

ALEUROCANTHUS WOGLUMI [HOM. : ALEYRODIDAE] AND *ENCARSIA OPULENTA* [HYM. : ENCYRTIDAE] : DENSITY-DEPENDENT RELATIONSHIP BETWEEN ADULT PARASITE AGGREGATION AND MORTALITY OF THE HOST

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Field and laboratory choice tests in which searching adult *Encarsia opulenta* Silvestri were exposed to variable densities of citrus blackfly, *Aleurocanthus woglumi* Ashby, indicated the following : (1) a direct functional relationship between adult parasite aggregation and host density, resulting in (2) a direct density-dependent mortality of *A. woglumi* within a single generation timespan. The implications of such nonrandom searching patterns by *E. opulenta* on stability of the host-parasite interaction on Texas citrus are discussed.

KEY-WORDS : Citrus, *Aleurocanthus woglumi*, *Aleyrodidae*, *Encarsia opulenta*, *Encyrtidae*, density dependence, aggregation, mortality factor.

Encarsia opulenta Silvestri, a specific solitary endoparasite of citrus blackfly, *Aleurocanthus woglumi* Ashby, is 1 of 4 exotic parasite species imported into Mexico from the India-Pakistan region during 1949-50 (Smith *et al.*, 1964). The ensuing initial decline of *A. woglumi* was attributed primarily to *Amitus hesperidum* Silvestri, although *E. opulenta* eventually became predominant in most areas, particularly the hot semiarid areas of northern Mexico (Flanders, 1969). Recent establishment of *E. opulenta* in south Texas (Hart, 1978) resulted in a complete biological control of *A. woglumi* on citrus, with host and parasite currently coexisting in a highly stable low-density interaction (Summy *et al.*, 1983a).

A delayed density-dependent response by populations of *E. opulenta* to *A. woglumi* is indicative of parasite regulation (K. R. Summy, Ph.D. Diss., 1982) but alone fails to account for the stability noted by Summy *et al.* (1983a). The present research was therefore conducted to investigate (1) density-dependent searching patterns of adult *E. opulenta* and (2) the impact of such behavior on mortality of *A. woglumi* and stability of the host-parasite interaction.

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MATERIALS AND METHODS

Choice tests in which searching adult parasites were exposed to groups of potted citrus plants with variable densities of preferred 1st- and 2nd-stage *A. woglumi* were conducted under the following conditions: (1) in greenhouse facilities maintained within a temperature range of ca. 23.9°-29.4°C, and (2) in an untreated natural infestation suppressed by *E. opulenta* to densities < 0.001 *A. woglumi* per leaf during the previous 12-month period. Laboratory replicates (n = 5) each consisted of 4 plants (densities of 0, 5, 25, and 250 *A. woglumi* per plant) spaced ca. 0.3 – m apart within 1 × 1 × 1 – m organandy cages. Twenty mated female *E. opulenta* (1-day old) were released into the center of each cage, and densities of adult parasites on individual plants were enumerated daily until all parasites were dead. Field replicates (n = 2) each consisted of 4 plants (densities of 0, 25, 100, and 1,000 *A. woglumi* per plant) situated ca. 1.5 – m apart within the canopy of selected citrus trees. No parasite releases were made in field studies. Monitoring procedures were similar to those used in laboratory replicates, with the exception that the observation period was terminated after ca. 40 days to prevent confusion of emerging parasite progeny with resident parent adults.

Exposed plants (field and laboratory studies) were held in 1 × 1 × 1 – m organandy cages under greenhouse conditions, and emerging parasite progeny were counted and removed daily to prevent reproduction by the latter. Life tables for each *A. woglumi* cohort were constructed using the following procedures: (1) enumeration of stage-specific survivorship using a nondestructive census procedure based on close-up 35mm photography (Summy *et al.*, 1983b), and (2) enumeration of parasite exit holes, followed by dissection of unemerged (dead) *A. woglumi* to determine actual intensity of parasitism. Real mortality of *A. woglumi* due to parasitism was transformed to k-values (difference of \log_{10} initial hosts and \log_{10} survivors from parasitism, *sensu* Varley *et al.*, 1974), and a 2-way regression test for direct density-dependence (Varley & Gradwell, 1968) was used to evaluate the functional relationship between k-values for parasitism and host density.

