

## ORIGINAL PAPER

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**Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing**

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**Abstract** Trap-nesting bees and wasps (Hymenoptera Aculeata) colonizing crop and fallow fields in an agricultural landscape were studied using 20 sown fields (pea, barley, rye, clover-grass mixtures, *Phacelia tanacetifolia*) and 20 fields with naturally developed vegetation (1- and 2-year old fields, both mown and unmown, and old meadows). Fourteen species of Apoidea, 4 of Sphecidae, 1 of Eumenidae and 4 of parasitoids were reared from reed nests exposed in these 40 fields of 10 field-types. Fields with naturally developed vegetation had twice as many species as sown fields, due to the distribution pattern of the 14 bee species, whereas the 9 predatory species (wasps and parasitoids) showed a rather uniform distribution. None of the trap-nesting bees were found in *Phacelia* fields, despite contrasting expectations of beekeepers. Old meadows showed a particularly high abundance and species richness, since only 10% of all traps were exposed, but 32% of all bee nests were sampled in old meadows, including 4 bee species that were not found elsewhere. Accordingly, species richness of fields with naturally developed vegetation showed a significant increase with age. Variability in Hymenoptera species numbers could be explained by corresponding differences in plant species numbers. The alternative hypothesis that field size or field connectivity influenced species richness was not supported. Habitats with great floral diversity appeared to offer better and richer food resources for the flower-visiting bees, whereas food availability apparently did not influence predatory wasps. The bees *Osmia caerulescens* and *Megachile versicolor* that had colonized early-successional fields took twice as long to provision cells as those that colonized late-successional meadows characterized by a greater plant species richness. In contrast, the eumenid wasp *Ancistrocerus gazella* took a similar period of time to provision cells in both field types. In addition, bee and wasp species of plant-species-poor fields were on average significantly larger

than those of plant-species-rich fields. Thus, body size appeared to be a good predictor of colonization ability. Management by cutting greatly increased plant species richness in early-successional set-aside fields and thus doubled species richness of bees. Cutting of early-successional habitats can be expected to benefit insects and plants in general, whereas older grassland should show the greatest insect diversity when both mown and unmown parts are present.

**Key words** Colonization · Succession · Body size  
Hymenoptera Aculeata · Set-aside

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**Introduction**

Set-aside forms an integral part of the agricultural reform package of the European Community, and aims to reduce agricultural surplus production. Since 1988, set-aside has been supported financially by government subsidies, so that short-term (1 year) and long-term (up to 5 years) set-aside fields have become a feature of the countryside that affects everyone associated with them (Kaule 1991; Clarke 1992). Both the colonization ability of animals and habitat suitability shape communities of such early-successional fields (see Clarke 1992). The effects of set-aside on the abundance of wild bees have received particular attention, since bees are of increasing importance for the pollination of both wild and cultivated plants in the agricultural landscape (e.g. Corbet 1987; Westrich 1989; Kevan et al. 1990; Torchio 1990; Corbet et al. 1991).

In this paper, we report the effects of set-aside, or the abandonment of cereal fields, on colonization by trap-nesting bees and wasps (Hymenoptera Aculeata). We expected a priori species richness to increase as vegetation develops naturally in formerly sown fields and as field age increases (see Anderson 1986; Brown and Southwood 1987; Southwood 1988). Nests made of reed internodes were exposed in 40 fields, and we studied the composition of the community in relation to field type.

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In particular, we were interested in differences between fallow sown with clover-grass mixtures or with *Phacelia tanacetifolia*, and fallow with naturally developed vegetation. Most farmers prefer sowing, because they expect this to suppress weeds. Further, we studied the impact of mowing and field age on colonization by trap-nesting bees and wasps. Set-aside fields with sown or naturally developed vegetation could be compared both with crop fields (negative null hypothesis) and with old meadows (positive null hypothesis).

