

## Strong interactions between species of phytophagous fly: a case of intraguild kleptoparasitism

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Reader, T. 2003. Strong interactions between species of phytophagous fly: a case of intraguild kleptoparasitism. – *Oikos* 103: 101–112.

In order to understand the role that interspecific competition plays in phytophagous insect communities, we need to consider the ways in which the nature of competition between species can be complicated by interactions with members of other trophic levels. In this paper, I describe how the competitive interaction between two species of gall forming fly, *Lipara lucens* and *L. rufitarsis*, is modified as a consequence of interactions with a host plant and natural enemies. The results of field experiments and observations of wild populations show that the two species compete strongly for stems of the common reed, *Phragmites australis*. *L. lucens* is competitively inferior, having significantly increased mortality in the presence of heterospecifics. No lasting negative effects of interspecific competition on *L. rufitarsis* could be found. In fact, the results show that *L. rufitarsis* can benefit from the presence of heterospecifics. It can usurp the galls of *L. lucens*, and experiences reduced mortality and increased fecundity as a result. Thus, *L. rufitarsis* can be described as a kleptoparasite. Kleptoparasitism in this system is mediated by the host plant and by the principal parasitoid of *L. rufitarsis*. *L. rufitarsis* can only benefit from the presence of its competitor because *L. lucens* induces *P. australis* to form a large, robust gall that repels the attacks of the ichneumonid wasp *Endromopoda phragmitidis*. These results show how facultative kleptoparasitism can modify the ecological consequences of interspecific competition for both individuals and populations.

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In the last few decades, there has been great debate about the general importance of the role that interspecific competition plays in ecosystems (Schoener 1982, 1983, Connell 1983, Roughgarden 1983, Gurevitch et al. 1992). Traditionally, the consensus has been that competition is weak, infrequent and inconsequential in phytophagous insect communities (Lawton and Strong 1981, Lawton and Hassell 1984). However, there is now good evidence that, although it is not always an important factor in population regulation, competition is intense in some communities (Damman 1993, Denno et al. 1995). Competition appears to be especially strong between species of phytophagous insect that are sedentary or confined, such as gall-formers, leaf-miners and stem-borers (Denno et al. 1995).

While simple theories of ecosystem function often rely on the assumption that interactions between species are pair-wise and direct, in reality they are frequently complex, subtle or indirect. For example, competition between species on the same trophic level is not always straightforward; species may compete via shared natural enemies (“apparent competition” – Holt 1977) or they may eat one another (“intraguild predation” – Polis et al. 1989). Apparent competition and intraguild predation appear to be common in communities of phytophagous insects (Polis et al. 1989, Chaneon and Bonsall 2000), as do indirect competitive or facilitative interactions that are mediated by the host plant (Denno et al. 1995). A major challenge in ecology is to understand how such intricate forms of ecological interaction

Accepted 21 March 2003

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ISSN 0030-1299

between species in the same trophic level, and more conventional direct competition for resources, affect individual fitness, population size and community structure (Wootton 1994, Abrams et al. 1996, Polis and Strong 1996).

One kind of interaction that has rarely been studied by population and community ecologists working with phytophagous insects is kleptoparasitism. Kleptoparasites, species that benefit from others not by direct predation or parasitism but by usurping resources, are common in the insect world (Ronquist 1994, Crespi and Abbot 1999, Sivinski et al. 1999). A number of examples of kleptoparasitic behaviour can be seen in the diverse invertebrate communities that are often associated with insect galls (Redfern and Askew 1992, Sanver and Hawkins 2000). For instance, some species traditionally classed as inquilines have been shown not only to share, but to steal galls that have been initiated by other species (Akimoto 1988, Ronquist 1994, Crespi and Abbot 1999). Despite the fact that the life-histories of many insect kleptoparasites have been described, little is known about the implications of kleptoparasitism at a population and community level in terrestrial ecosystems.

In this paper, the intricacies of a complex kleptoparasitic interaction in a phytophagous insect community are investigated. I describe the interaction between two species of fly, *Lipara lucens* Meigen and *Lipara rufitarsis* Loew (Diptera: Chloropidae), which form galls on the same host plant species and which apparently occupy very similar ecological niches. Firstly, I present the results of a field survey that explores the variability in space of the intensity of the interaction between *L. lucens* and *L. rufitarsis*, and reveals the impact that this interaction has on the survival of *L. lucens*, the inferior competitor in this system. Then, using the results of a field experiment, I investigate the relationship between the two species in more detail at two spatial scales. I examine the ways in which an interaction that is ostensibly asymmetrical interspecific competition is modified by attributes of the host plant and natural enemies to become something that resembles a predator-prey interaction. By understanding the consequences of this interaction for the survival and fitness of the species concerned, light is shed on the processes that are likely to promote coexistence in a community in which strong competition might be expected to lead to competitive exclusion.

## Methods

### Study organisms

*L. lucens* and *L. rufitarsis* induce characteristic apical, cigar shaped galls on stems of the common reed *Phragmites australis* (Cav.) Trin. ex Steud. (Mook 1967,

Chvála et al. 1974). Their life cycle is univoltine. Many eggs may be laid on a reed stem in spring, but only one gall can form on each stem and, by late summer, there is at most a single mature larva in each gall. The two species feed on the same host plant in the same kinds of habitats, and are difficult to separate ecologically (De Bruyn 1989). *L. lucens* is the larger species, and it induces large and heavily lignified galls. *L. rufitarsis* larvae initiate smaller, less robust galls and *L. rufitarsis* adults are about one-fifth the size of *L. lucens* adults. Inspection of galls collected in winter reveals that both species are attacked by a suite of natural enemies, including parasitoids and vertebrate predators (Mook 1967, De Bruyn 1994). Furthermore, the galls of *L. lucens* are sometimes found to be occupied by overwintering *L. rufitarsis* larvae (Chvála et al. 1974). In these instances, *L. rufitarsis* has defeated *L. lucens* in competition for the stem on which the gall has formed (Reader 2001). The proportion of *L. lucens* galls occupied by overwintering *L. rufitarsis* larvae thus provides a direct measure of the effects of interspecific competition on the survival of *L. lucens*. Unfortunately, an equivalent measure of the effects of competition on *L. rufitarsis* is not available, since *L. lucens* is never found overwintering in *L. rufitarsis* galls.

