

OBSERVATIONS OF SAGEBRUSH GALL MORPHOLOGY
AND EMERGENCE OF *RHOPALOMYIA POMUM*
(DIPTERA: CECIDOMYIIDAE) AND ITS PARASITOIDS

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ABSTRACT.—Galls induced by insects are specialized plant tissues thought to provide a suitable microclimate and high-quality food for insect development. Galls are also hypothesized to provide protection from predators, and particularly from parasitoids, because larger galls may be too deep for parasitoid oviposition (enemies hypothesis). However, galls may actually increase the risk of parasitism by making the location of gallformers more apparent (apparency hypothesis). *Rhopalomyia pomum* (Diptera: Cecidomyiidae) forms soft, lobed galls on big sagebrush (*Artemisia tridentata*: Asteraceae). The volume of the largest galls can be 600X that of the smallest. Here I explore the relationships of the number of lobes per gall and gall volume with the emergence of *R. pomum* and its parasitoids. I collected 159 galls from 4 locations in southern Utah in spring 2002, measured them, and monitored emergence from each. Lobing was not related to midge emergence ($F_{1,150} = 2.35, P = 0.13$) but was positively associated with parasitoid emergence ($F_{1,150} = 15.27, P < 0.001$), suggesting that early season parasitoids attacking before gall development may contribute to lobe formation by disrupting cues from eggs or larvae to the plant, or that flies in lobed galls are more accessible to oviposition by late season parasitoids. More midges emerged from larger galls than from smaller galls ($F_{1,150} = 22.0, P < 0.001$), but gall size was not related to parasitoid emergence ($F_{1,150} = 0.3, P = 0.6$), providing no support for either the enemies or apparency hypothesis.

Key words: gall, *Rhopalomyia*, *Artemisia*, *Cecidomyiidae*, *sagebrush*, *parasitoid*, *parasitism*.

Gall-forming insects stimulate their host plant to develop tumor-like growths that provide them with food and shelter (Abrahamson and Weis 1997). Morphology of the galls depends upon the species that induces it, and characteristics of galls are often used in identification of gallformers (e.g., Gagné 1989). Abrahamson and Weis (1997) argue that galls can be seen as adaptations of the insects that induce them rather than of the plant. However, there is ongoing debate about the adaptive nature of insect galls. Price et al. (1987) described the competing hypotheses and argued cogently that galls function to provide superior nutritional resources and a more suitable microclimate for gallformers. Subsequent research on nutritional quality of galls (Hartley and Lawton 1992, Hartley 1998, Schonrogge et al. 2000), water potential in galls (Fay et al. 1993), and distribution of galls in arid and mesic biomes (Fernandes and Price 1992, Price et al. 1998) lends support to those conclusions. However, there is ongoing debate over whether galls also act as a barrier to predation and parasitism, what Price et al. (1987) describe as the

“enemies hypothesis” (Askew 1965, Hawkins and Gagné 1989, Cornell 1990, Schultz 1992, Schonrogge et al. 1996, Stone and Cook 1998, Tschardt et al. 2001). Chemical composition, size, and hardness are several characteristics of galls that may influence rates of attack by parasitoids (Cornell 1983). Gall size seems particularly important, as parasitoids may not be able penetrate large galls deeply enough with their ovipositor to reach the gallformers, leading to lower rates of parasitism of insects in larger galls (e.g., Askew 1965, Price and Clancy 1986, Plakidas and Weis 1994, Abrahamson and Weis 1997). However, presence of a gall may also make insects more apparent to their natural enemies, as pointed out by Hawkins and Gagné (1989). Increasing gall size may increase apparency of galls, potentially increasing the risk of parasitism rather than decreasing it (Price et al. 1987), similar to the idea that the apparency of a plant influences the risk of herbivore attack (Feeny 1976). For simplicity I call this explanation for a positive association between gall apparency and natural enemy attack the “apparency

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hypothesis." Support for this idea comes from Hawkins and Gagné (1989), who found that cecidomyiid midges with more apparent galls have more species of parasitoids associated with them than cecidomyiids with less apparent galls, leaf rolls, or other unapparent modes of feeding. However, this pattern does not always hold because no significant differences in parasitism between galling and nongalling species of grass-feeding chalcids were found by Tschamtké et al. (2001). Lack of relationship between gall size and parasitism may be due to parasitism occurring during the "window of vulnerability" before the galls grow around the gallformers (Washburn and Cornell 1979, Craig et al. 1990, Briggs and Latto 1996).

