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INVERSELY DENSITY-DEPENDENT PARASITISM: THE ROLE OF PLANT REFUGES FOR HOSTS

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SUMMARY

(1) The response of a parasitoid species to host density was investigated for a host species concealed by plant tissues. The parasitoid was *Pteromalus* sp. and the host was a stem-galling sawfly, *Euura lasiolepis* on the willow, *Salix lasiolepis*.

(2) For three consecutive years in natural populations the parasitoid responded in an inversely density-dependent manner to host density, as density varied among patches of hosts on willow clones.

(3) There was a systematic positive relationship between mean gall diameter per willow clone and host density, such that hosts in high population patches were better concealed from parasitoids than hosts in low population patches. The size of the refuge from parasitoid attack increased as host density increased.

(4) The negative relationship between mean gall diameter per willow clone and percentage parasitism was significant in 1984, and when the 3 years of data from this study were combined, and when all data for seven generations of sawfly were grouped (1979–85).

(5) Plant traits and other concealing factors are important in defining the response of parasitoids to host density and may play a role in mechanistic and functional explanations of such responses.

INTRODUCTION

Lessell's (1985) review of responses of parasitoids to host density variation across patches showed that all possible responses occur in natural and laboratory systems: in the fifty-one cases examined 33% showed density dependence, 33% were inversely density-dependent, 29% were independent of density, and 4% were density-dependent at low host densities and inversely density-dependent at high host densities (a domed response). The model Lessells developed accounted for all these responses using the assumption that all hosts are equally available to parasitoids within a patch. She recognized that this is not always the case, and the intent of this paper is to explore with empirical field observations an example of hosts with very different availability within patches and between patches.

Of the thirty-two host species in Lessells' review, twenty are concealed in some way, most within plant parts: leaf-miners, stem-borers, gallers, seed-feeders and eggs in plant tissues laid by cicadellids and sawflies. Other cases include sawflies in cocoons hidden in the soil, flour moth larvae in a substrate, caddis flies in a case and paper wasp larvae in cells. Whenever a host is concealed, the potential exists for refuges or partial refuges from

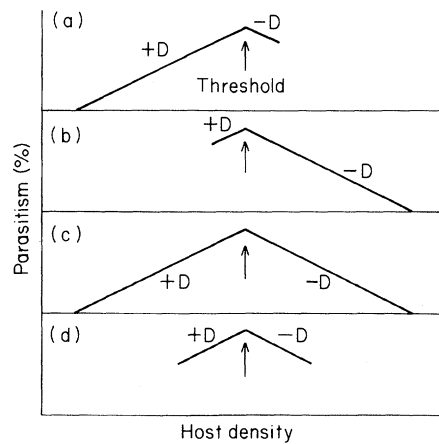
Plant refuges and parasitoid foraging

FIG. 1. Hypothetical responses of parasitoids to host density when a partial refuge for hosts is involved and starts to function at the threshold indicated and becomes stronger as host density increases. Thus, the probability of parasitoid success increases up to the threshold and decreases beyond the threshold in relation to host density. Cases A–D assume that different parts of a host density range are sampled in a given study, and illustrate the consequent parasitoid response observed. Case A will be density-dependent (+D); Case B, inversely density-dependent (–D); Case C, domed. Case D will probably appear to be density-independent because of variation round the mean trend. Other patterns would be apparent if hosts lived in effective refuges at low densities, but competition for these sites forced individuals into more vulnerable positions at higher densities.

parasitoid attack. For example, a host in a thick stem may have a lower probability of attack than one in a thin stem, or may be completely protected by the plant part.

Such refuges can produce all the possible parasitoid responses to host density if there is a systematic relationship between host density and the efficacy of the refuge (Fig. 1). This is probably more common than is realized at present. Many insects attack the most vigorous plant parts where they become most deeply concealed (e.g. Whitham 1978; Whitham & Mopper 1985; Craig, Price & Itami 1986), with the result that a host patch on a vigorous plant has a lower probability of attack by parasitoids than a host patch on a less vigorous plant.

Such refuges impose serious strictures on the way a parasitoid population can respond to host density. Understanding the mechanisms involved will then provide the functional explanation of why the parasitoid should respond in a particular way. Thus, the puzzle of the functional explanation of parasitoid foraging emphasized by Hassell, Lessells & McGavin (1985) is comparatively simple if refuges for hosts are involved. If the parasitoid response is inversely density-dependent, domed, or even density-independent, a partial refuge may be the reason why foraging does not meet the expectations for profitable or optimal searching.

