

Edge distributions of *Ceutorhynchus assimilis* (Paykull) and its parasitoid *Trichomalus perfectus* (Walker) in a crop of winter oilseed rape (*Brassica napus* L.).

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Abstract

The edge distributions of *Ceutorhynchus assimilis* and its parasitoid *Trichomalus perfectus* within a crop of winter oilseed rape were investigated between May and July using yellow water-traps arranged on a grid system. A randomisation test, which compared the observed arrangement of trap counts with permuted arrangements, was used to quantify the observed tendency of *C. assimilis* to congregate at the edges as it migrated into the crop; this tendency declined during the season. *Trichomalus perfectus* were distributed at the edge of the crop only during the early phase of its immigration in May, which occurred later than immigration of its host. It is considered that this simple means of quantifying insect spatial distribution could prove a useful tool in precision targeting of 1

insecticides.

Introduction

The cabbage seed weevil, *Ceutorhynchus assimilis* (Paykull) (Coleoptera: Curculionidae), is a pest of oilseed rape in Europe (Bromand, 1990; Winfield, 1992). It is univoltine; adults emerge from overwintering sites in the spring and migrate to rape crops to feed and oviposit. The females lay their eggs singly in the pods and the larvae cause economic damage by eating developing seeds.

The larval ectoparasitoid *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae) is the most abundant parasitoid of *C. assimilis* in Europe (Murchie & Williams, 1998). Like its host, it is univoltine and migrates to the rape crop in the spring, but later than its host. On locating a *C. assimilis* larva within a pod, the female parasitoid pierces the pod wall with her ovipositor, immobilises the larva and lays a single egg onto it. The parasitoid larva feeds externally on its host, eventually consuming all but the head capsule and skin. The percentage of *C. assimilis* larvae parasitised by *T. perfectus* can be large: in a recent study in the UK, it exceeded 50% in rape not treated with insecticides (Murchie *et al.*, 1997b).

In the UK, most crops of winter rape are treated with insecticides to kill *C. assimilis*, either prophylactically or when threshold numbers are reached (Alford *et al.*, 1991), and most treatments are applied to the entire area of the crop. Previous studies of the distribution of *C. assimilis* on winter rape, by sampling along line transects, have shown that during immigration to the crop in April and May, *C. assimilis* adults infest crop edges more than crop centres and that the proportion at the crop edge gradually diminishes as adults spread further into the crop during June and July (Free & Williams, 1979a). It has been suggested that their numbers could be effectively reduced by application of insecticide to crop borders only (Free & Williams, 1979a & b; Alford *et al.*, 1991).

Trichomalus perfectus migrates to winter rape during May, 2-4 weeks later than *C. assimilis* (Murchie *et al.*, 1997b) but there is no information about its spatial distribution on the crop relative to that of its host.

Precision farming involves the use of within-field spatial information to target husbandry measures (Sylvester-Bradley *et al.*, 1999). Technological advances, such as Global Positioning Systems and Geographical Information Systems mean that spatial information about crop characteristics can be collected and utilised. Inputs can be targeted to where they are most required thus reducing waste and pollution. This approach has been mainly confined to applications of fertilisers, herbicides and seeding densities. Insecticides are more difficult to target due to temporal and spatial fluctuations in pest densities. However, spatial targeting of insecticides against Colorado potato beetle significantly reduced insecticide inputs by 30-40% compared to whole-field applications but yields were unaffected (Weisz *et al.*, 1996).

This study used yellow water-traps, arranged in a grid pattern in and around a crop of winter oilseed rape to sample adult *C. assimilis* and adult *T. perfectus* simultaneously throughout spring and summer. The strength of edge effects were determined using a randomisation test which compared the cumulative distance of observed counts from pre-determined edge traps with the distances of 200 random permutations of the same values. More information about the within-field temporal and spatial distribution of *T. perfectus* relative to that of its host, *C. assimilis*, could facilitate the spatial targeting of insecticides to kill the pest but not the parasitoid.

