

Weed seed resources for birds in fields with contrasting conventional and genetically modified herbicide-tolerant crops

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The UK Farm Scale Evaluations (FSEs) have shown that the use of broad spectrum herbicides on genetically modified herbicide-tolerant (GMHT) crops can have dramatic effects on weed seed production compared to management of conventional varieties. Here, we use FSE data and information on bird diets to determine how GMHT cropping might change the food resources available to farmland birds. More than 60 fields of each of four crops, spring- and winter-sown oilseed rape, beet and maize, were split, one half being sown with a conventional variety, the other with a GMHT variety. Seed rain from weeds known to be important in the diets of 17 granivorous farmland bird species was measured under the two treatments. In beet and spring oilseed rape, rain of weed seeds important in the diets of 16 bird species was significantly reduced in GMHT compared to conventional halves; for no species did it increase. In winter oilseed rape, rain of weed seeds important in the diets of 10 species was significantly reduced in GMHT halves; for only one species did it increase significantly. By contrast, in maize, rain of weed seeds important in the diets of seven species was significantly greater in GMHT halves; for no species was it reduced. Treatment effects for the total weed seed energy available to each bird species were very similar to those for seed rain alone. Measuring the effects on individual bird species was outside the scope of this study. Despite this, these results suggest that should beet, spring and winter rape crops in the UK be largely replaced by GMHT varieties and managed as in the FSEs, this would markedly reduce important food resources for farmland birds, many of which declined during the last quarter of the twentieth century. By contrast, GMHT maize would be beneficial to farmland birds.

Keywords: genetically modified herbicide-tolerant crops; weed seeds; farmland birds; bird food

1. INTRODUCTION

Farmland biodiversity in the UK declined substantially during the last few decades of the twentieth century, largely because of agricultural intensification (Krebs *et al.* 1999; Donald *et al.* 2001; Robinson & Sutherland 2002). These declines occurred particularly among the arable weed flora (Donald 1998; Preston *et al.* 2002; Robinson & Sutherland 2002) and farmland birds (Gibbons *et al.* 1993; Fuller *et al.* 1995; Siriwardena *et al.* 1998a; Gregory *et al.* 2004).

The declines of seed-eating farmland birds have, in part, been driven by changes in adult survival (Siriwardena *et al.* 1998b, 2000; Newton 2004). As these species rely heavily on weed seeds for food, particularly outside the breeding season (Moorcroft *et al.* 2002; Robinson & Sutherland 2002), the estimated approximate 2% yr⁻¹ decline in the arable weed seedbank since the 1940s (Robinson & Sutherland 2002) has been inimical to them.

In addition, herbicide applications may have contributed to declines of several farmland bird species through reducing the abundance of invertebrate host plants, and thus chick food invertebrates and chick survival (Boatman *et al.* 2004; Morris *et al.* 2005).

Because of their efficient weed control (Dewar *et al.* 2000; Squire *et al.* 2003), it has been suggested that the broad-spectrum herbicides used in conjunction with genetically modified herbicide-tolerant (GMHT) crops might further exacerbate the long-term declines in the weed flora, and those species dependent upon them (Hails 2000; Watkinson *et al.* 2000). Alternatively, some authors suggest that GMHT cropping may benefit biodiversity because the flexibility in timing of applications of broad-spectrum herbicides could allow development of novel techniques designed to allow weeds and their associated wildlife to remain in fields for longer or to enhance seedbanks (Dewar *et al.* 2003; May *et al.* 2005).

The Farm Scale Evaluations (FSEs) of GMHT crops in the UK have shown that total weed seed rain in

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spring-sown beet, *Beta vulgaris* and oilseed rape, *Brassica napus* (Heard *et al.* 2003a), and dicot weed seed rain in winter-sown oilseed rape (Bohan *et al.* 2005) were substantially reduced in GMHT compared to conventionally managed varieties. These effects persisted in the seedbank the following year (Heard *et al.* 2003a; Bohan *et al.* 2005), leading, for the two spring-sown crops at least, to a predicted decline of an additional 7% yr⁻¹ in the weed seedbank in a typical cereal rotation with these two GMHT break crops (Heard *et al.* 2003b, 2005). By contrast, total seed rain in GMHT maize, *Zea mays*, and monocot seed rain in winter-sown oilseed rape were greater in GMHT compared to conventional, although these effects did not persist into the seedbank (Heard *et al.* 2003a; Bohan *et al.* 2005). All of these treatment effects were because of the herbicides used to manage the crops, rather than a direct result of the novel traits introduced into the GMHT cultivars.