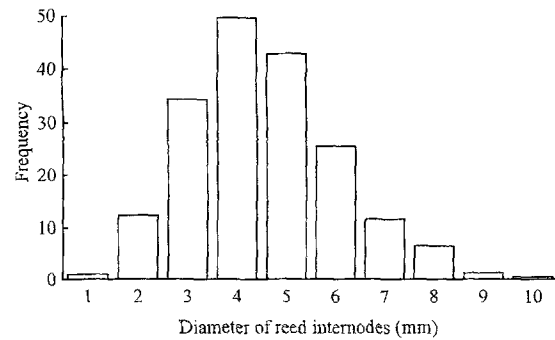
Trap-nesting bees (Apoidea) and wasps (Sphecidae, Eumenidae) use holes of a suitable diameter and can easily be observed and sampled using wood-borings, hollow reed or grass internodes etc. (Krombein 1967; Brechtel 1986; Westrich 1989). The linear nest built by the female consists of several cells provisioned with food for the larvae (nectar-pollen mixtures in the case of bees, insects or spiders in the case of wasps). After the females have placed food and an egg in the first cell, they construct a partition before starting the next cell, so that the brood chambers are separated from each other. Finally, the female seals the nest with a more or less species-specific, thick closing plug. Parasitoids mainly belong to the Hymenoptera; females lay their eggs in the cells and the predacious larvae consume their host and in most species also the host's food.

## Materials and methods

Traps exposed within each of the 40 fields consisted of six 850 ml tins filled with reed internodes. Each tin contained about 180 reed internodes (*Phragmites australis*) that were about 13 cm long and basally closed by a node. Each of three 1.5-m-long wooden posts put in the central area of a field (20–30 m apart) were equipped at the top with two tins with the openings oriented to south east and south west. Accordingly, the sample from each field consisted of Hymenoptera nests made in 1080 (i.e.  $180 \times 6$ ) exposed trap nests. The distribution of stem diameters is shown in fig. 1. The traps were set up in the fields during spring (17–18 April 1990) and sampled in autumn (3–4 October 1990), so the spring generation of bivoltine species was not considered. In the laboratory, reed nests were opened and examined for parasitization and for partial species identification. The internal diameter of the internode (mm) and cell length (mm) were measured using vernier callipers. After hibernation, adults emerged and could be fully identified (see Brechtel 1986). The mean lengths of females were taken as a measure of body size.

The crop and fallow fields were in the "Kraichgau", a region to the northeast of Karlsruhe, with a field size ranging from 2000 to 7000 m<sup>2</sup>. All fields were studied in 1990; the set-aside fields had been cereal fields before. Table 1 shows the 10 field types studied (with 4 replicates of each, i.e. 40 fields altogether). The number of plant species, percent cover of Asteraceae, and percent cover of Poaceae in a 49 m<sup>2</sup> plot was based on a 3-fold mapping of the flora (in May, July and October 1990, supplemented with additional data from 1991). Naturally developed set-aside fields were split in two types of vegetation management: (i) cutting in July (with the hay remaining on the fields) and (ii) uncut controls. Habitat connectivity was based on the calculation of the percentage of field margins adjoining neighbouring fields that were near-natural.

Time for cell provision was measured on 4 early-successional fields (1-year old set-aside fields with naturally developed vegetation) and on 4 late-successional fields (>30 years old meadows with fruit-trees). The nest of each female observed (75 specimens altogether) was marked with white correction fluid ("Tipp-Ex"),



**Fig. 1** Frequency distribution of the internal diameter of reed internodes used for trap-nesting (arithmetic means of 5 tins with  $5 \times 180$  internodes)

**Table 1** Sown and naturally developed field-types studied

Field types	Mean number of plant species/49 m <sup>2</sup>
Sown fields (1-year-old)	
1. Pea fields ( <i>Pisum sativum</i> )	11.2
2. Barley fields ( <i>Hordeum vulgare</i> )	13
3. Rye fields ( <i>Secale cereale</i> )	9.3
4. <i>Phacelia</i> set-aside fields ( <i>Phacelia tanacetifolia</i> ) <sup>b</sup>	6.8
5. Clover-grass set-aside fields (mainly <i>Trifolium repens</i> and <i>Lolium perenne</i> , or <i>Medicago sativa</i> ) <sup>a, b</sup>	17.6
Naturally developed fields	
6. One-year-old, unmown set-aside fields	33
7. One-year-old, mown <sup>a</sup> set-aside fields	37.5
8. Two-year-old, unmown set-aside fields	33.8
9. Two-year-old, mown <sup>a</sup> set-aside fields	42.3
10. Old meadows (>30 years) with several old fruit trees (apples, pears or cherries) <sup>a</sup>	50

<sup>a</sup> Set-aside fields and meadows were mown once a year (end of June, beginning of July) with the hay remaining on the fields (set-aside) or carried off (meadows)

<sup>b</sup> Sown during April and May 1990

and the period between the female's departure and return with food (pollen-nectar mixtures or prey insects) was timed. Observations were made on eight sunny days (from 19 June to 18 July) between 1000 hours and 1600 hours.

