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Parasitoid pressure and the radiation of a gallforming group (Cecidomyiidae: *Asphondylia* spp.) on creosote bush (*Larrea tridentata*)

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Summary. We tested the Enemy Impact Hypothesis, which predicts that communities of one tropic level are organized by the tropic level above. In the case of gallforming insect communities, the hypothesis predicts that gall morphology will diverge, minimizing the number of parasitoids shared among species. We used the monophyletic group of gallforming cecidomyiids (*Asphondylia* spp.) on creosote bush (*Larrea tridentata*) to test this hypothesis, predicting that species with thicker gall walls should exclude species of parasitoids with shorter ovipositors and have lower levels of parasitism. Of 17 parasitoid species reared from *Asphondylia* galls on creosote bush, 9 accounted for over 98% of parasitism. Seven of these 9 species had ovipositors long enough to penetrate 10 of 13 gall morphs measured. There was no significant relationship between gall wall thickness and number of associated parasitoid species ($r^2=0.01$, $P>0.05$, $n=13$). There was no relationship between gall wall thickness and types of parasitoid species colonizing galls: parasitoids with the shortest ovipositors colonized all types of gall morphs and were dominant members of the parasitoid assemblages in galls with the thickest walls. Ultimately, there were no significant differences in percent parasitism among *Asphondylia* species, regardless of gall wall thickness. We found no difference in numbers of associated parasitoids or percent parasitism in galls with different textures (e.g. hairy versus smooth), different locations on the plant or different phenologies. Our results suggest that enemy impact has not influenced the diversity of this gall community. Gall wall thickness, phenology, location on the plant and surface structure do not appear to influence the distribution of parasitoid species. Other explanations are offered to account for diversity in gall morphology among these species.

Key words: Parasitism – Gallforming – Community organization – Enemy impact hypothesis – *Larrea tridentata*

Many ecologists consider natural enemies to play an important role in structuring communities of herbivorous insects (Lawton 1978; Price 1980; Price et al. 1980; Lawton and Strong 1981; Strong et al. 1984). This view, represented by 'The Enemy Impact Hypothesis', contends that generalist predators or parasitoids will limit similarity among species within a community of herbivores by driving species to extinction or by strongly selecting for unique evolutionary responses that place species in enemy free space (Strong et al. 1984). While this concept has empirical support from several studies (Goeden and Louda 1976), more work is needed. Askew (1961) and Cornell (1983) extended this hypothesis to gallforming herbivores by suggesting that variation in gall morphology in communities of gallforming insects represents evolutionary responses to enemy impact.

Although many communities of gallforming herbivores exhibit considerable variation in gall morphology (Price et al. 1987), and thus, seem ideal for testing the Enemy Impact Hypothesis, no community-level tests of the relationship between natural enemies and gall morphology have been conducted to date. Investigations of enemy impact on individual species of gallformers have provided little insight into community-level patterns: some gall species are entirely free of parasitoids (Darlington 1975; Krombein et al. 1979), while others are heavily parasitized (e.g. Moser 1965; Askew 1980; Washburn and Cornell 1981; Hawkins and Goeden 1984; Abrahamson and Weis 1987; Hawkins and Lawton 1987), and others have some of the most complex parasitoid communities of any known herbivores (Price et al. 1987; Hawkins and references therein 1988). However, one pattern suggested by several studies is that species with larger than average galls deterred parasitoids because herbivores became inaccessible to parasitoid ovipositors (Jones 1983; Weis et al. 1985; Price and Clancy 1986; Price 1988).

Studies of parasitism in communities of gallforming insects may provide meaningful tests of the Enemy Impact Hypothesis because interactions between gall morphology and parasitoids are easily measured, and because many gallforming communities are comprised of monophyletic species (e.g. Felt 1940; Moser 1965; Mamaev 1968; Jones et al. 1983; Cornell 1985; Hawkins et al. 1986), and thus represent communities in which the consequences of evolutionary change are most easily measured. There are three predictions to consider when testing the Enemy Impact Hypothesis as applied to gallformers and parasitoids:

1. Gall species with thicker-walled galls should be attacked by fewer species of parasitoids.
2. Parasitoids with shorter ovipositors should be restricted to thinner-walled galls, while parasitoids with longer ovi-

