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PARASITOIDS OF THE BEDEGUAR GALL
(*DIPLOLEPIS ROSAE*): EFFECT OF HOST SCALE
ON DENSITY AND PREVALENCE

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Host plants have significant effects on parasitoid and herbivore distribution. There are just a few reports on tritrophic interactions. We aimed to study the relationships between rose host shrub and Bedeguar gall density with special attention to densities and prevalence of parasitoids at two scales: host shrub and gall. We found that gall density was inversely density dependent of shrub density. Parasitoid density was density dependent of both rose shrub and gall scales, while prevalence of parasitoids was density dependent at the shrub scale, but density independent at the gall scale. This pattern is likely to occur when parasitoids prefer those shrubs which are infected with galls and avoid uninfected shrubs and support optimal foraging theory.

Key words: tritrophic interactions, gall wasp, *Rosa* spp., parasitism, optimal foraging theory

INTRODUCTION

The theory on insect–plant interactions cannot show real progress without considering the third trophic level. Traits of individual plants may modify interactions between herbivores and their enemies operating directly on the herbivore, the enemy, or both (PRICE *et al.* 1980). Several works on parasitoid–herbivore systems are focusing on the effect of herbivore density on the parasitism rates by parasitoids (HASSELL 1978, STILING 1987, WALDE & MURDOCH 1988, PACALA & HASSELL 1991). Tritrophic interactions gained attention accentuating the effects of host plant quality, secondary metabolites, morphology and plant interspecific competition (PRICE *et al.* 1980, CRAIG 1994).

One of the most significant factor influencing the distribution of parasitoids and herbivores is the host plant. Furthermore, parasitoid movement and herbivore patch discovery are strongly influenced by habitat structure (CRONIN & STRONG 1999, KAREIVA 1987, PRICE *et al.* 1980). In a tritrophic system different predictions arise regarding the distribution of parasitoids among patches (DOAK 2000) considering direct density dependence (HASSELL 1978), inverse density dependence (STRONG *et al.* 1990) and resource concentration as opposed to density dependence (SHEEHAN & SHELTON 1989). The response to density of parasitoids

may be scale dependent (RAY & HASTINGS 1996); therefore, the adequate spatial scale is important in the study of such interactions (BIEDERMANN 2007, HEADS & LAWTON 1983, WALDE & MURDOCH 1988). Studies of tritrophic interactions found direct relationships between herbivore abundance and their parasitoid's host selection (plant and herbivore) or prevalence (the prevalence of parasitoids is defined as the relative frequency of parasitoids; in the literature prevalence is also mentioned as parasitism rate or parasitoid attack rate) (CAPPUCCINO 1992, SEGARRA-CARMONA & BARBOSA 1992, SHEEHAN & SHELTON 1989).

Patch choice is considered an independent area of optimal foraging theory (PYKE 1984). Parasitoids have to optimize their time allocated to search for hosts in order to increase oviposition efficiency when habitats are patchy (SPATARO & BERNSTEIN 2007). In the studied case parasitoids must choose between gall patches occurring on different host plants, where the quantity of galls per shrub may be a more relevant characteristic than their presence or absence. Parasitoids searching randomly possess a lower prevalence when host shows an aggregated spatial distribution (i.e., they are patchily distributed) because they lose time with searching on empty patches (MURDOCH & STEWART-OATEN 1989, HASSELL & PACALA 1990). Parasitoids searching non-randomly possess higher attack rates even if hosts appear aggregated (HASSELL & PACALA 1990, KAREIVA 1990). Therefore, the direct and indirect density dependence in the case of parasitoids on their insect hosts may root in optimal foraging (VELDTMAN & MCGEOCH 2004).

Increased host density increases (positive density dependence), decreases (inverse density dependence) or does not affect (density independent) parasitism by insect parasitoids (HASSELL & WAAGE 1984, RAY & HASTINGS 1996, STILING 1987). In the case of cynipid gall inducers, parasitoid abundance has shown both inverse density dependence (HAILS & CRAWLEY 1992) and density dependence (SCHÖNRÖGGE *et al.* 1996).