RESULTS

LABORATORY STUDIES

Cumulative mean densities of adult *E. opulenta* (= 'parasite days') on caged greenhouse plants ranged between 1.0 (host density (d) = 5) and 27.5 (d = 250) during a 30-day observation period (table 1, fig. 1a). The regression of \log_{10} parasite days on \log_{10} host density was significant (b = 0.60; r^2 = 0.86), indicating a linear functional relationship between the 2 variables (fig. 1 b). Real mortality of *A. woglumi* due to parasitism ranged between 20.0 % (d = 5) and 50.0 % (d = 250), with a significant regression (b = 0.14; r^2 = 0.99) between k-values for parasitism and host density (table 1, fig. 1 c). The criteria for direct density-dependence in the 2-way regression test are that (1) the regressions of \log_{10} initial hosts on \log_{10} survivors from parasitism and vice versa, produce slopes significantly different from b = 1.0, and (2) both regression lines lie on the same side of slope b = 1.0 (Varley & Gradwell, 1968). As indicated in fig. 1d, the regression of \log_{10} initial hosts on \log_{10} survivors from parasitism (b = 0.86; r^2 = 0.99), and \log_{10} survivors on \log_{10} initial hosts (b = 1.16; r^2 = 0.99) clearly met these criteria, thus establishing a direct density-dependent mode of action for parasitism.

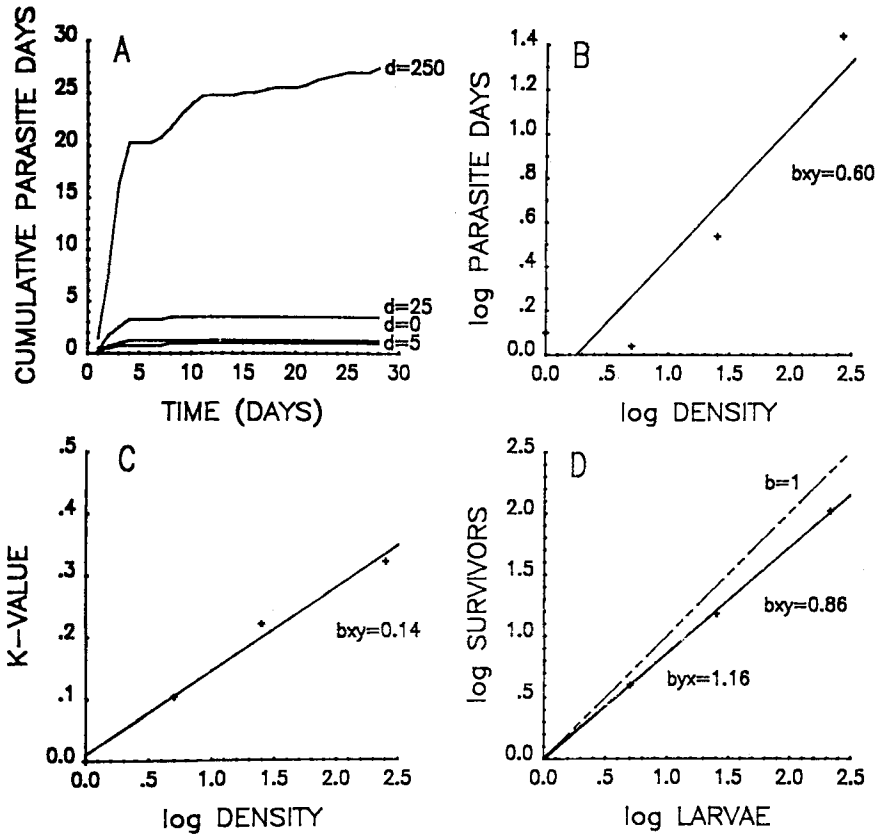


Fig. 1. Laboratory studies of aggregation by *Encarsia opulenta* and resulting mortality of *Aleurocanthus woglumi* : (A) cumulative parasite days on experimental plants exposed to 20 mated 1-day old female parasites for the duration of parasite adult lifespan ; (B) regression of parasite days on host density ; (C) regression of k-values for parasitism on host density ; and (D) 2-way regression test for direct density-dependence.

TABLE I

Cumulative mean daily densities ('parasites days') of Encarsia opulenta on caged citrus plants and resulting mortality of Aleurocanthus woglumi

Host Density	Cumulative Parasite Days	Percent Mortality	K-Value (a)
0	1.3	----	---
5	1.0	20.0	0.1
25	3.5	39.0	0.2
250	27.5	50.0	0.3

(a) Difference between \log_{10} initial numbers of hosts exposed to parasites and \log_{10} numbers of survivors from parasitism.

FIELD STUDIES

Placement of *A. woglumi*-infested plants in a stable low-density natural infestation resulted in an immediate response by adult *E. opulenta*, with 3 adults detected on plants after the 2nd day (fig. 2a). Cumulative parasite days ranged between 1.0 ($d = 0$ and 25) and 140.0 ($d = 1,000$) during a 40-day observation period (table 2), with a significant regression ($b = 0.77$; $r^2 = 0.80$) between \log_{10} parasite days and \log_{10} host density (fig. 2 b). Mean percent mortality of *A. woglumi* ranged between 69.2 % ($d = 25$) and 94.1 % ($d = 1,000$) (table 2), with a significant regression ($b = 0.42$; $r^2 = 0.94$) between k-values for parasitism and \log_{10} host density (fig. 2 c). The regression of \log_{10} initial hosts on \log_{10} survivors ($b = 0.58$; $r^2 = 0.97$) and \log_{10} survivors on \log_{10} initial hosts ($b = 1.68$; $r^2 = 0.97$) both met the criteria for direct density-dependence (fig. 2 d).