Cecidomyiid gall midges are among the most common and speciose of the gall-forming insects. They are an ancient group found worldwide (Gagné 1989) that includes economically important pests (e.g., *Mayetiola destructor* Say, the Hessian fly) and biological control agents of weeds (Peschken et al. 1989, Ehler and Kinsey 1993, Hinz and Müller-Schärer 2000, Skuhrová and Hinz 2000, Sobhian et al. 2000). Although some cecidomyiids are well studied, the biology and ecology of others are poorly understood, and new species and even genera continue to be described at a rapid pace (Fedotova 2000, Gagné 2002, Kolesik et al. 2002).

Rhopalomyia pomum Gagné (Cecidomyiidae), a common gall-forming midge of big sagebrush (*Artemisia tridentata* Nutt., Asteraceae), is unusual among gallformers in that it induces a wide range of gall morphologies. *Rhopalomyia pomum* galls can have from 1 to many lobes (Jones et al. 1983) and can range from 0.35 cm to over 3 cm in diameter, with volumes varying 600-fold (see below). The physiological mechanisms leading to this variation in gall morphology are not known. Here I employ the naturally occurring wide range of gall morphologies to explore associations between *R. pomum* gall size and lobing on parasitism in this system. I am particularly interested in determining whether there is either a negative or a positive association between gall size and parasitism, which would lend support to the enemies hypothesis or the apparency hypothesis, respectively.

STUDY SYSTEM

Artemisia tridentata Nutt. (big sagebrush, Asteraceae) is an erect, aromatic evergreen

shrub of great ecological importance throughout its range in western North America (Monsen and Shaw 2000). In the Great Basin, sagebrush-dominated vegetation accounts for approximately 46% of all habitats, and on the Colorado Plateau it accounts for approximately 12% of all habitats (West 1979). There are 3 parapatric subspecies of *A. tridentata*, each of which uses slightly different environments (McArthur and Sanderson 1999, Monsen and Shaw 2000). *Artemisia tridentata* is tolerant to browsing (e.g., Messina et al. 2002) and provides important forage and habitat for many vertebrates. In addition, it is host to specialized herbivorous insects including many gall-forming midges. For example, in Idaho, 26 species of gall midges develop on the 3 subspecies of big sagebrush (Jones et al. 1983).

Rhopalomyia pomum Gagné (Cecidomyiidae), a gall midge specific to *A. tridentata*, is among the more abundant galling species found throughout most of the range of its host plant (Gagné 1989). It forms galls on all 3 subspecies of *A. tridentata* and on hybrids between them (Graham et al. 2001). It is univoltine: eggs are laid on leaves in late spring, galls form in late summer and larvae develop and overwinter within them, pupation occurs in the galls, and pupae break through the gall surface the following spring prior to adult emergence (Jones et al. 1983). The galls are globular to lobed, soft and spongy, reddish, pale, or green, and covered in short trichomes (Fig. 1; Gagné 1989).

METHODS

Galls were collected on 7 May 2002 from approximately 20 plants at 3 locations in Garfield County, Utah (Table 1). The first 2 locations were in the Dixie National Forest, north of Bryce Canyon National Park, and the 3rd location was near the Lower Box entrance of the Box Death Hollow Wilderness. At that 3rd location, 2 collections were made: (1) from a population of sagebrush spanning about 1 ha in a dry wash, and (2) from 1 of 4 heavily galled plants along the roadside. To sample galls of all sizes without bias, I collected all of the galls from each of the shrubs sampled, a total of 159 galls.

I counted the number of lobes on each gall, and then I measured each gall across its widest dimension (x) and perpendicular to that (y). Gall volume was approximated using the



Fig. 1. An illustration of a highly lobed *R. pomum* gall, and a cross section of another gall. Reproduced from Gagné (1989) with permission from Cornell University Press.

formula for an ellipsoid ($4\pi abc/3$, where $a = x/2$, $b = y/2$ and $c = (x + y)/4$ [the average of the 2 measured radii]). Galls were placed in individual resealable sandwich bags with a piece of moist paper towel approximately 2 cm \times 2 cm. Galls were monitored daily or weekly for 5 weeks. Paper towel pieces were moistened as needed to maintain a humid but not wet environment in the bags. As *R. pomum* emerged, they were counted, sexed, and removed from the bags. Parasitoids and other insects were also counted and removed as they emerged. In the analyses described below, all parasitoid species were treated as a single group.