We studied a tritrophic interaction between the host shrub *Rosa* spp., the parthenogenetic gall wasp *Diplolepis rosae* (Hymenoptera, Cynipidae), which induces multi-chambered galls on rose shrubs and the parasitoids of rose galls. Females of *D. rosae* emerge from galls in early spring and lay their clutches in new rose buds within one or two months. The new gall finishes its development in late summer and pupae overwinter within the gall.

Usually parasitoid pressure on *D. rosae* galls is high (LÁSZLÓ & TÓTHMÉRÉSZ 2008, STILLE 1984). The inquiline species *Periclistus brandtii* is also frequent and plays an important role in shaping the community structure of *D. rosae* gall (LÁSZLÓ & TÓTHMÉRÉSZ 2006, STILLE 1984). Inquilines are gall wasps which do not induce galls; their larvae feed on the gall tissue inside the galls of other cynipids. The most frequent parasitoids of *D. rosae* are the ichneumonid *Orthopelma mediator*, the torymids *Glyphomerus stigma* and *Torymus bedeguaris* and the pteromalid *Pte-*

romalus bedeguaris (LÁSZLÓ & TÓTHMÉRÉSZ 2008, NORDLANDER 1973, STILLE 1984). In this study we focus on the parasitoids of *D. rosae*.

To explain why optimal foraging can cover the constant parasitoid prevalence at different shrub densities we outline a simple model. Let's take time as a limiting factor of parasitoid's oviposition success. Compare two plots with different shrub densities and with different gall densities. At the first plot we have fewer (for ex. 2) shrubs with a number of galls (for ex. 8) distributed uniformly on shrubs. At the second plot we have more shrubs (for ex. 4) with a number of galls inferior to the previous plot (for ex. 6) but distributed patchily. When a parasitoid ventures in the two plots we get the same parasitoid prevalence per gall per time only if it target firstly the galled shrubs. When the parasitoid searches all shrubs at the second plot its prevalence per gall is lower than in the first. When the oviposition per one gall takes a quarter of time unit and it searches non-randomly we get at the second plot a 0.66 parasitoid prevalence per gall in unit time. At the same conditions in the first plot we get 0.50 parasitoid prevalence per gall in unit time. In the case of prevalence per shrub in this way we get at the first plot a higher value and at the second a lower one.

Our null hypothesis was that parasitoid searching is random. If random, parasitoid prevalence on different scales (i.e. gall or shrub) would show the same direction in its change. Otherwise (alternative hypothesis), when parasitoids are able to distinguish between gall-infested and un-infested rose bushes, they are unlikely to spend time searching un-infested bushes, as optimal foraging theory would predict (COOK & HUBBARD 1977, HUBBARD & COOK 1978); thus, the prevalence of parasitoid density on Bedeguar galls exhibits different trends at increasing plant density.

The alternative hypothesis also involves that parasitoid prevalence should be inversely density dependent on the shrub scale. In a previous study we found that with increasing shrub density the galls become aggregated and there are fewer galls per plant in general (LÁSZLÓ & TÓTHMÉRÉSZ 2011). As the most shrubs will be gall free the parasitoid prevalence per shrub should decrease with increasing shrub density.

We had the following predictions: 1) with the increasing density of shrubs the prevalence of parasitoids per shrub will decrease; 2) with the increasing density of shrubs the prevalence of parasitoids per gall will be constant; 3) with the increase of rose shrub density the prevalence of galls per shrub decreases; 4) prevalence of parasitoids shows an antagonistic relationship with gall density per shrub.

More generally we aimed to find supporting evidences for the optimal-foraging theory within a tritrophic context considering that parasitoid behaviour and parasitoid attack rates are influenced by both of host plant and herbivore host attributes such as density.