*P. australis* is a clonal wetland plant capable of forming extensive, monospecific "reedbeds". The basal diameter of the annual stems of *P. australis* is constant throughout the growing season (Mook 1967), and it can be used at any point to predict final stem height, stem biomass and the probability that flowering will occur (Mook 1967, Tscharnke 1999). Thinner stems grow shorter and are less likely to flower (Reader 2001), and contain lower concentrations of silicates (Tscharnke 1988), which are an important defence against herbivory. Basal stem diameter is thus a useful index of reed stem fitness, and in several herbivore species it is known to correlate with survival and natural enemy attack rates and oviposition behaviour (Mook 1967, Tscharnke 1992, De Bruyn 1995). In this study, basal reed stem diameter is used to investigate the effect of host plant condition on the performance of *L. lucens* and *L. rufitarsis*.

### Natural variation in the intensity of competition

To assess the intensity of competition between the *L. lucens* and *L. rufitarsis* in different types of habitat, a survey of 14 field sites in Cambridgeshire, UK was conducted in early 2000. All adult and larval flies and parasitoids found during this survey, and during the experiment described below, were identified to species using Chvála et al. (1974) and De Bruyn (1989). Galls of the two species were collected and the proportion of *L. lucens* galls containing *L. rufitarsis* larvae was calculated as a measure of the intensity of competition. In the centre of each site, a sampling grid of 20–100 m<sup>2</sup>

was marked out (grid size was constrained by the amount of suitable habitat available). Reed stem density was measured in eight  $1 \times 1$  m quadrats positioned at random within each grid. In addition, four  $2 \times 2$  m quadrats were positioned at random in each grid and searched for galls of *L. lucens* and *L. rufitarsis*. All stems bearing galls were collected and dissected, and the identity of any larvae found inside recorded.

### A field experiment

During summer 2000, a field experiment was conducted in a large reedbed at Wicken Fen, Cambridgeshire, UK. The objective of the experiment was to test for the effects of intraspecific and interspecific competition on survival and female fitness (body mass) in *L. lucens* and *L. rufitarsis*. The approach was to manipulate adult densities, and consequently egg densities, in caged enclosures. In April 2000, 1000 galls each of *L. lucens* and *L. rufitarsis* were collected from Chippenham Fen, Cambridgeshire to provide animals for the experiment. These galls were dissected and healthy larvae were placed in plastic boxes in shade on the roof of the Zoology Department, Univ. of Cambridge. By the middle of May, adults began to hatch and the boxes were checked daily. Upon hatching, flies were sexed and placed in storage at  $4^{\circ}\text{C}$  until enough flies were collected to begin the experiment.

Manipulations of *L. lucens* and *L. rufitarsis* densities were achieved by placing reared adult flies in wooden framed cages ( $1 \times 1 \times 2$  m), covered with a fine plastic mesh (mesh size  $\sim 0.5$  mm), erected in the field. The vegetation at the site chosen had been cleared by burning the previous winter, and it was therefore devoid of *Lipara* galls before the experiment began. The experiment was factorial, with all nine possible combinations of three density treatments for each species being employed on each of three occasions (replicates). The density treatments were high (20 females, 20 males), low (5 females, 5 males) and zero. These densities are representative of those commonly encountered in the wild (Reader 2001). For each replicate, nine cages were positioned at 15 m intervals on a  $3 \times 3$  grid in the reedbed, and the nine density treatments applied to cages at random. After the release of flies, cages were left in position for 7 days to allow eggs to be laid. Cages were then removed and a subset of 50 stems in each plot covered by a cage (typically 25–50% of the total) was selected at random for inspection. Each stem was searched from base to tip for eggs of *L. lucens* and *L. rufitarsis*, and labelled according to the number found. For the second and third replicates of the nine density treatments, cages were repositioned 3 m away to the west, over fresh reed immediately after stems from the previous replicate had been examined. The experiment thus ran for a total of 21 days.

In September 2000, labelled stems from all experimental plots from were collected. In the laboratory, stem basal diameter was measured with vernier callipers, and all galls that had formed were dissected. Any larvae found inside were identified, weighed and kept in individual plastic boxes in an incubator at  $20^{\circ}\text{C}$  and 100% RH until they pupated and then emerged, at which point adult flies were sexed. Some flies failed to develop properly in laboratory conditions, but female flies that hatched successfully were kept alive in the incubator for 5 days, in order to allow the maturation of the initial egg load before they were dissected and the eggs counted under a binocular microscope. The relationship between final instar larval mass and adult fecundity was then established for each species to confirm that mass data could be used as a measure of fitness.

### Statistical analyses

The results of the field competition experiment were analysed at two spatial scales. Firstly, at a large (population) scale, the responses of average per capita production of galls, larvae and larval biomass per cage to average densities of conspecific and heterospecific eggs were investigated using generalised linear models (GLMs), assuming Gaussian errors. Replicate number was included in the analysis in order to assess the effects of variation in weather conditions etc. during the three weeks for which the experiment ran. Secondly, at a small scale, the interactions of individual flies on individual reed stems were investigated. The effects of host plant quality, as measured by basal reed stem diameter, and the numbers of conspecific and heterospecific eggs laid on the probability that reed stems would produce galls or larvae were examined. GLMs were again fitted to data, but errors were assumed to be binomial. The factors influencing the levels of parasitism suffered by *L. rufitarsis* were also investigated at both scales. In all analyses, two types of *L. rufitarsis* larvae were recognised. “Winners” were defined as those individuals that successfully survived their early instars, and any competitive interactions, to become the sole occupants of galls. “Mature larvae” were defined as those winners that successfully survived until the time of sampling. Some winners failed to reach maturity because they had been parasitised, or died for some other reason (e.g. fungal infection). The recognition of two stages in the maturation of *L. lucens* larvae was not necessary, since the vast majority ( $> 99\%$ ) of *L. lucens* winners remained healthy until sampling.

The procedure for fitting GLMs to data followed Crawley (2002). Firstly, the saturated GLM, including all possible interaction terms (excluding three way interactions in cases where degrees of freedom were limited), was fitted to the data. Model simplification by “back-

ward elimination” was then undergone. Terms were deleted systematically from the saturated model (highest order first) and only put back into the model if their deletion caused a significant reduction in the deviance explained. Deletions continued until only significant terms remained. The resultant “minimum adequate models” are presented in tables, and the relevant test statistics (as computed at the point of deletion) are given, either in tables or in the text, for all terms included in minimum adequate models, and for all non-significant main effect terms. In order not to violate the assumptions of this analysis, it was necessary to  $\log_e$  transform all continuous variables.

