

## The influence of host distribution, sex, and size on the level of parasitism by *Itopectis conquisitor* (Hymenoptera: Ichneumonidae)

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ABSTRACT. 1. Parasitism of the bagworm, *Thyridopteryx ephemeraeformis* Haw. (Lepidoptera: Psychidae), on red cedar was studied at Manassas, Va., U.S.A.

2. Fifteen parasitoids, five of which were hyperparasitoids, attacked the pupal stage of the bagworm. The Ichneumonid *Itopectis conquisitor* alone accounted for 58% of the parasitized bagworms.

3. Parasitism by *I. conquisitor* (Say) was inversely related to host size, but independent of host distribution within a tree. Male bagworms experienced disproportionately higher levels of parasitism than females. We conclude that it is small size that renders bagworms susceptible to parasitism rather than sex *per se*.

4. Ovipositor lengths of *I. conquisitor* were insufficient to penetrate the larger bagworm hosts (>57 mm); and in fact, as bagworm size increased, the proportion of the *I. conquisitor* population capable of penetrating the pupa declined abruptly. We suggest that the mechanical difficulties with oviposition, and perhaps the defensive capabilities of larger hosts, are responsible for the relationship between host size and per cent parasitism.

5. *I. conquisitor* could be an important selective agent for bagworm size at pupation, but it is not likely to act as a significant control agent of population density.

**Key words.** *Itopectis conquisitor*, microhabitat distribution, oviposition constraints, parasitoidism, size-limited parasitism, *Thyridopteryx ephemeraeformis*.

### Introduction

In their study of parasitism of the bagworm, *Thyridopteryx ephemeraeformis* (Haworth), Gross & Fritz (1982) observed that: (1) male pupae were proportionately more abundant at

the lower tree levels, while females were concentrated at the crowns; (2) the overall sex ratio of pupal and adult bagworms was 0.69 (M/F); (3) males were more heavily parasitized than females; (4) parasitism was highest at the bottom two-thirds of the tree for both males and females; and (5) there was no difference in level of parasitism between males and females at the middle level of the tree (the only comparison

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possible). They concluded from these results that the parasitoids must be searching selectively at the bottom two-thirds of the tree. This conclusion is consistent with a large body of literature that indicates that many parasitoids search selectively within plants and use particular cues to find their specific hosts (e.g. Varley, 1941; Weseloh, 1972; McClure, 1977; Elzen *et al.*, 1983).

Female bagworms are 12.5% larger than males. If parasitoids either prefer or are more effective on small bagworms, size-selective parasitism may have been an important factor contributing to the non-random pattern of parasitism observed by Gross & Fritz (1982). Females may be less susceptible to parasitization because of greater defensive capabilities, size constraints on parasitoid ovipositional activity, etc. (Schmidt, 1974). For example, Rotheray & Barbosa (1984) found that handling time of the gypsy moth pupae by *Brachymeria intermedia* (Nees) increased with increasing host size. Because male gypsy moths are smaller and less defensive toward attacking parasitoids than females, per cent parasitism was greater for the males.

It is natural to expect the opposite, namely that larger hosts are preferred. For many parasitoids there is a minimum host size requirement for the successful development within a host (Vinson & Iwantsch, 1980). In addition, parasitoid size and fecundity are often positively correlated with that of its host (Arthur & Wylie, 1959; Miles & King, 1975; Jowyk & Smilewitz, 1978). The latter factors imply that selection by parasitoids should, in general, be for larger hosts (Salt, 1958; Klomp & Tecrink, 1962; Herrebut, 1969; Arthur, 1981). Host size may also influence the sex ratio of the parasitoid offspring: more female parasitoids than males emerge from larger hosts (Balduf, 1937; Clausen, 1939; Purrington & Uleman, 1972). For these reasons host size is expected to be an important factor in the host acceptance process by parasitoids.