MATERIAL AND METHODS

There were eight sampling sites during two years (2004, 2005). Sampling sites were dry pastures or the forested edges of these pastures; the forest was an oak-hornbeam forest. There were scattered *Prunus spinosa* shrubs among *Rosa* spp. shrubs. Sampling sites and the number of surveyed plots are presented in Table 1.

Plots of 50×50 meters were randomly selected at each site (more than one plot per site). In each of the randomly chosen 50×50 meter plots we recorded the coordinates of each rose shrub with a GPS unit; we also counted the occurring *D. rosae* galls on them. We referred to the mean abundance of *Rosa* spp. as density of the shrubs in every plot. The density of galls on shrub individuals was determined on every plot by counting infected shrubs from all occurring shrubs and determining the shrubs with the same gall densities.

Galls were collected once from each plot in one of the sampling years. Gall collection was done in either February or March because gall inhabitants need cold temperatures in winter for pupation, and galls are more accessible before spring budding. All galls were sampled from each infected shrub (on each infected shrub we chose randomly one gall which was left for further analyses and for maintaining the host-plant under parasite pressure). After sampling, galls were introduced individually in plastic cups with cellophane cover, which enabled airing and were kept under standard laboratory conditions. Emerged individuals were separated and stored in 70% ethanol until identification.

The number and prevalence of parasitoids was determined on shrub and gall scale. For determining the number and prevalence of parasitoids per shrub we pooled the individuals of those parasitoids, which are attacking the gall inducer *D. rosae*. These were *Orthopelma mediator*, *Torymus bedeguaris*, *Gliphomerus stigma* and *Pteromalus bedeguaris* (NORLANDER 1973, STILLE 1984). The number and prevalence of parasitoids per shrubs was determined on each plot by counting the shrubs with parasitized galls, the number of parasitoids on these shrubs and the shrubs with the same parasitoid number. The number and prevalence of parasitoids per gall was determined by counting parasitized galls, parasitoids in these galls and galls which had the same parasitoid number. These calculations were done as required for the QP 3.0 software (RÓZSA *et al.* 2000). We discussed our findings on the scale of rose shrubs and on the scale of galls. The R language and environment for statistical computing (R DEVELOPMENT CORE TEAM 2010) was used for other statistical analyses.

We used Pearson correlation and linear regression analysis for the relationships between shrub density and gall number per shrubs, shrub density and parasitoid number per shrub and gall, and be-

Table 1. Sampling sites, their coordinates (latitudes, longitudes), and the number surveyed plots over the two years of study.

Site	No. of plots		Coordinates	
	2004	2005	N	E
Berettyóújfalu, Hajdú-Bihar county, Hungary	1	3	47.2476	21.5377
Tépe, Hajdú-Bihar county, Hungary	3	3	47.3301	21.5605
Târgu-Mureş, Mureş county, Romania	4	3	46.5126	24.5771
Cluj-Napoca, Cluj county, Romania 1	4	3	46.8018	23.6131
Cluj-Napoca, Cluj county, Romania 2	2	3	46.8317	23.6315
Cluj-Napoca, Cluj county, Romania 3	3	3	46.7328	23.5780
Cluj-Napoca, Cluj county, Romania 4	2	3	46.7672	23.4937
Emőd, Borsod-Abaúj-Zemplén county, Hungary	0	2	47.9522	20.8047

tween shrub density and parasitoid prevalence per shrub and per gall. Normality of data was obtained by log-transformation because the parasitoid densities and prevalences had quadratic correlations with rose shrub and gall densities. Normality of variables was tested by Kolmogorov-Smirnov test. The homogeneity of variances was tested by F-test on the log-transformed data. Nested linear mixed effect ANCOVA was used to compare the slopes of paired regressions, where the response variable was the parasitoid density or the prevalence calculated on the two scales, plots nested in sites were regarded as random variable and the covariate was either the shrub density or the gall per shrub number. Because we had different variances per stratum, and thus the homoscedasticity was not met we used the "varIdent" variance function class in our models (PINHEIRO & BATES 2000). For nested linear mixed modelling we used package "nlme" (PINHEIRO & BATES 2000). The nested linear mixed effect ANCOVA was used for the comparison of the regressions between parasitoid number and prevalence on shrubs and galls versus a) shrub density, b) number of galls per shrub and c) host (both shrub and gall) density.