In the analysis of data at the small spatial scale, the response variable in the GLMs used was the probability of “success”, where a success was defined as the production by a reed stem of a single gall, larva or parasitoid. The model was of this form because it was known in advance that only one larva could survive on a stem (i.e. a model predicting the probability of success for each egg rather than each stem would be inappropriate since it would allow a stem to produce more than one individual at high population densities). The saturated models fitted initially in the model selection procedure included quadratic terms (conspecific density squared and heterospecific density squared), in addition to all main effect and interaction terms, permitting the fitted models to incorporate deviations from a pure “contest” form of competition.

In order to analyse the results of the field competition experiment in a manner that would provide insights into the effects of intraspecific and interspecific interactions on flies at various stages of development both at the level of the population, and at that of the individual, it was necessary to conduct a very large number of statistical tests on the data collected. The overall chance of obtaining at least one false positive result (a “type-I” error) in such circumstances is obviously not accurately described by the p-values produced for each individual test. To provide a better guide as to the likelihood that each result obtained in the analysis of this experiment represents a type-I error, family-wise error rates for each major set of statistical tests that were conducted were computed using the Bonferroni inequality (Sokal and Rohlf 1995). Bonferroni adjusted significance thresholds (equivalent to  $p = 0.05$ ) are then given in the results section, alongside raw p-values. In the text, results are discussed with reference to raw p-values, and the assumption is made that this discussion will be interpreted with caution in the light of the nature of the analysis.

The relationship between body mass and egg load was analysed by fitting GLMs to data in the manner described above, assuming Gaussian errors. For *L. rufitarsis*, the saturated GLM fitted included a term describing the type of gall from which female flies had been reared. This was done in order to test whether the

nature of the relationship between body mass and fitness for females that had developed in their own galls was in any way different from that for those females that had usurped the galls of *L. lucens*. Data from the field survey describing the proportion of *L. lucens* galls that were occupied by *L. rufitarsis* were Freeman–Tukey transformed prior to analysis (Zar 1996). All statistical analyses were conducted using S-Plus version 4.0 for MS Windows (Mathsoft Inc., Seattle).

## Results

### Natural variation in the intensity of competition

The results of the field survey show that the intensity of interspecific interactions between *L. lucens* and *L. rufitarsis* varies tremendously from site to site. Unsurprisingly, the proportion of *L. lucens* galls occupied by *L. rufitarsis* in the different habitats surveyed was greater where the density of *L. rufitarsis* larvae was higher (Pearson’s correlation:  $r = 0.770$ ,  $p = 0.002$ ; Fig. 1). Levels of mortality of *L. lucens* associated with competition for reed stems were negligible ( $< 1\%$ ) at sites where *L. rufitarsis* was scarce and very high ( $> 50\%$ ) where *L. rufitarsis* was abundant. It is interesting to note that the relationship between *L. rufitarsis* density and competition related mortality in *L. lucens* may not be linear (Fig. 1). This suggests that, even at very high densities of *L. rufitarsis*, a proportion of *L. lucens* still have access to some kind of refuge from competition. The proportion of *L. lucens* galls occupied by *L. rufitarsis* was greater where vegetation was more mixed and where reed stem densities were consequently lower (Pearson’s correlation:  $r = -0.658$ ,  $p = 0.011$ ; Fig. 2). Competition between *L. lucens* and *L. rufitarsis* was least frequent in dense reedbeds where *P. australis* was totally dominant. This might be because *L. rufitarsis* is relatively scarce at sites where *P. australis* grows in dense stands, but there was no significant relationship

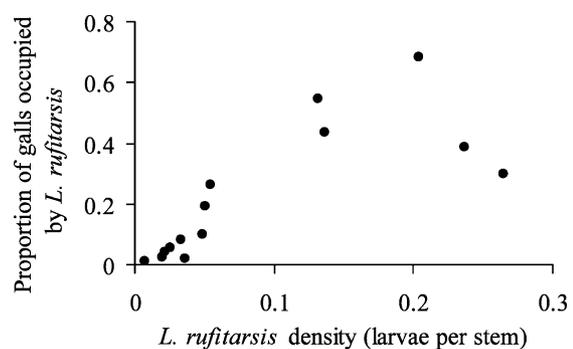


Fig. 1. The relationship between the proportion of *L. lucens* galls occupied by *L. rufitarsis* and the average density of mature *L. rufitarsis* larvae at 14 different field sites ( $n = 4$  samples per site).

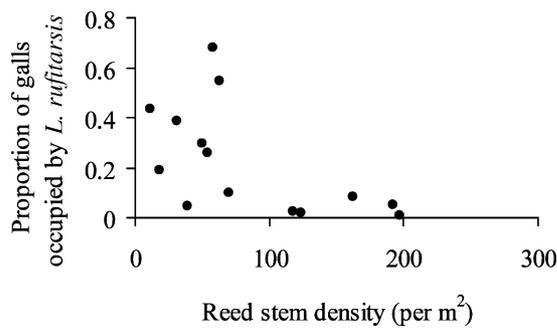


Fig. 2. The relationship between the proportion of *L. lucens* galls occupied by *L. rufitarsis* and the average density of reed stems at 14 different field sites ( $n = 8$  samples per site).

between stem density and *L. rufitarsis* density (Pearson's correlation:  $r = -0.516$ ,  $p = 0.071$ ).

### Experimental evidence of competition and kleptoparasitism

*Lipara lucens* and *L. rufitarsis* suffered high levels of mortality in experimental plots: approximately 10% ( $n = 2262$ ) of *L. lucens* eggs and less than 6% ( $n = 6558$ ) of *L. rufitarsis* eggs produced mature larvae. All but two of those *L. lucens* larvae that successfully occupied a gall went on to reach maturity, but *L. rufitarsis* suffered moderate levels of parasitism by the ichneumonid wasp *Endromopoda phragmitidis* Perkins (Table 1). For both *L. lucens* and *L. rufitarsis*, variation in body mass explained the majority of variation in female egg load five days after hatching ( $R^2 > 0.5$ ; Fig. 3 and 4). On average, *L. rufitarsis* females emerging from *L. lucens* galls were more than 50% heavier than those emerging from *L. rufitarsis* galls (Student's *t*-test:  $df = 23$ ,  $t = 5.923$ ,  $p < 0.001$ ) and they therefore carried

Table 1. The contents of galls collected from experimental plots. The category "others" corresponds to those galls in which some feeding had apparently occurred in the gall after gall-formation, but in which no clue as to the identity of the occupant (e.g. a corpse or a parasitoid) remained at the time of sampling.

