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Density and Survival of *Urophora stylata* (Diptera: Tephritidae) on *Cirsium vulgare* (Compositae) in Relation to Flower Head and Gall Size

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Abstract

Infestation of flower heads of *Cirsium vulgare* by *Urophora stylata*, and the subsequent mortality of *U. stylata* and its causes were studied at sites in Britain and West Germany. No clear relationships were found for infestation and mortality with the density or size of plants. The size of head, and the timing of its development are, however, important. Infestation is greater in large (and early maturing) heads than in small (and late developing) ones. Ectoparasites cause greatest mortality in galls in small heads; the endoparasite *Eurytoma tibialis* is indiscriminate, while deaths caused by Lepidoptera are greatest in large galls in large heads, although small heads with galls suffer more damage than those without. Overall survival of *U. stylata* is best in small galls in large heads and thus relates positively to levels of infestation. The relationship is not, however, perfect, and the reasons for this are discussed.

Densité et Taux de Survie de *Urophora stylata* sur *Cirsium vulgare* en Fonction de la Taille des Capitules et des Galles

l'infestation des capitules de *Cirsium vulgare* par *Urophora stylata*, et la mort subséquente de *U. stylata* et ses causes ont été étudiées en des emplacements de Grande-Bretagne et d'Allemagne de l'Ouest. Il n'existe aucun lien précis entre l'infestation ou le taux de mortalité et la densité ou la taille des plantes. Toutefois, la taille de la capitule et le moment de son développement constituent des facteurs importants. L'infestation est plus marquée dans les grands capitules (et à maturation précoce) que dans les petits capitules (et à maturation tardive). Les ectoparasites infestent principalement les plantes à petits capitules et entraînent leur mort, mais l'endoparasitoïde *Eurytoma tibialis* n'est pas sélectif en ce qui concerne la taille des capitules. Les grands capitules, atteints ou non de galles, et les petits capitules atteints de galles sont une source d'alimentation pour les chenilles qui constituent une important cause de mortalité sur certains sites. Les petites galles des grands capitules offrent les meilleurs possibilités de survie à *U. stylata* mais, en présence de fortes densités, ces conditions optimales sont rares; le rapport traite des raisons de ce phénomène.

Introduction

The gall fly *Urophora stylata* L. (Diptera: Tephritidae) infests flower heads of the Spear or Bull Thistle, *Cirsium vulgare* (Savi) Ten. (Compositae), in which its larvae induce hard, multilocular galls which reduce the production of viable seed by the plant (Redfern 1968, 1983; Zwölfer 1972).

Within the natural range of *C. vulgare*, the presence of this fly, and of other herbivores, may act to control the abundance of the plant (Zwölfer 1965; Redfern 1983). In North America where *C. vulgare* and other Cynareae (Compositae) introduced from Europe are serious agricultural weeds, *U. stylata* has been introduced as a biological control agent and achieves very high levels of infestation compared with most European populations (Harris 1984).

The life cycle and principal causes of mortality in *U. stylata* are well known (Persson 1963; Redfern 1968, 1983; Zwölfer 1972) and most causes can be determined after the event by inspection of gall-cells and their contents. Additional details of mortality and the biology of the parasitoids concerned are given in Claridge (1961), Varley (1937*b*, 1947) and Cameron and Redfern (1974).

Investigations of host-plant/gall fly interactions in *C. vulgare* and other Cynareae: Carduinae have concentrated on the effect on the plant (Zwölfer 1972; Baloch and Khan 1973; Harris 1980*a*, *b*; Myers and Harris 1980), on the regulation of the fly population (Varley 1947) and on aspects of the developing flower head which influence oviposition (Zwölfer 1972; Berube 1980). In this study, we concentrate on the effects of flower head size on probability of infestation, degree of infestation and subsequent mortality of *U. stylata* in populations within its natural range, and examine evidence that the pattern of infestation relates not only to food supply but also to the risk of death. The implications for the effectiveness of *U. stylata* as an agent of biological control of *C. vulgare* in areas where some mortality factors are absent is also briefly discussed, and related to more general hypotheses on foraging strategy (Hassell and Anderson 1984).

Table 1. Location of *Cirsium vulgare* (Savi) Ten. sites and dates of sampling.

Site	Grid reference	Altitude (m)	Habitat	No. plants in sample	Date of collection
Bayreuth University Campus, W. Germany (B82)	4470555326	350	Waste ground	5	10.viii.82
Rupertskapelle, W. Germany (R82, R83)	4456855310	390	Roadside verge	7 5	27.viii.82 14.viii.83
Oberwaiz, W. Germany (O82)	4462055340	430	Abandoned meadow	10	27.viii.82
Waldringfield, England (W82, W83)	150/TM 286443	< 15	Abandoned marshy meadow	8 5	20.xi.82 22.x.83

Materials and Methods

Spear thistle heads were sampled at four sites, three near Bayreuth, West Germany, and one at Waldringfield, Suffolk, England. All sites were sampled in 1982 and two resampled in 1983. Table 1 shows details of the sites.

At Bayreuth (B82) and Waldringfield (W82 and W83), the density of thistles was estimated using a point-centred method (Cottam and Curtis 1956), using random points within a gridded study area and measuring the distances from the points to the nearest thistle. The nature of the other sites made this technique impossible. At Oberwaiz (O82) and Rupertskapelle in 1982 (R82), an area was marked out and all thistles within it counted. No density estimate was carried out at Rupertskapelle in 1983 (R83).

At all sites except R82 and O82, an estimate of the degree of crowding, or proximate density, affecting each sample plant was obtained by counting the number of plants within a 5 m radius of the sample plant.

All heads of each sample plant were collected and bagged for subsequent laboratory examination. If numbers of heads were low, heads from the nearest neighbour were also collected, separately. In the laboratory, the size (maximum diam. between outer bracts) and state of development (bud, flower, dead) were recorded for each head, and their contained insect fauna was determined by dissection. For heads galled by *U. stylata*, the size of gall (maximum diam.), number of gall-cells and the fate of the contents of each were recorded. At some sites, drawings were made of each gall showing the position and fate of each cell. Other inhabitants of each head and any evidence of insect damage were also recorded. Methods of identifying causes of death are given in Redfern (1968).

Examination of the heads was a lengthy process and it was therefore necessary to deep-freeze some samples to preserve them prior to examination. This occasionally resulted in discolouration of *U. stylata* larvae, but comparisons with fresh-dissected material enabled such larvae to be assigned to appropriate categories without difficulty.

Although infestation by *U. stylata* varied between plants within each sample site, this variation was slight compared to between site variation and was, in any case, principally due to variation in infestation with head size, which is analysed in detail. For most purposes, therefore, all data from one site and year are pooled.

Results

Infestation by U. stylata *in Relation to Density, Size and Head Size of the Host Plant*

Table 2 gives the estimates of density, heads/plant, size of heads, % of heads infested and numbers of cells/head and cells/infested head. The point centre estimates were undoubtedly biased by the aggregated dispersion of the thistles and indicate only that density at Bayreuth (and, subjectively, at the other German sites) is considerably greater than at Waldringfield.

Estimates of proximate density, heads/plant and % of heads galled showed considerable variation between sites, but did not appear to be related.

