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Eurytoma serratulae and *E. robusta* (Hymenoptera, Eurytomidae): complementary host exploitation strategies of coexisting parasitoids and their impact on the host *Urophora cardui*

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Abstract

Our study investigates the host exploitation strategies of *Eurytoma serratulae* and *E. robusta* (Chalcidoidea, Eurytomidae), two parasitoid species that co-occur in gall populations of the tephritid *Urophora cardui* on *Cirsium* spp. The endoparasitoid *E. serratulae* detects the host larvae before an externally visible gall is formed. It profits from large galls, as its parasitization rate increases with increasing numbers of chambers per gall. Oviposition by the ectoparasitoid *E. robusta* does not occur until a distinct gall with chambers has been formed. Its parasitization rate reaches highest values in medium-sized galls. *Eurytoma robusta* is the dominant parasitoid in host populations with low and moderate gall densities, whereas *E. serratulae* is the superior exploiter of host populations with high gall densities. Within single galls *E. robusta* is an important hyperparasitoid of *E. serratulae*, but *E. serratulae* has no adverse influence on *E. robusta*. Parasitism by *E. serratulae* induces host larvae to promote gall growth, an effect that is profitable to both the parasitoid and the remaining host larvae in the gall. Parasitism by *E. robusta* often leads to smaller galls, as cases of unsuccessful parasitization result in empty gall cells.

Keywords

Introduction

A competitive coexistence of generalists and specialists is a common and well-studied feature of parasitoid guilds exploiting phytophagous hosts (e.g. Smith 1929, Zwölfer and Kraus 1957, Fisher 1961, Askew 1968, Godfray 1994). A particular case is the coexistence of pairs of competing congeners, a situation found in *Eurytoma* species (Chalcidoidea, Eurytomidae) associated with gall forming tephritids: thus *Eurytoma compressa* (Fabricius) (= *curta* (Walker)) and *E. robusta* Mayr coexist in hosts living in Cardueae flower head galls (Zwölfer and Arnold-Rinehart 1993), and *Eurytoma obtusiventris* Gahan and *E. gigantea* Walsh in stem galls of North American *Solidago* spp. (Abrahamson and Weis 1997). The parasitoids *Eurytoma serratulae* (Fabricius) and *E. robusta* regularly co-occur in gall populations of the tephritid *Urophora cardui* (Linnaeus) on shoots of Creeping Thistle (*Cirsium arvense*). Information on the biology of *E. serratulae* and *E. robusta* has been published by Claridge (1961), Redfern (1983), Redfern and Askew (1992) and Zwölfer (1979, 1988). In view of considerable differences in its larval biology *E. robusta* has been placed in a separate species group of *Eurytoma* (e.g. Zerova and Seryogina 2006). Both species are solitary parasitoids.

Our study investigates the mechanisms that make the coexistence of the two *Eurytoma* species possible. The characteristics of the multilocular gall of *U. cardui* allow comparing the behaviour of the two *Eurytoma* species on the level of the microhabitat of individual galls and on the macrohabitat level of the gall populations. For both levels we compare the exploitation strategies of *E. serratulae* and *E. robusta* using our large basis of field-collected data that allow the statistical evaluation of "natural experiments". We analyse the influence of gall size and gall densities in the field on the incidence, degree of parasitism and the exploitation pattern of the two *Eurytoma* species. In conclusion we compare the effect of *E. serratulae* and *E. robusta* on the growth of *U. cardui* galls and we discuss how the characteristic features of the multilocular galls of *U. cardui* and the specialized oviposition behaviour safeguard *E. serratulae* against an overexploitation of its resource.

Methods and material

Collections. For our study we combined cage observations on the behaviour of *E. serratulae* with the statistical analysis of field collected gall populations. For the evaluation of our field data we disposed of 693 gall samples (16 732 galls) of *C. arvense* and nine samples (374 galls) of *C. creticum*. The *C. arvense* galls were collected between the years 1969 and 2006 in France, Switzerland, northern Italy, Germany, Austria, Slovakia, southern England, and western Poland, the *C. creticum*-galls in 1984 and 1990 in northern Greece. Galls were collected from September / October to March / April. *Urophora cardui* populations frequently occur in the form of metapopulations (Eber and Brandl 1994), i.e. as a network of single demes (Saccheri and Hanski 2006). We treated a thistle patch with *U. cardui* galls as a "popula-

tion" if it was separated from a neighbouring patch with galls by at least 200 m. We counted the number of thistle shoots and galls / patch in the field, estimated the total number of shoots / patch and dissected the galls under a stereomicroscope. We assessed the gall content (living or dead larvae or pupae of *U. cardui*, *E. serratulae*, *E. robusta* and other parasitoids, empty chambers, eggs of *E. robusta*) and gall size (cell number and gall diameter). All data were assessed in SPSS files by the program DATA ENTRY and analysed by IBM SPSS statistics 21. For the path analysis we followed Sokal and Rohlf (1981).