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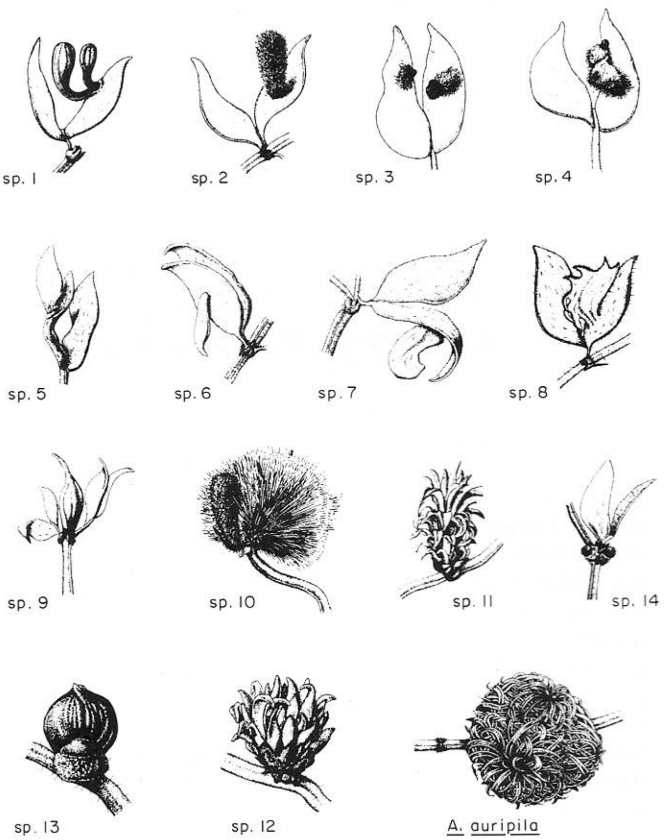

Fig. 1. *Asphondylia* galls on a creosote bush. Galls in the top row colonize leaf tops; galls in the second row colonize leaf bottoms; galls in the third row: the first two colonize flowers and seeds, and the second two colonize stems, galls in the fourth row colonize stems. (Illustration by Joel Floyd.)

positors should be more broadly distributed throughout the gall community.

3. Levels of parasitism should be lower in thicker-walled galls.

We studied a community of gallforming cecidomyiids (*Asphondylia* spp.) on creosote bush (*Larrea tridentata*) and addressed these predictions about parasitism. We also examined the relationship between parasitism and other variable gall traits, including phenology, location on the plant and gall surface texture. Levels of parasitism can be high, exceeding 80% in some cases, so strong selective pressure is potentially present.

Natural history

The 16 species of gallforming *Asphondylia* spp. (Cecidomyiidae) on creosote bush (*Larrea tridentata*) are a monophyletic group (most in Fig. 1) (R.J. Gagne, personal communication, National Museum and USDA, Washington, D.C.), and most were discovered by Waring. The colonial stemgalling species, *Asphondylia auripila* Felt, was described by Felt in the 1940s and the rest are currently being described by Gagne. Numbers are used here to distinguish new species.

In Arizona, *Asphondylia* species develop and emerge when creosote bushes are growing in response to increased temperature in the spring and in response to late summer rains. All leafgalling species (no 1–8) are bivoltine; flowergalling species (no 9, 10) also are bivoltine; and stemgalling species are univoltine, with species no 11, 12 and *A. auripila* developing and emerging in the late summer, while sp. no 13 is isolated from all others, emerging in January. Development and emergence in two other species have not been studied. Up to 10 *Asphondylia* species have been collected from individual creosote bushes and the geographic distributions of most species tend to be positively correlated with one another (Waring 1987).

Methods

To determine the number and types of parasitoid species (shorter versus long ovipositor) attacking *Asphondylia* species, galls were haphazardly collected from creosote bushes at three locations between 1982 and 1986: 1. Saguaro National Monument, approximately 10 km east of Tucson, Arizona; 2. Black Canyon City, approximately 15 km north of Phoenix, Arizona, and 3. Grand Canyon National Park, Arizona. Galls were stored in plastic bags at room temperature, and parasitoids allowed to emerge. Approximately 2300 parasitoids were reared from the galls of 13 *Asphondylia* species. Predators and nonhymenopteran inquilines were not considered in this study.