The mean number of cells/head also varied markedly between sites. In all cases, the index of dispersion (variance/mean) was significantly > 1, indicating that cells were highly clumped in heads. There was no evidence of any relationship between degree of clumping and mean number of cells/head. Mean cells/head and mean head size were correlated ($r_4 = 0.87$, $p < 0.05$), as were mean cells/gall and the ratio variance:mean for head size ($r_4 = 0.86$, $p < 0.05$). Infestation was greater in populations of thistles with larger heads and, in populations of thistles with a high mean number of cells/infested head, the variation in head size was large relative to the mean. Mean head sizes were lower in 1983 than 1982 in the two sites sampled in both years, though in R 83 it is possible that further growth might have altered the mean.

Infestation by U. stylata *in Relation to Developmental Stage and Size of Head*

Details of % of heads with galls and number of cells/gall in relation to size and developmental stage of head are given in Appendix 1. No differences in either size or % of heads with galls could be detected between dead heads and those in full flower and so they are combined for comparison with buds.

Heads in bud were generally smaller than those that have completed their development. They were also heads whose development was late. Table 3 shows the range of bud size; the proportion of buds in each size class declined as the season advanced, except that heads of diam. 7 mm or less were always buds and (with only one exception) were never galled. Given the large size of some buds in the earliest

Table 2. Estimates of density, heads/plant and mean head size (± S.E.) of *Cirsium vulgare* (Savi) Ten. at the study sites, together with the levels of infestation and cells/gall of *Urophora stylata* L. Point centre estimates were not made in O82, R82 and R83 nor were proximate density estimates made at R82 and O82. In O82, an estimate of proximate density can be derived from the number of plants in an 85 m^2 plot. Plants were selected non-randomly at R83.

Site	Point centre plants/ha	Proximate density/m	Mean heads per plant	Head size: Mean diam. (mm) $\bar{x}$	Head size: Variance S^2	Head size: $S^2/\bar{x}$	Overall % heads with galls	No. cells/head: Mean $\bar{x}$	No. cells/head: Variance S^2	No. cells/head: Index of dispersion $S^2/\bar{x}$	Mean no. cells/gall
B82	350	0.16 ±0.04	64.2 ±44.4	14.30 ±0.23	21.50	1.50	10.7	0.38	1.95	5.13	3.59
R83	—	0.06 ±0.02	260.6 ±59.7	13.35 ±0.12	13.78	1.03	32.3	0.90	3.38	3.77	2.78
R82	—	—	50.1 ±17.6	19.04 ±0.36	42.75	2.24	62.9	2.53	9.45	3.73	4.02
O82	—	0.16	13.4 ± 3.1	22.33 ±0.68	60.24	2.70	87.6	8.22	63.40	7.71	9.38
W82	20	0.07 ±0.02	76.5 ±23.2	17.17 ±0.17	18.20	1.06	13.7	0.39	1.51	3.82	2.88
W83	10	0.01 ±0.004	76.8 ±35.4	14.07 ±0.22	17.75	1.26	8.3	0.28	1.25	4.43	3.40

Correlation coefficients: Head size $S^2/\bar{x}$ against mean cells/gall $r = 0.86$, $p < 0.05$. Mean no. cells/head against mean head size $r = 0.87$, $p < 0.05$.

sample B82, it is clear that late developing heads are smaller and, in the case of those still in bud in October and November (W82 and 83), probably never reach maturity. Heads < 8 mm in diam. are therefore omitted from further analysis.

Since % of heads with galls increased with head size (see below), the effect of developmental stage was examined within size classes. There are 18 possible comparisons (sample/size class categories in which both buds and fully developed heads occur), but in many of them, one or other category was represented by very small numbers. In 14 cases, the fully developed heads had a higher % of infestation and in 4, the buds did so ($X_1^2 = 5.5$, $p < 0.05$). Only two comparisons were individually significant (Table 4), both in the direction of higher infestation in developed heads. The number of cells/gall did not differ between buds and developed heads of the same size.

Table 3. Percent of heads which are buds by site and head size class. Sites arranged by date of sampling (— = no sample).

Sample	Date	Size classes (mm)						
		<8	8–11	12–15	16–19	20–23	24–27	28+
B82	10 Aug	100	92.8	73.3	31.0	3.5	6.7	—
R83	14 Aug	100	99.1	71.3	10.4	0	0	—
R82	27 Aug	100	98.6	60.7	0	0	0	0
O82	27 Aug	100	86.7	37.5	0	0	0	0
W83	22 Oct	100	61.4	17.5	3.1	0	0	—
W82	20 Nov	100	60.8	4.1	0.4	0	0	—

Table 4. Comparison of proportion of galled heads in buds and developed heads in two size classes of head at R83 (see text).

Head size:	12–15 mm			16–19 mm		
	Galled	Not galled	Total	Galled	Not galled	Total
Buds	61	231	292	2	17	19
Developed heads	71	46	117	116	47	163
Total	132	277	409	118	64	182
X^2		60.5			27.4	
p		<0.001			<0.001	

In all sites (and in both years), % of heads with galls and the mean number of cells/gall increased with increasing head size (Appendix 1 and Fig. 1). The increase in % infestation was most marked in samples with low overall % of galled heads and least at Oberwaiz, where the mean head size and overall % infestation were very high. There was, however, no relationship overall between % infestation and mean head size between sites.

Between sites, there was no relationship between % infestation and mean number of cells/gall in small heads, but signs of a positive relationship developed as head size increased (Table 5). This suggests multiple laying at high densities, when nearly all heads are galled.

This marked preference for large heads might simply be a function of space available for infestation. The achenes are arranged in a single plane and so the area of receptacle base should relate linearly to space available. This was not measured directly but can be estimated from head diameter. Since numbers of heads in some size-classes are small, any trends have been examined by amalgamating size-classes, and comparing the number of cells found in small (8–19 mm) and large (20+ mm) heads with the numbers expected if cells were distributed in proportion to area available (Table 6). In each case, there is an excess of cells in the large heads; i.e. the preference for large heads cannot be accounted for by available area alone. X^2 values for each comparison were all formally significant but it is doubtful if cells can be considered as truly independent (see below). Infestation of buds was erratic and not strictly comparable between sites. There was a negative relationship between the overall density of cells/unit area and the ratio of densities in large:small developed heads ($r = -0.87$, df 4, $p < 0.05$). At high levels of infestation, discrimination between heads declines.