These changes in abundance of weed seeds could affect farmland birds by changing the food resources available to them. Here, we use FSE and other data to estimate the likely changes in these resources should GMHT cropping come to replace conventional crop management.

2. MATERIAL AND METHODS

(a) *Farm Scale Evaluation experimental design and weed seed rain*

Details of the FSEs have been published elsewhere (Firbank *et al.* 2003; Perry *et al.* 2003) but are outlined briefly here. Fields of maize ($n=68$), spring-sown (67) and winter-sown (65) oilseed rape, and beet (66) were studied. Each field was split in half. One half selected at random was sown with a conventional variety and managed according to current normal practice, the other with a GMHT variety with weeds controlled by a broad-spectrum herbicide, applied according to the simulated product label and advice from the industry representative body, the Supply Chain Initiative on Modified Agricultural Crops (SCIMAC). Seed rain measured during mid-May to late September was compared under the two treatments (Heard *et al.* 2003a). Measurements were taken at fixed locations within the crop and weed seeds were identified and counted at the species level. Although field margins were studied within the FSEs, for brevity they are not included here, though we note that treatment effects in the tilled but uncropped margins were similar to those observed within the crop (Roy *et al.* 2003).

(b) *Weed seed composition*

Since seeds from different weed species vary greatly in size and composition (Earle & Jones 1962; Glück 1985; Diaz 1990), the abundance of weed seeds alone may be a poor measure of the true resource available to foraging birds. Because of this, we obtained weights and compositions of seeds of 305 weed species important in bird diets and present in the FSE samples. The principal sources for this information were the US Department of Agriculture's 'New Crops Oilseed Database' (www.ncaur.usda.gov/nc/ncdb/search.html-ssi) and the Royal Botanic Garden at Kew's Seed Information Database (www.kew.org/data/sid/sidsearch.html). A small amount of additional information was obtained from published sources (e.g. Earle & Jones 1962; Diaz 1990).

For each species, seed weight and percentage content of protein, lipid and carbohydrate were obtained where available. For some species, data for several seed samples were documented; in such cases mean values have been used in all subsequent analyses. Species-specific weight and compositional data were available for seeds of 202 of the 305 species. Where seed weights were unavailable (two species), we calculated a surrogate weight as the mean of the weights of other species in its genus. Similarly, where compositional data were unavailable, we calculated surrogate percentages as the means of the other species in their genus (64 species) or, failing that, family (37 species).

(c) *Farmland bird diets*

The diets of 19 species of gamebirds, pigeons, larks, sparrows, finches and buntings were collated and updated from two earlier reviews (Wilson *et al.* 1996, 1999). These species were all those classified as 'primarily herbivorous' by Wilson *et al.* (1996) in their review of 42 species characteristic of lowland farmland in Britain, excluding quail, *Coturnix coturnix*, a rare long-distance migrant whose diet is particularly poorly known. Only plant taxa considered by these reviews to be important in the diet of each bird species are included in the following analyses. In the great majority of cases, the principal bird food resource provided by these plants is their seeds.

The bird species were: red-legged partridge, *Alectoris rufa*; grey partridge, *Perdix perdix*; pheasant, *Phasianus colchicus*; stock dove, *Columba oenas*; woodpigeon, *Columba palumbus*; collared dove, *Streptopelia decaocto*; turtle dove, *Streptopelia turtur*; skylark, *Alauda arvensis*; house sparrow, *Passer domesticus*; tree sparrow, *Passer montanus*; chaffinch, *Fringilla coelebs*; greenfinch, *Carduelis chloris*; goldfinch, *Carduelis carduelis*; linnet, *Carduelis cannabina*; bullfinch, *Pyrrhula pyrrhula*; yellowhammer, *Emberiza citrinella*; reed bunting, *Emberiza schoeniclus*; ciril bunting, *Emberiza cirilus* and corn bunting, *Miliaria calandra*.

The taxonomic level of knowledge of plants important in bird diets was variable, being known at the family level for all plants, but also at the genus level for selected families (Polygonaceae, Chenopodiaceae, Caryophyllaceae, Brassicaceae, Rosaceae, Fabaceae, Asteraceae, Poaceae). The level of taxonomic identification within the FSE data was thus finer than the level of taxonomic knowledge of bird diets.