Field censusing from 1982 to 1987 determined percent parasitism for *Asphondylia* species. Galls were sampled at Saguaro National Monument, near Tucson, Arizona, in August, except for *Asphondylia* sp. 13, which emerged and was sampled in January. Galls of each species were collected haphazardly from numerous plants in the area and from this data we estimated percent parasitism for each species per year. Parasitism was indicated by the presence of or evidence of a parasitoid in the gall.

We compared parasitism in a pair of probable sister species in this monophyletic group. These species (*Asphondylia* species 1 and 2) seem identical ecologically, often cooccurring on leaves and based on an electrophoretic analysis using 20 loci and a morphological analysis, they are more closely related to one another than to other species within the gall community on creosote bush (Waring, unpublished data; Gagné, personal communication). The only obvious difference between these two species is that one has a smooth, thin gall wall, while the other has a hairy, thicker wall (Fig. 1). The genetic and ecological similarity of these species, with differing morphologies, makes them ideal for comparing patterns of parasitism, because any patterns detected are less likely to be confounded by other ecological differences. Predicting that the species with the thicker, hairy wall would be more resistant to parasitism, we compared their parasitoid communities with a similarity index and compared percent parasitism in both species when ambient levels of parasitism were moderate and high.

Parasitoid ovipositor length and gall wall thickness were measured using a Lasico® digitizing micrometer. Ovipositors of parasitoids were prepared by relaxing specimens in Barber's solution (53 parts 95% ETOH, 49 parts distilled H20, 19 parts ethyl acetate, 7 parts benzene) for one minute and extending the ovipositor on a slide. Each ovipositor was measured from its tip to the base of the second valve (Weis et al. 1985). The diameters of fresh, cross-sectioned gall wall tissues and the resins, hairs or leaf-like structures overlying them were measured separately.

We also considered relationships between number of parasitoids and percent parasitism and the following gall traits: 1. gall phenology (develop and emerge in spring and again in summer, or in summer only or winter only), 2. location on the plant (tops of leaves, bottoms of leaves, stems, flower parts), and 3. gall surface texture (smooth, hairy, leafy, resinous).

Statistical analyses in this study involved the following: Gall wall thickness was compared using analysis of variance (Nie et al. 1975). The relationship between number of attacking parasitoids and gall wall thickness of each *Asphondylia* species was estimated with regression analysis (Nie et al. 1975). The distribution of each parasitoid species across the gall community, and its frequency in the parasitoid communities of individual gall species, were plotted graphically. The relationship between percent parasitism and gall wall diameter was measured with analysis of variance, with years as replicates, using transformed percent parasitism data (arcsin(square root(percent parasitism))) (Nie et al. 1975; Zar 1984). While transformation was required for parametric significance testing, we presented the untransformed percent parasitism means with 95% confidence intervals (Rohlf and Sokal 1969). The similarity of parasitoid assemblages of *Asphondylia* species no 1 and 2 was measured with a community similarity analysis, SIMI, in which paired uncommon communities have a value of 0 and identical communities have a value of 1 (Stander 1970). Analysis of variance tested for differences in number of attacking parasitoids and percent parasitism by gall phenology, location on plant and gall surface texture. Percentage data were transformed, and we presented nontransformed means.

Results

Asphondylia gall morphology

While the tissue portion of the gall walls did not differ significantly, hair, resin and/or leaf layers overlying galls did result in significant differences in wall thickness, based on measurements of 417 galls (Fig. 2). *Asphondylia auripila* had the thickest gall wall ($\bar{x}=3.23$ mm, s.d. $=1.27$), while the thinnest was that of *Asphondylia* sp. no 5, a leafgaller ($\bar{x}=0.66$ mm, s.d. $=0.02$) (Fig. 2).

Asphondylia's parasitoids

Seventeen parasitoid species, in 6 hymenopteran families, were reared from *Asphondylia* spp. (Table 1). Nine species accounted for over 98% of the parasitoids reared: the torymids, *Torymus atriplicis, T. umbilicatus,* and *T. capillaceus*; the eupelmid, *Eupelmus* sp.; the eurytomids, *Tenuipetiolus mentha* and *Rileya tegularis*; the pteromalid, *Pseudocatolaccus guizoti*; and the eulophids, *Tetrastichus cecidobroter* and *T.* sp 1. All major parasitoid species were collected from the three locales. The remaining species were uncommon in the gall community.