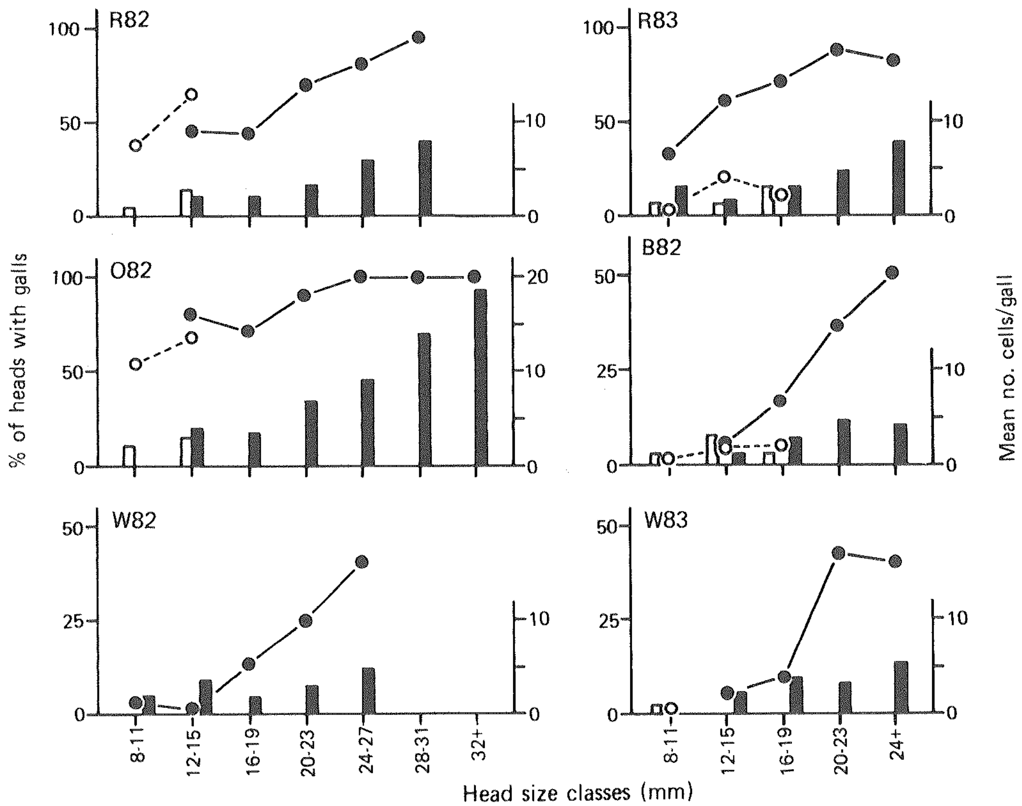

Fig. 1. Percent of heads with *Urophora stylata* L. and mean number of cells/gall by size of head in buds (○, □) and developed heads (●, ■) at six sites. R 82, R 83 = Rupertskapelle 1982 and 1983; O 82 = Oberwaiz 1982; B 82 = Bayreuth 1982; W 82, W 83 = Waldringfield 1982 and 1983.

Development of U. stylata *Relative to Head Size and Maturity*

At Oberwaiz and Waldringfield (both years) nearly all surviving *U. stylata* larvae were third instar and fully fed. In R 82, sampled at the same time as Oberwaiz, 11 third instar larvae out of 657 (1.7%) were not fully fed. Of these, seven were found in buds of 8–11 mm diam. (64% of all survivors in this size class). In the two earlier samples (B 82 and R 83), there were more larvae not fully fed (Table 7). In both, the proportion not fully fed declined with increasing head size. Samples were not large enough to investigate any differences between buds and developed heads of the same size, and it is an open question whether larvae in small heads develop more slowly or start their development later, or both.

Table 5. Correlations between % of heads with galls and mean number of cells/gall between sites by head size and development. In buds, there is no entry for W83 when there were no galls in buds.

Head stage	Size class	r	p
Buds	8–11	0.43	ns
Developed	12–15	0.31	ns
Developed	16–19	0.27	ns
Developed	20–23	0.70	ns
Developed	24–27	0.88	<0.05

Table 6. Distribution of cells by stage of head, head size and relative areas available to be galled. Since proportion of buds varies with season, mean cells/unit area, number of cells expected (on assumption of equal nos./unit area), X^2 and ratio cells/unit area in large and small heads are all based on developed heads only. B = buds, D = developed heads.

Site	Head size (mm)	Relative area	Cells/area	No. cells Observed	No. cells Expected	X^2 / p	Ratio cells/area in heads D 20+ / D 8–19
O82	B 8–19	25.1	1.07	27	—		
	D 8–19	69.7	1.02	71	94	6.2	
	D 20+	700.0	1.37	962	939	<0.05	1.34
	Mean		1.34				
R82	B 8–19	105.3	0.62	65	—		
	D 8–19	169.0	0.29	49	94	25.2	
	D 20+	1229.4	0.59	729	634	<0.001	2.03
	Mean		0.56				
R83	B 8–19	975.2	0.11	103	—		
	D 8–19	798.3	0.59	475	535	21.7	
	D 20+	360.8	0.83	300	240	<0.001	1.41
	Mean		0.67				
B82	B 8–19	397.5	0.04	15	—		
	D 8–19	246.8	0.09	23	56	32.0	
	D 20+	382.3	0.31	120	87	<0.001	3.44
	Mean		0.23				
W82	B 8–19	60.5	0.00	0	—		
	D 8–19	1075.9	0.06	62	126	65.8	
	D 20+	1085.3	0.18	191	127	<0.001	3.00
	Mean		0.12				
W83	B 8–19	120.6	0.002	1	—		
	D 8–19	551.2	0.08	45	74	42.5	
	D 20+	205.0	0.27	56	27	<0.001	3.37
	Mean		0.13				

Mortality in U. stylata

(a) General. The incidence of mortality and its causes at each site are given in Appendix 2 and summarized in Table 8. There was substantial variation between sites both in overall mortality and in that due to particular causes. Where sites were sampled in successive years, both overall mortality and that due to Lepidoptera and miscellaneous causes was higher in 1983.

Table 7. Numbers and proportions of *Urophora stylata* (L.) third instar larvae which are not fully fed in B82 and R83. (No dead not fully fed larvae were found in B82.)

Head size (mm)	Bayreuth 1982 Total surviving larvae	Larvae not fully fed No.	%	Total surviving larvae	Rupertskapelle 1983 Larvae not fully fed No.	%	Total dead larvae	Larvae not fully fed, dead No.	%
8 –11	2	2	100.0	4	3	75.0	8	5	62.5
12 –15	12	9	75.0	95	64	67.4	49	33	67.3
16 –19	15	7	46.7	141	40	28.4	78	36	46.2
20+	96	14	14.6	119	2	1.7	19	1	5.3

Overall mortality did not relate to cells/head or to cells/unit area, nor to time of sampling. Trends in overall mortality were followed by lepidopteran-caused deaths and those caused by unknown agencies, which were themselves weakly correlated (Table 8). Parasitism did not follow the same pattern; it correlated inversely with cells/unit area of head and this correlation was stronger in the ectoparasites than in the endoparasitic *Eurytoma tibialis* (Hymenoptera: Chalidoidea: Eurytomidae). Sparse infestations of *U. stylata* suffered more from parasitism than dense ones.

Further analysis of mortality is complicated. Cells in the same head were not independent in terms of mortality (there was an excess of all surviving and all dying in many cases), but the gall, or head, as a unit of sample was unsatisfactory because of the wide range of cells/head found. Standard statistical tests are thus technically invalid, even though the numbers of cells involved in particular comparisons were often large. Statistical tests were therefore generally avoided, the consistency of trends between samples being taken as the best guide to their reliability.

Table 8. (a) % mortality of *Urophora stylata* L. overall and by causes in relation to site and density/unit area of head. (b) Correlations between mortalities and density, and between selected mortality factors (all with 4 d.f.).

Site	Density cells/area	% mortality caused by						No. cells
		Overall	All parasites	Ectoparasites	*E. tibialis*	Lepidoptera	Other	
(a)								
O 82	1.33	50.4	5.5	5.0	0.5	29.3	13.9	1060
R 82	0.56	22.0	8.6	4.7	3.9	6.1	6.9	842
R 83	0.41	59.1	12.9	3.0	9.9	25.7	19.3	878
B 82	0.15	20.9	15.8	12.2	3.6	2.5	2.5	158
W 82	0.11	20.9	17.8	17.8	0.0	1.6	1.6	253
W 83	0.12	59.8	16.7	9.8	6.9	17.6	24.5	102

(b)

	Density	
	r	p
Overall	+ 0.26	ns
All parasites	− 0.94	< 0.01
Ectoparasites	− 0.60	ns
E. tibialis	− 0.32	ns
Lepidoptera	+ 0.65	ns
Other	+ 0.14	ns
Lepidoptera/other	+ 0.77	ns
Ectoparasites/*E. tibialis*	− 0.52	ns

(b) Mortality and head size. Figure 2 shows variation in mortality with flower head size. The two early samples (B 82 and R 83) showed no consistent trends but in the other four, mortality declined with increasing head size. *U. stylata* is safer in large heads and this is where it was found most frequently, both absolutely and in terms of cells/head area (see above).