Host ranges and distribution of *Eurytoma serratulae* and *E. robusta*. *Eurytoma serratulae* is an endoparasitoid of *Urophora cardui*. Claridge (1961) showed that *E. tristis* Mayr, which Mayr (1878) and other authors recorded from galls of *U. cardui,* is synonymous with *E. serratulae*. All reliable host records of *E. serratulae* refer to *U. cardui*, a tephritid whose host plants are *Cirsium arvense* (Claridge 1961), *C. creticum* (Zwölfer 1988) and *C. setosum* (Frenzel et al. 2000). The ectoparasitoid *Eurytoma robusta* can so far only be identified as a morphospecies, the host records in the literature may actually pertain to a cluster of undescribed siblings. Claridge (1961) describes *E. robusta* as attacking "a wide range of tephritid galls on Cardueae host plants". Zwölfer and Arnold-Rinehart (1993) list *E. robusta* from 14 Palearctic *Urophora* species on 22 Cardueae host plant species.

Both parasitoids have been reared from *U. cardui* galls on *C. arvense* in England (Claridge 1961), Switzerland, France, Germany and Austria (Zwölfer 1979, 1994), and Finland (Vikberg 2005). Additional records from *U. cardui* on *C. arvense* are from northern Italy, western Poland and Slovakia (H. Zwölfer, unpublished). The two *Eurytoma* species also coexist in *U. cardui* galls on *C. creticum* in northern Greece (Zwölfer 1988) and in *U. cardui* galls on *C. setosum* originating from the Ural Mountains (Frenzel et al. 2000). Thus, the two *Eurytoma* species attack *Urophora cardui* on all 3 host plants and in almost all regions where galls have been analysed. An exception is Denmark and Schleswig-Holstein (northern Germany), where Johannesen and Seitz (2003a, b) as well as we (H. Zwölfer, unpublished) found only *E. robusta* in *U. cardui* galls. There, the examined thistle patches with *U. cardui* may have been recently recolonized by *U. cardui* (Johannesen and Seitz 2003b). Parasitoids of minor importance in *U. cardui* galls are the ectoparasitoids *Torymus chloromerus* (Walker) (Torymidae) and *Pteromalus elevatus* (Walker) (Pteromalidae).

Biology of *Eurytoma serratulae* and *E. robusta*

Eurytoma serratulae is a koinobiont (Askew and Shaw 1986) endoparasitoid. Oviposition takes place in early summer, shortly after the start of the oviposition period of *U. cardui*. The *E. serratulae* females detect the host larvae in thistle shoots, before a visible growth of the gall had occurred (Zwölfer 1979) and deposit their eggs into the young host larvae. This early attack on the hosts has the advantage that there is no constraint

on the length of the ovipositor (Price and Clancy 1986). The young *E. serratulae* larva remains in developmental stasis within the growing *U. cardui* larva until the host larva is full-grown in early autumn. Then, the parasitoid larva consumes its host and induces a sclerotization of the cuticula of the host (Claridge 1961). This process might provide some protection against hyperparasitoids or predators penetrating into the gall. The mature parasitoid larva spends the winter within this mummy, which externally resembles a pupated *U. cardui* larva. Pupation of *E. serratulae* occurs in the following spring, emergence of the adults in early summer.

Eurytoma robusta is an idiobiont (Askew and Shaw 1986). Its females lay their eggs into the chambers of more advanced stages of *U. cardui* galls. The hatching larvae exploit the host larvae as an ectoparasitoid. The mature larvae hibernate within the gall chambers, they pupate in spring and the adults emerge 2–3 weeks later than those of *E. serratulae*. *Eurytoma robusta* is a hyperparasitoid of *E. serratulae*, if it consumes a host larva already attacked by a young larva of the congener. Within an individual gall an *E. robusta* larva may feed on and kill more than one host. Due to poor synchronization young host larvae are often killed and consumed before they have developed enough biomass to allow the maturation of the *E. robusta* larva. If nutritive gall tissue is still available, the *E. robusta* larvae may switch to it, thus acting as an inquiline (Redfern and Askew 1992). *Eurytoma robusta* often suffers from a high incidence of superparasitism. Zwölfer et al. (2007) give a detailed description of the biology of *E. robusta* and the part it plays in the population dynamics of its host *U. cardui*.