Materials and methods

Site

The study site was a field (1.1 ha) sown to winter oilseed rape (cultivar Libravo), at IACR - Rothamsted, Hertfordshire, England. The field was approximately rectangular in shape (150 m along its longitudinal axis and 85 m along its transverse axis) and bounded by a mature wood of beech and oak to the south, crops of winter wheat to the north and west, and winter beans to the east. There was a larger and more advanced crop of winter oilseed rape 100 m to the north.

Experimental design

Twenty three water traps were placed, in and around the crop, on selected intersects of a 10 m grid, on 24 April and removed on 10 July, 1992. Each trap was a yellow flat-bottomed bowl (diameter 210 mm, height 70 mm) with a holding capacity of *c.* 1500 ml, filled with water containing 5 g of sodium benzoate as a preservative, and a few drops of detergent to break the surface tension and aid insect capture. Traps were maintained at crop canopy height, emptied weekly and the catch stored in 80% methanol. *Ceutorhynchus assimilis* and female *T. perfectus* in the catch were counted; male *T. perfectus* were not counted because their identification from water traps was not reliable. *Ceutorhynchus assimilis* caught from 29 April to 26 June, their main oviposition period, were air-dried and sexed.

Analysis

To visualise the distributions of *C. assimilis* and *T. perfectus* on the crop, the numbers of each caught in the traps were entered into mapping software (Unimap 2000, Uniras Ltd., Slough) which produced contour maps by bilinear interpolation. Of the 31 maps produced, two are presented as examples (Figure 1).

The null hypothesis was that the counts in the traps were distributed randomly. To determine the strength of the edge effects, a randomisation test of this hypothesis was constructed, using Genstat 5 (Genstat 5 Committee, 1993). Edge effects were investigated only for the three crop-to-crop boundaries as fewer target insects were caught at the southern edge of the crop, AD (Figure 1), which was bounded by the wood. The procedure was as follows: 1) the minimum distance from each trap to the nearest of the set of ten traps on edges AB, BC and CD (within 10 m of any crop-to-crop boundary) (Figure 1) was calculated; 2) this distance was multiplied by the trap catch and the resulting products summed over all traps to give an overall measure of the degree which insects 5

occupied positions away from the edge (D_o); 3) trap counts were randomly permuted amongst the traps 200 times and step 2 recalculated for each permutation to yield values, D_n ; 4). The probability, P , of obtaining a spatial pattern as extreme as that observed, given the null hypothesis, was assessed by the position of D_o in the frequency distribution of the 200 ranked permuted values of D_n . This randomisation test is particularly sensitive to arrangements where the larger counts are located predominantly towards the edge of the crop; in such cases the value of D_o is small relative to D_n and therefore the value of P is small.

Simple correlation analyses on $\log_{10} (n+1)$ transformed counts, were used to assess the degree of association between distributions of different species and sexes. Analyses were done on trap catches on the same date. However, since *T. perfectus* attacks the later larval instars of *C. assimilis*, which take approximately three weeks to develop (Dmoch, 1965a), trap catches of female *T. perfectus* and of female *C. assimilis* three weeks before were also compared.

Results

Spatial pattern of single species

Ceutorhynchus assimilis

Ceutorhynchus assimilis first entered the crop in late April and early May. The strongest edge effect was in mid-May when all the largest counts were distributed along the crop-to-crop boundaries (Figures 1 & 2). It declined during the second half of May as *C. assimilis* numbers stabilised (Figure 2). However, in early June, this situation was reversed with catches again displaying a strong, albeit short-lived, edge distribution, which was followed by a substantial increase in catch the following week (Figure 2). Later in June and early July, the edge effect again declined overall whilst catches of *C. assimilis* remained large. Few *C. assimilis* were caught in mid-July.

More male than female *C. assimilis* were caught. The two sexes differed in their phenologies: 6

numbers of females caught increased, but only slightly, during June whereas those of males increased substantially between 5 and 12 June. The distributions of the sexes appeared to differ on most dates except in early June; relatively more of the females than of the males were caught at the edge of the crop (Figure 2).

Trichomalus perfectus

Fewer *T. perfectus* than *C. assimilis* were caught. The first *T. perfectus* were caught in early May; numbers remained small until early June and then increased steadily until mid-July (Figure 3). Throughout, *T. perfectus* were caught less often at the edge of the crop than *C. assimilis* (Figures 2 & 3), and were there predominantly on only one occasion in mid-May.