We have examined a field case in which a galling herbivore is attacked by an ectoparasitic wasp, *Pteromalus* sp. (Hymenoptera: Pteromalidae), which must pierce the gall from the external surface to reach its host (Price & Clancy 1986a). We showed that this small wasp had a mean (± 1 S.E.) ovipositor length of 1.89 ± 0.05 mm and thus could reach all hosts in galls up to 3.78 mm diameter. In fact, the threshold gall diameter was between 5 and 6 mm, above which the observed attack rate declined rapidly relative to that expected from random attack. Hosts were not necessarily centrally located in a gall so

they remained vulnerable to attack in galls larger than 3.78 mm. The refuge was partial from about 5 mm gall diameter to 7 mm, and complete in galls from 7 to 10 mm. We also showed that willow plants, hosts to the sawfly, differed significantly in the size of galls induced, and there was a long-term negative relationship (1979–83, five generations of host) between mean gall diameter per plant and percentage interval parasitism (parasitism of host larvae actually available when *Pteromalus* attacked).

Lessells' (1985) review, and studies by Hassell (1982, 1985) and Hassell, Lessells & McGavin (1985) placed the emphasis on spatial density relationships between hosts and parasitoid attack; they stimulated the present study which investigates the host population and parasitoid attack relationships between *Pteromalus* sp. and the galling sawfly, *Euura lasiolepis* Smith (Hymenoptera:Tenthredinidae). The willow, *Salix lasiolepis* Bentham, spreads vegetatively to produce clones that act as patches colonized by the sawfly and available to searching parasitoids. Each willow clone has a characteristic mean gall diameter, although this changes from year to year in response to environmental changes, particularly in water availability (Price & Clancy 1986a). The present study develops the detailed plant gall–herbivore–parasitoid relationship reported by Price and Clancy to investigate the population level interactions of the system.

METHODS

The study lasted 3 years and three host generations: 1983–85. It was conducted on the same fifteen willow clones per year on land owned by or adjacent to the Museum of Northern Arizona, north of Flagstaff (about 2100 m above sea level, 35°14' N, 111°30' W). All clones were within a radius of 500 m, and all either maintained populations of herbivores and parasitoids, or were touching other clones that did, so that colonization in each generation could occur readily.

Every year on every willow clone, galls were collected from all parts of each clone for dissection to determine the proportion of galls with larvae available to *Pteromalus*, and the proportion attacked by *Pteromalus*. First, diameter of all galls was measured to provide an estimate of how well hosts were concealed from attack by *Pteromalus*. *Pteromalus* attacks middle-sized larvae (instars III–IV) (Price & Craig 1984), so the proportion of these present per gall sample was estimated by opening galls. Sample sizes of 100 galls or more per clone were taken when available, but less than 100 galls could be found in some clones in some years. Replicate samples of 100 galls on one clone in 1980 showed only 6% maximum difference in estimates of percentage of larvae surviving to the stage available to *Pteromalus* (Price & Clancy 1986b). Dissections of galls were performed in March and April, toward the end of the sawfly generation when *Pteromalus* larvae were fully grown and conspicuous in galls. The percentage of middle-sized host larvae parasitized was calculated and termed *percentage interval parasitism*. It denotes parasitism on this interval of the life cycle, not parasitism on the original cohort starting the generation, or parasitism among the survivors of a cohort when the cohort is older than when it is attacked.

The number of galls per clone was estimated each year in March or April. A line was thrown over each clone repeatedly and in haphazard directions, and all shoots observed within 30 cm of the line until 1000 shoots had been examined. The number of galls per shoot was recorded. From the gall dissections the proportion of these galls occupied by host larvae at the time of *Pteromalus* attack was estimated, and then the density of hosts available to *Pteromalus* per 1000 shoots was estimated as the product of galls per 1000

TABLE 1. Regression equations for the relationships between sawfly host density (X) and percentage interval parasitism by *Pteromalus* (Y), in the years 1983–1985

Year	Regression equation	Sample size*	r^2	Probability
1983	$Y + 1 = 25.50e^{-0.0011(X+1)}$	8	0.92	< 0.01
1984	$Y + 1 = 23.92e^{-0.0014(X+1)}$	10	0.77	< 0.01
1985	$Y + 1 = 25.59 - 0.04(X + 1)$	9	0.65	< 0.01
All years	$Y + 1 = 20.96e^{-0.0013(X+1)}$	27	0.61	< 0.01

* Sample size was determined by the number of clones represented by 100 galls or more, except in 1985 when seven clones had 100+ galls, one had 85 galls, and another 53 galls. Gall densities declined in 1985, so the latter samples were used as they were the next largest samples available and they boosted clone sample size.