(d) *Analytical methods*

Analytical methods are based on those of the FSEs (Heard *et al.* 2003a; Perry *et al.* 2003), which compared the abundance of individual taxa in the GMHT and conventional halves. Here, for each bird species in each crop, the total abundance of all weed seeds important in its diet from each half field was calculated prior to comparison. In addition, the total energy contained within weed seeds important in each bird species' diet, in each half field, was calculated as the sum of the products of the number of seeds of each weed species and their energy content. Seed energy content was calculated as the sum of the energy contents of the seed lipid, carbohydrate and protein components, themselves calculated as the weight of each component (from seed weight and its percentage composition by weight) multiplied by component-specific conversion factors of 38.94 kJ g⁻¹ for lipid and 17.17 kJ g⁻¹ for carbohydrate and protein (Glück 1985). We consider total energy content to be a measure of weed seed energy available to birds.

Table 1. Total seed rain, per m², of weeds important in the diets of 17 species of farmland birds in beet, maize, spring and winter oil seed rape. (Values given are geometric means for GMHT and conventional (conv) field halves. Treatment ratios *R*—see text—with 95% CIs in parentheses are also given. **p*<0.05, ***p*<0.01, ****p*<0.001. *n*=number of split fields included in that bird species analyses. Bird species in winter oilseed rape for which the two most abundant bird-food dicots (*Stellaria* and *Senecio*) or monocots (*Poa* and *Alopecurus*) were important in their diets are marked d and m, respectively.)