Examination of individual causes of mortality required amalgamation of head size categories (Table 9). Excluding the two early sites where mortality may not be complete, ectoparasitism and miscellaneous deaths (mostly empty cells and shrivelled larvae) followed the trend seen in overall mortality, being lower in large heads. Deaths caused by *E. tibialis* showed no trend, however, and those caused by caterpillars actually increased in large heads in four of the samples. Causes of mortality are considered in more detail below.

(c) Mortality and cells/gall. Table 10 shows the variation in mortality with number of cells/gall. Some sites showed marked variation and others did not. Inspection of the original data indicated that for any given number of cells in a gall, mortality was lower in galls of larger size (measured diameter) and in larger heads. Gall diameter was, however, so closely connected to the other variables that it was not further analysed.

(d) Cells/gall, head size and mortality interactions. Cells/gall and head size were correlated and their covariation interacted with mortality. To retain large numbers of cells in each category, rather broad combinations of gall size and head size were used in analysis. To avoid excessive bias due to the lack of independence of cells in the same gall, only categories containing at least 20 cells in at least 5 galls were considered (Appendix 3).

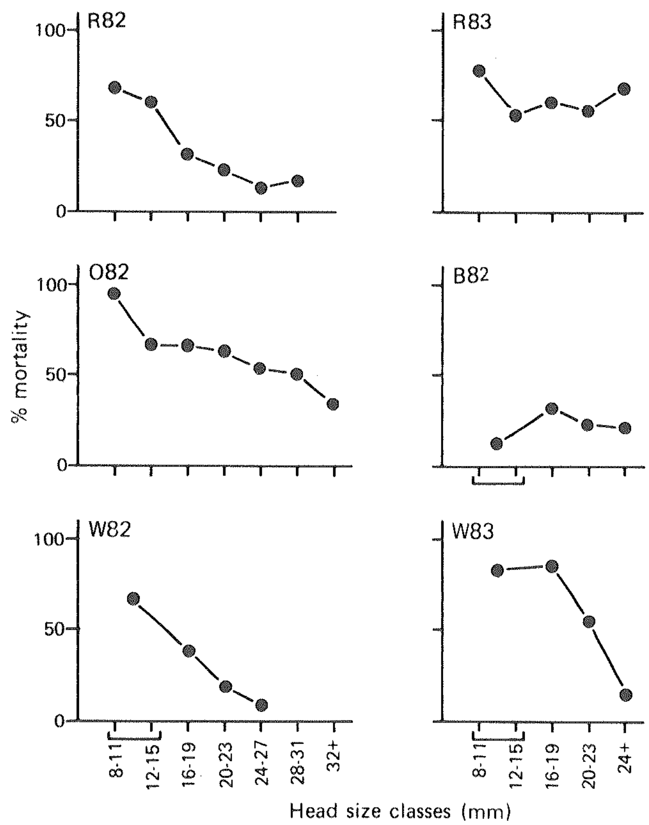

Fig. 2. Percent mortality of *Urophora stylata* L. by size of head. Sites as in Fig. 1.

Table 11 shows the variation in overall mortality at each site. With the exception of R83, within any cells/gall class, mortality declined with increasing head size but within any head size class, it increased with increasing number of cells/gall. In W83, where there were very few heads with more than six cells, a division on ± 3 cells showed the same trend.

Cells in buds showed higher mortalities in O82 and R82 than those in developed heads in the same size range. The buds did, however, have lower median sizes within the range than the developed heads, and the relative importance of size and development could not be assessed.

Table 9. Incidence of mortality (%), both overall and by course in small and large heads by site. The mean given in the last row is not weighted for sample size.

Head size:	8–19 mm						20+ mm					
	% mortality caused by						% mortality caused by					
Site	Overall	Ectoparasites	*E. tibialis*	Lepidoptera	Other	No. cells	Overall	Ectoparasites	*E. tibialis*	Lepidoptera	Other	No. cells
O 82	71.4	26.5	3.1	17.3	24.5	98	48.2	2.8	0.2	30.6	14.6	962
R 82	53.5	19.3	4.4	1.8	28.0	114	17.1	2.3	3.9	6.7	4.2	729
R 83	58.5	2.6	7.4	21.8	26.7	578	60.3	3.7	14.6	33.3	8.7	300
B 82	23.7	13.2	10.5	0.0	0.0	38	20.0	12.2	1.1	3.3	3.4	120
W 82	41.9	37.1	0.0	1.6	3.2	62	14.1	11.5	0.0	1.6	1.0	191
W 83	84.8	15.2	8.7	30.4	28.3	46	39.3	5.3	5.3	7.1	21.8	56
Mean	55.6	19.0	5.7	12.5	18.4	156	33.2	6.3	4.2	13.8	9.0	393

Numbers were reduced when specific causes of mortality were considered, and trends were more erratic (Table 12). Ectoparasites showed a consistent trend in the four later samples, with mortality being highest in small heads. In the early samples, the incidence of ectoparasitism may not have been complete at the time of sampling. Cells/gall had little effect. The endoparasite, *E. tibialis*, showed no clear trends and, in the two samples from Rupertskapelle where it was reasonably common, it appeared to be evenly distributed with respect both to head size and cells/gall. It was, however, rare in buds.

Table 10. Overall mortality (%) of *Urophora stylata* L. larvae in galls containing differing numbers of cells. Categories of cells/gall increase in range with increasing number to balance numbers in each category (— = no sample).

Sites	Number of cells/gall				
	1–2	3–5	6–9	10–14	15+
B82	16.1	8.9	22.9	47.6	—
R82	38.5	21.6	19.3	17.7	—
R83	58.1	58.9	57.2	70.0	—
O82	62.2	50.6	36.5	48.6	55.1
W82	34.2	15.0	18.6	—	—
W83	46.7	65.1	54.2	—	—

Table 11. Variation in overall mortality (%) with head size and number of cells/gall (— = no sample, B = buds, D = developed heads.)

Site	Cells/gall	Head size (mm)			
		B8–19	D8–19	D20–27	D28+
B82	1–6	—	30.4	11.4	—
	7–12	—	—	32.0	—
R82	1–6	67.7	34.7	14.4	4.2
	7–12	—	—	20.7	15.9
R83	1–6	46.6	60.5	59.6	—
	7–12	—	65.2	59.3	—
O82	1–6	100.0	67.5	31.8	16.7
	7–12	—	—	44.7	16.5
	13+	—	—	80.9	50.2
W82	1–6	—	41.9	14.6	—
	7–12	—	—	12.5	—
W83	1–3	—	72.2	20.0	—
	4+	—	92.9	46.3	—

Larger heads (and larger galls) might afford some protection from parasitism; if this is so, it appears to work only for the ectoparasites. In the three sites for which information is available and in which numbers of parasites are adequate, the ectoparasites tended to attack *U. stylata* larvae near the edge of the gall by comparison with *E. tibialis* (Table 13). Since number of cells/gall had little effect on ectoparasitism, it may be that in large heads the difficulty of detecting a small gall balances the difficulty of penetrating a large one.