Interactions between species and sexes

Numbers of male and of female *C. assimilis* caught were positively correlated (Table 1). Numbers of female *T. perfectus* caught were mostly negatively correlated with those of *C. assimilis* (total) and with those of *C. assimilis* (female) three weeks before (Table 1).

Discussion

Oilseed rape is an annual crop and *C. assimilis* and *T. perfectus* migrate to it in the spring, on dry days when the temperature exceeds 15° C (Free & Williams, 1979b). Many pests of oilseed rape (Bartlet, 1996) and their parasitoids (Murchie *et al.*, 1997a) locate the crop using visual and, particularly, olfactory cues. *Ceutorhynchus assimilis* is attracted by a range of volatiles from oilseed rape when presented in an olfactometer (Bartlet *et al.*, 1993, 1998) or in field traps (Smart *et al.*, 1997) and utilises odour-mediated upwind anemotaxis to locate them (Evans & Allen-Williams, 1993). This type of active habitat location probably explains the notable edge distributions demonstrated by *C. assimilis*; the edge is simply the first part of the crop which they encounter.

Habitat location by *T. perfectus* has not been investigated although it is known to use volatiles from 7

host frass to locate *C. assimilis* larvae inside pods (Dmoch & Rutkowska-Ostrowska, 1978).

Free & Williams (1979a) found that the proportion of *C. assimilis* at the edge of the crop was greatest during immigration and then diminished as weevils moved into the crop in June and July. Values from the randomisation test support this, with the edge effect decreasing as the season progressed. An exception to this trend was the distribution of *C. assimilis* on 5 June which was strongly clustered around the edge. Together with a sharp increase in the numbers of *C. assimilis* caught during the following week, this suggests a second migration into the crop. These weevils probably came from the winter rape crop 100 m to the north, which was at a more advanced stage, attracted to fresh flowers and younger pods for feeding and oviposition (Dmoch, 1965b). Alternatively, increased catches at this time may have been due to petal fall and the greater contrast of the yellow traps against the now more green background of the crop canopy (Dmoch, 1965a; Free & Williams, 1979b) but this does not explain the pattern of the distribution, nor is this sharp increase reflected by *T. perfectus* catches.

More male than female *C. assimilis* were caught. Dmoch (1965a) found that yellow water-traps caught relatively more males than sweep-netting and suggested that males may fly more. The even greater ratio of males to females caught after 12 June suggests that males migrate more than females to other crops. Although numbers of male and female *C. assimilis* caught were positively correlated, females were caught more often at the crop edges than males. However, it is unclear whether this is a true difference in distribution or a reflection of differences in the flight activity between the sexes; females may fly less once they reach the crop and start to search for oviposition sites.

Trichomalus perfectus were first caught during May, but their numbers did not increase substantially until early June, about four weeks after the initial immigration of *C. assimilis*; this concurs with other studies (Laborius, 1972; Dmoch, 1975; Murchie *et al.*, 1997b). Immigration of 8

T. perfectus is thus synchronised with the appearance of *C. assimilis* larvae in pods (Dmoch, 1975). The dissociation between the immigration flights of *C. assimilis* and *T. perfectus* provides an opportunity for the temporal targeting of insecticide to kill *C. assimilis* but not *T. perfectus*. This approach was proposed as part of an integrated strategy for the management of *C. assimilis* populations on winter rape (Alford *et al.*, 1996). This strategy is based on the work of Murchie *et al.* (1997b) who found that the application of a pyrethroid insecticide during early flowering to kill adult *C. assimilis* was less harmful to *T. perfectus* than the application of organophosphate insecticide after flowering to kill *C. assimilis* larvae within pods, because the pyrethroid was applied before the main flight of *T. perfectus* into the crop.