crop	bird species	<i>n</i>	geometric mean		multiplicative ratio of treatment effect, <i>R</i> (95% CI)		<i>p</i> -value
			conv	GMHT			
sugar and fodder beet	red-legged partridge	38	56.5	10.5	0.24	(0.12–0.46)	<0.001***
	grey partridge	56	98.0	20.9	0.24	(0.14–0.42)	<0.001***
	pheasant	60	179.2	35.0	0.21	(0.13–0.35)	<0.001***
	stock dove	52	86.5	24.2	0.31	(0.18–0.53)	<0.001***
	woodpigeon	40	45.8	15.0	0.38	(0.17–0.83)	0.022*
	turtle dove	49	83.6	19.1	0.26	(0.15–0.46)	<0.001***
	skylark	42	55.8	9.4	0.22	(0.12–0.41)	<0.001***
	house sparrow	45	78.9	12.8	0.20	(0.11–0.38)	<0.001***
	tree sparrow	51	79.2	20.6	0.30	(0.17–0.50)	<0.001***
	chaffinch	52	82.3	19.8	0.28	(0.17–0.45)	<0.001***
	greenfinch	60	115.1	42.7	0.39	(0.22–0.71)	0.0020**
	goldfinch	57	44.4	27.1	0.64	(0.42–0.98)	0.038*
	linnet	61	101.1	30.6	0.33	(0.21–0.51)	<0.001***
	bullfinch	63	151.2	91.2	0.61	(0.36–1.05)	0.056
	yellowhammer	49	80.8	18.7	0.27	(0.16–0.46)	<0.001***
	reed bunting	54	91.9	31.9	0.37	(0.22–0.65)	0.0020**
	cirl bunting	55	100.6	42.1	0.44	(0.21–0.91)	0.031*
forage maize	red-legged partridge	43	34.3	47.8	1.35	(0.74–2.49)	0.33
	grey partridge	49	54.6	123.1	2.17	(1.24–3.81)	0.0090**
	pheasant	52	103.4	203.9	1.94	(0.95–3.96)	0.056
	stock dove	52	54.8	119.9	2.11	(0.98–4.52)	0.048*
	woodpigeon	33	22.4	71.9	2.88	(1.14–7.28)	0.019*
	turtle dove	46	47.8	113.2	2.26	(0.86–5.92)	0.099
	skylark	40	37.3	84.0	2.13	(0.90–5.03)	0.071
	house sparrow	40	45.9	65.4	1.39	(0.75–2.57)	0.29
	tree sparrow	51	49.3	87.2	1.71	(0.83–3.53)	0.15
	chaffinch	51	53.5	92.9	1.69	(0.80–3.58)	0.18
	greenfinch	51	37.7	160.2	3.94	(1.89–8.21)	<0.001***
	goldfinch	53	50.6	68.7	1.33	(0.65–2.73)	0.43
	linnet	53	102.4	151.8	1.47	(0.70–3.07)	0.32
	bullfinch	54	82.8	302.7	3.54	(1.71–7.31)	<0.001*
	yellowhammer	46	50.7	109.1	2.07	(0.87–4.92)	0.098
	reed bunting	51	55.9	122.4	2.11	(1.01–4.40)	0.043*
	cirl bunting	49	59.1	161.1	2.62	(1.35–5.07)	0.0020**
spring oilseed rape	red-legged partridge	57	190.0	43.1	0.24	(0.13–0.47)	<0.001***
	grey partridge	64	392.3	104.3	0.27	(0.16–0.47)	<0.001***
	pheasant	65	493.0	123.6	0.26	(0.15–0.44)	<0.001***
	stock dove	63	300.8	79.5	0.27	(0.14–0.52)	<0.001***
	woodpigeon	49	128.8	77.8	0.62	(0.31–1.22)	0.17
	turtle dove	58	208.9	60.5	0.30	(0.17–0.56)	<0.001***
	skylark	58	227.4	40.4	0.19	(0.10–0.37)	<0.001***
	house sparrow	57	198.0	64.3	0.34	(0.19–0.62)	0.0030**
	tree sparrow	60	296.8	66.3	0.23	(0.12–0.45)	<0.001***
	chaffinch	61	303.1	67.1	0.23	(0.12–0.44)	<0.001***
	greenfinch	61	409.8	116.7	0.29	(0.16–0.52)	<0.001***
	goldfinch	57	73.8	25.3	0.38	(0.22–0.64)	0.0020**
	linnet	65	353.3	101.6	0.30	(0.18–0.50)	<0.001***
	bullfinch	64	807.1	182.2	0.23	(0.14–0.39)	<0.001***
	yellowhammer	57	193.7	58.1	0.31	(0.17–0.58)	<0.001***
	reed bunting	62	480.1	94.2	0.20	(0.11–0.38)	<0.001***
	cirl bunting	63	222.6	99.4	0.46	(0.27–0.77)	0.0030**
winter oilseed rape	red-legged partridge ^d	60	197.3	94.1	0.49	(0.25–0.96)	0.048*
	grey partridge ^m	64	543.0	844.5	1.55	(0.78–3.10)	0.21
	pheasant ^m	64	518.5	829.6	1.60	(0.79–3.21)	0.19
	stock dove ^d	62	336.7	106.0	0.32	(0.18–0.58)	0.0030**
	woodpigeon ^d	58	405.9	99.6	0.25	(0.13–0.49)	<0.001***
	turtle dove	49	52.3	51.8	0.99	(0.54–1.82)	0.98
skylark	45	34.8	43.3	1.22	(0.67–2.22)	0.52	

(Continued.)

Table 1. (Continued.)

crop	bird species	n	geometric mean		multiplicative ratio of treatment effect, R (95% CI)		p-value
			conv	GMHT			
	house sparrow ^m	63	210.2	593.2	2.79	(1.21–6.42)	0.017*
	tree sparrow ^d	59	238.6	89.9	0.39	(0.19–0.79)	0.0080**
	chaffinch ^d	58	302.0	82.9	0.28	(0.15–0.55)	0.0020**
	greenfinch ^d	61	669.3	134.1	0.21	(0.11–0.37)	<0.001***
	goldfinch ^d	48	142.8	15.9	0.14	(0.083–0.22)	<0.001***
	linnet ^d	60	425.5	157.0	0.38	(0.21–0.69)	0.0040**
	bullfinch ^d	64	2125.4	508.9	0.24	(0.14–0.41)	<0.001***
	yellowhammer ^m	47	62.6	91.4	1.43	(0.77–2.67)	0.25
	reed bunting ^d	61	1115.1	289.4	0.26	(0.14–0.49)	<0.001***
	cirl bunting ^m	63	505.0	799.6	1.58	(0.78–3.20)	0.22

Analyses were undertaken at the finest taxonomic level possible. Each weed species was allocated to its genus, this being the finest taxonomic resolution at which bird diet had been reviewed. Where the importance of a plant family in bird diet had been reviewed at the genus level, then the contribution towards the half field totals came only from the species within those genera. Where, however, a given plant family was known to be important in a particular bird species diet, but no review had been undertaken at genus level, then the contribution towards the half field totals came from all species within the family.