We investigated the details of parasitism in the same population of bagworms studied by Gross & Fritz (1982). In addition to bagworm sex and stratification within a tree, we include bagworm size as an experimental factor that may influence the level of parasitism by the bagworm's dominant parasitoid, *Itopectis conquisitor* (Say). We combine results from this study with that of another (Cronin, 1989) to assess the importance

of *I. conquisitor* to the population dynamics of the bagworm.

### Natural history of the bagworm and its principal parasite

*Thyridopteryx ephemeraeformis*. Comprehensive studies of the bagworm life cycle can be found in Haseman (1912), Jones (1927) and Kaufmann (1968). Only relevant aspects of their biology are reported here. Bagworms have been known to infest some 200 species of tree and shrub in southeastern United States, but in the Virginia area they are particularly abundant on red cedar, *Juniperus virginiana* L. Univoltine throughout their range, bagworms moult through seven instars during the summer months (Morden & Waldbauer, 1971). Males begin pupation in mid-August, but females begin 2–3 weeks later; both sexes eclose (at approximately the same time) around mid-September (J.C., pers. observ.). After mating, females lay their eggs in their pupal exuvia where the eggs overwinter and finally hatch in late May.

*Itopectis conquisitor*. *I. conquisitor* (Say) (Hymenoptera: Ichneumonidae) is a primary parasite of at least seventy-nine lepidopterans from twenty-two families (Krombein *et al.*, 1979). It also has been implicated as an occasional secondary parasite of other ichneumonid and braconid cocoons (Townes & Townes, 1960). *I. conquisitor* is multivoltine and is reported to have as many as five generations per year in Ontario (Arthur, 1965). Arthur (1963) reported that there is a period of 8–10 days after emergence from a host in which female wasps do not oviposit, even in the presence of host pupae. Laboratory rearings have permitted average life spans of 29 days for males and 56 days for females. The average number of eggs deposited by the synovigenic (= continuous egg production) females is 159.

Reported as a common parasite of the bagworm throughout most of its distribution (Kulman, 1965), *I. conquisitor* is the most prevalent parasitoid of the bagworm in northern Virginia (approx. 60%, see Results). As a consequence, we concentrated our analysis on the mortality of bagworms due to this parasitoid, but observed that the entire parasitoid complex of the bagworm seems to exhibit phenologies very similar to that of *I. conquisitor*.

## Methods

### Experimental design and procedure

The research was conducted in the Manassas Battlefield Park, Manassas, Virginia. The 3 acre study area was dominated by an even-aged stand of red cedar of an average height of 3 m. Virginia pine (*Pinus virginiana* L.) was interspersed at low to moderate densities within the site. In addition to infesting red cedar, bagworms were occasionally found on other species of plants, both herbaceous and woody.

To determine the influence of host stratification, sex and size on parasitoid success, we followed the basic design employed by Gross & Fritz (1982). On 20 September 1986, the date at which all bagworms had secured themselves (with a heavy band of silk) to their trees (signalling the beginning of pupation), all bagworms were collected from sixteen randomly chosen red cedar trees. For each tree, the overall crown height was measured and the tree was divided into three equal sections designated bottom, middle and top. The mean  $\pm$  1 SE height of the sixteen trees was  $2.90 \pm 0.12$  m. Bagworms collected from each section and tree were placed in separate polyethylene bags and returned to the laboratory. After bag length was measured, the pupae were excised from their bags, and stored in 5 dram scintillation vials at room temperature and humidity ( $24 \pm 3^\circ$  C; 70%). The vials were examined every other day for emerging parasitoids. Parasitoid species, sex and date of emergence were recorded, along with the sex of host pupae. A total of 1008 bagworms that achieved pupation were collected and analysed.