Contents	Gall type	
	<i>L. lucens</i>	<i>L. rufitarsis</i>
Mature <i>L. lucens</i>	228	0
Dead <i>L. lucens</i>	2	0
Mature <i>L. rufitarsis</i>	74	212
Dead <i>L. rufitarsis</i>	3	18
<i>L. rufitarsis</i> parasitised by <i>E. phragmitidis</i>	0	73
<i>L. rufitarsis</i> parasitised by other species	0	6
Empty (no evidence of feeding)	44	45
Others (evidence of feeding)	19	28
Total	370	382

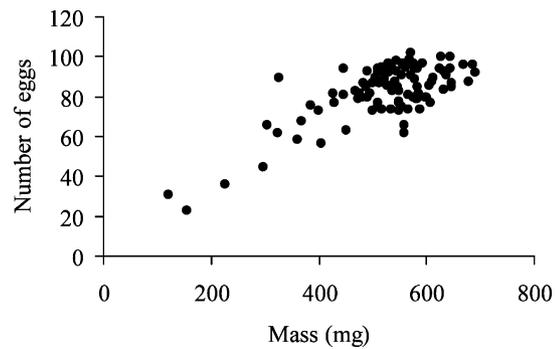


Fig. 3. The relationship between *L. lucens* female body mass (measured prior to pupation) and the number of eggs found in dissected ovaries five days after hatching (GLM:  $F_{(DF)} = 115.01_{(1,99)}$ ,  $p < 0.001$ ).

more eggs (Fig. 4). There was no suggestion that the nature of the relationship between body mass and egg load in *L. rufitarsis* varies with gall type (Fig. 4).

At a large spatial scale, there were no detectable effects of intraspecific competition on the per capita production of *L. lucens* galls, mature larvae or biomass (Table 2 and 3). There was evidence at this scale of the effects of interspecific competition on *L. lucens*, with the average larval biomass produced per egg being smaller at high densities of *L. rufitarsis* eggs. However, there were no significant effects of the density of heterospecifics on the numbers of *L. lucens* galls or mature larvae produced per egg. There was some variation between replicates in the production of *L. lucens* galls, mature larvae and biomass per egg; eggs from cages in the final (third) replicate were generally least likely to survive (Table 3).

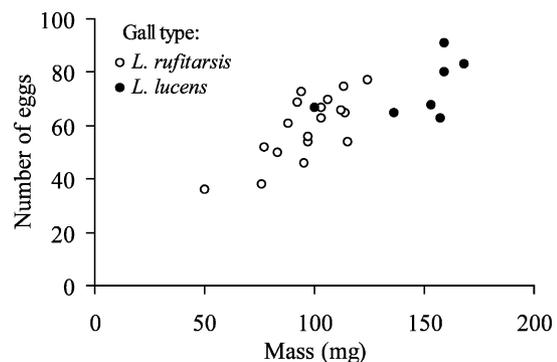


Fig. 4. The relationship between *L. rufitarsis* female body mass (measured prior to pupation) and the number of eggs found in dissected ovaries five days after hatching in two different kinds of gall. Egg load increased with body mass (GLM:  $F_{(DF)} = 29.63_{(1,23)}$ ,  $p < 0.001$ ). *L. rufitarsis* females that developed in *L. lucens* galls carried more eggs, since they had a higher body mass than those that developed in their own galls (see text). The slope (GLM:  $F_{(DF)} = 2.04_{(1,21)}$ ,  $p = 0.168$ ) and intercept (GLM:  $F_{(DF)} = 1.04_{(1,22)}$ ,  $p = 0.319$ ) of the relationship between body mass and egg load was not affected by gall type.

Table 2. Results of analysis of deviance (GLMs with Gaussian errors) at a large spatial scale in the per capita production of *L. lucens* individuals and biomass in experimental cages. Bonferroni adjusted significance threshold (for  $p = 0.05$ ) = 0.0024.

Term in GLM	Galls per egg		Mature larvae per egg		Biomass per egg	
	F <sub>(DF)</sub>	p	F <sub>(DF)</sub>	p	F <sub>(DF)</sub>	p
<i>L. lucens</i> density	2.886 <sub>(1,16)</sub>	0.109	1.422 <sub>(1,15)</sub>	0.252	0.199 <sub>(1,15)</sub>	0.090
<i>L. rufitarsis</i> density	0.340 <sub>(1,15)</sub>	0.568	2.959 <sub>(1,16)</sub>	0.105	5.088 <sub>(1,16)</sub>	0.038
Replicate	7.848 <sub>(2,17)</sub>	0.004	3.597 <sub>(2,17)</sub>	0.049	7.932 <sub>(2,16)</sub>	0.004

Table 3. The form of the linear predictor of the minimum adequate GLMs derived from analysis of deviance (covariance) where the response variable was average per capita production of *L. lucens* or *L. rufitarsis* galls, larvae or biomass, or parasitoids, in experimental cages ( $n = 50$  reed stems in each of 27 cages). All GLMs were fitted assuming Gaussian errors, except for that used in the analysis of parasitism of *L. rufitarsis*, which was fitted assuming binomial errors. Significant terms in models are represented by the following letters: l (average density of *L. lucens* eggs per stem), r (average density of *L. rufitarsis* eggs per stem),  $t_b$  (second replicate) and  $t_c$  (third replicate).

Response	Linear predictor for <i>L. lucens</i>	R <sup>2</sup>	Linear predictor for <i>L. rufitarsis</i>	R <sup>2</sup>
Galls per egg	0.150 + 0.038 $t_b$ - 0.046 $t_c$	0.480	0.137 - 0.060r	0.388
Winners per egg			0.138 - 0.059r	0.436
Mature larvae per egg	0.094 + 0.014 $t_b$ - 0.031 $t_c$	0.297	0.076 - 0.038r + 0.056l - 0.010 $t_b$ + 0.035 $t_c$ + 0.003r. $t_b$ - 0.023r. $t_c$	0.764
Biomass per egg	3.818 + 0.228 $t_b$ - 0.576 $t_c$ - 0.709r	0.567	1.784 - 0.664r + 1.028l	0.566
Parasitoids per winner			-0.420 - 2.026l	0.571