Distributions of many of these nine parasitoid species within the *Asphondylia* gall community were broad. The mean number of *Asphondylia* hosts attacked was 9.4 and ranged from 5 to 13 (s.d. $=2.6$, $n=13$, Table 1).

Eight of the nine principal parasitoid species are primary parasitoids (attacking intended host only), with several also being facultative hyperparasitoids (attacking other parasitoids already in gall) (Krombein et al. 1979; Hawkins and Goeden 1984). The other species, *Tetrastichus cecidobroter*, is a gallforming inquiline, whose presence in a gall also results in *Asphondylia* mortality (Gordh and Hawkins 1982; Hawkins and Goeden 1982). At least eight of these nine species commonly attack the *Asphondylia* gall complex on saltbush (*Atriplex*) (Hawkins and Goeden 1984), which is sympatric with creosote bush throughout much of the southwestern United States. They also attack *Asphondylia* species and other gallformers on other host plant species (Hawkins and Goeden 1984; Krombein et al. 1979).

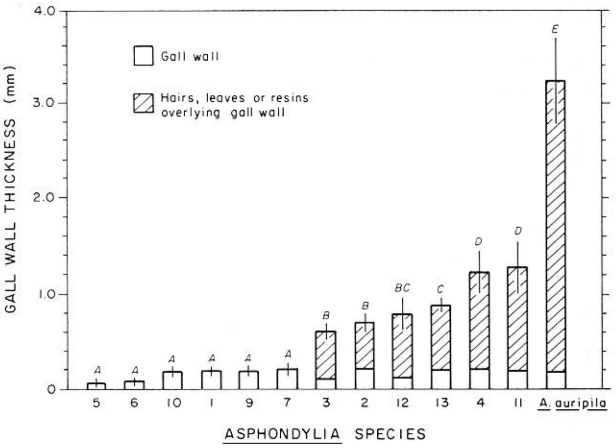

Fig. 2. *Asphondylia* species by gall wall thickness (Total wall thickness, $F_{13,404}=143.3$, $P<0.000$; Gall tissue thickness only, $P>0.05$)

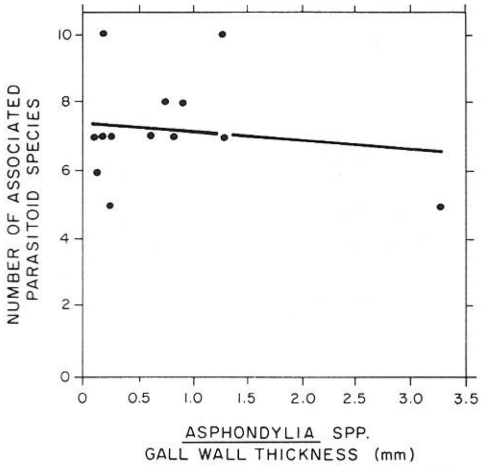

Fig. 3. Regression of number of parasitoid species reared from *Asphondylia* species with gall wall thickness ($y=7.97–0.607X$, $r^2=0.03$, $n=13$, $P>0.05$)

Predictions about parasitism and Asphondylia gall morphology

Prediction 1. Asphondylia species with thicker gall walls should be attacked by fewer species of parasitoids. No statistically significant relationship was detected between number of associated parasitoid species and gall wall thickness (Fig. 3). The mean number of parasitoid species reared from *Asphondylia* species was 7.2, and ranged from 5 to 10 (s.d. $=1.5$, $n=13$). The species with the thickest gall wall, *A. auripila*, did have relatively few associated parasitoids ($n=5$ species), although no fewer than a species with a gall wall that was 7 times thinner (*Asphondylia* sp. no 7).