The numbers of *C. assimilis* and *T. perfectus* caught were negatively correlated. This is surprising, as one would expect the parasitoid to be caught in the vicinity of its host. However, trap catches probably reflected the flight activity and not necessarily the oviposition activity of both *C. assimilis* and *T. perfectus*. Free & Williams (1979a) found that the distributions of adult and larval *C. assimilis* were not closely associated; in many crops, adults were most abundant at the edges but larval infestation was greatest in the centres. Since *T. perfectus* attack the larvae, this could explain the disparity in adult distributions. However, this raises concerns for monitoring adult *C. assimilis* using traps that attempt to measure density indirectly via flight activity. Probably, such monitoring is more reliable during *C. assimilis* immigration when its major activity is flight than later when the females are searching for pods in which to oviposit.

Targeting insecticide treatments to crop area, as well as in time, has potential for further reducing insecticide inputs with benefit for the parasitoid. The strong edge effects during immigration of *C. assimilis*, found in this study concurs with other studies that used different sampling methods (Risbec, 1952; Thiem, 1970; Kühne, 1977; Free & Williams, 1979a). They suggest that application of insecticide to the crop borders alone, early during flowering, could be an effective way 9

of spatially targeting the densest part of the *C. assimilis* population on the crop. Similarly, Buntin (1998) working in Georgia, USA, found that trap crops surrounding the main crop and treated with esfenvalerate during flowering, significantly reduced *C. assimilis* larval infestation in one year out of a four year study but had no adverse effects on *T. perfectus*. He suggests that, although trap cropping did not give adequate control at that site, where weevil larvae infested 54-90% of pods in plots not treated with insecticide, it could be effective with lower populations of *C. assimilis*. In the UK, annual surveys consistently find weevil numbers at or below the treatment threshold of two weevils per plant (Alford *et al.*, 1996) which would suggest that, in most fields, larvae infest well under 30% of pods (Cooper & Lane, 1991). In addition, parasitism rates are usually about 50% (Alford *et al.*, 1996) compared with a maximum of 6.7% found by Buntin (1998). Therefore, spatial targeting of insecticides via trap cropping or border applications may be a viable method of controlling *C. assimilis*.

One of the major difficulties in precision farming is sensing spatial variations (Sylvester-Bradley, 1999). This is especially difficult with a mobile and cryptic pest, such as *C. assimilis*. Weisz *et al.* (1996) scouted the crop by foot on a weekly basis to map Colorado potato beetle distribution before applying insecticides to specific within-field locations where and when pest population density exceeded the threshold. Such intensity of sampling is unfeasible for commercial production and, since remote sensing of insect distributions is not yet possible, growers wishing to spatially target insecticides are realistically confined to the crude spatial scales such as edge or centre. Many previous analyses have sought to quantify spatial distribution (Taylor, 1961; Lloyd, 1967; Iwao, 1968). However to target insecticide application, spatial knowledge of pest distribution must be indexed to crop boundaries. Mapping insect distribution is the most common method of doing this but maps can be misleading and statistical quantification is required. The randomisation test described in this study provides a simple and easy method of doing this.

More work is needed to determine how general the spatial dissociation between *C. assimilis* and *T. perfectus* is and to further quantify their edge distributions, particularly their width, on a range of crops of different sizes and infestation levels. It may be possible that models of insect spatial distribution could be constructed which utilise field and surrounding topography and climatic variables to predict pest distribution. However, any integrated pest management strategy incorporating spatial as well as temporal targeting of insecticide to kill *C. assimilis* must be compatible with the need to conserve the parasitoids of other pests on winter rape, which might be active at the time of insecticide application, such as those of *Meligethes* spp., as well as with the proposed introduction of unsprayed buffer zones of *c.* 6 m at crop borders, designed to avoid insecticide drift to field margins, which can provide reservoirs for natural enemies and other beneficial species (Evans and Scarisbrick, 1994).

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References

Alford, D.V., Cooper, D.A. & Williams, I.H. (1991). *Insect pests of oilseed rape*. Home Grown Cereals Authority, Oilseeds Research Review No. OS1.

Alford, D.V., Walters, K.F.A., Williams, I.H. & Murchie, A.K. (1996). A commercially viable low-cost strategy for the management of seed weevil populations on winter oilseed rape in the UK. In: *Brighton Crop Protection Conference - Pests & Diseases*, vol. 2 (session 6c), 18-21 November, Brighton, UK, pp. 609-614.

