20. The ecology of the pea galls of *Cynips divisa*

FRANCIS GILBERT, CHARLOTTE ASTBURY,
JENNY BEDINGFIELD, BRUCE ENNIS,
SAMANTHA LAWSON, and TRACEY SITCH

Department of Life Science, University of Nottingham, Nottingham, UK

Abstract

The results of a long-term study into the population ecology of pea galls is presented. Pea galls are produced by the agamic generation of the cynipid gall wasp *Cynips divisa* Hartig and they were studied over the period 1985–1991. Population biology is the sum effect of variations in fitness between individuals, variations which are determined by life history parameters. Components of fitness were measured for a large sample, calculating survival, size, fecundity, and maturity at eclosion: the fitness consequences of ovipositional decisions made in positioning the gall on different trees, leaves, and positions within leaves are analysed. Evidence for a 6–7 year population cycle is discussed.

Introduction

Understanding the structure and dynamics of communities of species is a central problem in ecology, particularly in view of new ideas about food webs (Pimm and Lawton 1979; Lawton 1989) and population dynamics (Hassell *et al.* 1991). Marrying up these contrasting disciplines in an integrated view of populations embedded within communities will be a difficult task, since ecologists have different ideas about the importance of the various forces involved (for example, top-downs vs bottom-up controls on population and community dynamics; Matson and Hunter (1991)). Recently there has been a lot of interest in interactions between more than two trophic levels, usually concentrating upon the nature of

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the interaction between plants, herbivores, and parasitoids (Price *et al.* 1980; Zwölfer 1987; Tscharntke 1992). Herbivores are subject to selection pressures from both the defensive mechanisms of the plant and attack by parasitoids. What determines their fitness under these conditions?

We have been studying this question since 1985 using the pea galls of the agamic generation of the cynipine gall wasp *Cynips divisa* Hartig, a relatively well-studied system (see Askew 1960, 1961*a,b*, 1965, 1975, 1985; Sitch *et al.* 1988). Gall systems are particularly useful for studying this since their position is fixed at the outset; the consequences of the decision-making process of oviposition or settlement by the female can then be assessed (for example Whitham 1980; Sitch *et al.* 1988). The relationship between the gall maker and the plant is a fascinating but elusive problem (Askew 1985; Crawley 1985; Abrahamson and Weis 1987; Weis *et al.* 1988; see reviews in Shorthouse and Rohfritsch 1992), as is the exact evolutionary advantage of creating the gall (Abrahamson and Weis 1987; Price *et al.* 1987; Cornell 1990; Hartley and Lawton 1992). Our studies on pea galls have been hampered by great year to year fluctuations in gall densities, including some years of very high mortality, but these changes in abundance have themselves proved very interesting. Long-term data on non-economic insect populations are becoming more available (for example Wolda 1983; Owen and Gilbert 1989), including some galling insects (Miyashita *et al.* 1965; Redfern and Cameron 1978; Washburn and Cornell 1981; Moran and Whitham 1988; Wool 1990).

We report here on data gathered between 1985 and 1991 to investigate two questions: first, is there any long-term pattern to population densities? and, second, is there any evidence for positional effects in components of fitness?

Materials and methods

Cynips divisa has a heterogonic life cycle with a sexual generation from red wart galls on oak buds, followed by an agamic generation from pea galls on the leaves (Askew 1985). The species has a wide distribution in the British Isles, from the Isle of Wight (D.E. Biggs, personal communication) to Scotland (C.K. Leach, personal communication). Mapping schemes are currently being undertaken (for example Bowdrey 1987; Griffiths *et al.* 1990), but it will be some time before we have an accurate indication of the distribution. Most records appear to be of a few scattered galls, quite unlike the situation in Oxford in 1958, where Askew (1961*a*) records them as very common.

We collected galled leaves from young oaks in Clumber Park, Nottingham during August and September, each year when they were available between 1985 and 1991. In 1991 galls were abundant on several trees, as in 1985 and samples were taken from eight different trees: a large sample was taken from one single tree with a high proportion of leaves galled. Galls were concentrated on the leaves of young oaks growing under the canopy of older larger oaks (Askew (1961*a*) notes that his pea galls were collected from oaks only 9 years old): because of the extreme patchiness of galled leaves between and within trees, only leaves with galls were collected. The position of galls (aborted or otherwise) was recorded according to the scheme reported in Sitch *et al.* (1988); briefly, the vein number, side of the leaf (left or right of the midrib) were all recorded for individual leaves. In addition, the length of the midrib and in most cases the maximum width of each leaf was measured. The width of individual galls was measured under the microscope using an eyepiece graticule and their weights measured using a Cahn 23 electrobalance: the weight of the wasp in the gall was later removed to leave the true weight of the gall alone. Galls were then dissected. At this stage the rare thin-walled galls of the related *Cynips agama* Hartig were obvious. The gall contents were identified to generic level using the key developed by Askew (1985; and personal communication) (see Sitch *et al.* 1988).

If the gall maker had survived, adult female wasps were in the gall awaiting emergence: females were removed and four measurements taken (wing length in mm, fresh body weight to the nearest 0.1 mg, fresh weight of the abdomen alone to the nearest 0.1 mg, and on dissection the number of eggs in the abdomen). No weights were taken in 1985; since survival was only again high in 1991, all analyses of fitness components refer only to this year. Parasitic inhabitants of the gall were identified, removed, and weighed (fresh weight) to the nearest 0.1 mg in 1988, but not in other years.

Females eclose from the pupa with an abdomen full of stored material from the pupal fat body, which they then use to mature their eggs. On natural emergence from the gall the eggs are completely or almost completely developed (personal observation). We counted the number of matured eggs in the ovarioles by dissecting the abdomen in Griffith's Ringer under a binocular microscope.

We then calculated several fitness components from these data: survival (the percentage of all galls that produce female wasps), fecundity (the number of eggs in the abdomen), size (body weight in mg), relative weight (standardized deviation from the double-log regression line that predicts body mass from wing length), allocation to reproduction (percentage of the total body mass represented by the abdomen), and degree of maturity (standardized deviation from the double-log regression line that predicts the number of eggs from wing length).

Calculations were performed using the SPSS statistical package implemented on an ICL mainframe computer. All mean values in the text and on graphs are quoted ± 1 standard error. Standard errors of proportions and percentages were calculated from the equation

$$SE = \sqrt{((p(p - 1/(n - 1))}$$

where p = proportion and n = sample size.