Seed rain data were log-transformed prior to analysis with the total count, c_{ij} , per half-field for treatment i at site j , transformed to $l_{ij} = \log_{10}(c_{ij} + 1)$. Sites for which the total whole-field count was zero or one were excluded. Geometric means were calculated from back-transformed arithmetic means of l_{ij} to give approximate indications of abundance for each treatment. The null hypothesis of no difference between treatments was tested with a paired randomization test, using as a test statistic $d = \sum_j [l_{2j} - l_{1j}] / n$ for n sites, the mean of the differences between the GMHT and conventional treatments on a logarithmic scale. Similar analyses were performed for seed energetic content; however, here the constant added for count data, 1, was replaced with half the minimum half-field energetic content recorded for each species and crop. Sites for which total whole-field energetic contents were zero were removed from the analysis. 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 intervals 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 $t_{0.05}$. Where $R > 1$, seed rain or energetic content was greater in the GMHT halves; where $R < 1$, they were greater in the conventional halves.

Within the text, 'significant' refers to a statistically significant effect at the 5% level ($p < 0.05$). However, actual p -values are given to assess the strength of evidence for treatment effects in each case.

3. RESULTS

(a) Seed rain

For collared dove and corn bunting, there were too few fields with weed seeds important in their diets to undertake analyses for any of the crops. The analyses presented here thus address the remaining 17 species.

For all 17 species in both beet and spring oilseed rape, rain of weed seeds important in their diets was less in GMHT compared to conventional halves, in all but one case (bullfinch in beet and woodpigeon in spring rape) significantly so (table 1). In winter oilseed rape, 11 out of the 17 species showed significant treatment effects, and for all except one of these species (house sparrow), rain of weed seeds important in their diets was significantly smaller in GMHT compared to conventional halves. Treatment ratios, R , varied from 0.20 for house sparrow (an approximate fivefold difference) to 0.64 for goldfinch in beet, from 0.19 for skylark to 0.62 for woodpigeon in spring rape and from 0.14 for goldfinch to 2.79 for house sparrow in winter rape. The geometric mean treatment ratios across bird species were 0.32, 0.29 and 0.56 for beet, spring oilseed rape and winter oilseed rape, respectively.

Results for maize contrasted markedly with the other three crops, with increased seed rain for all 17 species in GMHT compared to conventional halves (table 1), with R ranging from 1.33 for goldfinch to 3.94 for greenfinch. However, for only seven species were these increases significant. The geometric mean treatment ratio across species for maize was 2.06.

Winter oilseed rape was the only crop for which treatment ratios were sometimes above and sometimes below unity. These differences between bird species were dependent upon whether or not the two dicot genera, *Stellaria* and *Senecio*, or the two monocot grass genera, *Poa* and *Alopecurus*, with among the most abundant seed rain in this crop (Bohan *et al.* 2005), were important in their diets (table 1). Thus, for those 10 bird species for which the dicots *Stellaria* and *Senecio* or both were important in their diets, R was always less than 0.50 (across-species geometric mean of 0.28), whereas for those seven bird species for which neither dicot was important, R was always greater than 0.95 (geometric mean = 1.52). By contrast, for those five bird species for which the monocots *Poa* and *Alopecurus* were important in their diets, R was always greater than 1.4 (geometric mean = 1.73), whereas for 12 species for which neither monocot was important, R was less than 1.3 (geometric mean = 0.35).

(b) Energy available from weed seeds

For all 17 species in both beet and spring oilseed rape, the total energy available from weed seeds important in their diets was less in GMHT compared to conventional halves,

Table 2. Total seed energy (kJ), per m², from weeds important in the diets of 17 species of farmland birds in beet, maize, spring and winter oil seed rape. (See table 1 for further explanation.)