Analyses of variance and regression statistics were computed using "Statgraphics" software (STSC 1989; ANOVA with log-transformed values). Arithmetic means  $\pm$  standard deviations are given.

## Results

### Characteristics of the species

Six tins with  $6 \times 180$  reed internodes were exposed in each of the 40 fields, but only 292 of these 43 200 reed internodes were used by trap-nesting bees and wasps. Characteristic features of the species and distribution among field types are shown in Table 2. Fourteen species

**Table 2** Characteristic features of the bees (Apoidea), wasps (Sphecidae, Eumenidae) and parasitoids (Chrysididae, Gasteruptionidae, Eulophidae) reared from trap nests

Species	Number of nests/ cells	Number of males/ females	Body size (mm)	Mortality (%)	Cell diameter (mm)	Cell length (mm)	Endangered species <sup>a</sup>	Field types <sup>b</sup>	Food type (plant pollen or insect prey)
<b>Apoidea</b>									
<i>Anthidium lituratum</i> (Panzer)	16/123	70/46	6.6	5.7	5.46	8.04	2	3 7 9 10	Asteraceae
<i>Chelostoma fuliginosum</i> (Panzer)	7/33	22/10	7.5	3	4.07	9.38		9 10	<i>Campanula</i> sp.
<i>Heriades crenulatus</i> Nylander	10/48	23/9	7.0	33.3	4.75	8.46	3	9 10	Asteraceae
<i>Heriades truncorum</i> (Linnaeus)	22/130	74/35	7.1	16.1	3.91	8.54		9 10	Asteraceae
<i>Hylaeus angustatus</i> (Schenk)	6/23	12/5	5.0	26.1	2.95	6.97		7 10	>1 plant family
<i>Hylaeus communis</i> Nylander	1/7	4/1	6.0	28.6	3.8	6.8		5	>1 plant family
<i>Hylaeus confusus</i> Nylander	1/7	4/2	6.5	14.3	4.2	7.3		10	>1 plant family
<i>Megachile alpicola</i> Alfken	61/346	182/120	9.5	12.7	6.45	10.5	4	1 2 3 5 6 7 8 9 10	>1 plant family
<i>Megachile versicolor</i> Smith	50/258	150/86	10.5	8.6	7.5	11.2		2 5 6 7 8 9 10	>1 plant family
<i>Osmia caerulea</i> (Linnaeus)	37/167	110/36	7.7	12.5	5.06	8.71		9 10	>1 plant family
<i>Osmia gallarum</i> Spinola	2/17	9/4	6.6	23.5	4	6.16	2	10	Fabaceae
<i>Osmia leaiana</i> (Kirby)	2/9	6/1	10.0	22.2	4.75	9.8	3	10	Asteraceae
<i>Osmia rufa</i> (Linnaeus)	11/52	48/0	11.0	7.7	5.93	10.8		2 5 6 9 10	>1 plant family
<i>Stelis punctulatis</i> (Kirby)	1/1	1/0	--	--	--	--		6	<i>A. lituratum</i>
<b>Sphecidae</b>									
<i>Nitela borealis</i> Valkeila	3/5	2/3	4.1	0	3.37	12.1		5 10	Aphidina
<i>Psenulus pallipes</i> (Panzer)	7/60	9/41	5.9	16.7	3.96	6.66		5 9 10	Aphidina
<i>Trypoxylon figulus</i> (Linnaeus)	19/71	39/13	11.0	26.8	3.98	12.91		1 3 5 8 9 10	Araneida
<i>Trypoxylon medium</i> De Beaumont	28/174	96/42	7.5	20.7	4.41	11.01		1 3 4 6 8 9 10	Araneida
<b>Eumenidae</b>									
<i>Ancistrocerus gazella</i> (Panzer)	19/66	52/8	9.5	9.1	4.8	10.8		1 2 4 5 6 7 9	Lepidoptera
<b>Chrysididae</b>									
<i>Chrysis cyanea</i> (Linnaeus)	13/25	8/17	--	--	--	--		5 8 9	<i>Trypoxylon</i> sp.
<i>Chrysis ignita</i> (Linnaeus)	2/3	1/2	--	--	--	--		4 9	<i>A. gazella</i>
<b>Gasteruptionidae</b>									
<i>Gasteruption assectator</i> (Linnaeus)	1/2 <sup>b</sup>	2/0	--	--	--	--		5	<i>H. communis</i>
<b>Eulophidae</b>									
<i>Melittobia acasta</i> Walker	4/7	--	--	--	--	--		8 9	<i>Trypoxylon</i> sp., <i>A. gazella</i>