Significant effects of intraspecific competition on *L. rufitarsis* could be detected in all responses analysed at the large spatial scale (Table 3 and 4). Plots in which *L. rufitarsis* eggs were at high densities produced fewer *L. rufitarsis* galls, winners and mature larvae and less larval biomass per egg. The slope of the relationship between conspecific egg density and the production of mature *L. rufitarsis* larvae per egg varied significantly between replicates, although it was always negative (Table 3). While there were no detectable effects of interspecific competition on *L. rufitarsis* in experimental cages, there was a significant positive effect of *L. lucens* adult density on the number and biomass of mature *L. rufitarsis* larvae produced per egg. This positive effect was only detectable after parasitism and other forms of mortality affecting late instar larvae were taken into account: the density of heterospecifics had no significant effect on the production of *L. rufitarsis* galls or winners per egg. The specialist parasitoid *E. phragmitidis* attacked a significantly smaller proportion of *L. rufitarsis* larvae in plots with high densities of *L. lucens* eggs (GLM:  $F_{(DF)} = 14.658_{(1,11)}$ ,  $p = 0.003$ ), but levels of parasitism were not affected by *L. rufitarsis* density

(GLM:  $F_{(DF)} = 0.433_{(1,10)}$ ,  $p = 0.526$ ). Although there was some evidence that replicate number had an effect on the production of mature *L. rufitarsis* larvae per egg, replicate number did not significantly affect the production of *L. rufitarsis* galls, winners, or larval biomass (Table 3 and 4), or levels of parasitism of *L. rufitarsis* by *E. phragmitidis* (GLM:  $F_{(DF)} = 0.224_{(2,8)}$ ,  $p = 0.804$ ).

When analysed at a small spatial scale, the effects of host plant quality (as indicated by basal reed stem diameter) and competition between *L. lucens* and *L. rufitarsis* on the production of galls, winners and mature larvae of both species were generally highly significant. In the case of *L. lucens*, thick stems were less likely to produce a gall or mature larva than thin stems (Table 5 and 6). Stems upon which *L. rufitarsis* had laid eggs were also less likely to produce a *L. lucens* gall or mature larva, indicating that interspecific competition was operating, even before the point at which the signal that induces a gall to form is released. Unsurprisingly, stems that were not laid upon by *L. lucens* did not produce *L. lucens* galls or mature larvae. There was thus a positive effect of the number of *L. lucens* eggs on the probability that a stem would produce a gall or a

Table 4. Results of analysis of deviance (GLMs with Gaussian errors) at a large spatial scale in the per capita production of *L. rufitarsis* individuals and biomass in experimental cages. Bonferroni adjusted significance threshold (for  $p = 0.05$ ) = 0.0018.

Term in GLM	Galls per egg		Winners per egg		Mature larvae per egg		Biomass per egg	
	F <sub>(DF)</sub>	p	F <sub>(DF)</sub>	p	F <sub>(DF)</sub>	p	F <sub>(DF)</sub>	p
<i>L. lucens</i> density	1.319 <sub>(1,17)</sub>	0.267	0.494 <sub>(1,17)</sub>	0.492	10.945 <sub>(1,13)</sub>	0.006	10.862 <sub>(1,17)</sub>	0.004
<i>L. rufitarsis</i> density	11.417 <sub>(1,18)</sub>	0.003	13.899 <sub>(1,18)</sub>	0.002	18.861 <sub>(1,13)</sub>	<0.001	11.331 <sub>(1,17)</sub>	0.004
Replicate	0.100 <sub>(2,15)</sub>	0.905	0.129 <sub>(2,15)</sub>	0.880	1.662 <sub>(2,13)</sub>	0.025	0.566 <sub>(2,15)</sub>	0.580
<i>L. rufitarsis</i> density × replicate					4.444 <sub>(2,13)</sub>	0.034		

Table 5. The results of analysis of deviance (GLMs with binomial errors) at a small spatial scale in the proportion of stems carrying *L. lucens* eggs that produced *L. lucens* galls or mature larvae. Bonferroni adjusted significance threshold (for  $p = 0.05$ ) = 0.0036.

Term in GLM	Galls per stem			Mature larvae per stem		
	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$
<i>L. lucens</i> eggs	437.965 <sub>(841)</sub>	48.891 <sub>(1)</sub>	<0.001	290.163 <sub>(841)</sub>	36.641 <sub>(1)</sub>	<0.001
<i>L. rufitarsis</i> eggs	437.965 <sub>(841)</sub>	4.460 <sub>(1)</sub>	0.035	290.163 <sub>(841)</sub>	17.930 <sub>(1)</sub>	<0.001
Stem diameter	437.965 <sub>(841)</sub>	7.298 <sub>(1)</sub>	0.007	290.163 <sub>(841)</sub>	5.178 <sub>(1)</sub>	0.023
( <i>L. lucens</i> eggs) <sup>2</sup>	437.965 <sub>(841)</sub>	16.039 <sub>(1)</sub>	<0.001	290.163 <sub>(841)</sub>	17.143 <sub>(1)</sub>	<0.001

Table 6. The form of the linear predictor of the minimum adequate GLMs derived from analysis of deviance (multiple regression) where the response variable was the probability of survival of *L. lucens* or *L. rufitarsis* in the interval shown, or the probability of parasitism by *E. phragmitidis* ( $n = 847$  stems). All GLMs were fitted assuming binomial errors. Significant terms in models are represented by the following letters: l (number of *L. lucens* eggs per stem), r (number of *L. rufitarsis* eggs per stem) and w (stem diameter, square-root transformed). † Data describing *L. rufitarsis* survival from gall to winner/mature larva was available only from *L. rufitarsis* galls (it was not possible to quantify mortality of *L. rufitarsis* between gall initiation and successful gall occupation in cases where a *L. lucens* gall had formed).

Response	Linear predictor for <i>L. lucens</i>	R <sup>2</sup>	Linear predictor for <i>L. rufitarsis</i>	R <sup>2</sup>
Stem to gall	$0.127 + 1.082l - 0.083r - 1.716w - 0.083l^2$	0.149	$4.372 - 0.470l + 0.553r - 3.381w - 0.054r^2$	0.138
Stem to winner			$4.857 + 0.696r - 3.874w - 0.066r^2$	0.172
Stem to mature larva	$-0.169 + 1.319l - 0.340r - 1.849w - 0.121l^2$	0.210	$2.432 + 0.646r - 2.821w - 0.056r^2$	0.148
Gall to winner			$9.037 - 3.691w†$	0.048
Gall to mature larva		0.224	$-5.482 + 2.981w†$	0.036
Winner to mature larva	$7.642 - 3.945r - 3.158w + 1.638w.r$		$-11.633 + 0.994l + 6.089w$	0.176
Parasitism by <i>E. phragmitidis</i>			$10.318 - 0.597l - 6.189w$	0.277

mature larva. This effect was not linear, however, and a significant improvement in the deviance explained was obtained when an appropriate quadratic term (Table 6) was added to the GLMs of the probability that a stem would produce a *L. lucens* gall or a mature larva. This result suggests a deviation from pure contest intraspecific competition.