I analyzed the data in 2 main ways to explore the relationships between insect emergence, lobing, and gall size. First, to determine the association between the numbers of insects emerging and gall morphology, I employed Poisson regressions using the GENMOD procedure of SAS (SAS Institute, Inc. 1997). *Rhopalomyia pomum* and parasitoid counts were natural-log transformed to improve their linearity, and a DSCALE option was included in the model statements to account for overdispersion of the data. I examined effects of lobing, gall volume, and collection location on emergence of both *R. pomum* and its parasitoids. I calculated a version of R^2 for these models suggested by Christensen (1990) for log-linear models. Here R^2 is a measure of the

TABLE 1. Geographical coordinates of sample locations, elevations, and sample sizes (N).

Location	Latitude and Longitude	Elevation (m)	N
1	Lat: 37°36'35" Long: 111°54'19"	2009	47
2	Lat: 37°36'37" Long: 111°54'9"	2104	27
3a, 3b	Lat: 37°56'13" Long: 111°38'18"	1959	85

proportion of deviance explained by the model and is calculated as $(G^2_0 - G^2_M)/G^2_0$ (where G^2_0 = the deviance of the null model with the intercept term only and G^2_M = the deviance of the full model).

The 2nd set of analyses focused on the relationship between what emerged from the galls (irrespective of how many emerged) and gall morphology. To this end I categorized galls into 4 types according to what came out of each: only *R. pomum*, *R. pomum* and parasitoids, only parasitoids, or neither *R. pomum* nor parasitoids. I used a simple 1-way ANOVA (JMP Version 5; SAS Institute, Inc. 2002) to compare the lobing and volume of galls of the 4 types. Gall volume was natural-log transformed to improve the normality of the residuals.

RESULTS

In addition to *R. pomum* and its parasitoids, several other insects emerged from the galls. There were 2 predatory taxa that appeared either from within the galls or from between the lobes: a single Syrphidae fly larva and 5 Cantheridae beetle larvae. In addition, many early instar Myridae nymphs were found in the bags. Because these nymphs were not visible on the outside of the galls when placed into individuals bags, it is possible that they emerged from eggs hidden between lobes. Several adult *Apion* (sensu lato; Coleoptera: Brentidae) emerged that were likely to be inquilines (Jones et al. 1983). There were not enough predators or inquilines to warrant statistical analyses. At least 6 parasitoid taxa emerged. Three were uncommon (a Pteromalidae, a Eulophidae in the subfamily Euderinae, and an Ormyridae in the genus *Ormyrus*) and 3 were more common (a Eupelmidae in

TABLE 2. Significance of main effects from the Poisson regression models for (a) the number of *Rhopalomyia pomum* gall midges and (b) the number of parasitoids emerging from the galls. Deviance and Pearson's chi-square for both models divided by the degrees of freedom were <1 , indicating acceptable fit of the models. See text for details of R^2 calculations.

Source	df	F	Pr > F	R^2
a. Gall midges				
Collection	3,150	3.74	0.125	
Gall volume	1,150	22.00	<0.001	
Lobes	1,150	2.35	0.127	
				0.41
b. Parasitoids				
Collection	3,150	3.31	0.022	
Gall volume	1,150	0.31	0.58	
Lobes	1,150	15.27	<0.001	
				0.19

the subfamily Eupelminae and 2 Torymidae: 1 in the subfamily Toryminae and 1 in the genus *Megastigmus*). The 2 torimids made up approximately 80% of the parasitoids.

Rhopalomyia pomum emerging from a single gall were either all male or all female, with 1 exception in which a single male emerged along with 4 females. The average volume of galls producing females (3.0 cm^3) was not significantly different from that of galls producing males (2.6 cm^3 ; $F_{1,46} = 0.23$, $P = 0.64$). The sex ratio of the flies was slightly female biased overall (1.4), but it varied widely by collection location (collection location 1 = 0.36; 2 = 3; 3a = 0.8; 3b = 1.6).