<sup>a</sup> "Rote Liste" status category according to Schmidt (1981; 1984) (Sphecidae), Kunz (1989) (Chrysididae), Westrich (1989) (Apoidea), Schmidt and Schmidegger (1991) (Eumenidae)

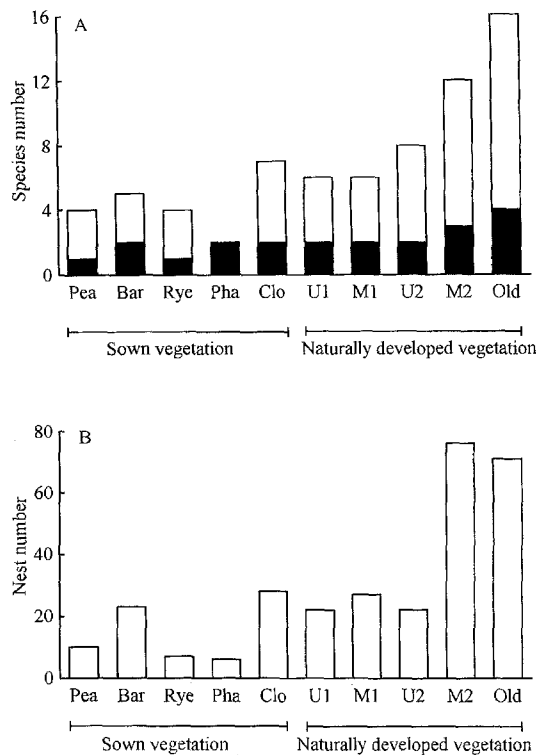
<sup>b</sup> See Table 1

of Apoidea, 4 of Sphecidae, 1 of Eumenidae and 4 of parasitoids were reared.

Altogether, 13.2% of the 1596 cells were empty due to the death of larvae (Table 2: mortality); causes of this mortality were presumably disease and unsuccessful at-

tacks of parasitoids. Successful parasitism was low (2%), although 4 species were involved. The diameter of the nests used was between 3.0 and 7.5 mm, and well within the size classes offered (see Fig. 1).

On three occasions we observed that nests started by



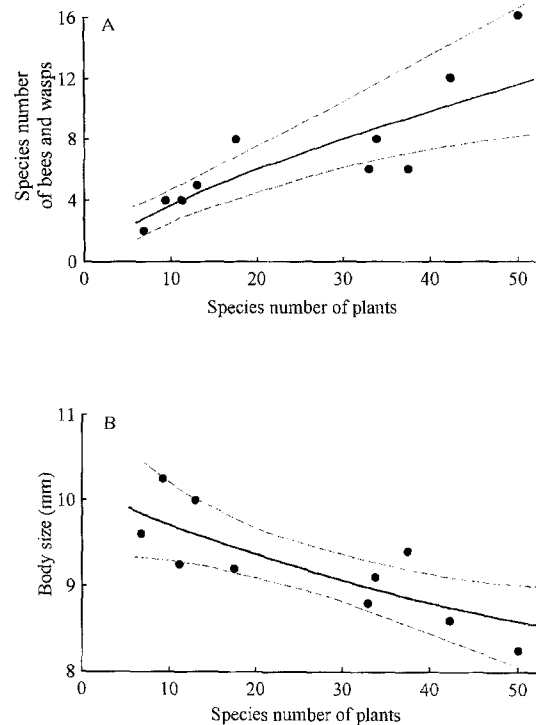
**Fig. 2A, B** Distribution of species number and nest number among field types. Field type abbreviations: see Table 1 **A** Total number of bee and wasp species reared (based on  $n = 40$  fields;  $F = 2.8$ ,  $P = 0.02$ ). *Black blocks*: predatory wasps and parasitoids, *white blocks*: bees. **B** Total number of nests (based on  $n = 40$  fields;  $F = 2.5$ ,  $P = 0.03$ )

one species were completed by another species: *Ancistrocerus gazella* completed 1 nest started by *Osmia rufa* (from 11 *O. rufa* nests), *Heriades truncorum* completed 1 nest started by *Megachile alpicola* (from 61 *M. alpicola* nests), and *H. truncorum* completed 1 nest started by *Trypoxylon* species (from 47 *Trypoxylon* nests).