Prediction 2. Parasitoids with shorter ovipositors should be restricted to thinner-walled galls, whereas parasitoids

Table 1. Parasitoid species collected from *Asphondylia* galls on creosote bush

Parasitoid species:	*Asphondylia* species attacked,	No. collected
Torymidae:		
Torymus larreae Grissell	9	1
T. umbilicatus (Gahan)	2, 3, 11, 12, 13, *A. auripila*	82
T. atriplicis (Hubner)	1, 2, 3, 4, 8, 10, 11, 12, 13, *A. auripila*	133
T. ferrugineipes (Hubner)	1	1
T. capillaceus (Hubner)	1, 2, 4, 6, 10, 11, 13, 14	82
Microdontomerus sp.	1	2
Pseudotorymus sp.	10	1
Pteromalidae:		
Pseudocatolaccus guizoti (Girault)	1, 2, 6, 8, 9, 10, 11, 13, 14	181
Eurytomidae:		
Rileya tegularis Gahan	1, 11, 12, 13, *A. auripila*	133
R. piercei Crawford	3, 4	9
Tenuipetiolus mentha Bugbee	1, 2, 3, 4, 7, 8, 9, 10, 11, 12, 13, *A. auripila*	588
Eulophidae:		
Tetrastichus cecidobroter (Gordh and Hawkins)	1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13	408
Tetrastichus sp. 1	1, 2, 3, 4, 5, 6, 8, 9, 10, 12	118
Tetrastichus sp. 2	9, 10, 13	6
Zagrammosoma multilineatum (Ashmead)	2, 3, 6, 8, 9	20
Eupelmidae:		
Eupelmus sp.	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, *A. auripila*	506
Chalcidae:		
Spilochalcis sp.	11	12

with longer ovipositors should be more broadly distributed in the gall community. Nearly all of the common parasitoids had ovipositors long enough to penetrate gall walls of 10 of 13 species measured (Fig. 4). Based on this alone, it seems unlikely that gall thickness could influence distributions of these parasitoids.

When considering ovipositor length, distributions and frequencies of parasitoid species across the gall community did not correspond to the diameters of gall walls they attacked, as one would predict if gall wall thickness was excluding species (Fig. 4). Some parasitoid species with the shortest ovipositors were the dominant parasitoid species reared from thick-walled galls, including galls with walls which appeared to be too thick to allow colonization by those species (e.g. *Rileyia tegularis* and *Tenuipetiolus mentha* in *A. auripila* galls, Fig. 4). These results indicate that thick gall walls are not excluding parasitoid species with shorter ovipositors, probably because attack occurs early in gall development or the parasitoids work their ovipositors down among the leafy structures overlying gall surfaces. Conversely, the species with the longest ovipositor (*Torymus umbilicatus*, Fig. 4), which should have had the broadest distribution in the gall community, was reared from 6 gall species, and was dominant only in one. This was the largest parasitoid and it may have been restricted to larger gall species, such as *A. auripila* and *A.* species no 11–13.

Prediction 3. Percent parasitism should be lower in *Asphondylia* species with thicker-walled galls. Percent parasitism

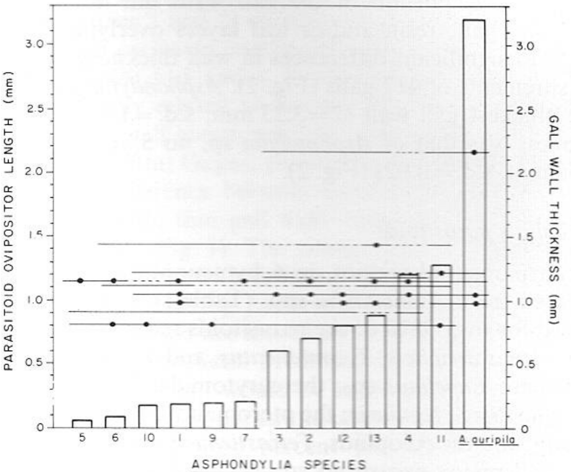

Fig. 4. The relationship between gall wall thickness, ovipositor length and distributions of parasitoids in the *Asphondylia* gall community on creosote bush. Vertical bars represent gall wall thickness by *Asphondylia* species (on *y* axis, right). Solid horizontal lines indicate the ovipositor length of parasitoids and extend across gall species that they were reared from (on *y* axis, left). Dotted lines indicate galls in which parasitoid were not reared. Solid cricles show gall species that a parasitoid was commonly reared from (making up at least 25% of the parasitoid community). In order of increasing mean ovipositor length: *Tetrastichus cecidobroter*, *T.* sp. 1, *Rileyia tegularis*, *Tenuipetiolus mentha*, *Torymus capillaceus*, *Eupelmus* sp., *Rileyia piercei*, *Torymus atriplicis*, *Pseudocatolaccus guizoti*, *T. umbilicatus*

