by bees.

Covariate analysis confirmed that foraging on Asteraceae in the conventional spring oilseed rape crops was particularly important, but the effects on butterflies (and bees) may have been buffered somewhat by the fact that both conventional and GMHT spring oilseed rape provide copious nectar and pollen during flowering and are larval food plants of *P. rapae* and *P. brassicae*. Whether the conventional and GMHT crops differ in attractiveness cannot be assessed from this dataset, but previous work suggests that this is unlikely (Picard-Nizou *et al.* 1995; Osborne *et al.* 2001) and no differences in flowering time were found between GMHT and conventional spring oilseed rape (Hawes *et al.* 2003). No differences were found between bee densities in maize crops, nor were there any effects on the number of mature plants per half-field (Heard *et al.* 2003*b*).

Transect counts are not indicators of butterfly or bee population densities *per se*, but rather of the foraging choices that they are making. Given that the herbicide management of GMHT beet and spring oilseed rape considerably reduced the forage available for these groups within the fields, these results may have implications for population abundances in the longer term. This experiment has shown that herbicide management of both GMHT and conventional varieties can lead, through a reduction in plant resources, to a lower occurrence of butterflies. If plenty of forage is available elsewhere in the landscape, then populations will be buffered, but if forage reductions occur over large areas, at the landscape scale for example, this may affect the reproductive success in the area and, consequently, populations in the following

year. The functional relationship between bees and butterflies (pollinators) and weed plants is considered further by Hawes *et al.* (2003).

Our results show that the forage provided by weed plants within fields may be important and should not be ignored. For example, the relative densities of butterflies foraging on plants within conventional beet, maize and spring oilseed rape crops were 50%, 21% and 38%, respectively, of those of the corresponding field boundaries (Roy *et al.* 2003). The scale of these differences is similar for bees (Roy *et al.* 2003). These results suggest that, although the resource in the field may be widely spread, because the cultivated area is so much greater than that of the uncultivated boundaries, the few weed plants that exist in the fields may be very important for nectar-foraging insects on a landscape scale. Consequently, the effectiveness of the management of weeds within the crop is likely to be important for populations of butterflies and bees that exploit them.

The low abundance of Heteroptera comprised a heterogeneous mix of species and feeding guilds. Although species-abundance and diversity analyses were not possible, the total numbers of Heteroptera and predatory Heteroptera were 70% lower in GMHT beet than in conventional beet. Although most species of Heteroptera rely on plants for part of their diet (Southwood & Leston 1959), very few species are regarded as crop pests (Moreby *et al.* 1997) and covariate analyses indicated that the considerably smaller weed biomass and weed-seed abundance in GMHT beet compared with the conventional treatment (see also Heard *et al.* 2003*a*) may have contributed to this effect. For *Leptopterna dolabrata* (Miridae: Stenodemini), the presence of grass seeds, with their high nitrogen content, is important for the maturation of nymphs to successful breeding adults (McNeill 1971). Invertebrate predators *per se* and aphids, which are an important food source for predatory Heteroptera (Ruth & Dwumfour 1989; Hesler *et al.* 2000), did not differ in abundance between the treatments in beet (Hawes *et al.* 2003), although the aphid covariate analysed in this paper did suggest that the treatment effect was related to prey abundance. Therefore, the interpretation of the results for predatory Heteroptera requires care.

The relative densities of Heteroptera within conventional beet, maize and spring oilseed rape were 31%, 18% and 39%, respectively, of those of the corresponding field boundaries (Roy *et al.* 2003), and as such represent significant reservoir populations of these non-target insects. Beet, the only crop in which the Heteroptera were affected by treatment, provides an important resource for farmland Heteroptera and their predators, notably farmland game birds (Wilson *et al.* 1999).