RESULTS

In the two years of the study we analysed $N = 42$ plots, in which there were 1004 rose shrubs from which 332 (33%) were infected by the gall wasp *D. rosae*. There were 449 galls containing other insect inhabitants than the gall inducer out of the 647 collected *D. rosae* galls. From these 647 galls emerged 8465 gall inhabitants including the gall wasp, its inquiline species and parasitoids of both.

From the total number of emerged specimens 25% were gall inducers and further 46% were the parasitoids of the gall inducer. Twenty-nine percent of the emerged gall inhabitants were inquilines and their parasitoids. From the parasitoids of the gall inducer *G. stigma* was the most abundant with 37%, *O. mediator* constituted 35%, while *T. bedeguaris* only 15%. The species *P. bedeguaris* was the least abundant with 13%.

Normality of variables. With the exception of shrub density (one-sample Kolmogorov-Smirnov test; $D = 0.17$, $p = 0.15$, $N = 42$), all variables showed significant departures from normal distribution. We used log-transformations on both variables in every pair of comparisons, because in most cases the relationships between variables were quadratic. Transformations dealt satisfactory with the departures from normality.

Density of galls. Number of galls per shrub decreased with increasing shrub density (Pearson correlation; $t_{40} = -6.86$, $r = -0.73$, $p < 0.0001$). The linear model explained 54% of the variance in gall number per shrub (linear regression analysis; $F_{1,40} = 47.14$, slope = -0.51) (Fig. 1).

Parasitoids on the shrub scale. Parasitoid number per shrub decreased with increasing shrub density (Pearson correlation; $t_{40} = -8.82$, $r = -0.81$, $p < 0.0001$). The linear model explained 66% of the variance in parasitoid number per shrub (linear regression $F_{1,40} = 77.81$, slope = -0.63) (Fig. 2a).

Parasitoid prevalence per shrub decreased with increasing shrub density (Pearson correlation; $t_{40} = -10.14$, $r = -0.84$, $p < 0.0001$). The linear model explained 72% of the variance in parasitoid prevalence per shrub (linear regression $F_{1,40} = 102.9$, slope = -0.47) (Fig. 2b).

Parasitoids on the gall scale. Parasitoid number per gall decreased with increasing shrub density (Pearson correlation; $t_{40} = -3.40$, $r = -0.47$, $p < 0.001$). The linear model explained 22% of the variance in parasitoid number per gall (linear regression $F_{1,40} = 11.59$, slope = -0.21) (Fig. 2c).

The parasitoid prevalence per gall was independent from shrub density (Pearson correlation; $t_{40} = -1.39$, $r = -0.21$, $p = 0.17$). However, based on linear regression the parasitoid prevalence per gall was also independent of the shrub density (linear regression $F_{1,40} = 1.94$, slope = -0.04) (Fig. 2d).

Comparison of shrub density effect. We found a significant difference between the two slopes of the regressions of shrub density with parasitoid number per shrubs and parasitoid number per gall (ANCOVA; $F_{2, 41} = 42.80$, $p < 0.0001$). Parasitoid number per shrub was more strongly correlated (negatively) with shrub density than was parasitoid number per gall (Fig. 3a).

The two slopes of the regressions of shrub density with parasitoid prevalence per shrubs and per gall also showed a significant difference (ANCOVA; $F_{2, 41} = 51.01$, $p < 0.0001$). Parasitoid prevalence per shrub was more strongly correlated (negatively) with shrub density than was parasitoid prevalence per gall (Fig. 3b).

