

Inverse Density-Dependent Parasitism of the Bagworm, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae)

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ABSTRACT This paper reports the results of a controlled manipulative experiment with the bagworm, *Thyridopteryx ephemeraeformis* (Haworth), on eastern redcedar, *Juniperus virginiana* L., to determine whether parasitism is density-dependent. Parasitoid foraging behavior indicated that two spatial scales were appropriate: individual trees and small patches of trees. Percentage of parasitism by *Itoplectis conquisitor* (Say) declined significantly as the density of female bagworms on individual trees increased. Although mathematically possible, this inverse density-dependent response appears too "vague" to promote the stability of the bagworm-*I. conquisitor* system. Other factors that may be involved in the regulation or control of the bagworm are discussed.

KEY WORDS Insecta, density-dependent parasitism, *Itoplectis conquisitor*, *Thyridopteryx ephemeraeformis*

PARASITOID AGGREGATION at patches of high host density has been an integral component of many models of host-parasitoid regulation (Hassell & May 1973, 1974; Rogers & Hubbard 1974). Theory suggests that an aggregative response at high host densities by natural enemies will stabilize interactions and promote coexistence of the host-parasitoid complex (Beddington et al. 1978; Hassell 1978, 1981; May 1978; Heads & Lawton 1983). Empirical data that support this theory, however, are scant and inconsistent. Although spatial density-dependence has been documented (Varley 1941; Hassell 1980, 1982; Stamp 1982; Heads & Lawton 1983), negative correlations and no correlation between the percentage of parasitism and host density appear more frequently in the literature (Morrison & Strong 1980; Stiling 1987; Walde & Murdoch 1988).

Because the failure to find a positive response could be the result of an inappropriate spatial scale (Morrison et al. 1980; Heads & Lawton 1983), researchers are now looking at a wider range of spatial scales (Heads & Lawton 1983; Murdoch et al. 1984; Reeve & Murdoch 1985; Smith & Maelzer 1986). For example, Heads & Lawton (1983) found that *Chrysocharis gemma* (Walker) (Hymenoptera: Eulophidae) had a density-dependent response for the holly leaf miner (Diptera: Agromyzidae) at the lowest levels, but the response became weaker as the spatial scale increased. In addition, Dempster (1983), Murdoch et al. (1984), Murdoch et al. (1985), and Reeve & Murdoch (1985) have argued that the host-parasitoid systems are typically unstable and that local extinctions are a common occurrence. Thus, at present, the theory

about the stability of spatial density-dependence in host-parasitoid systems is controversial and not well supported by empirical data.

Well-controlled field studies that assess parasitism with respect to host density and take into account the range of host densities found in natural populations and the searching behavior of the major parasitoids of the system are needed. The parasitoid complex of the bagworm, *Thyridopteryx ephemeraeformis* (Haworth), was chosen for evaluating the effect of host density on the level of parasitism for the following reasons: bagworm densities are easily manipulated; late instars are relatively sedentary; bagworm pupae are large and harbor a sizable complex of large parasitoids; levels of parasitism are relatively high (about 60%); and the dominant parasitoid, *Itoplectis conquisitor* (Say), is reported to have a high degree of associative learning (Arthur 1966, 1967). I report here the results of a controlled field experiment on the problem of density-dependent parasitism by *I. conquisitor* on the bagworm.

Materials and Methods

Study Site. Research was carried out in an abandoned corn field adjacent to Bull Run Creek in Manassas Battlefield Park, Manassas, Va. The field is now dominated by a nearly pure stand of several thousand eastern redcedar trees, *Juniperus virginiana* L., averaging 2.5-3.0 m in height. The rectangular field extends approximately 200 m E-W and 600 m N-S and is bordered on all four sides by large oaks, sycamores, and other hardwoods. The experimental plot was located in the southwestern corner of the redcedar stand.

Experimental Procedure. Three densities dis-

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tributed randomly among 15 patches of nine trees each were used in the experiment. As a result, parasitism could be examined at two spatial scales: among trees and among patches.