Because bag size itself may limit the success of parasitism by imposing mechanical barriers (e.g. toughness of integument, distance from the surface of the bag case to the centrally located pupa, etc.), we measured with a  $100\times$  dissecting microscope and ocular micrometer the ovipositors of ninety-six *I. conquisitor* females. We were unable to capture *I. conquisitor* searching for bagworm hosts using either yellow sticky or malaise traps; instead, we obtained a series of wasps from R. W. Carlson at the Smithsonian Institution. Because this sample was collected from Virginia and southern Maryland, it should approximate the ovipositor size distribution of *I. conquisitor* attacking bagworms. By taking the difference between the maximum diameter of

the bags and the pupae (and subtracting the thickness of the bag wall from it) of seventy-seven randomly collected unparasitized bagworms, a comparison of the distribution of ovipositor lengths to this distance necessary to reach the bagworm's pupae ( $D$ ) was possible; this reflected on whether parasitoid ovipositors were capable of penetrating all encasing bags and reaching the host pupae. We observed that the bagworm pupae can wriggle about freely within their bags and upon being attacked by a parasitoid will press themselves against the opposite wall of the penetrating ovipositor. The proportion of our sample of the *I. conquisitor* population that had ovipositor lengths greater than  $D$  was determined and compared against the distribution of  $D$  for the sample of bagworms. This comparison provided an index measure of the relative susceptibility of a bagworm of a given size class to parasitism by the *I. conquisitor* population.

To determine whether parasitoid size was related to that of its host, we measured, with calipers, host bag length and puparium length, and the total length of the emergent *I. conquisitor* adults (measured from head to tip of ovipositor).

### Statistical analysis

Because number parasitized is a discrete binomial variable, the logit transformation was used to convert the number parasitized into a continuous normally distributed variable (Cox, 1970). In the logit transformation,

$$z_i = \log((p_i + 1)/(n_i - p_i + 0.5))$$

$$v_i = (n_i + 2)/(n_i)(p_i + 1)(n_i - p_i + 0.5)$$

where  $z_i$  = transformed variable for analysis,  $p_i$  = number of bagworms parasitized in size category  $i$ ,  $n_i$  = total number of bagworms in category  $i$ , and  $v_i$  = variance of category  $i$ . The logit transformation was chosen over the traditional arcsine [square-root (proportion parasitized)] transformation because the logit is the more appropriate for unbalanced data (Cox, 1970). Because the number of bagworms used to calculate each parasitization rate ( $z_i$ ) differed so markedly, sample size was taken into account by weighting  $z_i$  by  $1/v_i$ , from the above variance equation (Cox, 1970).

The effect of host sex (fixed effect) and intra-tree microhabitat (random effect) on parasitization were analysed using SAS, Proc GLM (Statistical Analysis System, 1985 version). All

possible pairwise comparisons were tested using GT2 (Sokal & Rohlf, 1981, p. 245). In this ANOVA we use as the unit of replication the microhabitat positions on the tree (top, middle and bottom), such that the sample size is forty-eight (sixteen trees  $\times$  three positions). With the densities found in the experimental trees, bagworms within a tree are as functionally independent of those from the same tree as they are from neighbouring trees. The only conceivable way there could be dependence is if the chemistry of each red cedar tree were so unique as to alter the growth rates or attractability to parasites within and between trees. We find no evidence for differing growth rates of bagworms either within

trees (Table 3) or between trees ( $F_{15, 995} = 1.7333$ ,  $P > 0.05$ ), nor do rates of parasitism differ among trees ( $\chi^2 = 22.34$ ,  $P > 0.05$ ). We therefore suggest that this design is not pseudo-replicated.

The distribution of ovipositor lengths were compared against the distribution of the  $D$  using a Mann-Whitney  $U$  test (Sokal & Rohlf, 1981).

## Results

Numerous species of parasitoids and predators attacked the pupal stage of the bagworms (Table 1). Fifteen parasitoids (five of which are hyper-

TABLE 1. The parasitoids and invertebrate predators reared from bagworms collected in Manassas, Virginia (1985–86). Coding is as follows: Pr. = predator. Sc. = scavenger, PP = primary parasitoid, HP = hyper-parasite, GREG = gregarious, and SOL = solitary.