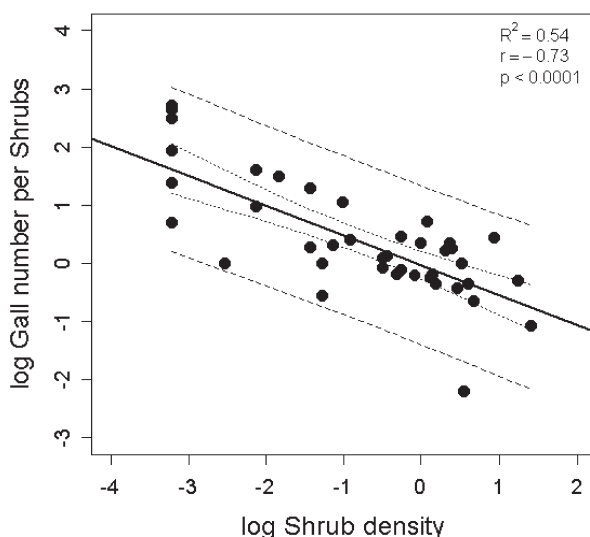


Fig. 1. Gall density per shrub as a function of rose shrub density per 50 m × 50 m plot (linear regression). The dotted lines represent the 95% CI, while the dashed lines represent the prediction intervals

Comparison of gall density effect. Both parasitoid numbers per shrub and per gall were positively correlated with gall number per shrub. However, the increase in parasitoid number per shrub was faster than the increase in parasitoid number per gall when plotted against gall number per shrub (ANCOVA; $F_{2,41} = 24.81$, $p < 0.0001$, Fig. 4a).

Parasitoid prevalence per shrub was positively correlated with gall density, whereas parasitoid prevalence per gall appeared constant regardless of increasing gall density, resulting in significant differences between the slopes of the two regression lines (ANCOVA; $F_{2,41} = 31.16$, $p < 0.0001$; Fig. 4b).