Results

E. serratulae and *E. robusta*: the influence of gall size (number of cells)

To assess the role of gall size for the parasitization pattern we use data from 260 gall samples with a total of 7,064 galls collected from 1976 to 1993 in eastern France, southern Germany and eastern Austria. The number of cells / gall ranged from one to 18 (mean + SE = 3.807+0.045, median = 3). A total of 25% of the galls had more than five cells and 10% more than 6 cells. Incidence of parasitism (% galls attacked) by *E. serratulae* increases steadily with increasing gall size, whereas attack rate by *E. robusta* reaches a maximum at intermediate gall sizes (Fig. 1). A corresponding pattern exists, if the average number of *Eurytoma* larvae / gall is examined (Fig. 2). The different trends of parasitization by *E. serratulae* and *E. robusta* are also recognizable in Fig. 3, which compares the average content of single galls of the different size classes. The graph includes the galls with empty cells, which usually are caused by *E. robusta* (Zwölfer et al. 2007). This species is represented together with a small (< 5%) proportion of *Pteromalus elevatus,* a rare ectoparasitoid of *U. cardui*. The clear winner of an increasing gall size is the host, *U. cardui* (Freese and Zwölfer 1996). Because of interactions with other mortality factors of *U. cardui*, the correlation of *E. serratulae* with gall size (cells / gall) is weak (Spearman rank correlation: r_s = 0.236, T = 20.72,
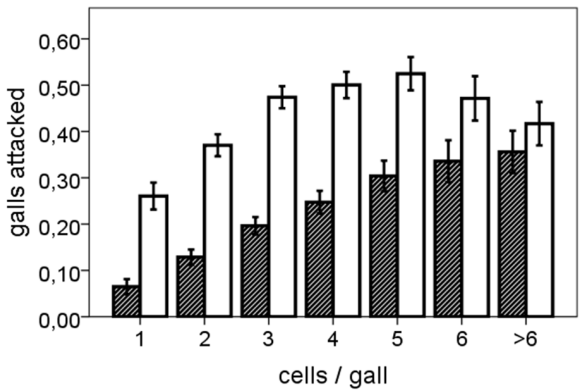
Figure 1. Average attack rate of galls by *E. serratulae* (black) and *E. robusta* (white) as function of cell numbers per gall. Analysed material: 260 gall samples with a total of 7,064 galls collected from 1976 to 1993 in eastern France, southern Germany and eastern Austria.
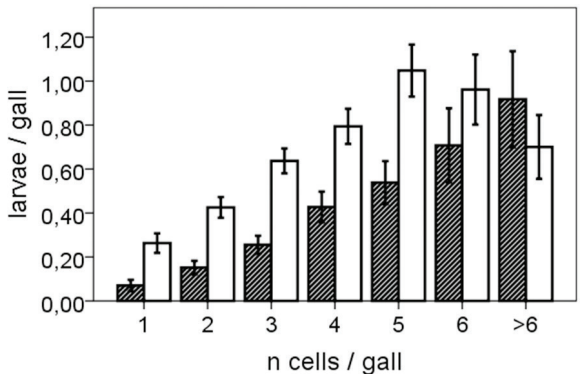
Figure 2. Average frequency of *E. serratulae* (black) and *E. robusta* (white) larvae as function of cell numbers per gall. Analysed material: 260 gall samples with a total of 7,064 galls collected from 1976 to 1993 in eastern France, southern Germany and eastern Austria.
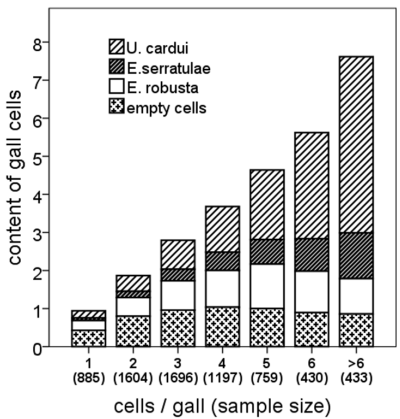
Figure 3. Average content of galls as a function of cell numbers / gall. (In parentheses: number of galls examined).
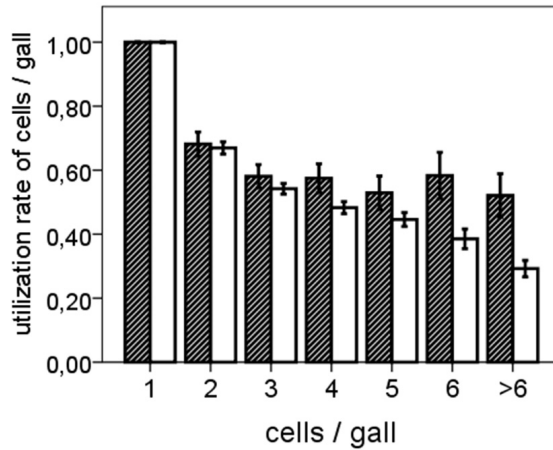
Figure 4. Average exploitation rate of galls attacked by *E. serratulae* (black) and/or *E. robusta* (white) as a function of gall size (cells / gall). Material: *E. serratulae*: 1407 galls; *E. robusta:* 1509 galls.