Results

1. *Overall patterns in fitness components*

Gall weight (all, 31.7 ± 0.6 mg, range 1–84; with surviving wasps, 47.4 ± 0.7 mg, range 19.5–77.0) was, not surprisingly, strongly related to gall diameter^3, an index of gall volume ($r^2 = 0.76$, $n = 849$). Gall weight was also related ($r^2 = 0.23$, $n = 397$, $p \ll 0.001$) to the weight of the female wasp, where she survived (slope $= 0.040 \pm 0.004$, intercept $= 1.72 \pm 0.18$). Female body weight (mean, 3.81 ± 0.04 mg, range 2.0–7.0) was slightly better fitted to an allometric rather than a simple linear function of wing length, since the slope of the double-log regression is only 0.84 ± 0.07 ($r^2 = 0.24$, $n = 496$, $p \ll 0.001$); deviations from this regression were saved, to give a measure of size-adjusted or relative weight. The number of eggs in the abdomen (mean 78 ± 2, range 3–243) was also better fitted as an allometric function of wing length ($r^2 = 0.18$, $n = 484$, $p \ll 0.001$, slope $= 2.24 \pm 0.22$, intercept $= 0.19 \pm 0.16$); deviations from this line were also saved as a measure of maturity. Allocation to the abdomen (mean 60.1 ± 0.3 per cent, range 21–84) was weakly positively related to wing length ($r^2 = 0.01$, $n = 496$, $p < 0.01$) with a slope of 0.011 ± 0.004.

Galls with surviving wasps were a mean of 5.73 ± 0.03 (range 3.2–9.4) mm in diameter. Galls containing parasitoids or inquilines were always on average significantly smaller whatever the species: the smallest galls were those where fungal attack appeared to have been the cause of death (mean 3.62 ± 0.07 mm).

2. *Differences between years*

Galls were nearly always on the same set of young trees; despite intensive search, other small oaks in the immediate vicinity were never galled. Figure 20.1 shows the variation in gall density and mortality on these trees during the study period. The data suggets that one cycle of a long-term population cycle occurred at this site and that a decline in gall-maker populations followed increased mortality rates by parasitoids.

There was no effect of leaf side (left/right) in any year. The distribution of galls on the different veins of the leaf showed highly significant

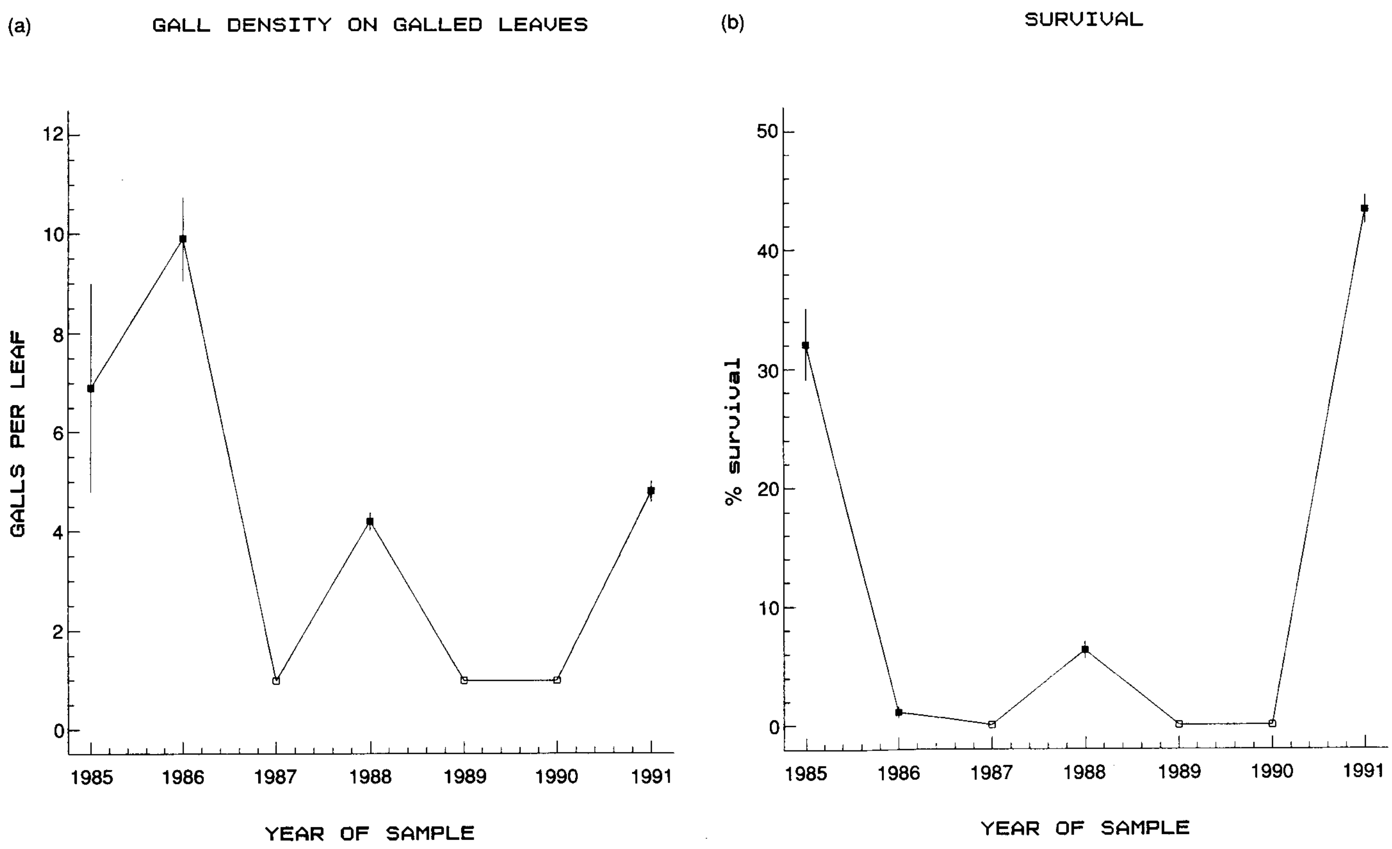

Fig. 20.1. (a) Gall density and (b) survival of the gall maker during the years of the study.

differences between the years: most galls were placed on veins 3–5 of the oak leaf in 1986 and 1988, but on veins 4–7 in 1991. Approximately 90 per cent were positioned on the half of the vein nearest the midrib, but there were also differences between years. Considering only the gall nearest the midrib, in 1991 this gall was on average approximately 12.4 ± 0.3 mm from the midrib, but less than 9.7 mm on average in 1986 and 1988 ($F_{2,1886} = 35.8$, $p \ll 0.001$). Restricting the analysis to single-gall veins, this difference still remained ($F_{2,1454} = 15.7$, $p \ll 0.001$). In 1991 the first gall was on average placed 38 per cent along the length of the vein, but only 26 per cent in 1988 ($F_{1,1104} = 125.5$, $p \ll 0.001$), with again a significant difference remaining for just the single-gall veins (35 per cent vs, 26 per cent; $F_{1,904} = 48.4$, $p \ll 0.001$).