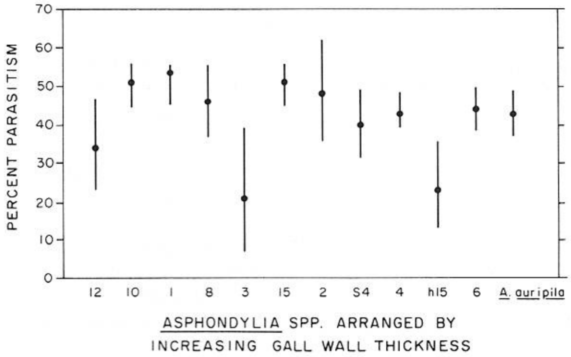

Fig. 5. Percent parasitism of *Asphondylia* spp., based on 2 to 6 years of data. These are nontransformed data, with 95% confidence intervals. The gall species are arranged according to increasing gall wall thickness. Analysis of variance on transformed data was not significant ($F_{11,33}=1.32$, $P=0.26$)

did not differ significantly among gall species, based on 2 to 6 years of data and examination of more than 6,400 galls (Fig. 5). The species with the thickest gall wall, *A. auripila*, had a parasitism level of 43%, while the average for all species was 41.5% (s.d. = 10.27, $n=12$). The three species with the lowest percent parasitism (spp. 4, 5 and 8) are all rare at the Tucson site. *Asphondylia* sp. 1, the commonest species at the site, was most heavily parasitized.

There was no significant relationship between number of parasitoids attacking a gall species and level of parasitism ($y=5.43+2.87X$, $r^2=0.05$, $n=11$, $P>0.05$).

Parasitism in Asphondylia sister species

The parasitoid communities of *Asphondylia* species 1 and 2 were virtually identical ($S=0.99$, based on 399 parasitoids reared from species 1 and 545 from species 2), indicating that they are attacked by the same species and in the same proportions, despite pronounced differences in gall morphology. They shared 6 species which accounted for over 96% of all parasitism in either species (Table 1).

There was no difference in percent parasitism between *Asphondylia* species 1 and 2 when ambient parasitism levels were moderate or high (% parasitism by species, $F_{1,1}=0.02$, $P>0.05$; % parasitism by intensity, $F_{1,1}=14.88$, $P>0.05$). At the Tucson site (moderate parasitism) percent parasitism of *Asphondylia* sp. 1 was 54% ($n=2{,}038$) versus 48% for sp. 2 ($n=91$) and at the Black Canyon City site (high ambient parasitism), 74% of *Asphondylia* sp. 1 were parasitized ($n=983$) versus 82% of *Asphondylia* sp. 2 ($n=365$). These results suggest that the hairy, thicker-walled gall of *Asphondylia* sp. 2 has not diminished its susceptibility to parasitoids and this does not change at different levels of ambient parasitism. We had predicted that if parasitism represents an important selective force in the evolution of gall morphology it should be most evident between such species.

Parasitism and other Asphondylia gall traits

We found no significant relationship between number of associated parasitoid species or percent parasitism and other gall traits including phenology, location on the plant and gall surface texture (Table 2), although considerable variation exists among species.

Table 2. Parasitism and *Asphondylia* gall texture and phenology and location on creosote bush

	No *Asphondylia* species:	Mean no parasitoid (S.D.)	Mean % parasitism (S.D.)[a]
1. Gall Surface Texture:			
Hairy	4	7.25 (0.50)	43.25 (13.60)
Resinous	1	8.00 (0.00)	43.00 (0.00)
Leafy	3	7.33 (2.52)	41.50 (2.12)
Bare	4	6.50 (2.89)	48.50 (10.54)
		$F_{3,8}=0.17$	$F_{3,8}=0.26$
		$P>0.05$	$P>0.05$
2. Gall Phenology:			
Summer only:	3	7.33 (2.52)	42.33 (2.08)
Spring and summer:	8	7.37 (2.20)	44.62 (10.87)
Winter:	1	8.00 (0.00)	43.00 (0.00)
		$F_{2,9}=0.04$	$F_{2,9}=0.05$
		$P>0.05$	$P>0.05$
3. Gall Location:			
Flowers	1	7.00 (0.00)	50.00 (0.00)
Flower Pedicels	1	7.00 (0.00)	46.00 (0.00)
Stems	4	7.50 (2.08)	42.50 (1.73)
Leaf Tops	4	8.00 (1.41)	44.25 (14.48)
Leaf Bottoms	2	6.50 (4.95)	42.00 (12.73)
		$F_{4,7}=0.14$	$F_{4,7}=0.12$
		$P>0.05$	$P>0.05$