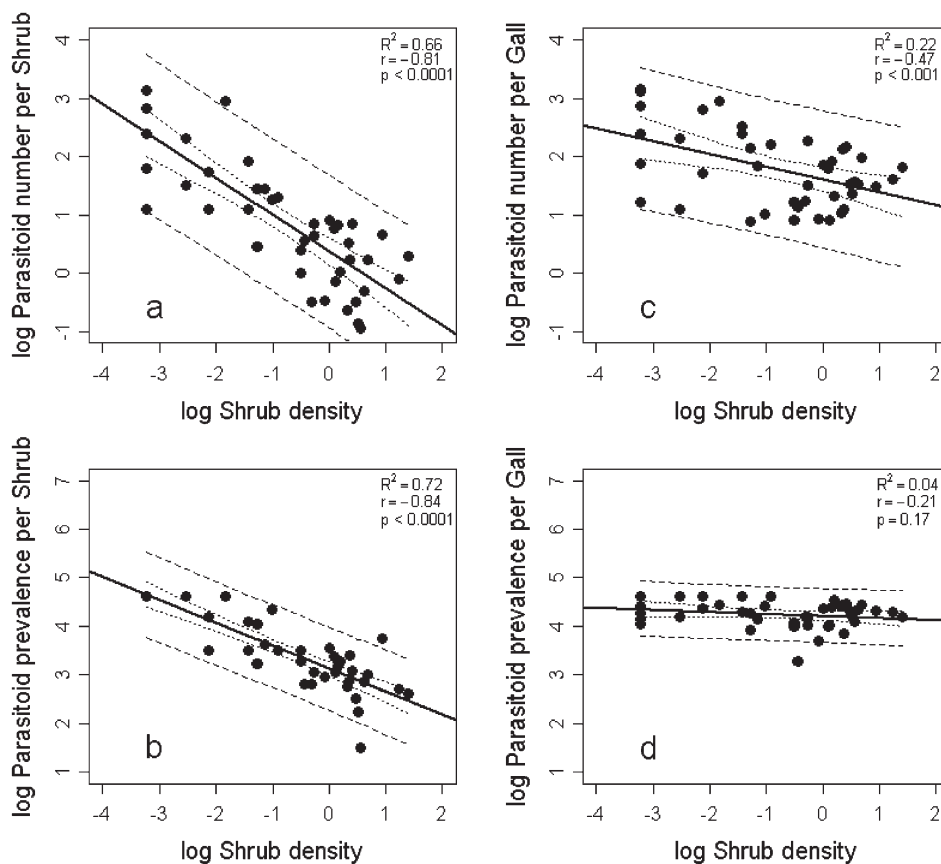


Fig. 2. a) Parasitoid number per shrub; b) parasitoid prevalence per shrub; c) parasitoid number per gall; d) parasitoid prevalence per gall as a function of rose shrub density per 50 m × 50 m plot (linear regressions). The dotted lines represent the 95% CI, while the dashed lines the prediction intervals

Comparison of shrub and gall density effects. Parasitoid prevalence per shrub was negatively correlated with shrub density, whereas parasitoid prevalence per gall appeared constant regardless of increasing gall density, resulting in significant differences between the slopes of the two regression lines (ANCOVA; $F_{2,41} = 49.78$, $p < 0.0001$; Fig. 5).

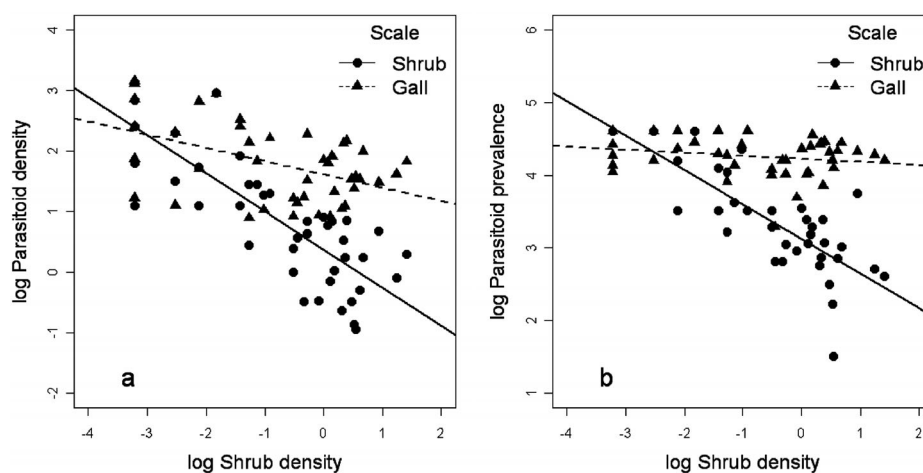


Fig. 3. a) Parasitoid numbers per shrubs (dots) and galls (triangles); b) parasitoid prevalences per shrubs (dots) and galls (triangles) versus rose shrub density per 50 m × 50 m plot (nested linear fixed effect ANCOVA)

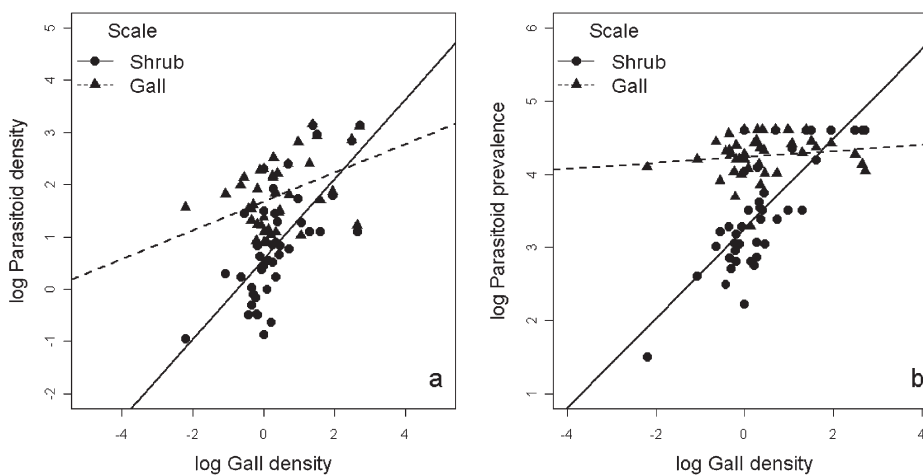


Fig. 4. a) Parasitoid numbers per shrubs (dots) and galls (triangles); b) parasitoid prevalences per shrubs (dots) and galls (triangles) versus gall numbers per shrub (nested linear fixed effect ANCOVA)