There was always a positive correlation between leaf size and gall number (1986, $r = 0.45$, $n = 43$, $p = 0.001$; 1988, $r = 0.37$, $n = 257$, $p \ll 0.001$; 1991, $r = 0.33$, $n = 353$, $p \ll 0.001$).

Survival rates decreased with gall density on leaves in years when survival was low to very low (in 1986, $F_{1,41} = 3.55$, $n = 42$, $p = 0.066$, slope $= -0.007 \pm 0.004$; and in 1988, $F_{1,266} = 23.6$, $p \ll 0.001$, slope $= -0.028 \pm 0.006$), but were unrelated to gall density in 1991 when survival was high ($F_{1,351} = 0.001$, $p > 0.05$). In 1988 a specific sample of low (1–3) and high (> 5) gall density leaves was taken, in which 37 survivors were found amongst a total of 535 galls: there was a highly significant difference in survival rates between low (17.5 per cent) and high (4.4 per cent) density leaves ($\chi^2_1 = 20.1$, $p < 0.001$).

In 1991, survival was not related to the number of galls on veins, but overall survival decreased with order on the vein (nearest the midrib 45 per cent, second position 38 per cent, third 29 per cent, fourth 20 per cent: $\chi^2_5 = 15.1$, $p < 0.01$).

Failure rates (galls aborted at an early stage of development) on each vein increased with the number of galls on the vein in 1986 ($\chi^2_4 = 10.8$, $p = 0.03$), but there was no detectable effect in 1988 ($\chi^2_3 = 6.5$, $p = 0.09$) or 1991 ($\chi^2_5 = 1.7$, $p = 0.9$).

3. *Fitness component differences in 1991*

(a) Tree differences Genetic, age, and environmental differences should lead to variation between trees in resistance; thus we predict that we should find significant differences in fitness components between trees. Across the eight trees sampled, there were strong differences in survival (from 0 to 53 per cent: $\chi^2_7 = 173$, $p \ll 0.001$). On average there were no differences between trees in female weights ($F_{6,693} = 1.45$, $p > 0.05$) or wing lengths ($F_{1,563} = 1.5$, $p > 0.05$). There were differences in the mean

relative weights (-1.2 ± 0.4 to $+0.4 \pm 0.3$ standard deviations; $F_{6,489} = 2.98$, $p > 0.01$), allocation (58 per cent ± 0.4 to 64 per cent ± 1; $F_{6,682} = 3.8$, $p = 0.001$), number of eggs (52 ± 11 to 106 ± 8; $F_{6,479} = 4.03$, $p < 0.001$), and maturity (-0.6 ± 0.1 to $+0.6 \pm 0.1$ standard deviations; $F_{6,479} = 4.4$, $p < 0.001$) for females on different trees. Because of these differences, we restricted most analyses of within-leaf positional effects to the large sample taken from one tree, although results from other trees match those presented here.

(b) Leaf size We predicted that larger leaves can provide more nutrients, which lead to larger heavier galls and heavier wasps that can allocate more to reproduction and mature faster. We had no specific prediction about how gall density should vary with leaf size, and therefore performed a two-tailed test. Gall density ($r = 0.41$, $n = 166$, $p < 0.001$) and the means per leaf for gall diameter ($r = 0.21$, $n = 166$, $p < 0.01$), gall weight ($r = 0.18$, $n = 96$, $p < 0.05$), female weight ($r = 0.15$, $n = 96$, $p = 0.07$), allocation ($r = 0.14$, $n = 91$, $p = 0.09$), egg number ($r = 0.20$, $n = 88$, $p < 0.05$), relative size ($r = 0.16$, $n = 91$, $p = 0.05$), and maturity ($r = 0.18$, $n = 88$, $p < 0.05$) were all siginificantly related to leaf area. These results are mirrored for all but gall diameter for the large sample from one tree.

(c) Gall number on the leaf We performed multiple regression using the mean values per leaf of the fitness components with leaf area and gall number as independent variables. The prediction is that fitness components should increase with leaf area (see above), but decrease with the independent effect of gall number. We used only the large sample data from one tree to avoid intertree differences. In all cases except female weight (where it was not significantly different from zero), the partial regression coefficient for gall number was negative, significantly so for survival (slope $= -0.034 \pm 0.009$, $p < 0.001$). This coefficient was also negative for gall weight (slope $= -0.5 \pm 0.38$, $p = 0.10$). All partial regression coefficients for leaf area were positive, most significantly different from zero.

(d) Overall effects of vein number For the large sample for one tree, we could analyse fitness differences on the different veins. We predicted that since most galls were on veins 4–7 in 1991, which are the longest veins, there would be differences in fitness components. Eight hundred and fifty-five galls were analysed from the midrib and veins 2 to 11. There were no differences in survival probability ($\chi^2_{10} = 14.8$, $p > 0.05$), female weight ($F_{9,469} = 0.63$, $p > 0.05$), relative weight ($F_{9,399} = 0.9$, $p > 0.05$), allocation ($F_{9,465} = 0.9$, $p > 0.05$), number of eggs ($F_{9,393} = 0.9$, $p > 0.05$), or maturity ($F_{9,393} = 0.9$, $p > 0.05$).

(e) Overall effect of distance along a vein Using the large sample, we tested the prediction that components of fitness would decrease in galls further away from the midrib. The reason for making this prediction arises from two hypotheses concerning the source of the nutrients flowing from the plant to the gall; either from the leaf down the veins or from the branch, up the veins. Either gives the prediction that it is better to be near the midrib, but if the former explanation is correct, the hypothesis is framed in terms of distances relative to vein length. The results might be biased by including all galls, since where there are several on a vein, distal galls are inevitably further away from the midrib than distal ones and any differences in fitness components with order on the vein (see below) will confound interpretation. We therefore used only data for veins with a single gall on them. There was no difference in distances ($F_{1,365} = 0.22$, $p > 0.05$) or relative distances ($F_{1,239} = 1.4$, $p > 0.05$) between survivors and non-survivors, although in both cases the mean values are in the expected direction (non-survivors further away from the midrib). Size, allocation, and the number of eggs were not affected by distance. Relative weight ($r = -0.25$, $n = 125$, $p < 0.01$) and maturity ($r = -0.15$, $n = 125$, $p < 0.05$) decreased with distance, as expected.