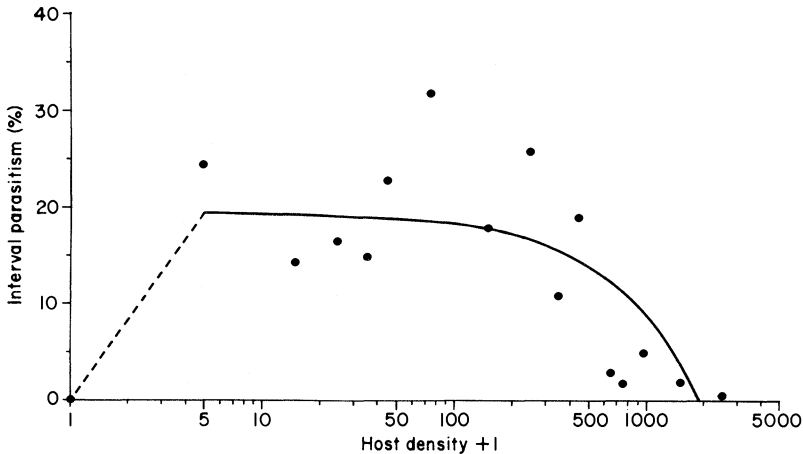


FIG. 2. Percentage interval parasitism in response to host density (+ 1) when sixteen host density classes were used and data grouped from fifteen clones for 3 years. Points for each class are plotted at its mid position. For the fifteen positive percentage interval parasitism (Y) values the regression equation with host density (+ 1) (X) was $Y = 19.61 - 0.01X$, $r^2 = 0.53$, $P < 0.01$. Note that the host density axis is on a logarithmic scale, making the linear relationship curvilinear on this scale.

shoots and the proportion occupied by middle-sized larvae. This provided the estimate of host density utilized in all analyses.

In all analyses mean estimates per clone were used for least squares linear regression, and the equation providing the highest correlation coefficient was used of the four types: arithmetic linear, logarithmic, power, and exponential. When zero values occurred in any estimate, $X + 1$ and/or $Y + 1$ transformations were used for the non-arithmetic regressions.

These analyses were based on dissection of a total of 1139 galls in 1983, 1298 galls in 1984, and 1036 galls in 1985. Whenever estimates per clone were made from less than 100 galls this will be stated in the results.

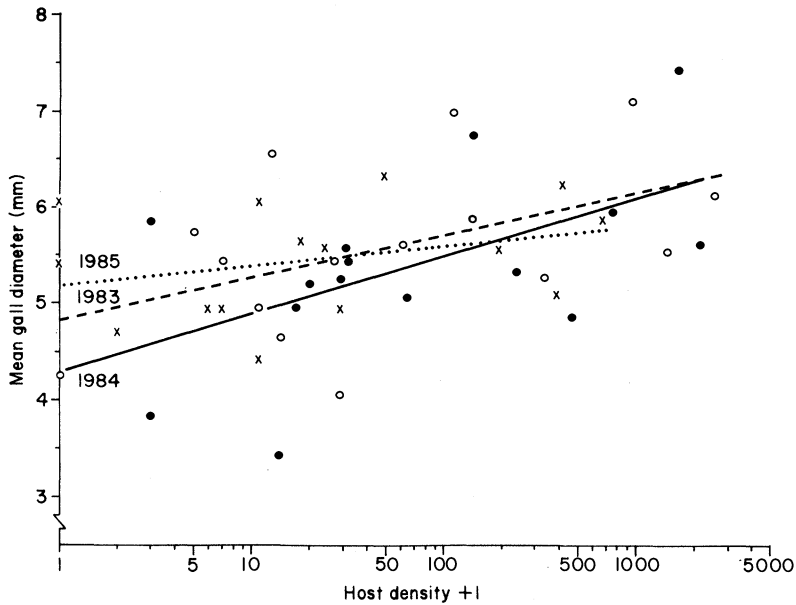


FIG. 3. The relationships between mean gall diameter per clone (Y) and host density ($+1$) (X) for the years 1983–85. Symbols and regression equations are as follows: 1983 (O—O), $Y = 4.82 + 0.19 \ln X + 1$, $n = 15$, $r^2 = 0.25$, $P < 0.05$; 1984 (●—●), $Y = 4.28 + 0.26 \ln X + 1$, $n = 15$, $r^2 = 0.30$, $P < 0.05$; 1985 (x ··· x), $Y = 5.19 + 0.09 \ln X + 1$, $n = 15$, $r^2 = 0.10$, N.S. The sample of fifteen clones per year was used because at least four replicates for the gall size estimate were available per clone. Gall diameters at 0 host density occurred when no available hosts existed in the galls.