The number of lobes on galls ranged from 1 to 7, while gall volume ranged from 0.025 cm^3 to 16.20 cm^3 . Poisson regression for the numbers of *R. pomum* emerging from each gall showed no significant relationship between lobing and the number of midges that emerged (Table 2a) but showed that more midges emerged from larger galls (Table 2a, Fig. 2a). In contrast, the parasitoid model showed that parasitoids were more abundant in highly lobed galls, but gall volume had little association with the numbers of parasitoids that emerged (Table 2b). Figure 2b illustrates the relationship between lobing and parasitoid emergence. For clearer visualization of the pattern, overlapping points were separated by adding a random number between -0.4 and 0.4 to the number of lobes for this graphic.

Twenty-two galls produced only *R. pomum*, 49 produced only parasitoids, 26 produced both *R. pomum* and parasitoids, and 62 produced nothing. Comparison of these 4 types showed that galls that produced both *R. pomum* and

parasitoids had significantly more lobes than galls producing either flies or parasitoids alone, with galls that produced nothing having the fewest lobes (Fig. 3a). Galls producing *R. pomum* alone or with parasitoids were significantly larger than galls producing only parasitoids or nothing (Fig. 3b).

DISCUSSION

Rhopalomyia pomum emerging from a single gall were typically unisexual. This sex segregation was also observed by Jones et al. (1983) in *R. pomum* populations in Idaho and has been observed for other Cecidomyiidae as well (e.g., *Mayetiola destructor*; Stuart and Hatchett 1991; and *Cystiphora sonchi*, McClay 1996). The mechanism by which unisexual broods are formed is not completely clear. In the subfamily Cecidomyiinae (which includes *Rhopalomyia*), sex seems to be determined by the number of chromosomes present. In most of the species, females have 8 chromosomes (4 autosomes and 4 sex chromosomes) and males have 6 (4 autosomes and 2 sex chromosomes; Matuszewski 1982). In the Hessian fly (*Mayetiola destructor*), crosses between different brood types (all female, all male, or bisexual) suggest autosomal genes have alleles that either maintain or eliminate the 2 paternally derived sex chromosomes (Stuart and Hatchett 1991). A similar sex determination system may be acting in *R. pomum*. The ecological and evolutionary significance of unisexual broods is unknown (McClay 1996).

The relationship between gall morphology and the number of individuals emerging differed for gall midges and their parasitoids.

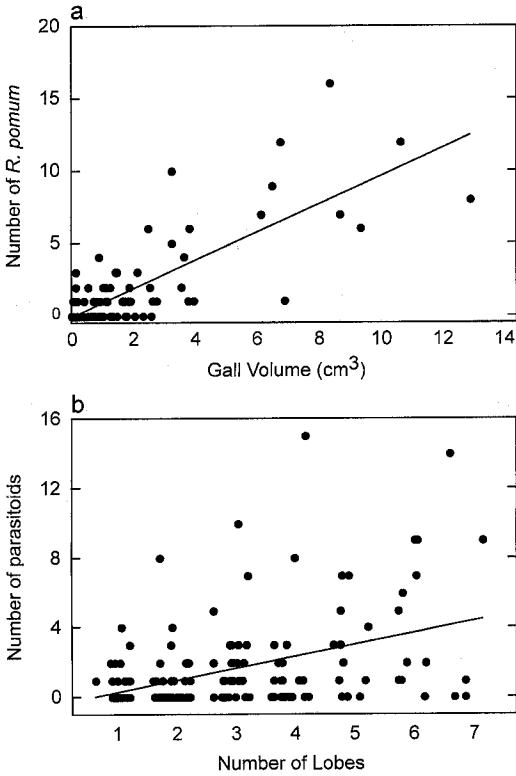


Fig. 2. (a) Relationship between gall volume and the number of *R. pomum* emerging. (b) Relationship between number of lobes on a gall and number of parasitoids emerging. To separate overlapping points, a random number between -0.4 and 0.4 was added to the number of lobes.