(f) Overall effect of the number of galls on a vein Again for the large sample from one tree, we analysed fitness differences resulting from different numbers of galls on a single vein. We predicted that competition for nutrients will lead to a decrease in fitness components. Survival did in fact decrease with increasing gall density ($\chi^2_5 = 19.8$, $p < 0.01$). There were significant effects on female weight ($F_{3,392} = 7.7$, $p \ll 0.001$) and relative weight ($F_{3,331} = 2.9$, $p < 0.05$), but none on allocation ($F_{3,388} = 1.0$, $p > 0.05$) or the number of eggs ($F_{5,323} = 0.95$, $p > 0.05$). The index of maturity showed significant differences between mean values ($F_{3,323} = 2.4$, $p = 0.06$), but these were not in the predicted order.

We also predicted that, if a significant proportion of nutrients come down the vein from the leaf during larval development, the effects of competition should be most severe on the gall nearest the midrib. We assigned galls to their sequence order along veins, the first being the nearest to the midrib, and tested whether the number of galls on a vein affects the fitness components of the first gall. Survival was not affected ($\chi^2_5 = 6.4$, $p > 0.05$). Female weights ($F_{2,490} = 5.5$, $p < 0.01$) and relative weights ($F_{2,326} = 5.3$, $p < 0.01$) were significantly different in the expected direction, but allocation, egg number, and maturity were not affected.

(g) Overall order effects Applying a similar argument to the effects of distance along veins, we predicted that there should be an effect of sequence order on a vein on components of fitness. The exact form this takes, unlike before, depends on which hypothesis concerning the source

of nutrients is thought to be correct. There were substantial differences in survival with order, and also in female weights, but not with other fitness components. However, these results are confounded by the impact of the number of galls on a vein.

A more sensitive test uses the cases where all females survived on a vein. There were 46 two-gall and two three-gall veins where this was true, not all with full data for each female. For two-gall veins, gall weights ($t_{17} = 3.2$, $p < 0.003$) and allocations ($t_{31} = 2.05$, $p < 0.05$) were significantly lower for the distal gall, but gall diameter, female weight, relative weight, egg number, and maturity were not different ($t < 0.83$, $p > 0.21$). In 1986 with rather few data, we suggested that having a companion on a vein disrupts the relationship between size and fecundity (Sitch *et al.* 1988). This is also apparent in these more extensive data, since there is a good correlation between weight and wing length for the proximal galls of the pair ($r^2 = 0.59$, $n = 26$, $p \ll 0.001$), but this disappears for the distal galls ($r^2 = 0.05$, $p > 0.05$).

(h) Interactions between gall number on veins and order Figure 20.2 shows fitness components split into categories of gall number on veins and order on veins. There are significant differences in survival, and the pattern is clear: the more galls and the further down in the sequence, the lower the survival.

The effect of other fitness componets was assessed by two-way ANOVA with leaf length as a covariate: only in the case of allocation was the effect of leaf length significant ($F_{1,379} = 12.9$, $p < 0.001$). There were no significant effects of gall number or order in the cases of wing length, allocation, number of eggs, or maturity. There was a significant effect of gall number on female weight ($F_{2,383} = 5.5$, $p < 0.01$) and a significant gall number × order interaction ($F_{1,383} = 4.64$, $p < 0.05$).

Gall weight and diameter for galls where female wasps survived were also analysed in this two-way design with leaf length as a covariate. Gall diameter was strongly affected by leaf length ($F_{1,383} = 13.0$, $p < 0.001$), but of the main effects only order is significant ($F_{2,383} = 4.8$, $p < 0.01$). Gall weight is significantly affected by gall number ($F_{2,136} = 4.9$, $p < 0.01$ and order ($F_{2,136} = 14.6$, $p < 0.001$), but there is no interaction ($F_{1,136} = 0.5$, $p >$ 0.05) and no apparent effect of the covariate ($F_{1,136} = 2.9$, $0.1 < p < 0.05$).

4. *Food web relationships*

In 1988 there were few surviving female wasps, but many parasitoids. We therefore weighed the parasitoid larvae to look for evidence of the interactions between them.

Synergus nervosus Hartig was found in the main chamber of 36 per cent of the galls, whilst *S. pallicornis* Hartig was found in the walls of 49 per