#### Distribution among field types

Field type was a factor explaining significant differences in both species richness and nest number (Fig. 2). In particular, sown fields (crop fields, and fallow sown with clover-grass mixtures or with *Phacelia*; field types 1–5 of Table 1) were colonized much less than the set-aside land with naturally developed vegetation (field types 6–10):  $4.6 \pm 2.1$  compared with  $7.9 \pm 2.3$  species ( $F = 6.8$ ,  $n = 40$ ,  $P = 0.01$ );  $4.1 \pm 5.7$  compared with  $12.2 \pm 10.6$  nests ( $F = 8.9$ ,  $n = 40$ ,  $P = 0.005$ ). Altogether, the 20 sown fields had 9 trap-nesting species from 74 nests, and the 20 naturally developed fields had 18 species from 218 nests.

These differences between field types were caused by the differential colonization success by the bees, but not by the distribution pattern of the wasps and parasitoids, which showed a rather uniform distribution (Fig. 2a, see Table 2). Bee species had a greater coefficient of varia-



**Fig. 3A, B** Species number and mean body size of bees and wasps in relation to the mean number of plant species/49m<sup>2</sup> per field type **A** Species number of bees and wasps:  $\text{Ln } y = 0.725 \text{ ln } x - 0.388$ ,  $F = 25.5$ ,  $r = 0.873$ ,  $n = 10$ ,  $P < 0.001$ . **B** Body size (mm):  $1/y = 0.00038 \times x + 0.099$ ,  $F = 17.4$ ,  $r = 0.828$ ,  $n = 10$ ,  $P = 0.003$ .

tion ( $\text{CV} = 0.8$ ,  $n = 10$  field types) than wasp species ( $\text{CV} = 0.4$ ,  $n = 10$ ). Sown fields were colonized only by 4 out of the 14 bee species (*Anthidium lituratum*, *Megachile alpicola*, *M. versicolor* and *Osmia rufa*). *Phacelia* fields attracted many honey bees, and bee-keepers claim that they are important for enhancement of all bee species, but none of the trap-nesting bees nested here. Ten bee species colonized only naturally developed fields. In particular, old meadows showed a great abundance and species richness of trap-nesting bees: they had only 10% of all traps, but 32% of all bee nests and 4 bee species that were not found elsewhere. Five endangered species were reared (with a “Rote Liste” status category, Table 2) and they were all bees; three of them nested mainly or completely in the old meadows.

#### Causes of the distribution patterns

The large differences between sown fields and fields with naturally developed vegetation, in terms of species richness and nest number, corresponded with differences in floral species richness (plant species/49m<sup>2</sup>:  $11.7 \pm 5.8$  versus  $39.0 \pm 9.2$ ,  $F = 103$ ,  $n = 40$   $P < 0.001$ ). In step-wise multiple regression, plant species richness proved to be the best predictor of total species richness of the trap-nesting Hymenoptera explaining 76% of the vari-

**Table 3** Time taken for cell provision (minutes) spent by two bee species (*O. caerulea*, *M. versicolor*) and one wasp species (*A. gazella*) in early-successional and late-successional habitats (1-year-old set-aside fields and old meadows). Arithmetic means  $\pm$  one standard deviation are given; differences in sample means; one-way analysis of variance)

	Early-successional	Late-successional	Significance level
<i>Osmia caerulea</i>	38.0 $\pm$ 8.0 (n=6)	15.0 $\pm$ 6.0 (n=14)	F=50.6 (P<0.001)
<i>Megachile versicolor</i>	33.6 $\pm$ 22.0 (n=11)	14.5 $\pm$ 4.1 (n=8)	F=58.3 (P=0.03)
<i>Ancistrocerus gazella</i>	20.3 $\pm$ 4.3 (n=19)	21.9 $\pm$ 3.5 (n=17)	F=1.52 (P=0.22)

ance (Fig. 3a). Alternative field characteristics (cover of Asteraceae, cover of Poaceae, habitat connectivity, habitat size) were either not significantly correlated with species number or did not significantly contribute to the explanation. Age of the naturally developed fallow was positively correlated with species richness of bees and wasps, since species numbers, not only of plants but also of bees and wasps, increased with age (from 1 year to 2 year old fallow up to the >30-year-old meadows:  $r_s = 0.477$ ,  $n = 20$ ,  $P = 0.03$ ).