Patch size was chosen on the basis of the observed searching behavior of individual parasitoids. *I. conquisitor* was observed to locate and search among trees for hosts that were in close proximity to each other and then disperse to other clumps of trees (patches). On this basis, the experimental patch was chosen to consist of nine redcedar trees (1.25–1.75 m tall) arranged in a square (1.5 m by 1.5 m) (3 rows \times 3 columns), with each tree 0.75 m from its nearest neighbors. The 15 patches of trees were arranged in three rows and five columns, with each patch separated from the others by 6 m of open space.

Three density levels were chosen in a geometric sequence (4, 8, and 16 bagworm pupae per tree, or 36, 72, and 144 pupae per patch) that reflected the natural densities observed in the field. The range of natural densities found adjacent to the study site were from 0 to 38 per tree, but high densities were rare and most of the trees sustained low levels of infestation (0–2 bagworms per tree). Because all of the trees were uniform in size and shape, the mean distance between bagworms was greatest for the treatment of 4 per tree and least for the treatment of 16 per tree. As a result, encounter rates by the randomly searching parasitoids was expected to be greatest for the treatment of 16 per tree.

From 22 June to 29 July 1986, all of the redcedar trees were cleared from a 1,170-m² area. Trees for each patch were excavated from the adjacent stand of redcedar and then transplanted into a series of 3 \times 3 arrays constituting the patches. A boundary zone that was 7.5 m wide and cleared of redcedars separated the patches from the main redcedar stand. Once all of the transplanted trees were established, each patch was randomly assigned (by a draw from a hat) to one of the three density levels, with each density level replicated five times.

On 7 August, 1,260 late seventh-instar bagworms were collected at random from a stand of redcedar 3 km away. The bagworms were placed at the prescribed density on each of the 135 trees in the 15 patches. They rapidly reattached themselves to their new hosts and resumed feeding.

One week later, approximately 10% of the bagworms across all densities had disappeared. The cause of this mortality was determined to be mice (*Peromyscus* sp.). Those bagworms that disappeared were replaced by newly collected ones. To minimize further mortality from the mice, trees were made inaccessible to them by clipping lower branches and applying Tanglefoot (Tanglefoot Company, Grand Rapids, Mich.) at their bases. However, some losses occurred despite these attempts. To determine if bagworms placed on the experimental trees had already been parasitized, 700 bagworms were collected on 12 August from the same source location and were reared in the

laboratory through pupation. No parasitoids were reared from these bagworms; thus it can be assumed that any parasitism found in the experimental bagworms had occurred after the establishment of the experimental densities.

The experimental bagworms began pupation on 13 August, and nearly all (approximately 95%) surviving bagworms had pupated by 13 September. On 20 September, all bagworms from each tree were collected, placed in polyethylene bags, and returned to the laboratory. Each pupa was placed individually in a marked 25-ml scintillation vial and stored at room temperature and $60 \pm 5\%$ RH. These vials were checked every other day for emergent parasitoids. All unknown parasitoids were identified by taxonomists of the Systematic Entomology Laboratory, USDA.

Statistical Analysis. The logit transformation was used to convert the number parasitized into a continuous normally distributed variable. This transformation was chosen over the conventional arcsine square-root transformation of the proportion parasitized because the logit is more robust for unbalanced data and is equally as effective in normalizing the data when the data are balanced (Cox 1970).

Because bagworm pupae suffered low levels of mortality across all density levels in the experimental plot (see Results), the integrity of the initial treatment conditions was not strictly met. Therefore, the a priori choice of statistical test (analysis of variance) was discarded in favor of linear regression analysis. In the absence of fixed treatment levels, this technique provides a more powerful test of the relationship between bagworm density and parasitism by *I. conquisitor*.

The total number of bagworms and the number parasitized by *I. conquisitor* were summed over the nine trees constituting each patch. Parasitization rates (logit transformed) were then compared with the total number of bagworms per patch for the 15 randomly assigned patches. At the smaller spatial scale, parasitism rates were calculated for each of the 135 trees in the experimental plot and related to individual tree densities of bagworms. Because trees were clustered in patches and contained similar densities of bagworms within each patch, the spatial distribution and density of bagworms on individual trees were not random. However, because patch densities were randomly assigned, the various density levels on trees were not entirely concentrated in a single location. In any event, this would only inflate the residual error term in the regression equation and reduce the power of the test statistic.