The probability that, once formed, a *L. lucens* gall would produce a mature *L. lucens* larva was not affected significantly by the density of conspecifics (GLM: Residual deviance<sub>(DF)</sub> = 83.912<sub>(78)</sub>,  $\Delta$  deviance = 0.256<sub>(1)</sub>,  $p = 0.613$ ; Bonferroni adjusted significance threshold [for  $p = 0.05$ ] = 0.0071; Table 6) or basal stem diameter (GLM: Residual deviance<sub>(DF)</sub> = 90.610<sub>(80)</sub>,  $\Delta$  deviance = 0.560<sub>(1)</sub>,  $p = 0.454$ ). However, *L. lucens* galls were less likely to produce a mature *L. lucens* larva on stems that had previously been laid upon by *L. rufitarsis* (GLM: Residual deviance<sub>(DF)</sub> = 90.610<sub>(80)</sub>,  $\Delta$  deviance = 19.208<sub>(1)</sub>,  $p = 0.035$ ), showing that the effects of interspecific competition continue to be felt after the point at which the signal that induces a gall to form is released. The magnitude of the effect of interspecific competition on *L. lucens* was not independent of stem diameter (GLM: Residual deviance<sub>(DF)</sub> = 84.168<sub>(79)</sub>,  $\Delta$  deviance = 6.441<sub>(1)</sub>,  $p = 0.011$ ). The significant interaction term in the relevant minimum adequate GLM (Table 6) indicates that the presence of *L. rufitarsis* eggs had a bigger negative effect on *L.*

*lucens* on thinner stems. This is to be expected given that, as the results discussed below suggest, mortality of young *L. rufitarsis* larvae is higher on thick stems.

Thick reed stems were less likely to produce *L. rufitarsis* galls, winners or mature larvae than thin stems (Table 6 and 7). *L. rufitarsis* galls were less likely to form on stems that had previously received *L. lucens* eggs, suggesting that the signal that induces the larger type of gall to form is dominant. There was no other evidence, however, of the negative effects of interspecific competition on the production of *L. rufitarsis* winners or mature larvae. As was the case for *L. lucens*, stems that had received conspecific eggs were more likely to produce *L. rufitarsis* galls, winners or mature larvae. However, analysis of deviance again suggested that the inclusion of quadratic terms in the GLMs of the probability that a stem would produce a *L. rufitarsis* gall, winner or mature larva was justified (Table 6).

On thicker reed stems, *L. rufitarsis* galls were less likely to yield *L. rufitarsis* winners, but more likely to yield mature larvae (Table 6 and 8). *L. rufitarsis* winners in both types of galls were also more likely to survive to maturity on thicker stems. This result is largely a consequence of the fact that parasitism by *E. phragmitidis*, the principal cause of mortality of *L. rufitarsis* winners in *L. rufitarsis* galls, was most likely to occur on thin stems (GLM: Residual deviance<sub>(DF)</sub> = 42.977<sub>(104)</sub>,  $\Delta$  deviance = 12.315<sub>(1)</sub>,  $p < 0.001$ ). There

Table 7. The results of analysis of deviance (GLMs with binomial errors) at a small spatial scale in the proportion of stems with *L. rufitarsis* eggs that produced *L. rufitarsis* galls, winners or mature larvae. Bonferroni adjusted significance threshold (for  $p = 0.05$ ) = 0.0017.

Term in GLM	Galls per stem			Winners per stem			Mature larvae per stem		
	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$
<i>L. lucens</i> eggs	544.176 <sub>(841)</sub>	16.836 <sub>(1)</sub>	<0.001	567.671 <sub>(841)</sub>	0.689 <sub>(1)</sub>	0.407	507.368 <sub>(841)</sub>	0.321 <sub>(1)</sub>	0.571
<i>L. rufitarsis</i> eggs	544.176 <sub>(841)</sub>	18.095 <sub>(1)</sub>	<0.001	568.450 <sub>(842)</sub>	36.754 <sub>(1)</sub>	<0.001	481.661 <sub>(842)</sub>	33.380 <sub>(1)</sub>	<0.001
Stem diameter	544.176 <sub>(841)</sub>	33.655 <sub>(1)</sub>	<0.001	568.450 <sub>(842)</sub>	46.056 <sub>(1)</sub>	<0.001	481.661 <sub>(842)</sub>	20.214 <sub>(1)</sub>	<0.001
( <i>L. rufitarsis</i> eggs) <sup>2</sup>	544.176 <sub>(841)</sub>	18.458 <sub>(1)</sub>	<0.001	568.450 <sub>(842)</sub>	35.325 <sub>(1)</sub>	<0.001	481.661 <sub>(842)</sub>	29.888 <sub>(1)</sub>	<0.001

Table 8. The results of analysis of deviance (GLMs with binomial errors) at a small spatial scale in the proportion of *L. rufitarsis* galls that produced *L. rufitarsis* winners or mature larvae, and the proportion of *L. rufitarsis* winners that produced mature *L. rufitarsis* larvae. Bonferroni adjusted significance threshold (for  $p = 0.05$ ) = 0.0024.

Term in GLM	Winners per <i>L. rufitarsis</i> gall			Mature larvae per <i>L. rufitarsis</i> gall			Mature larvae per winner		
	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$	Residual deviance <sub>(DF)</sub>	$\Delta$ deviance <sub>(DF)</sub>	$p(\chi^2)$
<i>L. lucens</i> eggs	80.141 <sub>(97)</sub>	0.001 <sub>(1)</sub>	0.980	129.025 <sub>(97)</sub>	0.630 <sub>(1)</sub>	0.427	98.395 <sub>(103)</sub>	9.883 <sub>(1)</sub>	0.002
<i>L. rufitarsis</i> eggs	80.142 <sub>(98)</sub>	0.650 <sub>(1)</sub>	0.420	129.654 <sub>(98)</sub>	3.232 <sub>(1)</sub>	0.072	102.272 <sub>(102)</sub>	3.788 <sub>(1)</sub>	0.051
Stem diameter	80.792 <sub>(99)</sub>	4.065 <sub>(1)</sub>	0.044	132.886 <sub>(99)</sub>	4.894 <sub>(1)</sub>	0.027	98.395 <sub>(103)</sub>	11.191 <sub>(1)</sub>	<0.001