Abundances of total Araneae and Linyphiidae were lower in GMHT spring oilseed rape than in the conventional equivalent in August. These differences were related to the weed biomass in this crop (see also Heard *et al.* 2003*a*). Herbicide use in crops, and the resulting reduction in the weed flora, have been shown to reduce spider abundance (Raatikainen & Huhta 1968; Feber *et al.* 1998; Moreby & Southway 1999). Weed control is associated with a decrease in vegetation height (Baines *et al.* 1998), and vegetation height has been shown to be a good indicator of structural diversity (Brown 1991). As vegetation structural diversity becomes more complex, opportunities for web-site selection and prey capture increase (Wise 1993; Samu *et al.* 1996). Indeed, vegetation structure has been shown to determine Araneae community structure (Bell *et al.* 2001), and decreasing vegetation height has been shown to decrease the abundance of a linyphiid spider (Haughton *et al.* 2001*a*). Crop height increased through the growing season (Hawes *et al.* 2003), but was less in GMHT spring oilseed rape than in its conventional equivalent in August, thus structural diversity was lower in GMHT spring oilseed rape. The Linyphiidae, which accounted for around half of the spiders recorded, are known to use vegetation for web-spinning (Greenstone 1984), and for some species it has been shown that migration from an area is greater when food resources are limited (Weyman *et al.* 1994). Thus, lower structural diversity and a reduction in potential web-building sites, coupled with a paucity of prey, may have influenced the differences in the abundances of all spiders and of the Linyphiidae. Numbers of Collembola captured by both pitfall trapping (Brooks *et al.* 2003) and Vortis sampling (this paper) increased in GMHT spring oilseed rape. Collembola are the preferred prey of many Linyphiidae (Alderweireldt 1994), but linking prey availability with spider abundance is difficult. For example, Weyman & Jepson (1994) artificially increased prey availability for a linyphiid spider, but noted that ballooning activity in relation to the enhanced food source varied with each day of the experiment. Indeed, the lack of effect of covariates representing the abundance of collembolan prey found here reflects the results of Brooks *et al.* (2003), who found a weak relationship for such covariates that was significant in only one crop on one occasion.

Relative densities of Araneae in the conventional beet, maize and spring oilseed rape crops were 26%, 14% and 31%, respectively, of those in the corresponding field boundaries (Roy *et al.* 2003). Spring oilseed rape crops were, therefore, the most valuable to Araneae of the three crops studied, and we found that the density of total spiders in the crop compared with that in the conventional field boundaries was lowered from 31% under conventional management to 21% under GMHT management.

(ii) *Responders showing increased abundance in GMHT treatments (R > 1)*

Taxa that showed increased abundances in GMHT crops (i.e. for which $R > 1$) generally had low dispersive abilities. The only arthropod order to be consistently more abundant under GMHT crop management was the Collembola in beet and maize. The families Entomobryidae, Isotomidae and Sminthuridae sampled by Vortis were each shown to be more abundant in GMHT crops. By contrast, although similar effects were observed in the Entomobryidae and Isotomidae captured by pitfall trapping, no treatment effect for the Sminthuridae was detected (Brooks *et al.* 2003), presumably because pitfall trapping of plant epigeal arthropods is not as efficient as Vortis sampling. The frequency of effects was not consistent across crops: most treatment effects were seen in maize and most probably resulted from the higher weed density and biomass in the GMHT treatment throughout the sampling season (see also Heard *et al.* 2003*a*), which could be used by both detritivorous Isotomidae (Hopkin 1997)

and herbivorous Sminthuridae. This effect could depend on the timings and efficiencies of herbicide management in the different crops. It might appear curious that there were more Isotomidae in GMHT beet in August, when weed density and biomass were lower than in the conventional crop (Heard *et al.* 2003*a*); however, earlier in the season, weed-seedling density was greater in the GMHT beet, presumably because the delayed herbicide application allowed an extended period of weed growth in the GMHT crop (Champion *et al.* 2003). It is likely that, by August, these weeds with a greater biomass were senescing or decayed, owing to the delayed herbicide treatment, and were therefore being used by the detritivorous Isotomidae.

Relative densities of Collembola in the conventional beet, maize and spring oilseed rape crops were 27%, 25% and 57%, respectively, of the densities in the corresponding field boundaries (Roy *et al.* 2003). Under GMHT crop management, we found that the abundance of Collembola was greater in each of the three GMHT crops than in the corresponding conventional crop. These findings are remarkably similar to those of Brooks *et al.* (2003), suggesting that these effects represent a robust finding for the Collembola. Consequently, the abundances of Collembola might increase under GMHT crop management.