These differences between fields were associated with the body size of bees and wasps. Mean body size of the Hymenoptera community that had successfully colonized the four fields of each field-type was negatively correlated with the number of plant species (Fig. 3b).

A further analysis tested the significance of this predictable correlation of body sizes with the richness of plant species. Bees colonizing plant species-poor fields can be expected (i) to need more time to provision cells and (ii) to be better colonizers of distant sources of pollen and nectar. Cell provision took *Megachile versicolor* and *Osmia caerulea* twice as long in early-successional habitats (1 year old set-aside fields with, on average, 35 plant species/49m<sup>2</sup>) as in late-successional habitats (old meadows with, on average, 50 plant species/49m<sup>2</sup>). *Ancistrocerus gazella*, a eumenid wasp with a rather uniform distribution among field types, took a similar time to provision cells in both field types (Table 3). Bees in old meadows needed only 15 min for cell provision instead of 35 min, and wasps in any field type took about 21 min to collect 1 caterpillar for a cell.

Comparison of the numbers of bee and wasp species found in mown and unmown fallow having naturally developed vegetation revealed no difference between mown and unmown 1-year-old fallow. But in the case of the 2-year-old fallow, mown fields had more than twice as many species as unmown fields (4.8  $\pm$  1.9 versus 1.8  $\pm$  1.2,  $F = 7.0$ ,  $n = 8$ ,  $P = 0.04$ ). The number of plant species nearly doubled when early-successional fallow was mown once at the beginning of July (Greiler and Tschardt 1991; Greiler 1994), but the effects of cutting the vegetation of 1-year-old fields could not be expected to influence bee colonization during the same year.

## Discussion

The results of this study show that set-aside fields with naturally developed vegetation had twice as many species of trap-nesting Hymenoptera as sown fields (crops and sown fallow). These differences between habitats were due to the differential colonizing ability of the 14 bee species, whereas the 9 species of "wasps" (Sphecidae, Eumenidae) and parasitoids showed a rather uniform distribution (Gathmann and Tschardt 1993). Variability in species number of these trap-nesting Hymenoptera was associated with corresponding differences in plant species number. Habitats with high floral diversity appeared to offer better and richer food resources for the flower-visiting (i.e. phytophagous) bees, whereas colonization by predatory wasps and parasitoids was apparently not influenced. Alternative hypotheses that field size or field surroundings influenced species richness were not supported. Habitat quality in terms of plant species number was the only predictor of Hymenoptera species number, although fragmentation and isolation of habitats are generally well-known causes of species losses (e.g. Wilcove et al. 1986; Thomas et al. 1992). The trap-nesting bees and wasps of all of the 40 fields came from reservoir populations from outside. Alternative nesting places appeared to be without importance: the 2-year-old and unmown fallow could be expected to offer dead (but very narrow) grass stems for nesting, but they were colonized even less than the mown fields. Furthermore, dead parts of fruit-trees in the four old meadows provided only very small bore-holes that could only be used by different, smaller species (Jagsch et al., unpublished). Besides species-rich vegetation, age was expected to be mainly responsible for the great Hymenoptera diversity observed in these >30-years-old meadows (see Westrich 1989): 10% of all traps sampled 32% of all bee nests, including 4 bee species that were not found elsewhere.

Management by cutting of set-aside fields with naturally developed vegetation promoted species richness of both plants and bees. Establishment of plants appeared to be facilitated by the suppression of the dominant annuals, particularly *Alopecurus myosuroides* (Greiler 1994). Destruction of these monoculture-like grasses reduced shading of the ground and allowed germination and establishment of further herbs (see also Harper 1977; Maas 1988). Cutting promoted species richness of bees and wasps only in the 2-year-old fields, since cutting of the 1-year-old fields (at the beginning of July) was too late to influence bee colonization in the same year. Management of early-successional habitats by cutting can be expected to benefit insects and plants in general (Greiler et al., unpublished; Greiler 1994). In contrast, cutting of older grassland favours mainly phytophagous insects, so that both long and short grass are important in maintaining species diversity (e.g. Morris and Rispin 1988).