was no evidence that the density of *L. lucens* eggs originally laid on a stem that subsequently produced a *L. rufitarsis* gall had an effect on the production of winners or mature larvae (Table 6 and 8). The fact that stems that received *L. lucens* eggs were likely to form *L. lucens* galls, however, led to a clear positive effect of interspecific interactions on *L. rufitarsis*. Not only were *L. rufitarsis* females reared from *L. lucens* galls much bigger and more fecund than those emerging from *L. lucens* galls (see above), but *L. rufitarsis* winners were more likely to survive to maturity on stems that had previously received *L. lucens* eggs. This is at least partly because *L. rufitarsis* is less likely to be parasitised by *E. phragmitidis* when developing on stems in the presence of heterospecifics (GLM: Residual deviance<sub>(DF)</sub> = 42.977<sub>(104)</sub>,  $\Delta$  deviance = 4.150<sub>(1)</sub>,  $p = 0.042$ ). The parasitoid seems incapable of attacking *L. rufitarsis* when it is developing in a *L. lucens* gall (parasitised *L. rufitarsis* larvae were never found in *L. lucens* galls). Levels of parasitism were unaffected by *L. rufitarsis* density (GLM: Residual deviance<sub>(DF)</sub> = 42.236<sub>(103)</sub>,  $\Delta$  deviance = 0.741<sub>(1)</sub>,  $p = 0.389$ ). The density of conspecifics did not have a significant influence on the probability that a *L. rufitarsis* gall would produce a winner or a mature larva, or on the probability that a winner would produce a mature larva (Table 6 and 8).

Although the results of the analysis of interactions between *L. lucens* and *L. rufitarsis* at the small spatial scale give clear evidence that competition, kleptoparasitism and host plant attributes have a significant effect on the performance of individuals in the field, it should

be noted that only some of the recorded variation in the performance of larvae can be attributed to such biological factors. The relatively low  $R^2$  values shown in Table 6 indicate that other, probably abiotic and density independent, factors are important in determining the likelihood that larvae of these species successfully mature. Nevertheless, the analysis of data at the large spatial scale shows that interspecific interactions have the potential to play a important role in determining *L. lucens* and *L. rufitarsis* population size (note the higher  $R^2$  values in Table 3).

## Discussion

### A case of intraguild kleptoparasitism

The results described here demonstrate that the interaction between *L. lucens* and *L. rufitarsis* for a shared host plant resource is more complex than straightforward competition. It is well known that interspecific competition is often highly asymmetrical (Lawton and Hassell 1981), and that in many cases interactions that appear to be competitive are actually ammensal (Denno et al. 1995). Even in comparison with cases of ammensalism, however, the asymmetry in the interaction between *L. lucens* and *L. rufitarsis* is extreme. There is no evidence of the negative effects of interspecific competition on *L. rufitarsis*, and the species actually gains from the presence of *L. lucens*, both in terms of survival and fitness. As a result, the interaction resembles that be-

tween predator and prey rather than that between competitors.

These findings suggest that *L. rufitarsis* is rather like an intraguild predator: it can gain both from attacks on its “prey” (*P. australis*), and from encounters with the competitor (*L. lucens*) with which it shares its prey. Despite superficial similarities, however, there is a significant difference between *L. rufitarsis* and the typical intraguild predator. Intraguild predators make direct energetic gains from the consumption of members of the same guild (Polis et al. 1989). In contrast, the benefits enjoyed by *L. rufitarsis* in its interaction with *L. lucens* come about indirectly, via the responses of the host plant and natural enemies. By “stealing” the larger gall of *L. lucens*, *L. rufitarsis* gains access to larger quantities of nutritious plant tissues and enemy-free space (sensu Jeffries and Lawton 1984) than would be available in the absence of heterospecifics. It is thus perhaps most appropriate to think of *L. rufitarsis* as an “intraguild kleptoparasite”.

A kleptoparasite can be defined as an animal “that habitually robs others (of a different species) of food” (Brown 1993). Kleptoparasitism is found in many invertebrate taxa, but is particularly widespread amongst the Diptera (Sivinski et al. 1999), the Hymenoptera (Ronquist 1994 and references therein), and the Arachnida (Grostal and Walter 1997, Tso and Severinghaus 1998). Amongst gall forming insects, kleptoparasitism, also called “gall-parasitism” in this context (Akimoto 1988), seems to be fairly common. The galls of some thrips (Crespi et al. 1997, Crespi and Abbot 1999), aphids (Akimoto 1988) and cynipid wasps (Ronquist 1994) are subject to “invasion” by conspecifics, or, more commonly, by individuals of other closely related species. This study has shown that such invasions also occur in the gall forming Diptera, emphasising that the phenomenon may be common across a broad range of taxonomic groups.

Given that kleptoparasitism is widespread in terrestrial invertebrates, it is not surprising that interest has been expressed in its natural history and evolution (Ronquist 1994, Crespi and Abbot 1999). However, the effects of this kind of interaction on fitness and survival have rarely been quantified. The results described here demonstrate the far-reaching consequences of kleptoparasitism for individuals and populations. The successful invasion by *L. rufitarsis* of a *L. lucens* gall leads to the death of its occupant, and the presence of a population of the kleptoparasitic species leads to a significant decline in *L. lucens* survivorship. The occupation of a large *L. lucens* gall by *L. rufitarsis* gives rise to a large increase in body mass, and therefore to significantly enhanced fecundity. In addition, the protection from parasitoids that the larger gall affords is responsible for a significant increase in survivorship in *L. rufitarsis* populations when *L. lucens* is present. This effect may be even greater in wild populations that are exposed to

bird predation, which can account for very high levels of mortality (> 50%) of individuals in *L. rufitarsis* galls, but which seldom affects *L. lucens* galls (Tscharnkte 1997, Reader 2001).

### The role of the host plant and natural enemies

Analysis of data from the field experiment revealed effects of host plant quality, as measured by basal reed stem diameter, on almost all response variables. In general, mortality of young larvae of both *L. rufitarsis* and *L. lucens* is higher on thicker reed stems. There is good experimental evidence that this is because, from the point of view of a fly larva, thicker reed stems are more difficult to attack (De Bruyn 1995). Thin *P. australis* stems are associated with various forms of environmental stress (Haslam 1972, 1975), and reed stem diameter can be thought of as a measure of host plant vigour. The relationship between the performance of *L. lucens* and *L. rufitarsis* and stem diameter is thus typical of the many insect–plant systems in which more vigorous plants are better able to defend themselves against herbivore attack (White 1984, Price 1997, but see Price 1991). It is worth noting that the effects of host plant vigour on the larvae of *L. rufitarsis* are greater than they are on the larvae of *L. lucens* (Table 6). It is not clear why this is, but the fact that the two species show different responses to resource heterogeneity suggests some potential for resource partitioning in this system.