DISCUSSION

Bedeguar gall parasitoid density was density-dependent both at the rose shrub and gall scales, while prevalence of parasitoids was density dependent only at the rose shrub scale. At the gall scale parasitoid prevalence showed density independence. This pattern may occur if parasitoids exhibit differential preference to rose shrubs in the presence of galls. Optimal foraging theory predicts that parasitoids directly choose infected rose shrubs and don't forage on uninfected shrubs. The accurate and effective recognition of galled roses requires cues from the infected shrub individuals or directly from galls. This may support the presence of attractants which enhances the activity of natural enemies of these herbivores.

D. rosae galls showed inverse density dependence, the more rose shrubs were, the less galls occurred. This finding is in concordance with the results of WILLIAMS and CRONIN (2004) who found that combined density of *Diplolepis* spp. galls on *Rosa arkansana* showed inverse density dependence with rose density. It was found in a study of the relationship between rose shrub density and Bedeguar gall density that this inverse density dependence is connected to the aggregation of galls at high host densities on only a few shrubs, which may be linked to fitness

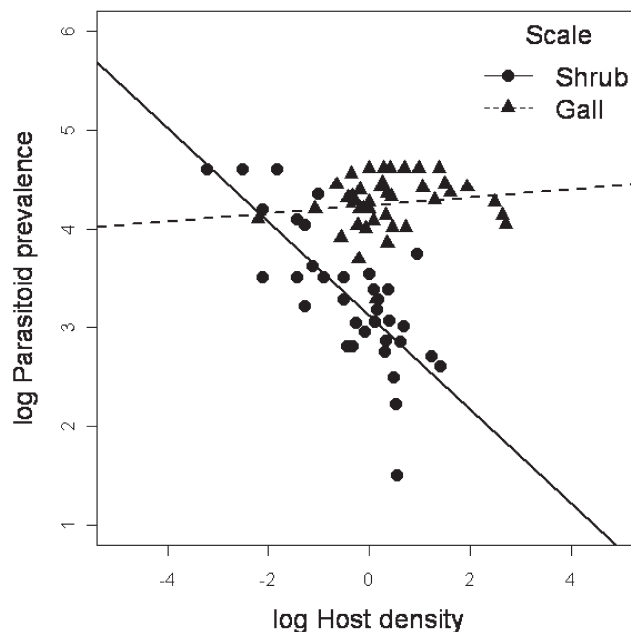


Fig. 5. Parasitoid prevalence per shrubs (dots) and galls (triangles) as a function of rose shrub densities per 50 m × 50 m plot and gall densities per shrub (nested linear fixed effect ANCOVA)

components of host shrubs (LÁSZLÓ & TÓTHMÉRÉSZ 2011). Contrary to our results direct density dependence was found in the case of *Urophora cardui* on *Cirsium arvense* (EBER & BRANDL 2003) and *Eurosta solidaginis* on *Solidago altissima* (CRONIN & ABRAHAMSON 2001). These contradicting findings may be due to factors such as growth form of the plants, biology of the gall formers, or number of gall chambers.