The abundances of the Carabidae were shown to be greater in GMHT maize in August, a time when weed density was greater than in conventional maize (Heard *et al.* 2003*a*), although the total weed biomass in maize did not explain Carabidae abundance. The Carabidae is a generalist group with a diversity of habitat preferences, life histories and feeding strategies (Thiele 1977). Increased and more diverse vegetation have been suggested to be important for their abundance. Shah *et al.* (2003) recorded greater abundances of Carabidae in organic cereals, where there has been shown to be increased weed flora (Moreby *et al.* 1994), than in conventional cereals. Nevertheless, the absolute values of the estimated multiplicative ratio, R, were always less than 1.5, and, consequently, the effect of managing GMHT crops on this family was relatively slight. In terms of the strength of the treatment effect, the results for total Carabidae sampled by Vortis paralleled those for total pitfall-trapped Carabidae (Brooks *et al.* 2003), although many more individuals and species were caught by pitfall traps. The composition of the Carabidae fauna sampled by Vortis (this paper) was different from that sampled by pitfall traps. Vortis samples were dominated by the diurnal *Bembidion* species (Baker & Dunning 1975), whereas pitfall-trapped samples were dominated by nocturnal *Pterostichus* species (Brooks *et al.* 2003).

Relative densities of Carabidae in the conventional beet, maize and spring oilseed rape crops were 50%, 58% and 63%, respectively, of the densities in the corresponding field boundaries (Roy *et al.* 2003), and, out of the taxa studied here, Carabidae had the highest within-field densities relative to the non-cropped field boundaries. Given the large area of the crops compared with that of the field boundary, these crops are clearly important for the smaller Carabidae, and we found in this study that the abundance of Carabidae was greater under GMHT maize crop management than under conventional crop management. However, it is important to note that pitfall-trapped total Carabidae showed a treatment difference only in beet,

with lower numbers being found in the GMHT crop (Brooks *et al.* 2003).

(b) *Taxa showing no treatment effects*

In contrast to those taxa and functional groups that showed strong responses to the management of GMHT beet, maize and spring oilseed rape, the majority of the taxa studied were less sensitive to the changes in management. Out of the 99 analyses presented here that had a sample size of more than eight, 73 comparisons showed no significant treatment effect and $0.67 < R < 1.5$. Those groups that were found to be largely insensitive to the difference in herbicide management between GMHT and conventional crops tended to be generalist predators, such as the Carabidae (Thiele 1977) and spiders (Sunderland *et al.* 1986), which are not wholly dependent on the weed flora.

(c) *Comparing pitfall trapping with Vortis sampling*

Using pitfall trapping, Brooks *et al.* (2003) found broadly similar results to those presented here for the Collembola, but strikingly different results for the Carabidae and Araneae. While few carabids showed large effects when sampled by Vortis, strong and consistent effects were found using pitfall trapping (Brooks *et al.* 2003). Similarly, few large effects were found for the Araneae, and these in spring oilseed rape alone, when sampled using Vortis. With pitfall trapping, a larger number of significant results was observed for the Araneae, with more being found in maize and beet, where no significant effects were detected using Vortis.

For the Carabidae and Collembola, the values of the treatment effect, d, were similar for the two sampling methods, but for the Araneae the values of d were different, with pitfall trapping yielding larger estimates. This result probably reflects the systematic differences in detection ability between pitfall trapping and Vortis observed in beet and maize, and may be a result of the vegetation structure in these crops. The variabilities of the sampling methods used at the intensities employed in the FSEs differed significantly, with Vortis being clearly and systematically more variable. Despite the marked difference between pitfall count and Vortis abundance (the pitfall count was often an order of magnitude greater), the lower variability of the pitfall counts was unlikely to be caused by this difference in magnitude because of the logarithmic transformation used in the analyses. As noted in Brooks *et al.* (2003), the two methods measure different aspects of abundance. Pitfall traps measure 'activity density', whereas Vortis provides an absolute measure per unit area. This means that the relative efficiency of Vortis sampling and pitfall trapping may differ for different assemblages of species sampled from different vegetation-structure microhabitats.

The comparisons of d presented above should be treated with care, and not over-interpreted, given that the data were not randomly selected and related to species deliberately chosen for their potentially large treatment effects. The non-random selection of data should not, though, affect the estimated variabilities of the Vortis and pitfall methods, as evaluated by the confidence intervals of d.