The number of lobes per gall was not related to the number of *R. pomum* that emerged; however, it was positively associated with parasitoid emergence. More parasitoids emerged from galls with more lobes than from galls with fewer lobes. Two mechanisms that could lead to this association are possible: (1) attack by early season parasitoids before gall formation may actually cause the formation of lobes by reducing the physiological cues that lead to gall growth, so that instead of a single large gall, several smaller ones are formed that are attached to each other; and (2) attack by later season parasitoids may be higher on lobed galls (whatever the mechanism of lobe formation), because the distance from the exterior to the gallformer will be smaller on average than in single large galls. Distinguishing between these possibilities is difficult, because timing of parasitoid attack and the window of vulner-

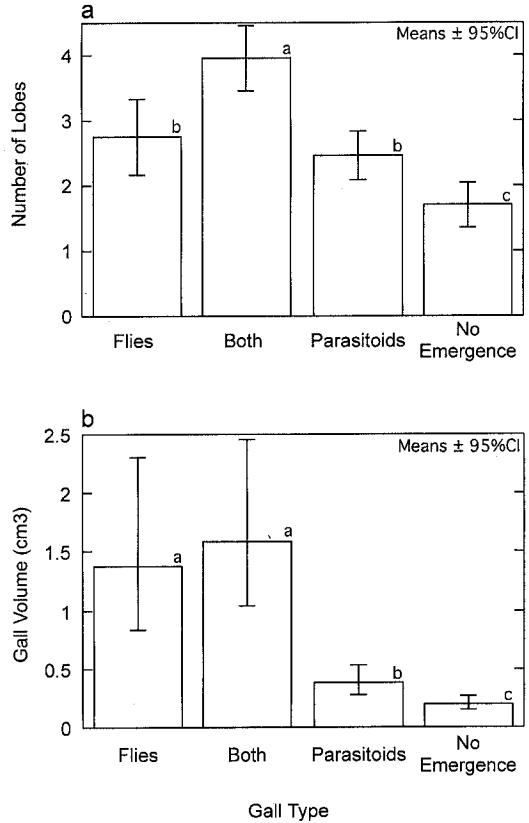


Fig. 3. Average lobing (a) and gall volume (b) of galls that produced only *R. pomum*, *R. pomum* and parasitoids, only parasitoids, or neither *R. pomum* nor parasitoids. Bars with different letters are significantly different at the $\alpha < 0.05$ level using Tukey's HSD.

ability of the midge to different parasitoid species currently is unknown.

Examining the lobing of the 4 types of galls (midges only, midges and parasitoids, parasitoids only, no emergence) showed that galls producing both flies and parasitoids had the most lobes on average. Since the galls producing only parasitoids had fewer lobes than galls producing both flies and parasitoids, mechanism 1 above cannot be the only means of lobe formation. Another possibility is that distinct lobes may form when eggs in a clutch are slightly separated on a leaf.

Larger galls produced more *R. pomum* per gall. This may simply be due to larger galls forming around larger clutches of eggs, as appears to be the case in the congener *R. californica* (Ehler and Kinsey 1993), or to larger

galls increasing the chances for midge survival. Gall size was not related either positively or negatively to parasitoid emergence, supporting neither the enemies hypothesis nor the apparency hypothesis. It may be that most parasitism takes place during the window of vulnerability before galls develop, leading to dissociation between parasitoid emergence and gall size.

The larger volume of galls producing *R. pomum* with or without parasitoids (Fig. 3b) suggests that developing larvae may produce the physiological cues that increase gall size throughout their own development. If all gall midge larvae die (through parasitism or other means), the drop in cues may lead to the reduced size of galls that produced only parasitoids, and neither flies nor parasitoids.

Interactions between plants, gall midges, and parasitoids are clearly complex. From this correlative study it is not possible to discern cause and effect. Are galls that produce *R. pomum* larger than others because more midge larvae are present to give the proper cues for gall growth, or do large galls produce more *R. pomum* because the midge larvae develop more successfully in larger galls? These alternatives are not mutually exclusive. Multiple factors may interact to give the patterns seen here.

The data suggest that *R. pomum* gall size does not influence overall parasitoid emergence either negatively (enemies hypothesis) through providing a barrier too thick for oviposition, nor positively (apparency hypothesis) by making the whereabouts of the flies more obvious. However, the parasitoid data were not analyzed separately by individual species due to total sample sizes available. Individual species may be influenced by gall size positively or negatively, depending on factors such as their host-finding mechanisms and their timing of attack.

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