[a] *F* test results are based on analysis of arcsin-square root transformed percentage data, although nontransformed means and standard deviations are presented

Discussion

We found no evidence that parasitoid pressure has influenced the evolution of gall wall thickness or other gall traits in the gallforming community on creosote bush. Thus, we conclude that the Enemy Impact Hypothesis is not supported by this study. The differences in gall morphology we observed seem nonadaptive with regards to parasitoids. These results contrast with suggestions of Cornell (1983) and Askew (1961), while supporting our earlier proposal (Price et al. 1987) that there is little evidence to support the Enemy Impact Hypothesis with regard to diversity in gall communities, and so alternative explanations must be sought.

Some parasitoid species we report on here attack early instar gallformers (e.g. *Rileyia tegularis*), while other species are dependent on later instar larvae (e.g. some *Torymus* species) (Hawkins and Goeden 1984) and so gallformers are susceptible to parasitism throughout much of their life history. We commonly observed the presence of early instar parasitoids associated with late instar larvae or pupae in the largest gall, *Asphondylia auripila*, indicating that these gallformers are attacked throughout their development. Regardless of when the galls are attacked, the wide distributions of parasitoid species in the gall community on creosote bush indicates that gall morphology is not detering them.

Three alternative explanations may account for some of the diversity in gall morphology on creosote bush: 1. Some gall morphologies reflect the structure of the plant part that they derive from. For instance, galls that originate from leaf buds on stems (*Asphondylia* sp. 11) are very leafy;

fruit galls are extremely hairy, as are fruits; and most leaf galls have essentially the same texture as do leaves (Fig. 1). However, other galls do not resemble the plant surfaces they derive from and so their morphology requires other explanations. 2. Some gall morphologies may protect gallformers from heat and solar radiation, because all of the hairy leaf gall species occur on leaf tops (*Asphondylia* species 2–4) (Fig. 1). These species have colonized tops of leaves through separate radiations from different plant parts (Waring, unpublished data), rather than radiating within the leaf 'habitat'.

Still other types of gall morphologies offer no insights into their derivation or function and the third proposed explanation is that some variation has arisen through genetic drift. Gall morphologies are clearly delineated between species, suggesting that they may have arisen with speciation events. Perhaps they arose through genetic drift as populations became isolated and gall morphology, beyond the basic protective envelope of plant tissue, has no adaptive function at all.

It seems that galls must become quite large, and do so very quickly, to deter parasitoids and such a trait simply has not arisen in the *Asphondylia* complex on creosote bush. However, in the *Asphondylia* complex on saltbush, *A. neomexicana* stimulates a thick, hairy gall (about 10 mm in diameter), that does deter both species and numbers of parasitoids (Hawkins et al. 1986; Hawkins and Goeden 1984). Within *Quercus robur*, it is clear that gall size varies greatly among different cynipid species (Askew 1961). This variation seems to reside in the genotype of the gallformer, although the host plant may also play a role. Weis and Abrahamson (1986) showed that some individuals of *Eurosta solidaginis* can stimulate the growth of large, parasitoid-proof galls on *Solidago altissima* stems, and yet avian predators selectively attack these larger galls; and variability in plant reactivity can compromise the expression of this trait. Their work elegantly demonstrates how complicated these processes can be. The unpredictability of the evolution of the trait for large gall stimulation combined with these other selective factors means that the role of natural enemies in structuring gall communities is likely to remain highly idiosyncratic.

There is no evidence that natural enemies have influenced gall morphology in the gall community on creosote bush. Parasitism in this study and others (Waring 1987; Hawkins and Goeden 1984) may be a density-dependent phenomenon, with parasitoids tracking gall populations more than regulating them. Large numbers of ecologically similar *Asphondylia* species co-occur on creosote bushes, and though they do not appear to have not acquired enemy free space, they persist. These patterns are not compatible with the predictions of the Enemy Free Space hypothesis.

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