(*d*) *Detection of treatment differences*

All treatment differences greater than a factor of 1.5 ($R < 0.67$ or $R > 1.5$) for $n > 30$ were significant. Low values of n were a reflection of the inherently low populations of some taxa, especially the bees, and the patchy distributions of other groups, e.g. some species of Carabidae, within crops. Despite occasional small sample sizes, the densities of arthropods sampled by Vortis were comparable with those found in other experiments, for example, SCARAB (Frampton 2001).

The apparent lack of strong interactions between the treatments and associated whole-field covariates was an important finding. The lack of a difference in response between fodder and sugar beet suggests that the management of these crops is sufficiently similar for them to be treated as one crop for analysis. Treatment × year and treatment × environmental zone interactions were also absent. The consistency of the treatment effects over a range of sites with differing degrees of weed vegetation implies that the indirect effects studied here remain proportionate across zones and years. In only one out of the 23 significant treatment results were treatment × distance interactions apparent, little more than expected by chance. Indeed, the treatment × distance interactions showed little consistency through the season, and would require experimental-manipulation studies to determine whether they are real effects or artefacts of the number of analyses examined. The significance of these analyses for the aerial and epigeal arthropods is that they indicate that the results may be scaled up to a wider population of sites across the UK.

(*e*) *Long-term effects of GMHT cropping*

Our results suggest that, for the majority of the aerial and epigeal arthropods studied here, there would be little or no small-scale short-term effect of a change to GMHT management in beet, maize or spring oilseed rape crops. The analyses show that generalists, less-sedentary taxa and groups with diverse feeding strategies that do not rely solely on pollen and/or nectar as a food source, such as Carabidae and Araneae, were not affected by the treatment in some crops. However, several effects were observed: the actively foraging taxa, such as bees and butterflies, showed lower abundances under GMHT beet and spring oilseed rape management, while those that could use the greater abundance of dead plant matter in GMHT crops, such as the detritivorous isotomid Collembola, benefited from the management of these crops (see also Brooks *et al.* 2003). This is consistent with Hawes *et al.* (2003), who found a positive relationship between the biomass of weed vegetation and the abundance of detritivores *per se* in GMHT crops. It should be noted, though, that the return of seed to the seedbank by weed plants in GMHT crops could have a marked effect on the long-term dynamics of weeds, and presumably associated arthropods, under large-scale GMHT cropping (Squire *et al.* 2003). Weed-seed return is lower in GMHT crops (Heard *et al.* 2003*a*) and this might lead to lower weed abundances in subsequent years.

Despite the study of arthropods in the FSEs being a within-year experiment, conducted at individual sites, the relationship between the recorded geometric-mean abundances and the multiplicative treatment ratio, R, suggests that long-term effects of GMHT management may be predictable from the recorded data, provided that certain assumptions are made within a mathematical-modelling framework. To test these expectations or to develop future approaches to test the environmental impact of other genetically modified traits, it will be necessary to adopt species that are sensitive to management in both possible directions and readily measured using simple protocols. Collembola and butterflies, for example, were clearly sensitive and provided adequate power for the detection of effects, and might be appropriate for future studies.

(*f*) *Conclusions*

The FSEs have shown that GMHT management has no strong effect on the majority of the higher taxa of aerial and epigeal arthropods, but significant effects were found on the abundances of at least one group within each taxon studied. Indeed, for some important taxa, such as the pollinator bees and butterflies and the detritivore Collembola, clear effects of GMHT management were observed, with either increasing or decreasing captures according to the crop and to the phenology and ecology of the species concerned. The effects were indirect and related to herbicide management. The smaller counts of bees and butterflies in GMHT beet and spring oilseed rape were associated with differences in the abundances of flowering weeds between the two treatments. The consistently larger abundances of detritivore Collembola recorded in all GMHT crops were related to differences in weed biomasses between the two treatments. These results apply generally to agriculture across Britain, and could be used in mathematical models to predict the possible long-term effects of adopting GMHT crops. However, the results for bees and butterflies relate to foraging preferences and might or might not translate into effects on population densities, depending on whether adoption would lead to forage reductions over large areas. These species, and the detritivore Collembola may be useful indicator species for future studies of GMHT management.

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GLOSSARY

ANOVA: analysis of variance
BMS: Butterfly Monitoring Scheme
FSE: Farm Scale Evaluation
GMHT: genetically modified herbicide tolerant