While there is a clear negative relationship between reed stem diameter and survival in young *L. lucens* and *L. rufitarsis* larvae, the effects of variation in host plant quality on survival after gall formation has been initiated are less obvious. This is because host plant attributes interact in a complex manner with competitive and predator–prey interactions involving *L. lucens* and *L. rufitarsis*, as is often the case in tritrophic systems of this sort (Price et al. 1980). For example, in *L. lucens* galls, the survival of *L. lucens* is apparently dependent on the interplay of stem diameter and the density of competitors. The effects of competition with *L. rufitarsis* are less severe when reed stem thickness is high, since most *L. rufitarsis* larvae probably die prior to any competitive interaction in such circumstances.

Although plants might be expected to evolve characteristics that facilitate the activities of the natural enemies of herbivores, the interests of host plants and natural enemies may be conflicting (Strong and Larsson 1994, van der Meijden and Klinkhamer 2000). In this study system, it appears that increased plant resistance to herbivory is associated with a decline in the success of natural enemies. Thicker, more vigorous stems are better able to defend themselves against attack by *L. rufitarsis*, but the *L. rufitarsis* galls formed on thick stems afford the herbivore some protection from para-

sitism by *E. phragmitidis*. Little is known about the habits of *E. phragmitidis*, but it does possess a rigid ovipositor (~3 mm long), which may be used to drill through the surface tissues of reed stems during the search for hosts. It could be that, in galls on thick stems, *L. rufitarsis* is sufficiently far from the surface of the stem that *E. phragmitidis* is limited in its ability to attack its host by the length of its ovipositor.

With the recognition that complex, indirect interactions may have an important role to play in terrestrial ecosystems, much attention has recently been focused on the process of apparent competition. Apparent competition between herbivores, where the impact of a shared natural enemy on one prey species is enhanced as a result of the presence of a second prey species, appears to be common and may have an important role to play in regulating populations and structuring communities (Holt 1977, Chaneton and Bonsall 2000). In this study system, the opposite kind of interaction appears to occur, with one herbivore unwittingly benefiting another by providing it with access to enemy free space. The presence of *L. lucens* clearly has a negative affect on the ability of *E. phragmitidis* to parasitise *L. rufitarsis*. While apparent competition may lead to competitive exclusion (Bonsall and Hassell 1997), interactions such as that between *L. lucens* and *L. rufitarsis* could actually act to enhance diversity by reducing the effects of natural enemies on some herbivore species.

### Competition, kleptoparasitism and coexistence

The findings of this study support a growing body of evidence suggesting that strong, highly asymmetric interference competition is common between confined phytophagous insects (Damman 1993, Denno et al. 1995). At some of the field sites surveyed, where more than 50% of *L. lucens* galls were occupied by *L. rufitarsis* larvae, interspecific interactions must have a serious impact on the population dynamics of both species. The discovery that *L. lucens* and *L. rufitarsis* compete strongly for reed stems at some sites, and that *L. lucens* suffers far more from the interaction than *L. rufitarsis*, prompts the question: how do the two species coexist? Conventional ecological theory suggests that, in the absence of some special coexistence mechanism, if the effects of interspecific competition on *L. lucens* are greater than the effects of intraspecific competition on *L. rufitarsis*, coexistence should not be possible (Gause 1934). Conventional theory, however, describes systems in which interspecific competition is assumed to be a more straightforward process than it is between *L. lucens* and *L. rufitarsis*. The kleptoparasitic nature of the relationship between the two species means that the theoretical line that divides competition interactions from

predator-prey interactions is blurred in this system. It is possible that the likelihood of coexistence is altered by the dependence of *L. rufitarsis* on the benefits that it gains from the presence of *L. lucens*.

In contrast to those habitats in which interspecific interactions are strong, competition and kleptoparasitism appear to have very little influence on the performance of *L. lucens* and *L. rufitarsis* in dense reedbeds. In these habitats, *L. lucens* and *L. rufitarsis* populations must therefore be limited by factors other than competition for food. Because natural enemies are relatively scarce in many habitats (De Bruyn 1989), and because it seems unlikely that there is a strong dynamic link between *Lipara* spp. and their long-lived, clonal host plant, the identity of this limiting factor remains something of a mystery. Plant defence related mortality, which is likely to be density independent, will be particularly prevalent in dense reedbeds, where *P. australis* is normally vigorous and reed stems are consequently thick. It is possible that this mortality, combined with high levels of density independent background mortality resulting from the effects of adverse weather conditions etc., keeps population densities in most reedbeds in most years below the levels at which density dependent processes are likely to operate. In habitats in which *P. australis* is stressed, and reed stems are thin, plant defence related mortality will be less important, and populations may be permanently at or near the carrying capacity of the environment, and continually subject to density dependent mortality.

### Conclusions

Herbivores, whether they are in direct competition or not, are often engaged in an array of indirect interactions with members of the same guild that are mediated by host plants and natural enemies. As this study and others have shown, such interactions have important effects on the individual, and have the potential to play a crucial role in determining population size and species coexistence. The fact that pair-wise interactions amongst the invertebrate assemblages associated with insect galls often involve a mixture of predator-prey, competitive and facilitative effects highlights the need for further research into the processes that determine the structure and function of these fascinating communities. Gall formers, like those studied here, and their natural enemies and inquilines, continue to provide ecologists with important insights into the workings of terrestrial ecosystems. Perhaps future work will enable us to generalise about the effects that the kind of kleptoparasitic relationship observed between *L. lucens* and *L. rufitarsis* can have on the nature of invertebrate communities.

*Acknowledgements* – Thanks go to Chris Graham, Anna McIvor, Genevieve Morris, Ollie Morris, Stephan Müller, Chris Stewart, Matt Symonds and Jim Usherwood for their assistance in the field, and to Pej Rohani and Laurie Friday for their advice and encouragement. Dieter Hochuli and Heloise Gibb provided helpful comments on the manuscript. This work was supported by a NERC research studentship (GT 04/97/61/FS) and The National Trust.

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