Deaths caused by Lepidoptera showed one consistent trend: an increase as number of cells/gall increased, though there was a weak trend (reversed in W83) for small

Table 12. Incidence of particular causes of mortality (%) by site, head size and number of cells/gall (— = no sample).

Site	Ectoparasites				Eurytoma tibialis				Lepidoptera				Others			
	Head size (mm)															
	Buds	Developed heads			Buds	Developed heads			Buds	Developed heads			Buds	Developed heads		
Cells/gall	8–19	8–19	20–28	28+	8–19	8–19	20–28	28+	8–19	8–19	20–27	28+	8–19	8–19	20–27	28+
B 82																
1–6	—	13.0	7.1	—	—	17.4	1.4	—	—	0.0	2.9	—	—	0.0	0.0	—
7–12	—	—	18.0	—	—	—	2.0	—	—	—	4.0	—	—	—	8.0	—
R 82																
1–6	24.6	12.2	1.9	0.0	1.5	0.2	5.1	0.0	3.1	0.0	3.8	0.0	47.7	14.2	2.8	4.2
7–12	—	—	2.7	3.4	—	—	3.8	0.8	—	—	8.0	9.2	—	—	5.7	2.5
R 83																
1–6	1.9	1.9	4.1	—	1.9	8.2	15.1	—	14.5	22.9	30.1	—	28.2	27.5	10.3	—
7–12	—	10.9	3.0	—	—	13.0	14.1	—	—	28.3	33.1	—	—	13.1	8.9	—
O 82																
1–6	37.0	27.5	5.9	8.3	0.0	7.5	0.0	0.0	11.1	12.5	17.6	4.2	51.8	17.5	5.9	0.0
7–12	—	—	2.6	1.1	—	—	0.0	0.0	—	—	27.2	5.5	—	—	13.2	8.8
13+	—	—	4.4	2.0	—	—	0.0	0.4	—	—	51.4	34.0	—	—	25.2	12.3
W 82																
1–6	—	37.1	12.6	—	—	0.0	0.0	—	—	1.6	1.3	—	—	3.2	0.7	—
7–12	—	—	7.5	—	—	—	0.0	—	—	—	2.5	—	—	—	2.5	—
W 83																
1–6	—	22.2	6.2	-	—	5.5	6.2	—	—	27.8	8.3	—	—	27.8	25.1	—

heads to be less attacked. Most of the caterpillars seen were *Eucosma cana* (Haworth) (Lepidoptera: Tortricidae) and damage to heads and the frass produced were easily recognised in the absence of caterpillar. At least one other species was present but unidentified.

The caterpillars feed on the receptacle, achenes and florets. They eat gall tissue where present and may incidentally kill *U. stylata* larvae. Damage by caterpillars was recorded for all heads, with and without galls. It may have been underestimated (in terms of final effects) in the earliest samples, although there was no relationship between proportion of heads damaged and time of sampling.

In general, frequencies of damaged heads increased as head size increased (Fig. 3). Amongst the larger heads, there was no evidence that galled heads were more liable to damage but, in four of the six samples, smaller heads with galls were significantly more liable to damage than those without (Table 14). When *E. cana* infested smaller heads, it appeared to prefer those with galls.

Table 13. Numbers of parasitized *Urophora stylata* L. larvae in different positions in galls. The categories are arbitrary, hence only differences between parasites can be tested. Drawings of galls were not made in B82, and in W82 no *Eurytoma tibialis* were recorded.

Site	Endoparasite *Eurytoma tibialis*		Ectoparasites		X^2 contingency
	Central	Edge	Central	Edge	
R82	18	15	2	37	21.7 $p < 0.001$
R83	22	65	0	26	8.2 $p < 0.01$
O82	3	2	10	44	4.5 $p < 0.05$
W83	1	6	4	6	ns trend reversed

Table 14. Percent of heads damaged by Lepidoptera by head size and infestation with *Urophora stylata* L. R = ratio galled: ungalled; p = probability less than given figure (X^2 contingency tables); ns = not significant. (Numbers of heads involved given in Appendix 1.)

Head size	8–19 mm				20+ mm			
	Not galled	Galled	R	p	Not galled	Galled	R	p
B82	13.6	25.0	1.8	ns	37.8	60.7	1.6	ns
R82	17.3	24.2	1.4	ns	62.2	67.1	1.1	ns
R83	19.3	42.4	2.2	0.001	88.9	85.5	1.0	ns
O82	14.2	54.8	3.9	0.02	100.0	88.0	0.9	ns
W82	21.5	39.4	1.8	0.05	26.4	38.2	1.4	ns
W83	25.4	73.3	2.9	0.001	47.6	60.0	1.3	ns

As expected, the incidence of damage in gall heads and lepidopteran-caused mortality were correlated (Fig. 4). The relationship appears curvilinear (log transformed slopes > 1), suggesting that when the proportion of heads damaged was high, the amount of damage done to each head (which was not estimated) was also high.

The residual mortality (mostly empty cells and shrivelled larvae) showed broadly the same trends as overall mortality. Although the incidence of this mortality between sites correlated well with lepidopteran-caused deaths, its incidence within sites was different in that buds were usually the worst affected.

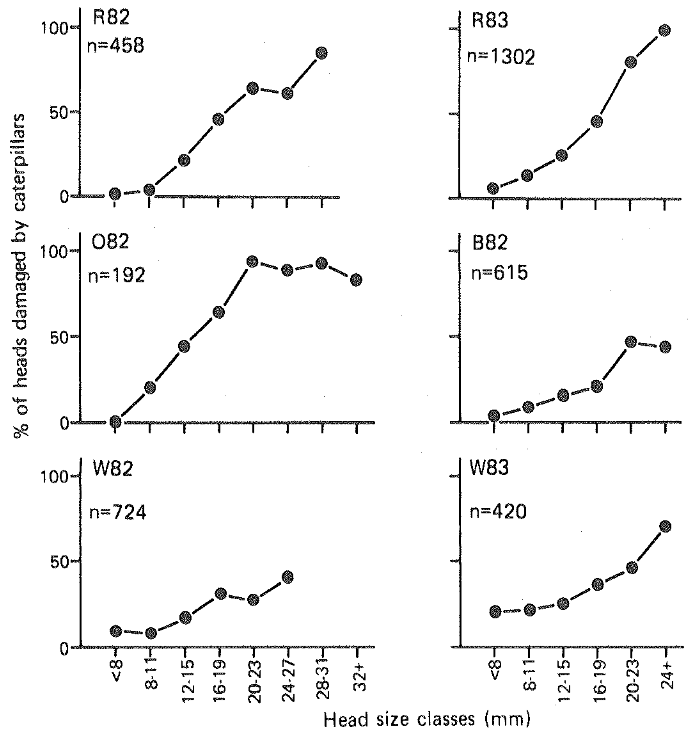

Fig. 3. Percent of heads with lepidopteran damage by size of head (including heads < 8 mm diam. not included elsewhere). Sites as in Fig. 1.