$p < 0.001$, $N = 6971$). It becomes much stronger ($r_s = 0.604$, $T = 12.305$, $p < 0.001$, $N = 270$), if the analysis is restricted to galls parasitized by *E. serratulae* without other mortality factors (e.g. *E. robusta* or empty chambers).

The mean exploitation rate of the cells of a gall drops in both *Eurytoma* species with an increasing number of cells / gall (Fig. 4). In *E. robusta* it decreases from 60–70% in small galls to 20% in galls with more than seven chambers. In *E. serratulae* the trend remains constant with a rate of about 40% in medium-sized and large galls. Therefore *E. serratulae* profits from *U. cardui* populations with large galls more than *E. robusta*. The difference between the two species is significant ($p < 0.001$).

E. serratulae and *E. robusta*: interactions at the level of single galls

Since *E. robusta* oviposits later than *E. serratulae*, we expected an asymmetric relationship between the two *Eurytoma* species. For a statistical test the effect of gall size on the rate of parasitization had to be removed. If galls occupied by *E. serratulae* without its congener are compared with galls jointly occupied by both species together (Fig. 5), the presence of *E. robusta* in a gall leads to a lower proportion of *E. serratulae* larvae (means of 1.87 vs 2.18 larvae / gall, ANOVA: $F = 16.5$, DF = 1 / 1405, $p < 0.001$). We interpret the difference as loss of *E. serratulae* due to hyperparasitism by *E. robusta*. For *E. robusta* the presence of *E. serratulae* has no significant effect (means of 1.74 and 1.75 larvae / gall, ANOVA: $F = 0.11$, DF = 1 / 2979, $p = 0.743$). Since cases in which all *E. serratulae* larvae have been eliminated by *E. robusta* could not be assessed, the data in Fig. 5 do not represent the entire extent of mortality of *E. serratulae* due to *E. robusta*.
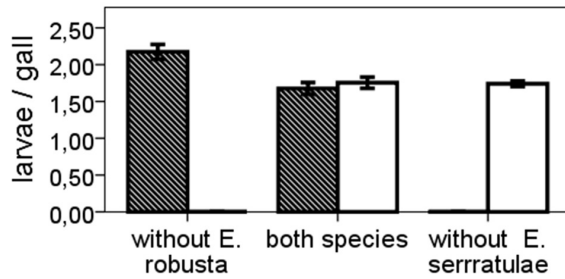
Figure 5. Asymmetric interaction between the *E. serratulae* (black) and *E. robusta* (white): Average numbers of *E. serratulae*/gall without *E. robusta* (381 galls); *E. serratulae* together with *E. robusta* (324 galls); *E. robusta* without *E. serratulae* (2454 galls).
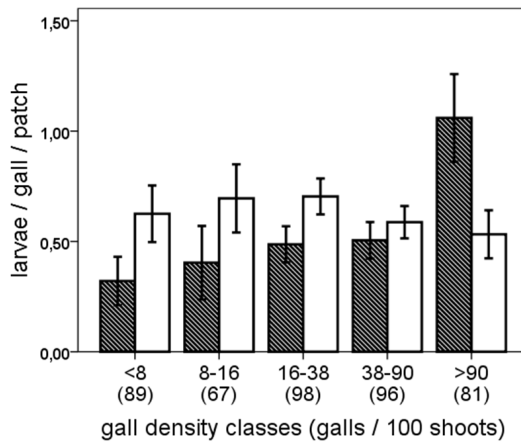

Figure 6. The influence of gall density / thistle patch (= galls / 100 thistle shoots) on *E. serratulae* (black) and *E. robusta* (white). (In parentheses: number of galls examined).