On the one hand parasitoid number per shrub showed inverse density dependence with shrubs. This means that the more shrubs were, the less parasitoids per shrub occurred. On the other hand parasitoid number per gall showed inverse density dependence with shrubs too. This means that the more shrubs were, the less parasitoids per gall occurred. This is possible because as density of shrubs increased the density of galls decreased. In this way the decrease in gall density strengthened the decrease of parasitoid number per gall. A similar result is known for the gall inducing cynipid wasp *Andricus quercuscalicis* on *Quercus cerris*. The parasitoid abundance of the pteromalid *Mesopolobus xanthocerus* showed inverse density dependence in the majority of spatial scales (HAILS & CRAWLEY 1992). In the case of inverse density dependence for parasitoid density of *A. quercuscalicis* (HAILS & CRAWLEY 1992) the galls were belonging to the sexual form which induces single chambered galls on male catkins of *Quercus cerris*. Both density dependence and independence responses were reported for parasitoids of the dipteran gall former *Giraudiella inclusa* on phragmites plants (TSCHARNTKE 1992). Half of the parasitoid species were density independent while the other half showed either inverse or positive density dependence on the gall's scale.

Parasitoid prevalence at the gall scale was density independent of both shrub density and gall density. Here we focus on the lack of correlation. In a study of *A. quercuscalicis*, attack rates by *Cecidostiba hilaris*, showed slight positive density dependence to the number of inquilines per gall (gall scale), while those by *Mesopolobus jucundus* showed no such trend (SCHÖNROGGE *et al.* 1996). In the lack of data regarding multi chambered galls this example is interesting, because inquilines (*Synergus* sp.) of the asexual galls of *A. quercuscalicis* inhabit gall wall tissues resembling multi chambered gall structure, while the inducer develops in the middle of the gall in a single chamber surrounded by small inquiline chambers. Both density dependence and independence were found for the parasitoids of inquilines in these asexual galls, which partially support our finding for *D. rosae* parasitoids in multi chambered galls at the gall scale. Parasitoid rates on the dipteran gall former *G. inclusa* were reported density independent at the gall scale (TSCHARNTKE, 1992). Another example of density independence of parasitoid rates is the single chambered galls of the gall wasp *Cynips divisa* where the inquilines *Synergus nervosus* and *S. pallicornis*, and the parasitoids *Eurytoma brunniventris* showed no significant relation to the gall number per leaf of *Quercus robur* (SITCH *et al.* 1988).

At the shrub scale, parasitoid prevalence was inversely density dependent of shrub density and density dependent of gall density. This would mean that prevalence of parasitoids may decrease with increasing host density which may result from handling limitations, causing decreased parasitoid efficiency in exploiting high host densities (STILING 1987, TAYLOR 1993).

Studies focusing on the relationships between parasitoid densities or prevalence and gall inducer density incorporating host plant abundance are still rather scarce. Thus, the lack of reliable case studies on density dependence of parasitoid abundance and prevalence on either shrub or gall scale may hamper the development of a comprehensive theory on galling tritrophic relationships.

Differences in the effect of density at the two scales may arise from differential selection of host plant by parasitoids. The lack of correlation between parasitoid prevalence (on gall scale) and host density (both shrub and gall) stands if the host plant selection by parasitoids target infected rose shrubs with a higher probability than uninfected shrubs. The constant prevalence may be not sustained if host plant selection is random, because, at higher shrub densities, where galls are aggregated and numerically inferior to lower densities (LÁSZLÓ & TÓTHMÉRÉSZ 2011), searching parasitoids would spend more time on uninfected shrubs, therefore prevalence would decrease. In this case parasitoids may identify rose plants, rather than galls, as islands, which is in concordance with the statement of PRICE *et al.* (1980) that insect parasitoids have particular searching patterns which constrain them on a single plant species or only a part of the plant species. This involves optimal search among shrubs rather than among galls. The success of search may be enhanced by the volatiles released by host plants or plant's visual cues which add to the signals emitted by galls (TURLINGS *et al.* 1993). Studies which confirm differential selection of host plant by parasitoids mostly treat non gall assemblages (HOLLABACH *et al.* 2002, LIU & JIANG 2003, RODRIGUEZ-SAONA *et al.* 2005).

Finally, since the pattern of parasitism by parasitoids of the Bedeguar gall on rose shrubs is density independent at the smaller gall scale, and inversely density dependent at the larger shrub scale, we conclude that the parasitoids perform their host selection presumably at the galled shrub scale and not at the gall scale.

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