	Reared as:
I. COLEOPTERA	
Cleridae	
<i>Enoclerus</i> sp.	Pr. and Sc.
Cantharidae	
<i>Chauliognathus</i> sp.	Pr. and Sc.
II. DIPTERA	
Chloropidae	
<i>Pseudogaurex anchora</i> (Leow)	GREG PP. and Sc.
Sarcophagidae	
<i>Sarcophaginae</i> sp.	GREG PP.
III. LEPIDOPTERA	
Pyrilidae	
<i>Dicymolomia julianalis</i> (Wilk.)	Pr. and Sc.*
IV. HYMENOPTERA	
Ichneumonoidea	
Ichneumonidae	
<i>Scambus hispae</i> (Harris)	GREG PP
<i>Itoplectis conquisitor</i> (Say)	SOL PP
<i>Chirotica thyrdopteryx</i> (Riley)	GREG PP
<i>Gambrus ultimus</i> (Cr.)	SOL PP
<i>Theronia atalantae</i> (Cr.)	SOL PP
Chalcidoidea	
Chalcididae	
<i>Brachymeria ovata</i> (Say)	SOL PP
<i>Spilochalcis mariae</i> (Riley)	SOL PP [HP]
<i>Spilochalcis flavopicta</i> (Cr.)	SOL PP
<i>Spilochalcis</i> sp.	SOL PP
Torymidae	
<i>Monodontomerus minor</i> (Ratzeburg)	GREG PP and HP
Pteromalidae	
<i>Pteromalus</i> sp.	GREG PP and HP
Eurytomidae	
<i>Eurytoma pini</i> Bugbee	GREG PP and [HP]
<i>Eupelmus amicus</i> Gir.	GREG PP and HP

\* Predaceous on eggs.

[ ] Uncertain record.

parasitic) and three predaceous invertebrate larvae were identified. The relative abundance of each parasitoid was: *I. conquisitor*, 58%; *Sarcophagid* sp., 19%; *Pteromalus* sp., 10%; *Eurotoma pini* Bugbee, 2%; *Brachymeria ovata* (Say), 1%. *Pseudogaurex anchora* (Loew), *Spilochalcis* sp., *Eupelmus amicus* Gir. and *Monodontomerus minor* (Ratzeburg) together accounted for another 2%; the identity of 8% of the parasitoid species could not be determined.

Male and female bagworms in the pupal stage were distributed differently within a tree. Females occurred in significantly increasing numbers from the bottom third of the tree to the top third ( $F_{2, 47} = 63.69$ ;  $P < 0.0001$ ; log transformed data), but males were uniformly abundant throughout the three sections ( $F_{2, 47} = 2.41$ ;  $P = 0.14$ ; Table 2). Comparing males to females at each section of the tree we find significantly more females at the top third of the tree ( $P < 0.0001$ ), equal numbers of each at the middle third ( $P > 0.05$ ), and fewer females at the bottom third ( $P < 0.0001$ ) (Table 2). With males and females combined, there were significantly fewer bagworms at the bottom third of the tree compared to the top third ( $P < 0.05$ ). Males and females were equally abundant at the onset of

pupation, but 2.3 times as many females emerged as males (Table 3).

The relationship between parasitization and bagworm sex and position on the tree (bottom, middle, top) was analysed using a mixed factorial ANOVA. Bagworm sex was the only factor that influenced the rate of parasitism in this model (Table 4). Both the distribution of bagworms within a tree and the interaction between bagworm sex and microhabitat did little to explain the variation in parasitization rates. Males consistently incurred higher levels of parasitism than females across all three levels of the tree; although only at the bottom was this difference significant (Table 2). When all males and all females were pooled and compared, the rate of parasitism was significantly higher for males ( $P < 0.01$ ; Table 2).

Female bagworms were significantly larger than males at all three positions on the tree (Table 2;  $P < 0.0001$ ). Because bagworm distribution within a tree had no influence on the rate of parasitism or bag size for either males or females (Tables 2 and 4), positions were pooled for each sex. Males were significantly shorter than females based on a Mann-Whitney  $U$  test (Table 2;  $U = 9.72$ ,  $P < 0.0001$ ). To determine

TABLE 2. Bagworm number, case length, and proportion parasitized by *I. conquisitor* for male and female bagworms distributed among the three tree positions (bottom, middle and top). Sixteen red cedar were randomly sampled, and the data represent means  $\pm$  1 SE. Within columns, means with different letters are significantly different based on SNK ( $P < 0.05$ ).