Bartlet, E. (1996). Chemical cues to host-plant selection by insect pests of oilseed rape. *Agricultural Zoology Reviews* 7: 89-116.

Bartlet, E., Blight, M.M., Hick, A.J. & Williams, I.H. (1993). The responses of the cabbage seed weevil (*Ceutorhynchus assimilis*) to the odour of oilseed rape (*Brassica napus*) and to some volatile isothiocyanates. *Entomologia Experimentalis et Applicata* 68: 295-302.

Bartlet, E., Blight, M.M., Lane, P. & Williams, I.H. (1998). The responses of the cabbage seed weevil *Ceutorhynchus assimilis* to volatile compounds from oilseed rape in a linear track olfactometer. *Entomologia Experimentalis et Applicata* 85: 257-262.

Bromand, B. (1990). Diversities in oilseed rape growing within the western Palearctic region. *IOBC/WPRS Bulletin* 13: 7-31.

Buntin, G.D. (1998). Cabbage seedpod weevil (*Ceutorhynchus assimilis*, Paykull) management by trap cropping and its effect on parasitism by *Trichomalus perfectus* (Walker) in oilseed rape. *Crop Protection* 17: 299-305.

Cooper, D.A. & Lane, A. (1991). Monitoring of oilseed rape pests in England and Wales. *OILB/WPRS Bulletin* 14: 5-13.

Dmoch, J. (1965a). The dynamics of a population of the cabbage seedpod weevil (*Ceuthorrynychus assimilis* Payk.) and the development of winter rape. Part I. *Ekologia Polska - Seria A* 8: 249-287.

Dmoch, J. (1965b). The dynamics of a population of the cabbage seedpod weevil (*Ceuthorrynychus assimilis* Payk.) and the development of winter rape. Part II. *Ekologia Polska - Seria A* 13: 463-489.

Dmoch, J. (1975). Badania nad pasożytami chowacza podobnika (*Ceuthorrynychus assimilis* Payk.). II. Czas występowania i rozwoju chowacza podobnika i jego pasożytów na rzepaku ozimym. *Roczniki nauk Rolniczych, Seria E* 5: 113-124.

Dmoch, J. & Rutkowska-Ostrowska, Z. (1978). Host-finding and host-acceptance mechanism in *Trichomalus perfectus* Walker (Hymenoptera, Pteromalidae). *Bulletin de l'Academie Polonaise des sciences* 26: 317-323.

Evans, K.A. & Allen-Williams, L.J. (1993). Distant olfactory response of the cabbage seed weevil, *Ceutorhynchus assimilis*, to oilseed rape odour in the field. *Physiological Entomology* 18: 251-256.

Evans, K.A. & Scarisbrick, D.H. (1994). Integrated insect pest management in oilseed rape crops in Europe. *Crop Protection* 13: 403-412.

Free, J.B. & Williams, I.H. (1979a). The distribution of insect pests of oil-seed rape (*Brassica napus* L.) and the damage they cause. *Journal of Agricultural Science, Cambridge* 92: 139-149.

Free, J.B. & Williams, I.H. (1979b). The infestation of crops of oil-seed rape (*Brassica napus* L.) by insect pests. *Journal of Agricultural Science, Cambridge* 92: 203-218.

Genstat 5 Committee (1993). *Genstat 5 Release 3 Reference Manual*. Clarendon Press, Oxford.

Iwao, S. (1968). A new regression method for analysing the aggregation pattern of animal populations. *Researches on Population Ecology* 10: 1-20.

Kühne, W. (1977) Untersuchungen Zur Befallsverteilung der Rüsselkäfer *Ceutorhynchus napi* Gyll., *Ceutorhynchus quadridens* Panz. und *Ceutorhynchus quadridens* Payk. innerhalb grossflächiger Winterrapsbestände. *Archiv für Phytopathologie und Pflanzenschutz* 13: 109-115.