E. serratulae and *E. robusta*: comparison of gall populations

Our material allows comparing the two *Eurytoma* spp. with regard to gall density / thistle patch, which is a rough estimate of the quantity of galls in a thistle patch (*E. serratulae* = 688 samples; *E. robusta* = 1093 samples). The analysed samples represent average densities of locally and temporally fluctuating parasitoid-host complexes (Zwölfer 1994, Zwölfer et al. 2007). If analysed for five classes of sample sizes (Fig. 6) the average parasitism of *E. serratulae* and *E. robusta* is significantly different only in populations with low and high gall densities. In isolated galls and small clusters of galls *E. robusta* reaches larval densities twice as large as *E. serratulae*. The opposite situation occurs in thistle patches where the host population has reached peak gall densities. The rate of parasitism by *E. serratulae* increases steadily with increasing gall densities (Spearman correlation: r_s = 0.399, N = 670 populations, $p < 0.001$), whereas *E. robusta*
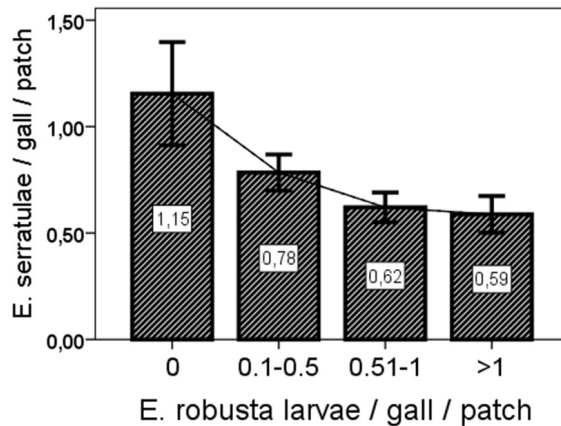
Figure 7. Average numbers of *E. serratulae* larvae / gall in *U. cardui* populations with different parasitization rates of *E. robusta.* (Sample sizes: 227, 332, 295, 209 gall populations).

reaches highest values in patches with intermediate gall densities (F = 3.589, DF = 4 / 437, p = 0.007). *Eurytoma serratulae* profits from phases with high gall density, while *E. robusta* takes over at low and intermediate gall densities. The pattern suggests differences in the host searching behaviour of the two species, but an additional effect that favours *E. serratulae* at high host densities may be the reduced load of hyperparasitism by *E. robusta*. A general linear model was used to disentangle the effects of sample size and gall density. Sample size is statistically not significant (*E. serratulae*: DF = 4, F = 0.577, p = 0.679; *E. robusta*: DF = 4, F = 0.500, p = 0.736), but the effect of gall density is highly significant (*E. serratulae*: DF = 4, F = 10.428, p < 0.001; *E. robusta*: DF = 4, F = 3.739, p < 0.001), and the interaction between the two factors is weak (*E. serratulae*: DF = 15, F = 1.740, p = 0.040; *E. robusta*: DF = 15, F = 1.774, p = 0.035).

Fig. 7 shows that the average number of *E. serratulae* larvae / gall / sample reaches the highest value in gall populations without *E. robusta* and sinks significantly with increasing numbers of *E. robusta* larvae (N samples: 227, 332, 295, 209, DF = 3, F = 4.723, p = 0.003). We interpret the data as an average mortality of 40–50% due to hyperparasitism and empty cells caused by *E. robusta*. If the average density of *E. robusta* larvae is compared for samples without (N = 357) and with (N = 691) *E. serratulae*, there is an increase of 0.57 to 0.65 *E. robusta* larvae /gall / sample. This weak statistical effect (DF = 1, F = 4.033, p = 0.045) with the factor "*E. serratulae*" is due to the fact that *E. serratulae* has the tendency to occur in higher numbers in galls with more chambers, which favour also *E. robusta*.

Hyperparasitism by *E. robusta* masks in most gall populations the superior capacity of *E. serratulae* to use the cells of the multilocular *U. cardui* galls. In 119 gall populations with less than 0.011 *E. robusta* larvae / gall / sample an average of 27.9% of the available cells where parasitized by *E. serratulae*, whereas *E. robusta* (605 populations with low or without parasitism by *E. serratulae*) used only 21.8%. The difference is significant (*T*-test: p < 0.001).
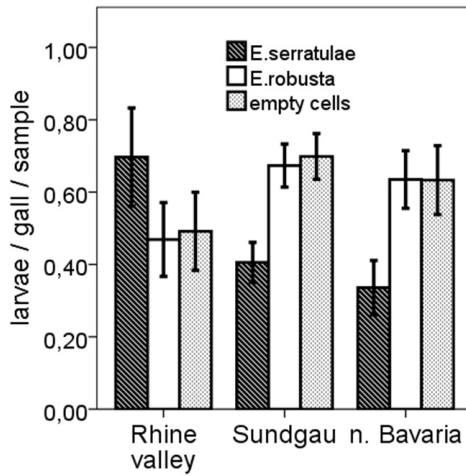
Figure 8. Parasitization of *U. cardui* samples by *E. serratulae* and *E .robusta* in 3 different regions of western Europe. Sundgau (France, region of Belfort): 307 samples, 6463 galls (1970–2004); Upper Rhine Valley (region n.w. Freiburg): 78 samples, 1885 galls (1972–1992); North eastern Bavaria (region s.e. Bayreuth): 216 samples, 4131 galls (1978–2004).