crop	bird species	n	geometric mean		multiplicative ratio of treatment effect, R (95% CI)	p-value	
			conv	GMHT			
sugar and fod- der beet	red-legged partridge	46	0.29	0.05	0.19	(0.091–0.40)	<0.001***
	grey partridge	60	0.76	0.12	0.17	(0.082–0.36)	<0.001***
	pheasant	62	1.43	0.23	0.16	(0.087–0.31)	<0.001***
	stock dove	60	0.56	0.14	0.27	(0.14–0.51)	<0.001***
	woodpigeon	47	0.16	0.07	0.45	(0.19–1.11)	0.078
	turtle dove	54	0.72	0.16	0.25	(0.13–0.46)	<0.001***
	skylark	50	0.88	0.12	0.16	(0.077–0.31)	<0.001***
	house sparrow	51	0.28	0.04	0.16	(0.086–0.31)	<0.001***
	tree sparrow	57	0.44	0.11	0.26	(0.13–0.51)	<0.001***
	chaffinch	59	0.44	0.10	0.24	(0.13–0.44)	<0.001***
	greenfinch	63	1.07	0.25	0.24	(0.12–0.46)	<0.001***
	goldfinch	61	0.35	0.21	0.61	(0.34–1.10)	0.10
	linnet	64	0.88	0.30	0.35	(0.20–0.60)	<0.001***
	bullfinch	63	1.15	0.56	0.50	(0.29–0.87)	0.012*
	yellowhammer	52	0.72	0.16	0.24	(0.13–0.42)	<0.001***
	reed bunting	58	0.52	0.12	0.26	(0.13–0.50)	<0.001***
	forage maize	cirl bunting	60	0.56	0.20	0.35	(0.16–0.74)
red-legged partridge		50	0.20	0.22	1.14	(0.59–2.23)	0.68
grey partridge		50	0.35	0.96	2.70	(1.32–5.50)	0.0070**
pheasant		53	0.80	1.47	1.85	(0.82–4.15)	0.12
stock dove		53	0.52	1.15	2.23	(0.95–5.24)	0.069
woodpigeon		38	0.07	0.27	3.52	(1.25–9.91)	0.018*
turtle dove		50	0.40	0.92	2.22	(0.81–6.06)	0.098
skylark		47	0.52	0.80	1.50	(0.61–3.66)	0.36
house sparrow		45	0.15	0.23	1.53	(0.77–3.02)	0.23
tree sparrow		52	0.35	0.60	1.68	(0.74–3.85)	0.20
chaffinch		52	0.40	0.68	1.68	(0.71–3.99)	0.22
greenfinch		52	0.37	1.35	3.56	(1.56–8.15)	0.0030**
goldfinch		54	0.60	0.60	1.00	(0.43–2.33)	0.99
linnet		53	1.23	1.55	1.24	(0.53–2.89)	0.61
bullfinch		54	0.76	2.51	3.30	(1.57–6.96)	0.0030**
yellowhammer		51	0.40	0.80	1.89	(0.82–4.37)	0.12
reed bunting		52	0.35	0.72	2.05	(0.88–4.77)	0.080
spring oilseed rape	cirl bunting	50	0.44	1.03	2.35	(1.02–5.40)	0.035*
	red-legged partridge	60	1.19	0.23	0.20	(0.093–0.42)	<0.001***
	grey partridge	65	4.22	0.72	0.17	(0.091–0.32)	<0.001***
	pheasant	65	4.82	0.88	0.18	(0.099–0.33)	<0.001***
	stock dove	64	3.42	0.76	0.23	(0.11–0.49)	<0.001***
	woodpigeon	55	0.60	0.35	0.61	(0.30–1.24)	0.17
	turtle dove	61	2.11	0.64	0.31	(0.16–0.60)	0.0020**
	skylark	62	3.38	0.72	0.22	(0.10–0.47)	0.0020**
	house sparrow	60	1.03	0.25	0.25	(0.12–0.53)	0.0020**
	tree sparrow	63	1.87	0.33	0.18	(0.085–0.38)	<0.001***
	chaffinch	64	2.19	0.38	0.18	(0.088–0.36)	<0.001***
	greenfinch	65	3.26	1.03	0.32	(0.16–0.63)	0.0030**
	goldfinch	59	0.80	0.20	0.26	(0.13–0.53)	<0.001***
	linnet	65	3.90	0.96	0.25	(0.14–0.44)	<0.001***
	bullfinch	65	5.05	1.23	0.25	(0.16–0.41)	<0.001***
	yellowhammer	61	1.55	0.48	0.32	(0.17–0.60)	0.0020**
	reed bunting	65	2.15	0.33	0.16	(0.074–0.33)	<0.001***
winter oilseed rape	cirl bunting	65	1.47	0.76	0.53	(0.27–1.03)	0.062
	red-legged partridge	62	0.92	0.60	0.64	(0.32–1.32)	0.21
	grey partridge	64	3.22	4.26	1.31	(0.64–2.68)	0.46
	pheasant	64	3.02	4.46	1.48	(0.73–3.02)	0.28
	stock dove	63	4.22	1.39	0.34	(0.17–0.65)	0.0030**
	woodpigeon	61	2.27	0.44	0.20	(0.099–0.41)	<0.001***
	turtle dove	53	0.52	0.52	1.02	(0.51–2.05)	0.96
	skylark	52	0.36	0.38	1.05	(0.58–1.91)	0.87
	house sparrow	64	1.11	2.31	2.03	(0.83–4.98)	0.11
	tree sparrow	60	0.96	0.38	0.41	(0.19–0.88)	0.031*
	chaffinch	61	1.47	0.39	0.27	(0.13–0.55)	0.0020**