Sex	Position on tree	Bagworm number	Bagworm length	Proportion parasitized
Males	Bottom	9.90 $\pm$ 1.92 <sup>h</sup>	41.97 $\pm$ 0.40 <sup>a</sup>	0.34 $\pm$ 0.06 <sup>c</sup>
	Middle	16.13 $\pm$ 3.67 <sup>ab</sup>	41.09 $\pm$ 0.30 <sup>a</sup>	0.30 $\pm$ 0.04 <sup>ab</sup>
	Top	7.63 $\pm$ 1.91 <sup>h</sup>	42.25 $\pm$ 0.45 <sup>a</sup>	0.30 $\pm$ 0.07 <sup>ab</sup>
	Total	33.66 $\pm$ 6.85 <sup>d</sup>	41.60 $\pm$ 0.21 <sup>a</sup>	0.33 $\pm$ 0.05 <sup>d</sup>
Females	Bottom	0.69 $\pm$ 0.20 <sup>c</sup>	48.18 $\pm$ 1.99 <sup>b</sup>	0.09 $\pm$ 0.07 <sup>h</sup>
	Middle	9.90 $\pm$ 2.35 <sup>b</sup>	47.02 $\pm$ 0.49 <sup>b</sup>	0.19 $\pm$ 0.05 <sup>b</sup>
	Top	19.60 $\pm$ 4.30 <sup>a</sup>	46.62 $\pm$ 0.34 <sup>b</sup>	0.20 $\pm$ 0.05 <sup>b</sup>
	Total	30.19 $\pm$ 6.10 <sup>d</sup>	46.80 $\pm$ 0.28 <sup>b</sup>	0.20 $\pm$ 0.05 <sup>b</sup>

TABLE 3. The distribution of the sexes among pupae and emergent adults of the bagworm *Thyridopteryx ephemeraeformis*.

Class	Sex	No.	Proportion	$\chi^2$	Significance
Pupae	Male	525	0.52	1.75	0.5 < $P$ < 0.1
	Female	483	0.48		
Adults	Male	114	0.30	57.0	$P < 0.001$
	Female	260	0.70		

TABLE 4. Analysis of variance for the effect of bagworm sex and microhabitat distribution on parasitization. Data were logit transformed and weighted (see Methods). Type III sums of squares were used for unbalanced data (Sokal & Rohlf, 1981).

Source of variation	DF	MS	F	P
Model	5	0.458	3.81***	<0.004
Sex	1	1.648	13.70***	<0.001
Microhabitat	2	0.058	0.48	0.63
Sex × microhabitat	2	0.264	2.19	0.12
Error	42	0.120		
Total	47			

TABLE 5. Analysis of covariance (Proc GLM, SAS, 1985) for the effect of bagworm sex (main effect) and bag length (covariate) on the rate of parasitism.

Source of variation	DF	MS	F	P
Model	2	0.623	58.09***	<0.0001
Sex	1	0.023	2.11	0.17
Bag length	1	1.249	116.38***	<0.0001
Error	13	0.011		
Total	15			

the influence of bagworm size (covariate) and sex (fixed effect) on the rate of parasitism, an ANCOVA (Sokal & Rohlf, 1981) was performed. Bagworm length was scaled into eight 5 mm size classes for each sex and the logit parasitism was calculated for each sex × size class. Sex had no influence on the rate of

parasitism, but bag length explained over 88% of the variation (Table 5). Weighted least squares regression on all bagworms combined shows a strong negative correlation between bagworm length and the rate of parasitism ( $r^2 = 0.93$ ,  $P = 0.0004$ ; Fig. 1).