E. serratulae and *E. robusta:* regional differences

The parasitization rates of *E. serratulae* and *E. robusta* vary temporally and locally with the population dynamics of *U. cardui* (Zwölfer et al. 2007). These fluctuations are superimposed by regional differences (Fig. 8). Examples are the *U. cardui* populations in the floodplain forests of the upper Rhine Valley, where the host occurs in relatively stable source-sink systems. In these forests the average density / gall / sample of *E. serratulae* (mean = 0.744, SE = +0.069 was distinctly higher than that of *E. robusta* (mean = 0.427, SE = +0.052). In northern Bavaria (Bayreuth – Pegnitz) *U. cardui* occurs in a fragmented, agriculturally influenced landscape in mostly short-living population systems and metapopulations. Here *E. robusta* dominated with a mean density of 0.661, SE = +0.04 over *E. serratulae* (mean = 0.364, SE = +0.043). The Belfort-Sundgau region holds an intermediate position (*E. serratulae*: mean = 0.459, SE = +0.031. *Eurytoma robusta*: mean = 0.638, SE = +0.027). If our whole material collected in western and central Europe (*E. serratulae* = 772 gall samples, *E. robusta* = 755 gall samples) is compared, the average mortality of *U. cardui* due to *E. robusta* plus the empty cell factor (= 38.9%) is more than twice as high as that of *E. serratulae* (14.8%).

Effect of *E. serratulae* and *E. robusta* on gall growth

In galls of *U. cardui* the number of *E. serratulae* larvae / gall is positively correlated with the gall diameter ($r = 0,428$, $p < 0.001$, $N = 1407$). But the variable "*E. serratulae* larvae / gall" is also correlated with the variable "cells / gall" ($r = 0,481$, $p < 0.001$, N

Table 1. The effect of cells / gall and *E. serratulae* larvae / gall on gall diameter. Multiple regression: dependent variable: gall diameter, N = 2.733, multiple R = 0.67115, adjusted R² = 0.45024, SE = 3.02533.

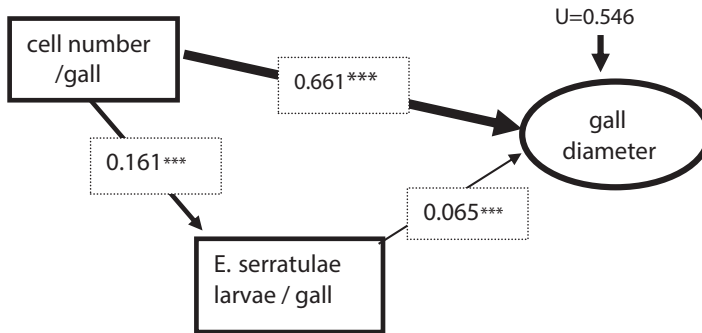| Variable	B	SE (B)	Beta	T	Sign
cells / gall	1.15157	0.02496	0.6606	46.147	< 0.001
E. serratulae / gall	0.18681	0.04095	0.0653	4.562	< 0.001
(Constant)	9.00247	0.11135		80.851	< 0.001

Figure 9. Direct and indirect effects between cells / gall, *E. serratulae* / gall and gall diameter. Path diagram: all three path coefficients (beta values) are significant at *p* < 0.001. Multiple R² = 0.4546. U (coefficient of non-determination) = 0.5456 (*N* = 2,733 *U. cardui* galls with *E. serratulae*).

= 2733), which in turn strongly affects the gall diameter (*r* = 0,674, *p* < 0.001, *N* = 2733). Together the two variables account for about 45% of the variation of the gall diameter (R² = 0.454). A multiple regression (Table 1) and a path analysis allow to separate the effect of the two variables and to calculate the impact of the variable "*E. serratulae* larvae / gall". Fig. 9 shows the three path coefficients (= standard partial regression coefficients). A comparison of the strength of the coefficients affecting the gall diameter allows the conclusion that the parasitoid larvae / gall can contribute about 10% to the gall diameter. Since *E. serratulae* attacks the *U. cardui* larvae before the gall is formed, this effect is not due to the selection of larger galls but to a stimulatory influence on gall growth.

An independent additional test is the comparison of galls with and without parasitoids (Fig. 10). Multivariate tests (GLM, Wilks-Lamda) for the gall size classes 2–5 (2 = 158, 3 = 158, 4 = 84, 5 = 45 galls, DF = 441) indicate (*F* = 14.364 and *p* < 0.001) a high statistical significance: Galls parasitized exclusively by *E. serratulae* have larger diameters than unparasitized galls and galls parasitized exclusively by *E. robusta* have lesser diameters than galls without parasitoids. This negative effect of *E. robusta* is not due to an ovipositional preference for smaller galls but to a premature elimination of young *Urophora* larvae that results in empty cells (Johannesen and Seitz 2003a, Zwölfer et al. 2007).

Table 2. Correlation of body weight of unparasitized *U. cardui* and *E. serratulae* larvae within *U. cardui* mummies with gall parameters.