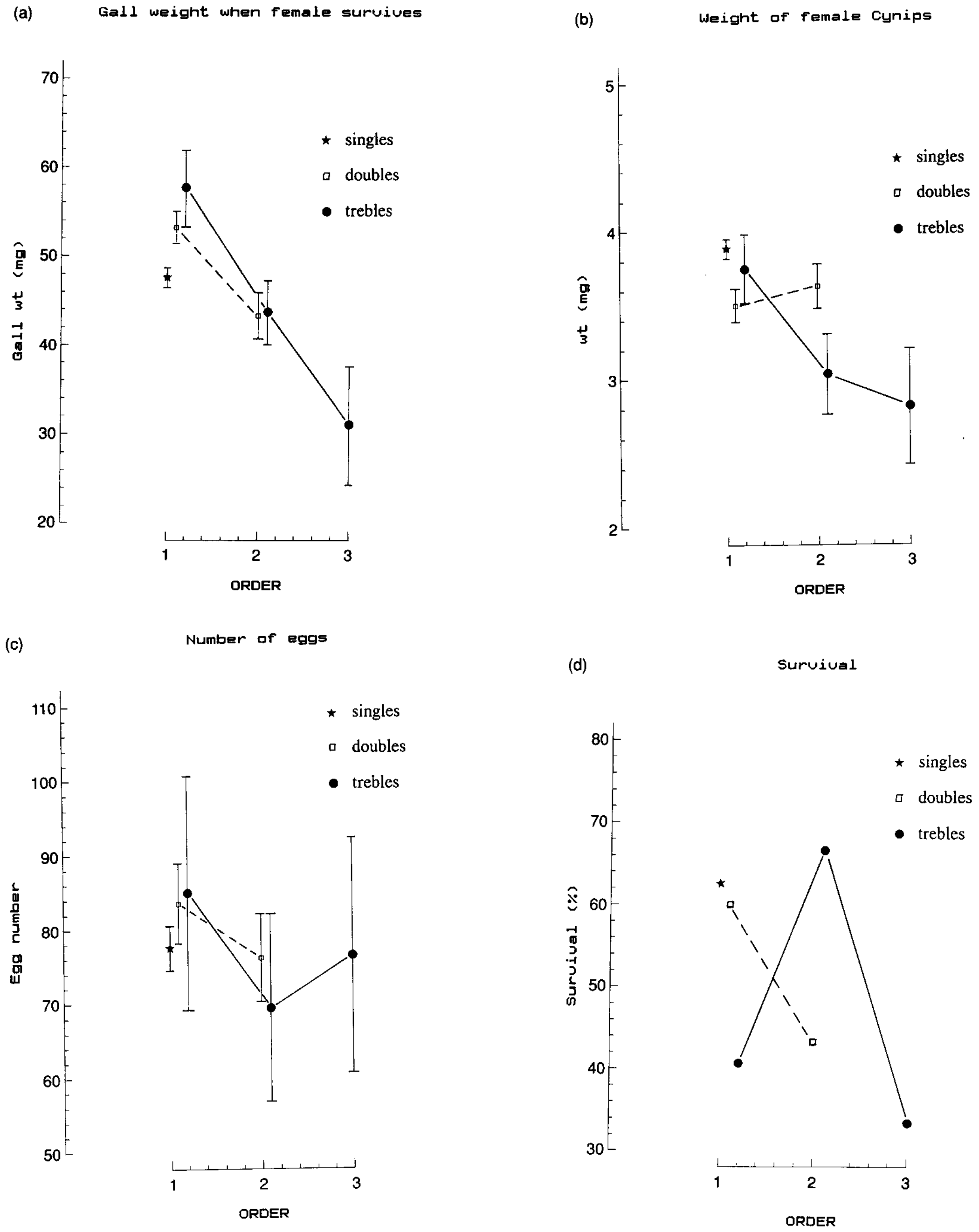

Fig. 20.2. Plot of fitness components split into categories of the number of galls on a single vein and the order on the vein: (a) gall weight for surviving gall makers, (b) weight of female wasp, (c) number of eggs carried by dissected females, (d) survival.

Table 20.1. Multiple regression equations assessing the effect of gall diameter and the number or weight of *S. pallicornis* on the weight of the other inhabitants

	Independent variables				
Dependent variable	Gall diameter	Other independent variable	Intercept	R^2	F
S. pallicornis wt n = 97	0.13 ± 0.06	*S. nervosus* wt nsd from 0.0	nsd from 0.0	0.45	6.6**
S. pallicornis wt n = 49	0.28 ± 0.06	*Eurytoma* wt − 0.17 ± 0.07	− 0.84 ± 0.30	0.44	10.6***
S. pallicornis wt n = 97	0.15 ± 0.04	Number of *S. pallicornis* nsd from 0.0	− 0.38 ± 0.16	0.50	15.6***
S. nervosus wt n = 60	0.41 ± 0.07	Number of *S. pallicornis* 0.06 ± 0.03	− 0.95 ± 0.32	0.59	40.3***
Eurytoma wt n = 49	0.88 ± 0.17	Number of *S. pallicornis* − 0.35 ± 0.08	− 2.78 ± 0.80	0.42	16.4***

All figures cited are significantly different from zero at the 5 per cent level, except where indicated by 'nsd from 0.0'.
** = $p < 0.01$; *** = $p < 0.001$.

cent of the galls. Unlike in 1986, *S. pallicornis* were not solely confined to galls already containing *S. nervosus*, even though there was a strong positive association ($\chi_1^2 = 42.2$, $p < 0.001$). Both *Synergus* species were found in relatively large galls ($F_{1,413} > 11.5$, $p < 0.001$). *Eurytoma brunniventris* Ratzeburg were found in 24 per cent of the galls, virtually always in the main chamber.

The mean weights (mg) of the different larval gall inhabitants were *Eurytoma*, 1.09 ± 0.11 (range, 0.27–4.46), $n = 49$; *S. nervosus*, 1.27 ± 0.06 (range, 0.22–1.95), $n = 60$; and *S. pallicornis*, 0.40 ± 0.02 (range 0.04–1.00), $n = 97$. There were between one and six *S. pallicornis* in an individual gall ($n = 138$). Both the combined weights of *S. pallicornis* ($F_{1,58} = 16.9$, $p < 0.001$) and individual weights ($F_{1,95} = 30.9$, $p \ll 0.001$) are strongly related to gall diameter. Similar positive regressions are found for *S. nervosus* ($F_{1,59} = 61.12$, $p \ll 0.001$) and *Eurytoma* ($F_{1,48} = 10.9$, $p < 0.05$).

We investigated the effect of competition in *S. pallicornis* by removing the effect of gall diameter via multiple regression (Table 20.1). We looked for the effect of *S. pallicornis* on the other inhabitants by regressing gall diameter and the number of *S. pallicornis* on the weights of *S. pallicornis*, *S. nervosus*, and *Eurytoma*. Regressing gall diameter and weights of *S. nervosus* or *Eurytoma* on the weight of *S. pallicornis* assessed the effect of competition on *S. pallicornis*. Significant regressions are detected by testing whether the slope is different from zero via a *t*-test.

Greater numbers of *S. pallicornis* had no effect on the weights of individual *S. pallicornis* ($t = 0.73$, $p > 0.05$). However, there was a significant negative effect on *Eurytoma* weights ($t = 4.12$, $p < 0.001$) and a significant positive effect on *S. nervosus* weight ($t = 2.25$, $p < 0.05$). The effect of the other inhabitants on *S. pallicornis* was very different. No effect of *S. nervosus* could be detected ($t = 0.35$, $p > 0.05$), but there was a negative effect of *Eurytoma* ($t = 2.5$, $p < 0.05$). This latter negative effect is presumably a competitive effect via the food supply, since *Eurytoma* was virtually never found as a direct parasitoid of *S. pallicornis* (although Askew (1961*a*) notes that it frequently is).

Discussion

There have been a number of recent reviews of the biology of gall systems, each from a slightly different perspective (Askew 1975, 1985; Abrahamson and Weis 1987; Weis *et al.* 1988; various papers in Shorthouse and Rohrfritsch 1992). Because of the general lack of long-term data, few of these reviews are able to assess the population biology of gall systems. However, more long-term studies are becoming available and will perhaps lead to new syntheses in the near future. Within populations, individual 'fitness' is determined through individual variation in life history parameters such as developmental rate, fecundity, and probability of survival. Population biology can be addressed through considering the life history consequences of oviposition site selection (Weiss *et al.* 1988). These consequences are particularly transparent in the case of gall systems because the gall is sessile.