Results

Although densities were initially set at 4, 8, and 16 pupae per tree (36, 72, 144 pupae per patch), only 95% of the bagworms survived to pupation. A small part of this 5% loss was attributed to mice,

Table 1. Relationship between bagworm density and level of parasitism by *I. conquisitor* at two spatial scales: patches (a cluster of nine trees) and individual trees. Linear regression analysis performed on logit-transformed data

Spatial scale	Bagworm sex	n	Slope	Intercept	r^2 ^a	p ^b
Patch	♂	15	-0.0006	0.077	0.0001	0.9255
	♀	15	-0.0009	-2.176	0.0050	0.7907
Tree	♂	104	-0.1274	0.629	0.0384	0.0836
	♀	134	-0.0808	-0.833	0.2764***	<0.0001

^a Asterisks indicate a significant correlation at $P < 0.001$.

^b Significance level was adjusted to 0.01 to control for experiment-wise error.

but the cause of the majority of the losses was unknown. Despite these losses, final bagworm densities in the three density groups were significantly different from one another ($F_{2,12} = 682.85$, $P < 0.0001$). Significantly more females had been collected and used in the experiment than males (81% females, 19% males; $\chi^2 = 457.9$; $P < 0.0001$); therefore, parasitization was compared for females and males separately. Separating the two for analysis may be ecologically important because males pupate earlier than females (Cronin & Gill in press) and therefore may be subject to different parasitoids or searching behaviors.

Six species of parasitoids were found to attack the bagworms in the experimental plot. *I. conquisitor* was dominant, accounting for 79% of the parasitism. The remaining 21% was contributed by the following: *Pteromalus* sp. (a facultative hyperparasitoid—only its influence as a primary parasite is included here), 10%; Sarcophaginae sp., 3%; *Brachymeria ovata* (Say), 1%; Chalcididae sp., 1%; and unidentified species, 6%. The parasitoid complex showed a highly significant preference for males (61% parasitism) over females (10% parasitism) ($\chi^2 = 301.9$; $P < 0.0001$), and *I. conquisitor* alone showed similar bias (males 45% versus females 9%; $\chi^2 = 188.1$; $P < 0.0001$). Because *I. conquisitor* was responsible for four-fifths of the parasitism, only its effect with respect to density-dependence is reported in my analysis.

Parasitism by *I. conquisitor* at the level of the patch was unrelated to male or female bagworm density (Table 1). At the smaller spatial scale (among individual trees), parasitism was inversely related to female bagworm density but was independent of the density of males (Table 1).

Discussion

The fivefold difference in level of parasitism between male and female bagworms observed in the field is consistent with those found in other studies (Gross & Fritz 1982, Cronin & Gill in press). Cronin & Gill (in press) conclude that this results from the difference in size between female and male bagworms rather than from sex itself, or the difference in phenology of pupation by the two sexes. The distance between the pupa and exterior bag of larger hosts is too great for *I. conquisitor* to reach

the pupa with its ovipositor. It is because males are significantly smaller than females that they incur higher levels of parasitism.

The rate of parasitism by *I. conquisitor* declined significantly as the density of female bagworms increased per tree. Despite the high level of significance associated with this pattern, there was a great deal of scatter around the regression line as evidenced by the low r^2 value (Table 1). Although the trend was similar, male bagworm density showed no significant relationship with the level of parasitism. In a related study which had a modest sample size, Cronin & Gill (in press) found that parasitism was independent of the density of bagworms per tree ($n = 16$; slope = -0.0005 ; $r^2 = 0.03$; $P = 0.58$). Together, these results indicate that density influences on the rate of parasitism by *I. conquisitor* on bagworms are detectable only when sample sizes are large and are inverse in sign.

Because the distribution of bagworm densities at both spatial scales was highly correlated (trees of low bagworm density make up patches of low density, etc.), parasitoid response at either spatial scale should have been indistinguishable (but see Results). For example, if *I. conquisitor* aggregated to redcedar trees containing high bagworm densities, the aggregative response also should have been observed at the larger spatial scale (patch of trees) simply because the spatial scales were correlated. This is not to imply that the two scales were indistinct. The nature of the design dictated that the pattern of parasitism should have been the same regardless of the scale at which the parasitoid was actually responding.