RESULTS

Host density and percentage parasitism

In the three host generations studied there was a consistent inverse density dependence in *Pteromalus* attack (Table 1). Sawfly density accounted for 65–92% of the variance in percentage interval parasitism within years and 61% of the variance when years were combined. To examine the general response of the parasitoid at densities lower than represented by the clones used in Table 1, data from all clones and all years were grouped into sixteen host density classes (Fig. 2). Levels of parasitism were generally high when host density ranged from about 4 to 500 hosts per 1000 shoots, but low at higher densities, and of course zero when no hosts were available. Using the fifteen positive values of percentage interval parasitism, host density accounted for 53% of the variance (Fig. 2).

At low host densities (<30 hosts per 1000 shoots) percentage parasitism varied enormously, between 33 and 0% and in one case 100%. This was partly because of small sample sizes available, but also because of the potential for parasitoid populations to go locally extinct on a clone as host densities decline.

Host density and gall diameter

A positive relationship between mean gall diameter per clone and host density also existed in each year of study (Fig. 3). The relationships were significant in 1983 and 1984, but not in 1985. This meant that hosts became more deeply concealed from parasitoid attack as host density increased. This relationship probably existed because sawflies more

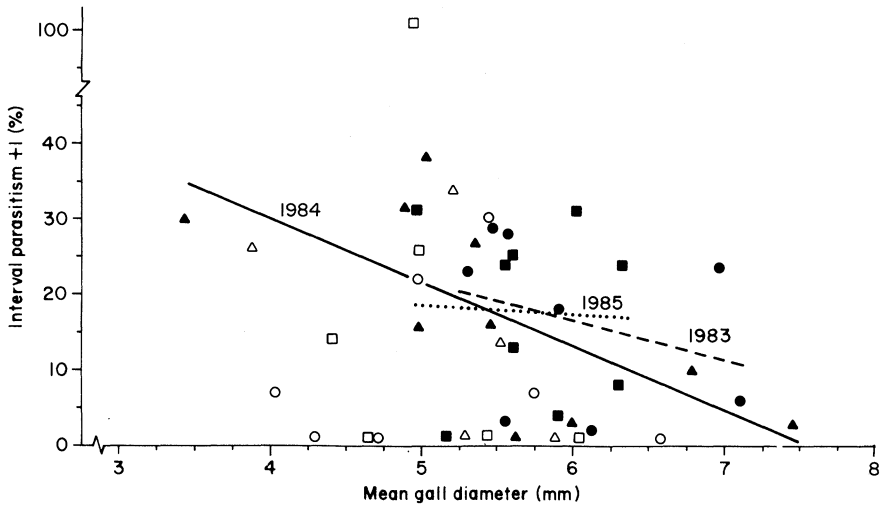


FIG. 4. Relationships between mean gall diameter per willow clone (X) and percentage interval parasitism per clone (Y). Data for all fifteen clones per year are given. Closed symbols represent data with large gall sample sizes as described in Table 1, and used in the regression. Open symbols are for clones with smaller sample sizes and are not included in regressions. 1983 (●---●); 1984 (▲—▲); 1985 (■···■). The regression equations were as follows: 1983, $Y+1=70.66-30.24 \ln X$, $n=8$, $r^2=0.09$, N.S.; 1984, $Y=62.91-8.43X$, $n=10$, $r^2=0.47$, $P<0.05$; 1985, $Y+1=29.68-6.78 \ln X$, $n=9$, $r^2=0.002$, N.S.

frequently attack the longest shoots available per clone and the clones with the longest mean shoot lengths (Craig, Price & Itami 1986; Price & Clancy 1986b). This means that vigorous clones support higher sawfly densities than old and senescent clones, and galls develop to a larger size on vigorous shoots. Mean gall diameters per clone remain stable relative to other clones from year to year (Price & Clancy 1986a), and sawfly densities per clone also correlate from year to year (Craig, Price & Itami (1986), e.g. 1983/84 correlation, $r^2=0.91$, $P<0.001$, $n=15$), so the extent of the partial refuge from parasitoid attack remains characteristic for each willow clone patch. Hosts are better protected where plant vigour and therefore host density are higher.