The timing of oviposition and habitat selection during oviposition are key components of the life history of gall makers (Weis *et al.* 1988). We have no data on the consequences of variation in the timing of oviposition in *Cynips divisa*. In *C. divisa* oviposition occurs during May (Askew 1985) when oak leaves are expanding; presumably the precise timing of gall initiation relative to bud burst is important, if not critical, like many other gall systems (for example, Whitham 1980).

Whitham's (1980) elegant study found that increasing numbers of galls on a leaf affected various fitness components such that mean fitnesses per leaf were equalized whatever the gall density. The influences on fitness in *Cynips divisa* are best summarized by a path diagram (Fig. 20.3) of the inferred relationships between components, based on the results of several stepwise multiple regressions. We have not tested any particular path model since this would involve some circularity. The major components are the negative effects of gall density on leaves and on veins,

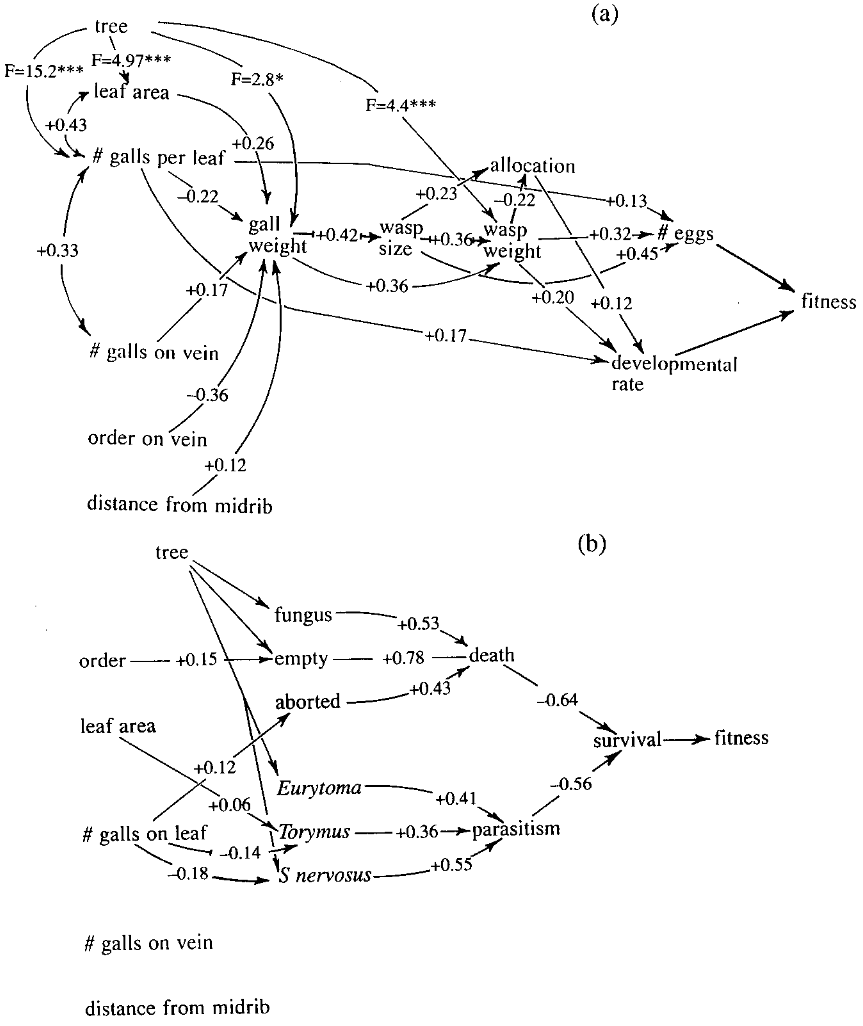

Fig. 20.3. Path diagram detailing influences upon components of fitness in *Cynips divisa*, as inferred from 1991 data. Double-headed arrows indicate correlated variables, single-headed arrows indicate inferred causal relationships. Figures are path coefficients (standardized partial regression coefficients) or correlation coefficients. Arrows drawn from 'Tree' indicate a significant variance component or chi-squared for the effect of different trees after all other influences have been taken into account. (a) Components of reproduction, (b) components of survival.

order effects, the positive influence of leaf area on fitness, and strong differences between trees. Which vein the female chooses has no effect.

As can be seen from the results for the only fitness component we can assess over several years (survival), the way in which these influences affect survival differs from year to year. The existence of this variability makes us cautious about interpreting too definitively the results of the analyses on other fitness components; the way in which gall order on a vein, for example, affects female weight might change from year to year. Why should there be this variability? We suggest that this is mainly a host plant factor and, in particular, the timing of oviposition relative to bud burst. We plan manipulative experiments to test this in future years.

Our results from a year when mortality was very high can be used to show the way in which other components of the food web interact. Askew (1961*a*) drew a very detailed food web for the gall of *Cynips divisa* on the basis of his extensive rearing programme involving more than 2000 galls (see Fig. 20.4a). We are unable to match his superbly detailed study, but we are able to suggest that there are some extra and subtle interactions between the web species (Fig. 20.4b). We base our conclusions on the analysis of larval weights. As would be expected on a simple resource availability argument, larval weights increase with an increasing gall size, evident in both species of *Synergus* and *Eurytoma.* One would expect therefore that where two individuals occur together in the same gall, there might be competition for resources. *Eurytoma* is a parasitoid, feeding directly on either the gall maker *Cynips* or on the inquiline *S. nervosus*; Askew (1961*a*) notes that it also can feed on plant tissue of the gall. The *Synergus* species are inquilines, feeding on gall tissue in the wall (*S. pallicornis*) or the inside (*S. nervosus*) and are unable to create the gall themselves, but may modify it (Askew, 1961*a*, 1985).

After removing the effect of gall diameter, the weight of *S. nervosus* **increases** when there are more *S. pallicornis* present in the walls, but there is no reciprocal effect. This positive facilitative influence on *S. nervosus* suggests that *S. pallicornis* may be able to induce the plant to produce more gall tissue. There is therefore here a positive feedback of density on resource availability (see Bianchi *et al.* 1989), as is the case with the gall makers proper. The form of the relationship implies that each additional *S. pallicornis* in the wall increases the mean weight of *S. nervosus* by 5 per cent. Thus, at least some *Synergus* species are not solely parasitic on the gall, but can induce the plant to provide them with food; they may merely be unable to initiate the process of gall formation. Presumably there is a spectrum of abilities, from true gall makers that need no assistance at all in creating a gall, to true inquilines that cannot play any part in inducing plant growth. Such a spectrum might perhaps be expected, since the inquilines appear to have evolved from gall makers (Askew 1985).