The causes of the good correlation between plant species numbers and the numbers of bee and wasp species were studied more thoroughly. Bees nesting in 1-year-old fallow took twice as long to provision cells with food

as bees nesting in old meadows (significant differences were found for *Osmia caerulescens* and *Megachile versicolor*), whereas the eumenid wasp *Ancistrocerus gazella* took a similar time in both field types. Further, mean body length of the trap-nesting species was closely correlated with the mean species number of plants per field type. These results support the hypothesis (Westrich 1989) that only plant-rich habitats offer sufficient and suitable pollen resources to make a bee-rich community possible. In addition, plant species-poor habitats were evidently colonized only by large species, thereby supporting general hypotheses on the positive correlation of dispersal ability and body size (see den Boer 1990 with respect to carabid beetles, Steffan-Dewenter and Tscharntke 1994 with respect to butterflies). Availability of suitable pollen can be expected to be a major force structuring bee communities, whereas the specific nature of nectar sources is of minor importance (Westrich 1989). The results suggest that the reduced pollen quality and quantity in early-successional habitats shaped not only species number of the community, but favoured selectively large species. Large bees invade new habitats faster and can nest far from their forage source due to their greater dispersal ability. Species number of both bees and plants increased with the successional age of the habitat. Pollen and nectar availability should also increase with succession, since annuals offer less nectar than perennials and are visited less often by long-tongued bees (Parrish and Bazzazz 1979, Fussell and Corbet 1992). But conservation strategies also have to consider the exceptions: the rare and endangered bee *Andrena tscheki* prefers pollen from small-sized annual Cruciferae like *Capsella bursa-pastoris* (Westrich 1989; K. Schmidt personal communication) and therefore may greatly benefit from early-successional set-aside fields. Bees and wasps nesting in sandy soils even prefer vegetation-free areas, shown by experiments with manually removed plant cover (Wesserling and Tscharntke 1994).

Farmers often prefer sown fallows, because they are afraid of weeds when the vegetation is allowed to develop naturally (starting a secondary succession; see Brown and Southwood 1987). Furthermore, bee-keepers emphasize that fields sown with *Phacelia tanacetifolia* promote not only honeybees, but also solitary wild bees and nature conservation in general (e.g. Bauer and Engels 1991). Despite such statements, *Phacelia*-fields proved to be species-poor habitats in which none of the nesting bees were found, presumably because these habitats (i) were dominated by a foreign plant species with a presumably non-nutritious pollen resource for wild bees (equally, *Phacelia* plants were almost never attacked by phytophagous insects), (ii) had very few plant species (see Table 1), and (iii) flowered for only a short time (June and July). Availability of large amounts of *Phacelia* nectar during June and July appeared to be attractive only to the large and social Apidae (honeybees and bumblebees), which range over several fields for forage sources.

Accordingly, set-aside fields with naturally developed vegetation provide more species-rich communities than sown fields. In general, diversity increases with age of succession (Brown and Southwood 1987), but early-successional habitats harbour a few typical species. Furthermore, mowing once a year leads to an increase in both plant and bee species richness. Consideration of the differential habitat use of bees, wasps and many other insect taxa (Greiler et al. 1992; Greiler 1994; Steffan-Dewenter and Tscharntke 1994; Greiler et al., unpublished) shows that only a mosaic of different habitats can generally guarantee high species diversity in an agricultural landscape.

Mortality due to unknown causes (diseases, parasitization failures etc.) was low (maximum 33%, Table 2) and within the range (8–60%) found by other authors (Danks 1971; Tasei 197; Schneider 199; Westrich 1979). Similarly, the very low (2%) mortality caused by parasitoids is not unusual. Westrich (1979) argues that parasitoid mortality may become much more important, when trap nests stay in a habitat for more than 1 year.

Because of the relatively low mortality rate and the ease of construction, trap nests of this design are recommended as a means of augmenting the number of bees and wasps (see also Dorn and Weber 1988 who give information on augmentation of the crop-pollinating *Megachile rotundata*). In the agricultural landscape, most habitats lack suitable nests, and this appears to be a major factor limiting bee abundance. In addition, experimental exposure of such trap nests also provides an opportunity for experimental evaluation of habitat quality.

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