Laborius, A. (1972). Untersuchungen über die Parasitierung des Kohlschotenrüsslers (*Ceuthorrhynchus assimilis* Payk.) und der Kohlschotengallmücke (*Dasyneura brassicae* Winn.) in Schleswig-Holstein. *Zeitschrift für angewandte Entomologie* 72: 14-31.

Lloyd, M. (1967). 'Mean crowding'. *Journal of Animal Ecology* 36: 1-30.

Murchie, A.K., Smart, L.E. & Williams, I.H. (1997a). Responses of *Dasyneura brassicae* and its parasitoids *Platygaster subuliformis* and *Omphale clypealis* to field traps baited with organic isothiocyanates. *Journal of Chemical Ecology* 23:917-926.

Murchie, A.K. & Williams, I.H. (1998). A bibliography of the parasitoids of the cabbage seed weevil (*Ceutorhynchus assimilis* PAYK.). *IOBC/WPRS Bulletin* 21: 163-169.

Murchie, A.K., Williams, I.H. & Alford, D.V. (1997b). Effects of commercial insecticide treatments to winter oilseed rape on parasitism of *Ceutorhynchus assimilis* Paykull (Coleoptera: Curculionidae) by *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae). *Crop Protection* 16: 199-202.

Risbec, J. (1952). De l'évolution des insectes nuisibles au Colza et des moyens de lutter contre eux. *Comptes Rendues de l'Académie d'Agriculture de France* 39: 403-407.

Smart, L.E., Blight, M.M., & Hick, A.J. (1997) Effect of visual cues and a mixture of isothiocyanates on trap capture of cabbage seed weevil *Ceutorhynchus assimilis* (Paykull) (Coleoptera: Curculionidae). *Journal of Chemical Ecology* 23: 889-902.

Sylvester-Bradley, R., Lord, E., Sparkes, D. L., Scott, R. K., Wiltshire, J. J. J. & Orson, J. (1999). An analysis of the potential of precision farming in northern Europe. *Soil Use and Management* 15: 1-8.

Taylor, L. R. (1961). Aggregation, variance and the mean. *Nature* 189: 732-735.

Thiem, E. (1970). Die Bedeutung der Feldrandbehandlung für die Bekämpfung von *Dasyneura brassicae* Winn. (Dipt., Cecidomyiidae) und *Ceuthorrhynchus assimilis* Payk. (Col., Curculionidae) im blühenden Raps und der Einfluss dieser Insektizidmassnahme auf das Vorkommen von *Trichomalus perfectus* Walker (Hym., Chalcidoidea, Pteromalidae) an den Larven des

Kohlschotenrüsslers. *Archiv für Phytopathologie und Pflanzenschutz* 6: 83-98

Weisz, R., Fleischer, S. & Smilowitz, Z. (1996). Site-specific integrated pest management for high-value crops: Impact on potato pest management. *Journal of Economic Entomology* 89: 501-509

Winfield, A.L. (1992). Management of oilseed rape pests in Europe. *Agricultural Zoology Reviews* 5: 51-94.

Table 1. Correlations between *Ceutorhynchus assimilis* and its parasitoid, *Trichomalus perfectus*, which were caught in yellow water-traps ($n=22$ or 23) in a crop of winter oilseed rape during the summer of 1992.