In contrast, the weight of *Eurytoma* decreases as the numbers of *S. pallicornis* rise, and the weights of *S. pallicornis* decrease as the weight of *Eurytoma* increases. We interpret this as supporting the idea that part of the food of *E. brunniventris* consists of plant material, for which it is in direct competition with *S. pallicornis*. Each additional individual *S. pallicornis* in

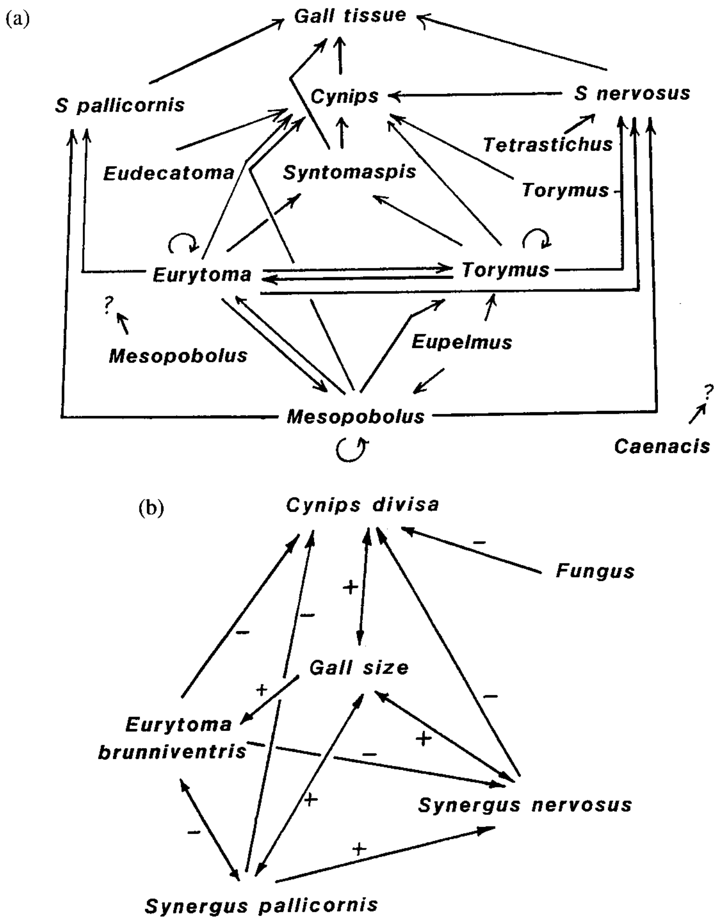

Fig. 20.4. (a) Food web based on *Cynips divisa* galls, redrawn from Askew (1961), (b) Food web of the commoner inhabitants of *Cynips divisa* galls. Signs show the nature of the interaction, either positive/facilitation (+) or negative/competition (–). Arrows point to a confirmed significant interaction; absence of an arrow means that no interaction has been detected.

the gall reduces the mean size of *Eurytoma* by 32 per cent, but a 10 per cent increase in the weight of *Eurytoma* decreases the mean weight of *S. pallicornis* by only 5 per cent. This interaction is therefore very potent and asymmetric.

How do these components combine to produce fluctuations in population size? In a widely cited paper, Washburn and Cornell (1981) interpreted their 3-year data from a site in New York State (USA) as implying that populations of the cynipid *Xanthoteras* were evanescent at one site, starting at high population density in one year, to be followed by declining populations to extinction 2 years later. They attributed this decline to the action of natural enemies, particularly the inquiline *Synergus*. A similar situation could pertain in Clumber Park. The entire park is a patchwork of young oaks of different genotypes and ages, and *Cynips* populations could shift patchily from year to year (cf. Huffaker 1958), the small-scale equivalent to the Rothamsted moth and aphid data (see Taylor 1986). However, unless the scale of this population patchiness is large, we do not feel that this is a correct interpretation since other trees in the vicinity were searched intensively and unsuccessfully for galls.

Alternatively, gall maker populations could really be responding to age-related long-term changes in host plant chemistry or other factors related to resistance or they could be undergoing population cycles that crash almost to extinction in particular years. The very high mortalities of 1986 and 1988 are clearly not unusual in *Cynips*, since Askew (1961*a*) also recorded a very low rate of survival (2–3 per cent) in *C. divisa* galls in Whytham Wood (Oxford) in 1958. Survival is improved at low gall densities on leaves and this suggests a possible mechanism for cycling. Although there are only 7 years of data, we suggest that there might well be a 6–7-year cycle of population density. In fact, many longer-term population studies on gall systems are consistent with long populations cycles. Washburn and Cornell (1981) could have been looking only at the decline phase of a 6–7-year cycle in the cynipid *Xanthoteras*; a 2-year or longer cycle may be pertinent for the cynipid *Dryocosmus* in Japan (Miyashita *et al.* 1965). The very interesting long-term data for the cynipid *Disholcaspis* (Frankie *et al.* 1992) on urban live oaks show great variation from tree to tree in any one year (for example, 0.6–88.6 per cent survival) and from year to year; again, the data suggest an overall long-term cycle. A cycle has been inferred also from a 9-year study of *Cynips quercusfolii* in The Netherlands (Wiebes-Rijks and Shorthouse 1992). In other non-cynipid gall systems the story is similar. In pemphigid aphids on *Pistacia* there is evidence for a 2- or 4-year cycle (Wool 1990); although the authors interpret population fluctuations in terms of rainfall, there is evidence for a 4-year cycle in *Pemphigus betae* on *Populus* in Utah (see Fig. 3 in Moran and Whitham 1988). Finally, a 12–14-year cycle is suggested by the data for populations of yew gall midge *Taxomyia* (Redfern and Cameron 1978; Cameron and Redfern 1978). We suggest that the interaction between plants, gall makers, and their parasitoids and inquilines will often generate long-term population cycles. Most authors (for example, Washburn and Cornell 1981; Frankie *et al.* 1992; Wiebes-Rijks and Shorthouse 1992) attribute changes in gall density to the action of natural enemies; while this appears to be similar to the situation in *Cynips divisa* in Clumber Park, experimental studies will probably be necessary to assess the relative impact of natural enemies as against host plant factors.

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References

Abrahamson W.G. and Weis, A.E. (1987). Nutritional ecology of arthropod gall makers. In *Nutritional ecology of insects, mites and spiders*, (ed. F. Slansky and G. Rodriguez), pp. 235–58. Wiley, New York.