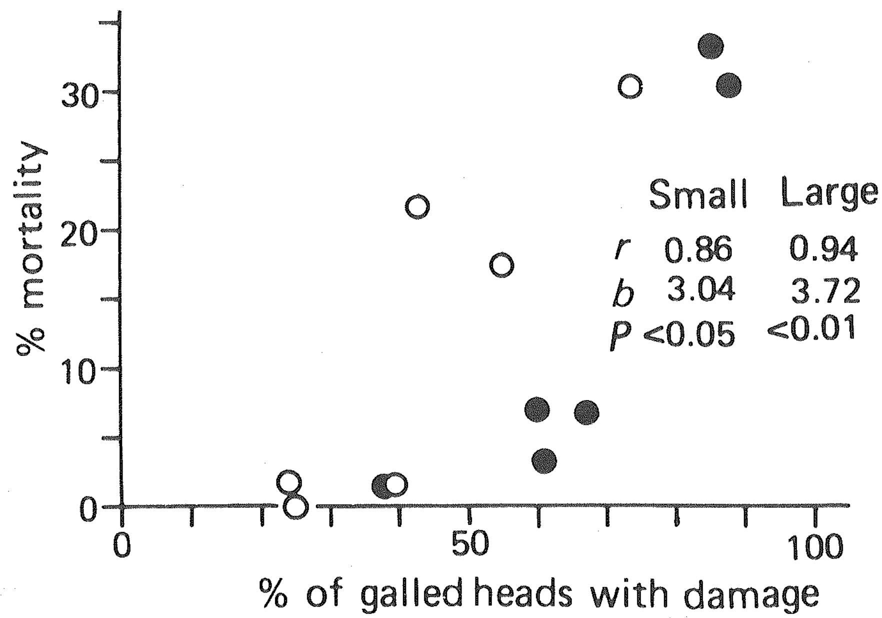

Fig. 4. Percent mortality of *Urophora stylata* L. caused by caterpillars against % of galled heads with lepidopteran damage, for small (8–19 mm, ○) and large (20+ mm, ●) heads.

Discussion

With certain particular exceptions, discussed below, this study revealed clear and consistent patterns of infestation of *C. vulgare* heads by *U. stylata* and demonstrated connections between these and the incidence of larval mortality in *U. stylata*. Before conclusions are drawn, however, it is necessary to consider certain incomplete aspects of this study.

Most importantly, not all the possible factors affecting the likelihood of infestation have been considered. The positions of the heads on the plants were not noted; they are probably related to timing of development and to ultimate sizes achieved but could have an effect on likelihood of infestation independently of those variables.

There is also relatively little information here on the timing of development relative to infestation. Other studies (Varley 1947; Zwölfer 1972; Baloch and Kahn 1973; Berube 1980; Harris 1980*a*, 1984) have shown that oviposition is only successful over a narrow range of bud development both in this species and in other tephritid/composite systems. *U. stylata* adults are, however, present for about two months and it seems that heads developing at most periods within the overall flowering season are at risk of infestation. Only very late-developing buds are free, as in W82 and W83, and observations here and elsewhere (Harris 1984) suggest that mown thistles surviving and flowering late may avoid infestation completely. The proportion of late-flowering heads which set seed is unknown; one could speculate that length and timing of flowering season might be affected in populations subject to persistent and heavy infestation.

In many of our sites, levels of infestation differed between plants and this seems to relate to the mean size of heads. This, in turn, may reflect a diversity in the timing of development between plants which would affect levels of infestation and consequent loss of fertility; that heavy infestation has substantial effects on fertility is well documented (Zwölfer 1972; Harris 1984).

It also seems likely that infestation affects head size. At O82, all the largest heads were infested. In other gall fly/seed head systems, developing galls sequester plant resources (Harris 1980*b*) and it is possible that infestation increases the size of infested heads while reducing the size, and possibly number of, later-developing uninfested heads. The small numbers and large size of heads found at O82 may be a product of heavy infestation. Nevertheless, large uninfested heads occurred at all other sites and it seems unlikely that the difference in mean diameters of infested and uninfested heads was simply a consequence of infestation itself. It is possible, however, that the between-site correlation of mean head size and level of infestation was due, in part, to such a direct effect, a conclusion supported by the higher variability of head size in heavily infested populations.

Attempts to estimate the density of plants in the study areas were not wholly successful. This is a recurrent problem for *C. vulgare*, populations of which tend to be patchy, transient and situated in places (e.g. roadside verges) where orthodox sampling techniques are difficult to apply. There was no evidence in our results of any clear relationship between density (either over a large area or in terms of nearest neighbours) on pattern and level of infestation (Myers and Harris 1980), although other work (Harris 1984) suggests that populations of *C. vulgare* need to be relatively large and persistent to support populations of *U. stylata*. Size of plant (as measured by number of heads) also appeared to be irrelevant to the pattern of infestation, as Harris (1984) also concluded. Both these aspects of host-plant biology need more investigation.

Finally, these studies, by their timing, did not give a complete account of larval and pupal mortality, and some cover a greater span of time than others. In the earliest samples (B82 and R83), ectoparasitism may have been incomplete and, in all but the latest samples (W82 and W83) more damage by Lepidoptera was possible.

These reservations limit our understanding of the causes of patterns of infestation and mortality, but not of their character or consequences. In each site, levels of infestation and numbers of cells/infested head increased with increasing head size. The distribution of cells was clumped, and the greater intensity of infestation of large heads was not simply a product of their greater area.

This selectivity may result from oviposition behaviour or from egg and larval mortality prior to gall formation, or both. Eggs may be laid singly or in small groups (5–10, Persson 1963). Zwölfer (1972) describes the stimuli which determine choice of head by *U. stylata* but there is little evidence on searching strategies of females; in *U. affinis* Frauenfeld, there is no correlation between fly density and *Centaurea* flower head density (Myers and Harris 1980). Likewise, we do not know if female *U. stylata* can detect the presence of other eggs, though the related *U. quadrifasciata* (Meigen) (Varley 1937*a*) and *Tephritis dilacerata* Loew (Berube 1978) apparently cannot. Galls with large numbers of cells are likely to be the product of more than one laying and, since these are frequent, it suggests that *U. stylata* has, at most, very limited powers of detecting earlier oviposition.

There are many accounts indicating that tephritids select particular bud sizes and developmental conditions for oviposition (Varley 1937*a*; Zwölfer 1972, 1977; Myers and Harris 1980; Berube 1980) but it is not clear how these sizes relate, if at all, to achieved size in the fully developed head.

Very little is known of larval competition prior to gall formation. Random laying of clutches will produce a clumped distribution of individuals but, at high levels of infestation, such clumping will be reduced by larval competition. The decline in selection of large heads with increasing levels of infestation seen here suggests that such competition may be occurring, and a decline in clumping at peak densities is recorded for *U. quadrifasciata* on *Centaurea* by Myers and Harris (1980).

Competition before gall formation cannot be a sole explanation of any decline in clumping, since individual heads, even at high intensities of infestation, may have 2–3 times more cells than the mean for their size (maximum of 46 cells in one head at O82). Possible competition after gall formation is considered further below.

Patterns of mortality in these samples have a general resemblance to those recorded for *U. stylata* elsewhere (Redfern 1968; Zwölfer 1972; Cameron and Redfern 1974) and for *U. jaceana* (Varley 1947). Attacks by parasitic Hymenoptera and lepidopteran larvae are the most important causes of mortality between the formation of the gall and the death of the plant. Both overall mortality and that due to particular causes varies considerably between samples. The incidence of mortality appears to be unrelated to levels of infestation, except for that caused by parasites (and particularly ectoparasites), which is heaviest at low levels of infestation. The conclusions of Varley (1947), coupled with the generally higher levels of infestation by *U. stylata* in introduced populations of *C. vulgare* in North America, where parasites are absent (Harris 1984), suggest that parasites regulate the density of *U. stylata*; if so, populations within the natural range must occasionally break through levels within which parasite regulation operates, as seen here at Oberwaiz and Rupertskapelle. At Oberwaiz, levels of infestation matched those seen in introduced populations. Extended studies of populations over several generations are needed to enable firm conclusions to be drawn.