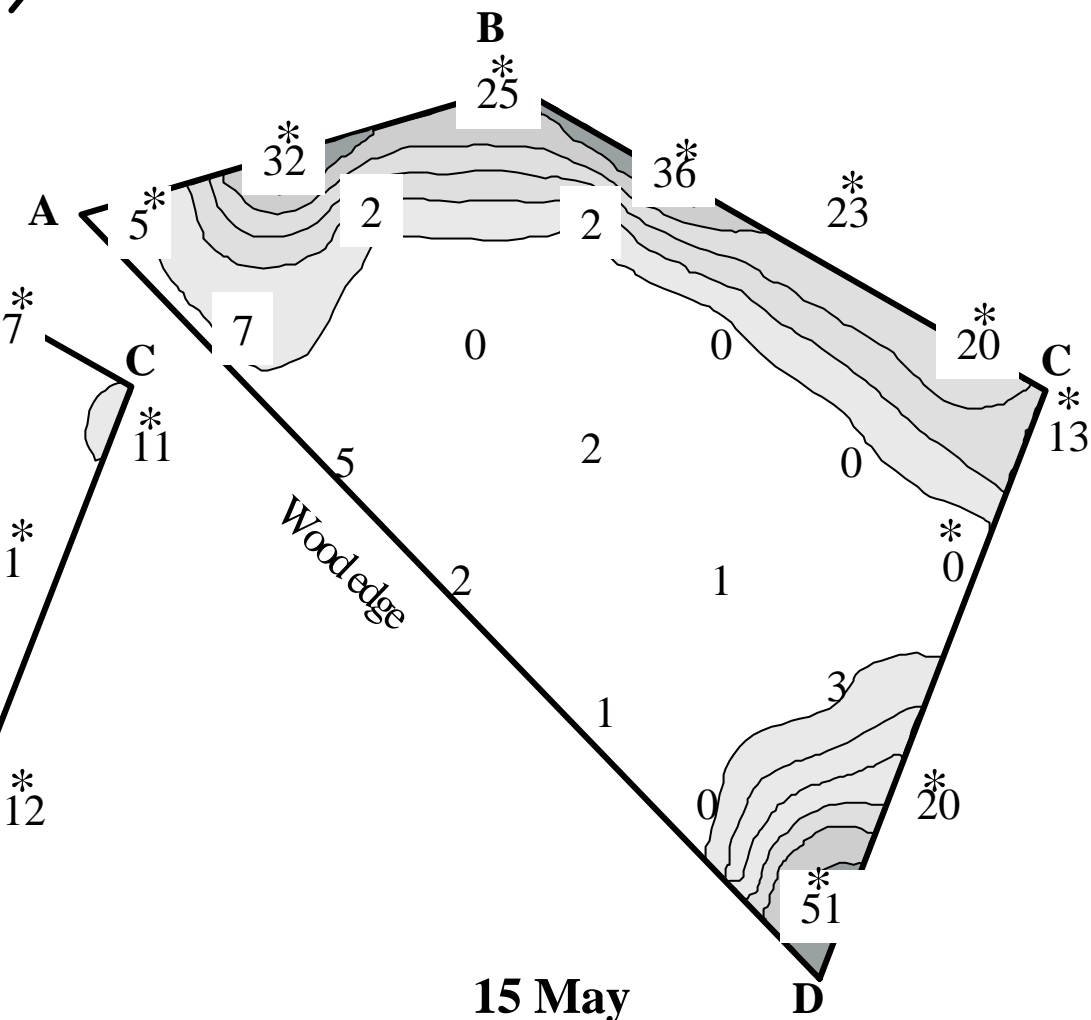
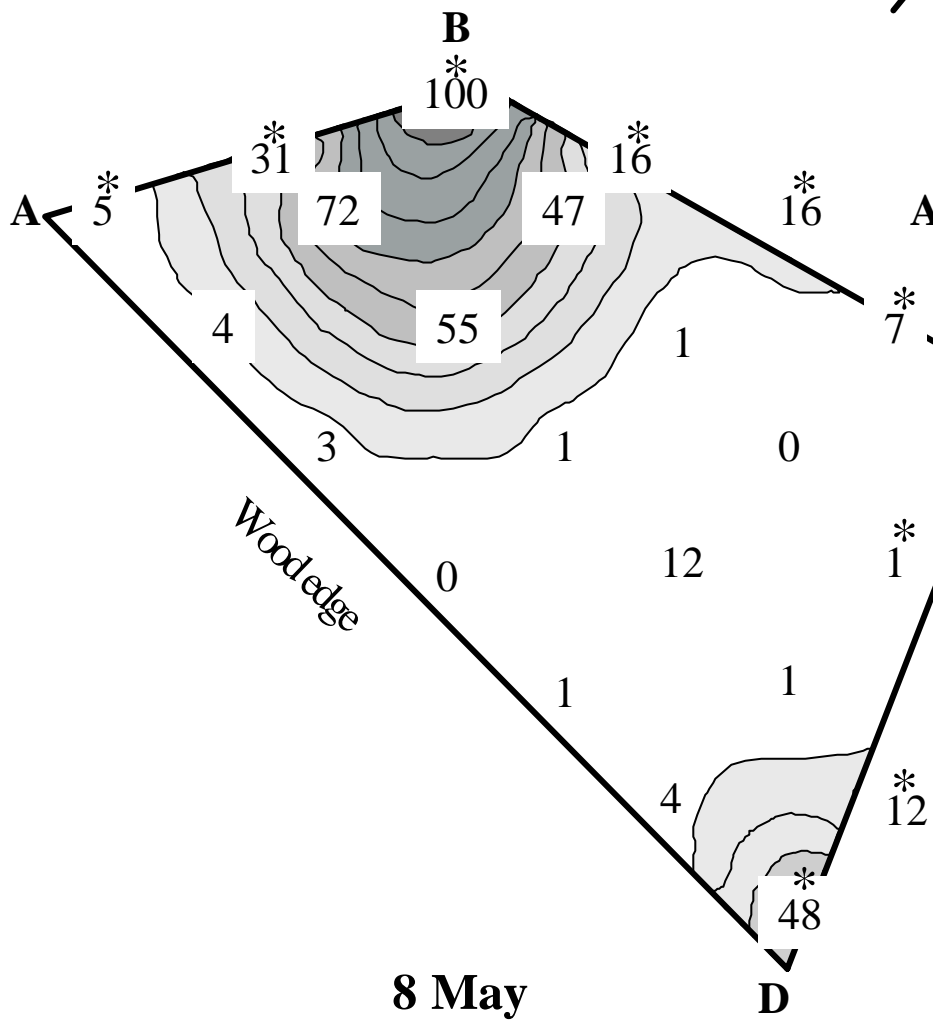
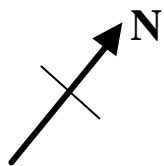
Date	<i>C. assimilis</i> male v's female		<i>C. assimilis</i> v's <i>T. perfectus</i>		<i>C. assimilis</i> (female) (3 weeks before) v's <i>T. perfectus</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
8 May	-	-	-0.139	0.53	-	-
15 May	-	-	0.387	0.07	-	-
22 May	-	-	0.309	0.16	-	-
29 May	0.317	0.15	-0.246	0.27	-	-
5 June	0.752	<0.01	-0.141	0.52	-	-
12 June	0.636	<0.01	-0.375	0.09	-	-
19 June	0.704	<0.01	-0.013	0.95	-0.278	0.21
26 June	0.836	<0.01	-0.319	0.14	-0.380	0.07
3 July	-	-	-0.089	0.69	-0.488	0.02
10 July	-	-	0.334	0.12	-0.206	0.38