	U. cardui (*N* = 66)	*E .serratulae* (*N* = 15)
Weight (mg) vs gall length (mm)		
r	0.0892 (*p* = 0.464)	**0.8452 (*p* = 0.0001)**
slope	0.048 (SE = 0.067)	0.2253 (SE = 0.0395)
Weight (mg) vs gall diameter (mm)		
r	0.1701 (*p* = 0.1722)	**0.6233 (*p* = 0.013)**
slope	0.1972 (SE = 0.1428)	0.4503 (SE = 0.1561)
Weight (mg) vs cell sum/gall		
r	0.0679 (*p* = 0.588)	**0.5633 (*p* = 0.0393)**
slope	-0.2201 (SE = 0.4043)	1.1746 (SE = 0.5127)

In a subsample of 81 galls we assessed larval biomass of the host and *E. serratulae*, gall diameter and length, and cell sum / gall. The average fresh weight of 66 mature unparasitized third instar larvae of *U. cardui* was 13.465 mg (SE = +0.545 mg) and that of 15 full grown *E . serratulae* larvae (inclusive of the sclerotized host skins) 5.207 mg (SE = +0.452 mg). Gall length (mean 24.302 mm, SE = +0.88 mm) ranged from 14.8 to 35.2 mm. Gall diameters (mean 13.82 mm, SE = +0.408 mm) ranged from 7.9 to 20.3 mm. Correlations of larval weight of *E. serratulae* in sclerotized host skins with the gall parameters diameter, length, and cell sum produced positive correlations (Table 2). We interpret this difference as another indication that host larvae, under the influence of the endoparasitoid *E. serratulae*, stimulate gall growth more strongly than *U. cardui* larvae without the endoparasitoid.

Discussion

Mechanisms allowing a balance in multi-parasitoid systems are compensations between intrinsic and extrinsic superiorities (Smith 1929). Examples can be found in most parasitoid complexes where parasitoid species with different life histories competitively coexist (e.g. Zwölfer and Kraus 1957, Askew 1968, Godfray 1994). Another important aspect is the temporal niche divergence of coexisting parasitoids, i.e. the exploitation of different host stages (e.g. Pschorn-Walcher and Altenhoffer 1989) or different developmental phases of plant galls (e.g. Askew 1975). Simulation models (Hassell 1986, 2000) demonstrate that patchy host distributions, metapopulation structures and host refuges may stabilize parasitoid-host interactions and contribute to prevent overexploitation of host populations.

In our study we show that the particular characteristics of multilocular plant galls provide an additional stabilizing mechanism for competing parasitoid species, since the two *Eurytoma* species exploit the cells of an individual gall in different ways. *Eurytoma robusta* is intrinsically superior, i.e. where its larva comes into contact with an *U. cardui* larva containing a young *E. serratulae*, it eliminates both. An advantage is also the ca-

pacity of the *E. robusta* larva to feed as an inquiline on the nutritive tissues of the gall. For its oviposition *E. robusta* is dependent on galls with fully developed cells, where synchronisation problems can lead to mortality of the young host larvae and starvation of the *E. robusta* larvae. Frequent and often high superparasitism of *E. robusta* (Zwölfer et al. 2007) can result in a considerable waste of eggs. As an initiator of empty cells *E. robusta* is an important mortality factor of *U. cardui* (Fig. 8). Parasitism by *E. robusta* and empty cells due to host killing without successful development of the parasitoid larva can cause up to 100% host mortality of small *U. cardui* populations. In experimental *U. cardui* populations in the Swiss Jura (Zwölfer 1994) and in several of our monitored populations in Northern Bavaria (Zwölfer et al. 2007) an overexploitation by *E. robusta* resulted in the complete breakdown of local *U. cardui* subpopulations and the associated monophagous parasitoid *E. serratulae*. In such cases its relatively broad host range allows *E. robusta* to switch to other host species. With regard to its host *U. cardui*, *E. robusta* is a poorly adapted generalist parasitoid but nevertheless an important mortality factor.