The most important conclusion to be drawn from this study is that risk of dying is not the same for all *U. stylata* larvae. Except in B82 and R83 (sampled early), larvae in buds and small heads had a greater risk of dying than those in large heads and, within the large heads, those at high densities (cells/head) were more at risk than those at low densities. We cannot yet be sure that this non-random distribution of risk is a direct consequence of head size *per se*, as factors such as timing of development and position on plant of the heads may also be important. What we do know is that this distribution of risk matched the distribution of *U. stylata* larvae in the four later samples: larvae were concentrated where the risk of dying is least.

Many studies have investigated the searching behaviour and success rate of insect parasites in relation to the density, distribution and availability of their hosts, and to their own density and mutual interference (Krebs 1978; Hubbard and Cook 1978; Hassell and Anderson 1984). Such studies have often attempted to determine to what extent the parasite is pursuing an 'Optimum Foraging Strategy' which will maximize its success in the prevailing circumstances.

For herbivores such as *U. stylata*, risks of death are arguably as important a determinant of success as the detection and utilization of food. To what extent does *U. stylata* possess an 'Optimum Infestation Strategy'? The evidence here is incomplete, because we do not have data on mortality over the whole life cycle and, in the early samples (B 82 and R 83), there may have been serious underestimates of several mortality factors. The individual causes of mortality also varied considerably between sites, and each cause had a different pattern of incidence with respect to head size.

The consistent preference for large heads (even when account is taken of area of head available) would appear to be a successful strategy for minimizing attack by ectoparasites and will be, therefore, most successful where this cause of death is greatest, both relatively and absolutely. It appeared to be neutral with respect to attack by *E. tibialis* and counterproductive with respect to attacks by lepidopteran larvae, whose effects were greatest in large heads, especially when number of cells/head was large. The effects of larval competition (before or after gall formation) are at present indeterminate but might also limit the advantage of selective oviposition in large heads, especially at high levels of infestation.

It is worth noting that deaths caused by ectoparasites were the least variable between sites and, therefore, the most predictable over the longer term in which selection for a strategy might operate. Such deaths were also most significant when the levels of infestation were low, which was when the concentration of larvae in large heads was greatest. By contrast, other causes of mortality were more variable between samples and were greatest relative to ectoparasitism in R 83, where it appeared that risk of death was the same in all head and gall sizes. The incidence of mortality other than that caused by ectoparasites may explain, therefore, why small heads were also galled; there are circumstances in which it may have been advantageous or, as in R 83, in which infestation was optimal in the sense that risk was the same throughout and presumably at an overall minimum.

If such a strategy is innate and unresponsive to short-term fluctuations in causes of mortality, it may limit the usefulness of *U. stylata* as an agent of biological control in areas lacking parasites. Small heads may escape infestation even when there is larval competition in large ones, and seed production will be greater than if larvae were distributed at random (Zwölfer 1972). It will be interesting to see if *U. stylata* modifies its strategy in circumstances, as in North America, in which parasites are absent.

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Appendix 1. Number of buds and developed heads of increasing size infested by *Urophora stylata* L. at six sites. (All plants at each site combined.)

Site		Head size (mm)							
		2–7	8–11	12–15	16–19	20–23	24–27	28–31	32+
Bayreuth 1982									
Buds	No. heads	201	129	96	22	2	1	0	0
	No. galls	0	2	4	1	0	0	7	
	% heads with galls		1.6	4.2	4.5				
	No. cells		2	12	1				
	No. cells/gall		1.00	3.00	1.00				
	No. cells/head		0.02	0.13	0.04				
Developed heads	No. heads	0	10	35	49	55	14	0	0
	No. galls		0	2	8	20	7		
	% heads with galls			5.7	16.3	36.4	50.0		
	No. cells			2	21	91	29		
	No. cells/gall			1.00	2.62	4.55	4.14		
	No. cells/head			0.06	0.43	1.65	2.07		
Rupertskapelle 1982									
Buds	No. heads	124	71	17	0	0	0	0	0
	No. galls	1[1]	27	11					
	% heads with galls	0.8	38.0	64.7					
	No. cells	1	35	30					
	No. cells/gall	1.0	1.30	2.72					
	No. cells/head	0.008	0.49	1.76					
Developed heads	No. heads	0	1	11	43	98	72	21	0
	No. galls		0	5	19	68	58	20	
	% heads with galls			45.5	44.2	69.4	80.6	95.2	
	No. cells			10	39	233	340	156	
	No. cells/gall			2.00	2.05	3.38	5.86	7.80	
	No. cells/head			0.91	0.91	2.35	4.72	7.43	

Rupertskapelle 1983									
Buds	No. heads	323	321	292	19	0	0	0	0
	No. galls	0	11	61	2				
	% heads with galls		3.4	20.9	10.5				
	No. cells		15	82	6				
	No. cells/gall		1.36	1.34	3.00				
	No. cells/head		0.05	0.28	0.32				
Developed heads	No. heads	0	3	117	163	48	16	0	0
	No. galls		1	71	116	42	13		
	% heads with galls		33.3	60.7	71.2	87.5	81.3		
	No. cells		3	120	352	199	101		
	No. cells/gall		3.00	1.69	3.03	4.74	7.77		
	No. cells/head		1.00	1.03	2.16	4.15	6.31		
Oberwaiz 1982									
Buds	No. heads	63	13	6	0	0	0	0	0
	No. galls	0	7	4					
	% heads with galls		53.8	66.7					
	No. cells		15	12					
	No. cells/gall		2.14	3.0					
	No. cells/head		1.15	2.0					
Developed heads	No. heads	0	2	10	14	18	25	29	12
	No. galls		2	8	10	16	25	29	12
	% heads with galls		100.0	80.0	71.4	88.9	100.0	100.0	100.0
	No. cells		4	32	35	109	226	404	223
	No. cells/gall		2.00	4.00	3.50	6.81	9.04	13.93	18.58
	No. cells/head		2.00	3.20	2.50	6.05	9.04	13.93	18.58
Waldringfield 1982									
Buds	No. heads	83	45	6	1	0	0	0	0
	No. galls	0	0	0	0				
Developed heads	No. heads	0	29	139	226	153	42	0	0
	No. galls		1	2	30	58	17		
	% heads with galls		3.4	1.4	13.3	24.8	40.5		
	No. cells		2	7	53	109	82		
	No. cells/gall		2.00	3.50	1.77	2.87	4.82		
	No. cells/head		0.07	0.05	0.23	0.71	1.95		

Appendix 1 (continued)

Site		Head size (mm)							
		2–7	8–11	12–15	16–19	20–23	24–27	28–31	32+
Waldringfield 1983									
Buds	No. heads	58	70	20	3	0	0	0	0
	No. galls	0	1	0	0				
	% heads with galls		1.4						
	No. cells		1						
	No. cells/gall		1.00						
	No. cells/head		0.01						
Developed heads	No. heads	0	44	94	95	26	10	0	0
	No. galls		0	5	9	11	4		
	% heads with galls			5.3	9.5	42.3	40.0		
	No. cells			11	34	35	21		
	No. cells/gall			2.20	3.78	3.18	5.25		
	No. cells/head			0.12	0.36	1.34	2.10		

[1]This gall is omitted from all analyses.