Total body length of *I. conquisitor* adults

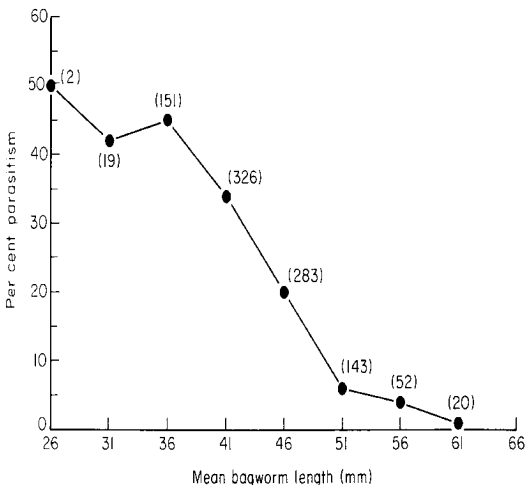


FIG. 1. The per cent parasitism as a function of bag length for both male and female bagworms combined. Bag lengths were categorized into 5 mm wide size classes and sample sizes for each size class are in parentheses.

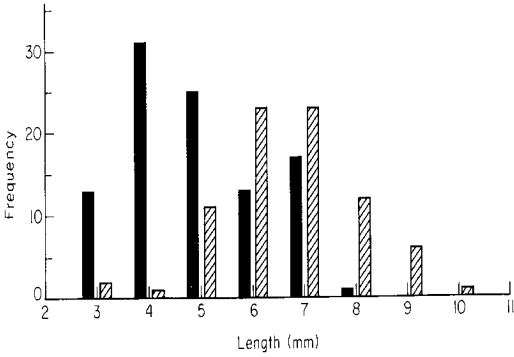


FIG. 2(a). A comparison of the frequency distribution of *I. conquisitor* ovipositor lengths (black bars) and the maximum distance necessary to reach the pupae ( $D$ ) (hatched bars). See Methods section for calculation of  $D$ .

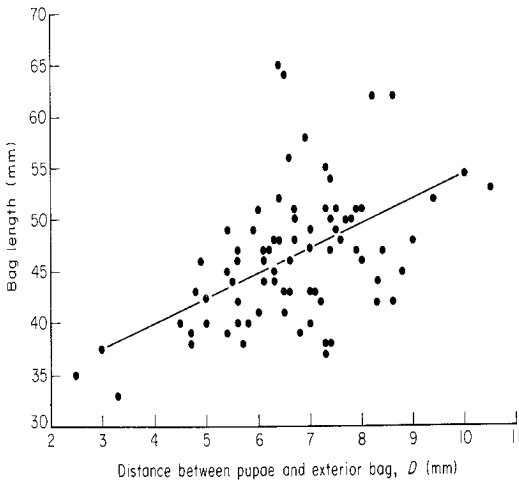


FIG. 2(b). The relationship between bag length and maximum distance necessary to reach pupae ( $D$ ) (see Methods section for calculation) for male and female bagworms combined. Line fit by least squares regression (Sokal & Rohlf, 1981).

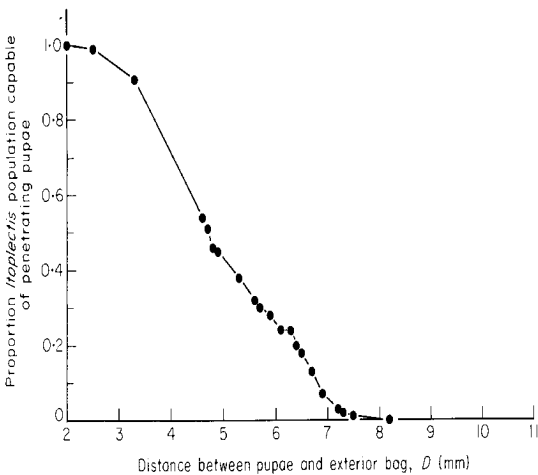


FIG. 2(c). The proportion of the *I. conquisitor* population with ovipositors long enough to penetrate a bagworm of pupae of a given size versus the  $D$ .