The life history of its congener *E. serratulae* is perfectly integrated with that of *U. cardui*. The female of *E. serratulae* detects the young host larvae already before an externally visible gall is formed and is able to parasitize a greater proportion than *E. robusta* of the host larvae available in an individual gall. In this way *E. serratulae* profits from grown up *U. cardui* populations with large multi-chambered galls. The capability to induce a sclerotization of host cuticula, once the host larva is consumed, provides a certain protection of the hibernating *E. serratulae* larva, e.g. against hyperparasitoids or predators. The emergence of adults is well synchronized with the emergence of the host flies. The increasing parasitism by *E. serratulae* in thistle patches with higher gall densities (Fig. 6) indicates a host searching behaviour influenced by the concentration of the host resource. Within a local host population galls with more cells contain over proportionally more *E. serratulae* larvae. This relationship suggests that thistle shoots with larger clutch sizes of *Urophora* are better recognizable and more attractive for *E. serratulae* females. The positive density dependence on the macrohabitat and microhabitat levels relieves the host *U. cardui* at low densities and contributes to stabilize a host-parasitoid system (Hassell 2000). Within individual galls the exploitation rate of *E. serratulae* is inversely density-dependent, making possible an increasing host refuge for *U. cardui* with increasing numbers of cells / gall (Fig. 3). The reason for this inverse relationship may be egg limitation of the *E. serratulae* females leading to some sort of "predator satiation" and/or the difficulty to locate all the tiny host larvae of a large clutch. The survival advantage of *U. cardui* larvae in galls with higher cell numbers can be important for the population dynamics of the host; as such galls contribute considerably more to the reproductive fitness of *U. cardui* than small galls (Freese and Zwölfer 1996). Since the absolute numbers of *E. serratulae* / gall also increase, larger galls with higher cell numbers are ultimately profitable to both the parasitoid and the host. Tabuchi and Amano (2004) report a similar relationship for the gall midge *Asteralobia sasakii* and its parasitoids on *Ilex*.

A particular feature of *E. serratulae* is its capacity to contribute to the growth of *U. cardui* galls (Table 1, Fig. 10). Host manipulation by endoparasitoids is a common
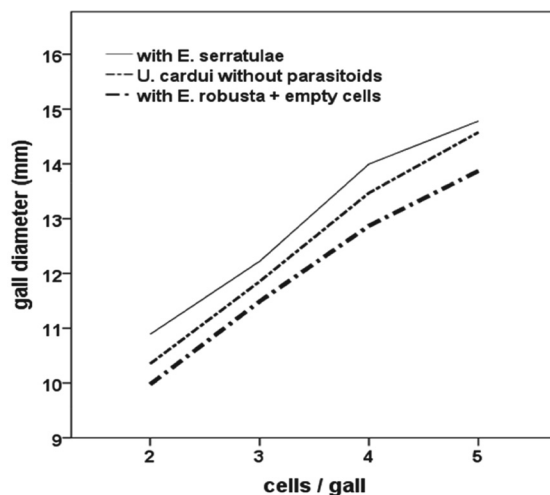
Figure 10. Average gall diameter in galls with *E. serratulae* (3512 galls), with unparasitized *U. cardui* (3449 galls) and with *E .robusta* plus empty cells (4288 galls).

phenomenon, as parasites tend to alter their hosts in ways beneficial to their own fitness. A special type of this manipulation consists in the prolongation of the feeding stages of the host, which allows the parasitoid larva to accumulate additional food resources (Beckage and Riddiford 1983, Slansky 1986, Godfray 1994). We assume that *E. serratulae* larvae stimulate *U. cardui* larvae to produce additional gall growth in a comparable way. Since larger galls provide better protection and possibly also an improved nutritional situation for *U. cardui* (Freese and Zwölfer 1996) they are profitable for both *U. cardui* and *E. serratulae.* The life history of *E. serratulae*, and the fact that it was able to follow its host to all three host plants and to cover the whole distribution area of *U. cardui*, indicate that the parasitism of *U. cardui* by *E. serratulae* forms an evolutionarily ancient and stable association.

It is interesting to compare *E. serratulae* with *Eurytoma obtusiventris* Gahan, the monophagous and highly specialised parasitoid of another gall-inducing tephritid, *Eurosta solidaginis* (Fitch), on North American *Solidago* spp. (Uhler 1951, Abrahamson et al. 1989, Abrahamson and Weis 1997). Both parasitoid species are koinobiont endoparasitoids, both attack the young host larvae of a gall-maker before gall formation starts, both are more frequent in large host galls and both are exposed to congeneric hyperparasitoids (*E. robusta* and *E. gigantea* Walsh, respectively), which deposit their eggs later into the galls. An important difference between the two parasitoid-host systems lies in the gall structure. The multi-chamber gall of *U. cardui* can secure the survival of some host larvae, whereas the single-chamber gall of *E. solidaginis,* once attacked, provides no chance of a host-escape. Differences exist also in the exploitation strategies of the two parasitoids. No influence on gall growth is described for *E. obtusiventris*; its higher frequency in larger galls is interpreted as a mere result of interactions with other mortality factors of the *Eurosta* galls (Abrahamson et al. 1989). It might, however, be

worthwhile checking whether *E. obtusiventris* larvae could manipulate *Eurosta* larvae to produce larger goldenrod galls in a comparable way as *E. serratulae* influences the growth of *U. cardui* galls.

Our study shows that the specialised *E. serratulae* in its closely-knit and evolutionarily stable parasitoid-host system with *U. cardui* follows a "sustainable" exploitation strategy, which is absent in the poorly adapted generalist *E. robusta*.

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