Appendix 2. Infestation of thistle heads (buds + developed heads) and survival and mortality (numbers) of *Urophora stylata* L. (*Us*) in heads of increasing size (mm).

Head diameter (mm)	No. heads	Galled heads No.	Galled heads %	Cells/gall No.	± SE	Cells/head	No. cells	No. *Us* survived	No. parasitized by[1] Total	*Et*	*Pe*	*Tc*	*Er*	No. killed by Lep.	Other
Bayreuth 1982	10 August														
2–7	201	0	0		—	—	0	—	—	—	—	—	—	—	—
8–11	139	2	1.4		—	0.01	2	2	0	0	0	0	0	0	0
12–15	131	6	4.6	2.33	1.81	0.14	14	12	2	0	0	1	1	0	0
16–19	71	9	12.7	2.44	0.56	0.31	22	15	7	4	0	2	1	0	0
20–23	57	20	35.1	4.55	0.61	1.59	91	70	15	1	0	11	3	2	4
24–28	16	8	46.6	4.14		1.93	29	26	1	1	0	0	0	2	0
Rupertskapelle 1982	27 August														
2–7	124	1	0.8	1	—	0.008	1	—	—	—	—	—	—	—	—
8–11	72	27	37.5	1.30	0.13	0.49	35	11	10	0	2	8	0	1	13
12–15	28	16	57.1	2.50	0.32	1.43	38	15	10	1	1	8	0	1	12
16–19	43	19	44.2	2.05	0.25	0.91	39	27	7	4	1	2	0	0	5
20–23	98	68	69.4	3.38	0.45	2.35	233	180	21	15	1	5	0	19	13
24–27	72	58	80.6	5.86	0.36	4.72	340	294	18	11	2	5	0	14	14
28–32	21	20	95.2	7.80	0.70	7.43	156	130	6	2	1	3	0	16	4
Rupertskapelle 1983	14 August														
2–7	323	0	0	0	—	—	—	—	—	—	—	—	—	—	—
8–11	324	12	3.7	1.50	0.23	0.06	18	4	0	—	—	—	—	6	8
12–15	409	132	32.3	1.53		0.49	202	95	11	9	1	0	1	40	56
16–19	182	118	64.8	2.71		1.76	358	141	47	34	3	6	4	80	90
20–23	48	42	87.5	4.73		4.14	199	87	33	27	3	3	0	61	18
24–29	16	13	81.3	7.77		6.31	101	32	22	17	3	2	0	39	8

Appendix 2 (continued)

Head diameter (mm)	No. heads	Galled heads No.	Galled heads %	Cells/gall No.	± SE	Cells/head	No. cells	No. *Us* survived	No. parasitized by[1] Total	*Et*	*Pe*	*Tc*	*Er*	No. killed by Lep.	Other
Oberwaiz 1982 27 August															
2–7	63	0	0	—	—	—	—	—	—	—	—	—	—	—	—
8–11	15	9	60.0	2.11	0.42	1.27	19	1	6	0	0.7	5.3	0	2	10
12–15	16	12	75.0	3.67	1.04	2.75	44	15	14	3	2.7	8.3	0	5	10
16–19	14	10	71.4	3.50	0.95	2.50	35	12	9	0	5.4	2.6	1	10	4
20–23	18	16	88.9	6.81	1.28	6.05	109	40	3	0	2.4	0.6	0	28	38
24–27	25	25	100.0	9.04	1.01	9.04	226	107	11	0	3.4	7.6	0	88	20
28–31	29	29	100.0	13.93	1.30	13.93	404	203	9	2	1.4	5.6	0	132	60
32+	12	12	100.0	18.58	3.24	18.58	223	148	6	0	2.4	3.6	0	46	23
Waldringfield 1982 20 November															
2–7	83	0	0	0	—	—	—	—	—	—	—	—	—	—	—
8–11	74	1	1.4	2.00		0.03	2	0	2	0	0	2	0	0	0
12–15	145	2	1.4	3.50		0.05	7	3	3	0	3	0	0	1	0
16–19	227	30	13.2			0.23	53	33	18	0	15	3	0	0	2
20–23	153	38	24.8	2.87		0.71	109	89	19	0	15.8	3.2	0	1	0
24–28	42	17	40.5	4.82		1.95	82	75	3	0	2	1	0	2	2
Waldringfield 1983 22 October															
2–7	58	0	0	—	—	—	—	—	—	—	—	—	—	—	—
8–11	114	1	0.9	1		0.01	1	0	0	0	0	0		1	0
12–15	114	5	4.4	2.20		0.01	11	2	4	0	0	4	0	1	4
16–19	98	9	9.2	3.78		0.35	34	5	7	4	0	3	0	12	10
20–23	26	11	42.3	3.18		1.34	35	16	6	3	0	3	0	1	12
24–29	10	4	40.0	5.25		2.10	21	18	0	0	0	0	0	3	0

[1] *Et* = *Eurytoma tibialis*; *Pe* = *Pteromalus elevatus*; *Tc* = *Torymus chloromerus*; *Er* = *Eurytoma robusta*; Lep. = Lepidoptera larvae

Appendix 3. Survival and mortality (numbers) of *Urophora stylata* L. (*Us*) in relation to number of cells per gall and head size. B = buds, D = developed heads, other abbreviations as in Appendix 2.

Cells/gall	Head diameter (mm)	No. cells	No. *Us* survived	No. *Us* died	Deaths caused by *Et*	*Pe*	*Tc*	*Er*	Lep.	Other
Bayreuth 1982										
B1–6	8–19	15	13	2	0	0	1	1	0	0
D1–6	8–19	23	16	7	4	0	2	1	0	0
D1–6	20+	70	62	8	1	0	5	0	2	0
D7–12	20+	50	34	16	1	0	6	3	2	4
Rupertskapelle 1982										
B1–6	8–19	65	21	44	1	3	13	0	2	25
D1–6	8–19	49	32	17	4	1	5	0	0	7
D1–6	20–27	312	267	45	16	2	4	0	12	11
D1–6	28+	24	23	1	0	0	0	0	0	1
D7–12	20–27	261	207	54	10	1	6	0	21	16
D7–12	28+	119	100	19	1	1	3	0	11	3
Rupertskapelle 1983										
B1–6	8–19	103	55	48	2	1	0	1	15	29
D1–6	8–19	428	169	259	35	1	6	1	98	118
D1–6	20+	146	59	87	22	4	2	0	44	15
D7–12	8–19	46	16	30	6	2	0	3	13	6
D7–12	20+	135	55	80	19	2	2	0	45	12
Oberwaiz 1982										
B1–6	8–19	27	0	27	0	4	6	0	3	14
D1–6	8–19	40	13	27	3	3	8	0	5	8
D1–6	20–27	85	58	27	0	5		0	15	7
D1–6	28+	24	20	4	0	2		0	1	1
D7–12	20–27	114	63	51	0	3		0	31	17
D7–12	28+	91	76	15	0	1		0	5	9
D13+	20–27	136	26	110	0	6		0	70	34
D13+	28+	512	255	257	2	10		0	174	71
Waldringfield 1982										
D1–6	8–19	62	36	26	0	18	5	0	1	2
D1–6	20+	151	129	22	0	17	2	0	2	1
D7–13	20+	40	35	5	0	1	2	0	1	1
Waldringfield 1983										
D1–6	8–19	36	7	29	2	0	7	0	10	10
D1–6	20+	48	26	22	3	0	3	0	4	12