Legends to Figures

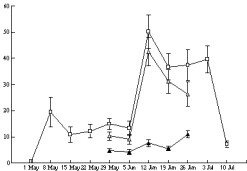
Figure 1. Distribution of catches of *Ceutorhynchus assimilis* in yellow water-traps in a crop of winter oilseed rape for two dates during 1992. Values are absolute insect catches in traps and darkening shade suggests greater insect activity/density. Trap positions marked with an asterisk are designated edge traps as used in analysis (see text).

Figure 2. Mean catches of *Ceutorhynchus assimilis* (total: ; male Δ ; female \blacktriangle) in yellow water-traps ($n=22$ or 23) in winter oilseed rape during 1992. Error bars are \pm one standard error. Table values are probabilities of the observed data under the null hypothesis of randomness; a value of <0.05 indicates a significant edge distribution.

Figure 3. Mean catches of *Trichomalus perfectus* in yellow water-traps ($n=22$ or 23) in winter oilseed rape during 1992. Error bars are \pm one standard error. Table values are probabilities of the observed data under the null hypothesis of randomness; a value of <0.05 indicates a significant edge distribution.



Mean number of *C. acinosa*



P (total)		0.035	0.005	0.105	0.190	0.015	0.135	0.290	0.935	0.870	0.940
P (male)					0.355	0.015	0.170	0.400	0.945		
P (female)					0.015	0.025	0.045	0.020	0.935		

Mean number of female *F. pygmaea*