Gall diameter and percentage parasitism

The relationship between mean gall diameter and percentage interval parasitism was negative and significant in 1984, accounting for 47% of the variance in parasitoid attack (Fig. 4). In the other 2 years the relationship was not significant, and difficult to detect because samples with many galls showed such a small range in mean gall sizes; 1.82 mm in 1983 and 1.38 mm in 1985. In contrast, the range in gall diameters in 1984 was 4.00 mm. The decline in the lowest gall diameters in 1984 beyond the range in other years no doubt resulted from poor growth of willows in dry sites after low precipitation in the winter of 1983/84 (Price & Clancy 1986a,b). This extended the gall diameter range for 1984 by 1.45 mm, making the pattern easier to detect. When 1984 data on mean gall diameter (X_1) and host density (X_2) were entered as independent variables in a multiple linear regression with percentage interval parasitism (Y) as the dependent variable, both X_1 and X_2 had negative slopes, indicating that when gall diameter is held constant a negative density dependence

is evident in the parasitoid response in addition to the gall diameter effect ($Y+1 = 53.79 - 5.80X_1 - 0.01X_2$, $n = 10$, $r^2 = 0.62$, $P < 0.05$).

When the 1983–85 years of data were combined the relationship between mean gall diameter (X) and percentage interval parasitism (Y) was negative and significant ($Y = 53.54 - 6.49X$, $n = 27$, $r^2 = 0.20$, $P < 0.05$). In addition, when these data were coupled with results from 1979 to 1982 in Price & Clancy (1986a) to cover seven generations of sawfly–parasitoid relationships, the regression equation accounted for 31% of the variance in percentage interval parasitism (using only samples of 99 galls per clone or larger $Y = 60.30 - 7.46X$, $n = 48$, $r^2 = 0.31$, $p < 0.01$). The negative relationship between mean gall diameter per clone and percentage interval parasitism is long-standing, and strong, for it is detectable in spite of many environmental variables which probably increase the variation in response of the parasitoid to host populations.

DISCUSSION

This study has shown that a concealed herbivore in a gall has a decreasing probability of attack by a parasitoid as gall diameter increases and that this pattern correlates positively with herbivore density. There existed a systematic relationship between host density and a partial refuge from parasite attack as suggested in the introduction (Fig. 1).

Such relationships may be more common in nature than the literature has revealed. Bark beetles in deep bark near the base of trees may be denser and better protected from parasitoids than in thinner barked parts of the tree (Berryman 1982). Cicadellids attacking more rapidly growing plants may, hypothetically, oviposit deeper in more succulent tissues, and reach higher populations on vigorous plants. Conversely, the ultimate result of population increase in favourable sites may be competition for oviposition sites and displacement of some oviposition to less-protected sites, so a density-dependent response by parasitoids becomes possible.

The existence of partial refuges provided by plants for concealed herbivores, or other substrates in which hosts exist, may force the parasitoid into a relatively impotent role in the population dynamics of the host. In the *Euura-Pteromalus* example this is the case. The parasitoid is very ineffective at high host densities when sawfly populations are self-sustaining on individual clones. At low populations on poor quality willow clones where *Pteromalus* may parasitize 30% of the available sawflies, maintenance of the population is probably largely by immigration rather than by local reproduction. Although this point needs more study, it seems that *Pteromalus* can attack many hosts only where they are probably doomed also by other factors, particularly low-quality resources. The partial refuge provided by galls seems to force *Pteromalus* into a more passive role in its host population dynamics than is generally thought to be the case for parasitoids.

This example reinforces our argument that the three trophic levels of plants, herbivores and their parasitoids interact in complex ways and need to be understood as a unit, rather than in pairwise comparisons of only host and parasitoid (Price *et al.* 1980; Price & Clancy 1986a). Three trophic level interactions represent evolutionary units in Thompson's sense (1982, 1986a,b). By understanding the ecology of such units we can begin to understand the evolutionary forces that shape them. This will provide the basis for a functional ecology which can answer such questions as why parasitoids should respond to host populations in an inversely density-dependent manner.

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