Askew, R.R. (1960). On the Palaearctic species of *Syntomaspis* Forster (Hym., Chalcidoidea, Torymidae). *Entomologists' Monthly Magazine*, **96,** 184–91.

Askew, R.R. (1961*a*). On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. *Transactions of the Society for British Entomology*,**14,** 237–68.

Askew, R.R. (1961*b*). A study of the biology of the species of *Mesopobolus* Westwood (Hymenoptera: Pteromalidae) associated with cynipid galls on oak. *Transactions of the Royal Entomological Society of London*, **113,** 155–76.

Askew, R.R. (1965). The biology of the British species of the genus *Torymus* Dalman (Hymenoptera: Torymidae) associated with galls of Cynipidae (Hymenoptera) on oak, with special reference to alternation of forms. *Transactions of the Society for British Entomology*, **16,** 215–32.

Askew, R.R. (1975). The organisation of chalcid-dominated parasitoid communities centred upon endophytic hosts. In *Evolutionary strategies of parasitic insects and mites*, (ed. P.W. Price), pp. 130–53. Plenum, New York.

Askew, R.R. (1985). The biology of gall wasps. In *The biology of gall insects*, (ed. T.N. Ananthakrishnan), pp. 223–71. Edward Arnold, London.

Bianchi, T.S., Jones, C.G. and Shachak, G. (1989). Positive feedback on consumer population density on resource supply. *Trends in Ecology and Evolution*, **4**(8), 234–8.

Bowdrey, J.P. (1987). Oak galls of Essex. *Essex Biological Record Centres Publication* **6.** Colchester Museum Service, Colchester.

Cameron, R.A.D. and Redfern, M. (1978). Population dynamics of two hymenopteran parasites of the yew gall midge *Taxomyia taxi* (Inchbald). *Ecological Entomology*, **3,** 265–72.

Cornell, H.V. (1990). Survivorship, life history, and concealment: a comparison of leaf miners and gall formers. *American Naturalist*, **136,** 581–97.

Crawley, M.J. (1985). Reduction of oak fecundity by low-density herbivore populations. *Nature*, **314,** 163–4.

Frankie, G.W., Morgan, D.L., and Grissell, E.E. (1992). Effects of urbanization on the distribution and abundance of the cynipid gall wasp, *Disholcaspis* *cinerosa*, on ornamental live oak in Texas, USA. In *Biology of insect-induced galls*, (ed. J.D. Shorthouse and O. Rohfritsch), pp. 258–79, Oxford University Press, Oxford.

Griffiths, R., Jones, L., and Leach, C.K. (1990). *An introduction to the study of plant galls in Leicestershire.* Leicester Polytechnic, Leicester.

Hartley, S.E. and Lawton J.H. (1992). Host-plant manipulation by gall-insects: a test of the nutrition hypothesis. *Journal of animal Ecology*, **61,** 113–19.

Hassell, M.P., Comins, H.N., and May, R.M. (1991). Spatial structure and chaos in insect population dynamics. *Nature*, **353,** 255–8.

Huffaker, C.B, (1958). Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, **27,** 343–83.

Lawton, J.H. (1989). Food webs. In *Ecological concepts*, (ed. J.M. Cherrett), pp. 43–78. Blackwell, Oxford.

Matson, P.A. and Hunter, M.D. (1992). The relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology*, **73,** 723–66.

Miyashita, K., Ito, Y., Nakamura, K., Nakamura, M., and Kondo, M. (1965). Population dynamics of the Chestnut Gall-wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera; Cynipidae). III. Five year observation on population fluctuation. *Japanese Journal of Applied Entomology and Zoology*, **9,** 42–52.

Moran, N.A. and Whitham, T.G. (1988). Population fluctuations in complex life cycles: an example from *Pemphigus* aphids. *Ecology*, **69,** 1214–18.

Owen, J. and Gilbert, F.S. (1989). On the abundance of hoverflies. *Oikos*, **55,** 183–93.

Pimm, S.L. and Lawton, J.H. (1979). Are food webs divided into compartments? *Journal of Animal Ecology*, **49,** 879–98.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N., and Weiss, A.E. (1980). Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11,** 41–65.

Price, P.W., Fernandes, G.W., and Waring, G.L. (1987). The adaptive nature of insect galls. *Environmental Entomology*, **16,** 15–24.

Redfern, M. and Cameron, R.A.D. (1978). Population dynamics of the yew gall midge *Taxomyia taxi* (Inchbald) (Diptera: Cecidomyiidae). *Ecological Entomology*, **3,** 251–63.

Shorthouse, J.D., and Rohfritsch, O. (1992). *Biology of insect-induced galls.* Oxford University Press, Oxford.

Sitch, T.A., Grewcock, D.A., and Gilbert, F.S., (1988). Factors affecting components of fitness in a gall making wasp (*Cynips divisa* Hartig). *Oecologia*, **76,** 371 -5.

Taylor, L.R. (1986). Synoptic dynamics, migration and the Rothamsted insect survey. *Journal of Animal Ecology*, **55,** 1–38.

Tscharntke, T. (1992). Coexistence, tritrophic interactions and density dependence in a species-rich parasitoid community. *Journal of Animal Ecology*, **61,** 59–67.

Washburn, J.O., and Cornell, H.V. (1981). Parasitoids, patches and phenology:

their probable role in the local extinction of a cynipid gall wasp population. *Ecology*, **62,** 1597–607.

Weis, A.E., Walton, R., and Crego, C.L. (1988). Reactive plant tissue sites and the population biology of gall makers. *Annual Review of Entomology*, **33,** 467–86.

Whitham, T.G. (1980). The theory of habitat selection examined and extended using *Pemphigus* aphids. *American Naturalist*, **115,** 449–66.

Wiebes-Rijks, A.A., and Shorthouse, J.D. (1992). Ecological relationships of insects inhabiting cynipid galls. In *Biology of insect-induced galls*, (ed. J.D. Shorthouse and O. Rohfritsch), pp. 238–57, Oxford University Press, Oxford.

Wolda, H. (1983). 'Long-term' stability of tropical insect populations. *Research in Population Ecology* (suppl.), **3,** 112–26.

Wool, D. (1990). Regular alternation of high and low population size of gall-forming aphids: analysis of ten years of data. *Oikos*, **57,** 73–9.

Zwölfer, H. (1987). Species richness, species packing, and evolution in insect–plant systems. *Ecological Studies*, **61,** 301–19 (ed. E.D. Schulze and H. Zwölfer). Springer-Verlag, Berlin.