(Continued.)

Table 2. (Continued.)

crop	bird species	n	geometric mean		multiplicative ratio of treatment effect, R (95% CI) p-value		
			conv	GMHT			
	greenfinch	61	3.98	0.80	0.20	(0.11–0.38)	<0.001***
	goldfinch	52	0.64	0.09	0.16	(0.087–0.28)	<0.001***
	linnet	61	2.83	1.03	0.37	(0.20–0.69)	0.0050**
	bullfinch	64	11.14	2.75	0.25	(0.15–0.41)	<0.001***
	yellowhammer	52	0.44	0.72	1.57	(0.75–3.27)	0.22
	reed bunting	62	2.99	0.80	0.27	(0.14–0.52)	<0.001***
	cirl bunting	64	1.95	3.06	1.59	(0.79–3.18)	0.19

in all but two cases (woodpigeon and goldfinch in beet and woodpigeon and cirl bunting in spring rape) significantly so (table 2). In winter oilseed rape, 9 out of the 17 species showed significant treatment effects; for all of these, the energy available from weed seeds important in their diets was significantly lower in GMHT compared to conventional halves. The geometric mean treatment ratios across species were 0.26, 0.25 and 0.55 for beet, spring oilseed rape and winter oilseed rape, respectively.

Once again, the results for maize, contrasted with those from the other three crops, with increased availability of energy from weed seeds for 16 of the 17 species in GMHT compared to conventional halves (table 2); for the remaining species, goldfinch, R was 1. However, for only five species were these increases significant. The geometric mean treatment ratio across species for maize was 1.95.

The results for seed energy were very similar to those for seed rain abundance alone. Across species, within each crop, R values for seed rain abundance and seed energy were strongly correlated ($r=0.92, 0.92, 0.91$ and 0.97 for beet, maize, spring and winter oil seed rape, respectively; all $n=17, p<0.001$). Despite this similarity, R values for seed energy in beet and spring oilseed rape were slightly, but significantly lower than those for seed rain, especially so in beet (beet, paired $t_{16}=3.96, p=0.001$; spring rape, paired $t_{16}=2.32, p<0.05$). There were no such differences for maize ($t_{16}=0.99, p=0.34$) or winter oilseed rape ($t_{16}=1.14, p=0.27$).

4. DISCUSSION

In beet and spring oilseed rape, rain of weed seeds important in the diets of all 17 granivorous bird species studied was markedly less (approximately a threefold difference across species) in the GMHT compared to conventional treatments. These differences were significant for all but one bird species in both crops. In winter oilseed rape, although rain of weed seeds important in bird diets was also lower in GMHT treatments, the effect was less marked overall, with a twofold difference. Despite this, for 10 out the 11 species where the differences were significant, rain of weed seeds important in their diets were less in GMHT. In maize, by contrast, rain of weed seeds important in the diets of all 17 species was higher in the GMHT compared to conventional treatments, though only significantly so for seven species. This was because the broad spectrum herbicide used on GMHT maize, glufosinate ammonium, was less effective at weed control than those used on conventional maize, mostly triazine herbicides such as atrazine (Heard *et al.* 2003a; Perry *et al.* 2004). Despite weed seeds varying in

size and composition, results for seed rain and energy available from seeds were remarkably similar for all four crops.