However, rates of parasitism by *I. conquisitor* differed between trees and patches. This may reflect a true difference in parasitoid response between the two spatial scales (because they are not perfectly correlated), or it may simply be the result of the difference in statistical power between the two regression equations as a consequence of the marked difference in degrees of freedom (see Table 1).

The detection of an inverse density-dependent response to the bagworm by *I. conquisitor* is in agreement with a number of empirical studies of spatial density-dependence (Walde & Murdoch 1988). Recent reviews by Stiling (1987) and Walde & Murdoch (1988) have pointed out that in field

studies of parasitism, the proportion of studies demonstrating direct density-dependence is approximately equal to those showing inverse density-dependence (approximately 25%).

Inverse density-dependence has generally been attributed to one of several factors involving the behavior of the parasitoid. First, an inverse pattern of parasitism may be the result of an increase in the handling time by the parasitoid as the density of hosts within a patch increases, either through mutual or pseudo-interference (Hassell 1971, Hassell & May 1973). Second, the declining rates of parasitism with increasing host density may be the result of egg limitation in parasitoids (Morrison & Strong 1980, Morrison et al. 1980, Hassell 1982, Smith & Maelzer 1986). Third, an inverse response could be a consequence of parasitoids "spreading the risk." If local population (patch) survival is highly variable, parasitoids may scatter their eggs among many patches to ensure survival of some of their offspring (Reddingius & den Boer 1970, Chesson 1978). None of these three processes is mutually exclusive; any or all may contribute to inverse density-dependence.

The bagworm-*I. conquisitor* system reported here was not designed to distinguish among the three processes, but additional observations argue against the second point. Dissections of the ovaries of recently emerged female *I. conquisitor* showed that egg numbers exceed 60 per female (unpublished data). In addition, laboratory studies (Leius 1961) indicate that feeding on hosts or nectar and pollen, or both, increases egg production (i.e., *I. conquisitor* is synovigenic). Thus, this wasp is not an egg-limited parasitoid. Also, local extinction of patches (trees) of bagworms appears to be a characteristic of bagworm populations; preliminary studies in two separate stands of redcedar showed that 71:75 (95%) and 82:211 (39%) of the populations on trees with at least one bagworm egg case (an average of 654 ± 37 SE) became extinct by the following year (unpublished data). This high rate of local extinction may be the result of various density-independent mortality factors. As such, persistence does not appear to be a property of bagworm populations (at that scale). This high rate of local extinction lends some support to the "spreading of risks" hypothesis. Further study of the direct foraging behavior of *I. conquisitor* will be necessary to assess whether handling time constraints or spreading of risks is responsible for this pattern.

The spatial scales used for this study of parasitism of the bagworm were deliberately chosen to be relevant to the actual searching behavior of *I. conquisitor*, following the recommendations of Heads & Lawton (1983). Therefore, I conclude that stabilizing density-dependence by *I. conquisitor* does not occur over the natural range of prey densities.

It has been suggested (mathematically) that inverse density-dependence can be stabilizing (regulatory), and that stability increases as more and

more hosts occur in patches of low density (Hassell 1985, Chesson & Murdoch 1986). However, the stronger the inverse response, the higher the equilibrium densities of host and parasite will be (Hassell 1985). Stability occurs because a partial refuge is created (the higher density patches) that prevents parasitoids from driving the host population to extinction. An additional refuge is created in the bagworm-*I. conquisitor* system as a result of *I. conquisitor*'s preference for smaller bagworms (i.e., males) (Cronin & Gill in press). As a result, larger bagworms (females) escape parasitism. Because bagworm size varies greatly among host plants (Cronin & Gill in press), this refuge also is host plant dependent. This size refuge, too, can promote stability (Murdoch in press) but again will result in higher equilibrium densities.

The "vague" (sensu Strong 1984) inverse response of parasitism to bagworm density appears not to be strong enough to stabilize the interaction. In addition, the equilibrium densities predicted by inverse density-dependence in combination with the size refugia may be too high for either parasite or host to realize in natural populations. For these reasons, *I. conquisitor* may not be responsible for maintaining bagworm populations at low levels. Other mortality factors such as the amount of precipitation during hatching (unpublished data) and the abundance of larval predators (birds and mice) appear to be more important sources of mortality for the bagworm on eastern redcedar.

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