The impacts of GMHT cropping on rain of weed seeds important in bird species' diets were broadly consistent with those on weed seeds more generally (Heard *et al.* 2003a; Bohan *et al.* 2005); GMHT cropping reduced weed seed rain, both overall and for granivorous birds, in beet and spring oilseed rape, but increased it in maize. Results for winter oilseed rape were somewhat different. Total seed rain in this crop was similar in the two treatments (Bohan *et al.* 2005) yet, for 10 out of the 11 bird species with significant treatment effects, rain of weed seeds important in their diets was less in GMHT compared to conventional. This apparent discrepancy is because although total weed seed rain in winter oilseed rape was not affected by treatment, that from monocots (principally the grasses, Poaceae) was greater, while that from dicots was less, in GMHT compared to conventional treatments. Although grass seeds are taken by granivorous bird species, they are substantially less important in their diets than dicot seeds. For example, while the monocot genus *Poa* was important in the diets of five of the granivorous bird species studied, many more dicot genera were important in the diets of five or more bird species. Thus, *Sinapis* and *Cerastium* were important in the diets of five species; *Brassica*, 6; *Rumex*, 7; *Chenopodium*, 10; *Stellaria*, 11 and *Polygonum* 13 (data from Wilson *et al.* 1996, 1999, unpublished work). Even though rain of monocot weed seeds was higher in GMHT than conventional treatments, the preference of most granivorous birds for dicot seeds that were much rarer in GMHT treatments meant that, overall, weed seed resources for these birds were reduced under GMHT cropping. Interestingly, two of the most abundant monocot genera, *Poa* and *Alopecurus*, were important in the diets of five of the six bird species for which GMHT winter oilseed rape cropping increased rain of weed seeds important in their diets ($R>1$). By contrast, neither of these two monocot genera was important in the diets of the eleven species for which GMHT cropping reduced rain of weed seeds important in their diet ($R<1$).

Given that weed seeds vary greatly in weight and composition, it was perhaps surprising that the results for seed rain and seed energy were so similar. The only systematic difference between these two measures was that R values for seed energy in beet and spring oilseed rape were slightly, but significantly, lower than those for seed rain, especially so in beet. This suggests that for these two GMHT crops, the energetic resource available to birds

would be reduced even further compared to conventional than suggested from the simple reduction in seed numbers.

These results suggest that should beet, spring and winter rape crops in the UK be largely replaced by GMHT varieties and managed as in the FSEs, this would markedly reduce important food resources for granivorous farmland birds, many of which declined during the last quarter of the twentieth century. By contrast, GMHT maize would increase food resources for birds.

However, given that measuring the effects on individual birds, populations and their trends was outside the scope of this study, we cannot be certain of the effect of these differences in food resources on bird population levels. In particular, birds respond to availability and accessibility of food resources, not merely their abundance (e.g. Wilson *et al.* 2005). Furthermore, with the notable exception of the cardueline finches (linnet, greenfinch and goldfinch) and turtle dove, which are almost wholly granivorous even when feeding young, relatively few birds actually forage in the growing crop for weed seeds. The most important consequence of a change in seed rain is thus probably through the impact this has on weed seed abundance post-harvest. Since the marked differences between GMHT and conventional field halves in seed rain may well be modified by a range of biological processes, such as predation and germination and post-harvest management options (e.g. whether or not crop stubbles are left), the eventual impacts on birds may not be as straightforward as suggested by seed rain data alone. Nevertheless, the effects of treatment on the input of seeds to fields later exploited by birds were, in many cases, so marked, and the importance of weed seeds to granivorous birds so well documented, that we feel our interpretation of the results remains valid. In principle, data such as these could be used to model the likely impacts on individual bird species' populations (e.g. Watkinson *et al.* 2000), though we have not done so here.

The results presented here are dependent upon the crop management adopted within the FSEs. Since management of conventional halves followed normal practice current at the time, and management of GMHT halves followed the advice of the industry's representative body, it is likely that the comparisons presented are realistic. However, as the triazine herbicides used on conventional maize are being phased out by the European Union, the results found in the FSEs for maize, and by implication here, may not hold in the future. A recent analysis of a relatively small subset of the FSE data, however, has suggested that a ban on triazine herbicides would be likely to reduce, but not negate the relative benefits of GMHT cropping (Perry *et al.* 2004). A range of alternative GMHT management regimes have been tested for beet, particularly with a view to enhancing weed seed resources for birds (May *et al.* 2005). While such regimes tend to be specialized, they could nevertheless be made a condition of growing GMHT beet, or be supported through agri-environment schemes.

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