TABLE 2

Cumulative mean daily densities ('parasites days') of *Encarsia opulenta* in selected citrus trees and resulting mortality of *Aleurocanthus woglumi*

Host Density	Cumulative Parasite Days	Percent Mortality	K-Value (a)
0	1.0	---	---
25	1.0	69.2	0.5
100	47.0	92.8	1.1
1,000	140.0	94.1	1.2

(a) Difference between \log_{10} initial numbers of hosts and \log_{10} survivors from parasitism.

DISCUSSION

Parasite aggregation, and resulting density-dependent mortality of the host, has long been recognized as an important stabilizing mechanism in host-parasite interactions (Hassell, 1978). Such aggregation conceivably provides a twofold impact on stability: (1) localized host aggregations are detected by parasites with higher probability than less dense 'patches', and suppressed before significant numerical increases occur, and (2) higher probability of survival of hosts in less dense 'patches' reduces chances of overexploitation by parasites, thus mitigating against possible local extinction of both host and host-specific parasite. Life tables compiled for *A. woglumi* populations under effective regulation by *E. opulenta* (K. R. Summy, Ph.D. Diss., 1982) indicated significantly lower average mortality among parasite-undetected cohorts (67.1 %) than among contemporary cohorts detected by at least 1 parasite (96.3 %). No temporal or spatial refugia for *A. woglumi* were apparent, suggesting that rarity *per se* represents a principal refuge for the host in stable, low-density infestations under effective biological control.

Field and laboratory experiments reported herein both indicate a strong tendency of searching *E. opulenta* females to aggregate in high-density host patches, the net result of which is a direct density-dependent mortality of its host, *A. woglumi*. A key distinction between the delayed density-dependent population response by *E. opulenta* to *A. woglumi* (an intergeneration phenomenon) and direct density-dependent mortality resulting from adult parasite aggregation is that the latter involves a behavioral response operative through space within a single generation timespan. Such nonrandom searching patterns by the parasite are presumably a major determinant of the inherent stability characteristic of the interaction between *A. woglumi* and *E. opulenta* on Texas citrus (Summy *et al.*, 1983a).

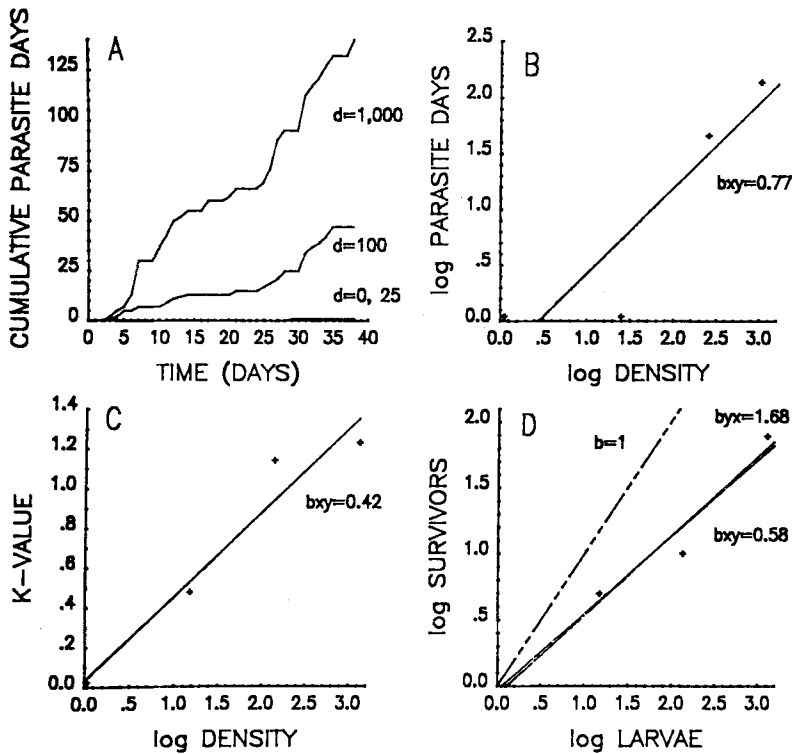


Fig. 2. Field studies of aggregation by *Encarsia opulenta* and resulting mortality of *Aleurocanthus woglumi*: (A) cumulative parasite days on experimental plants exposed to resident parasites during a 40-day observation period in selected citrus trees; (B) regression of parasite days on host density; (C) regression of k-values for parasitism on host density; and (D) 2-way regression test for direct density-dependence.

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RÉSUMÉ

Aleurocanthus woglumi [Hom. : Aleyrodidae] and *Encarsia opulenta* [Hym. : Encyrtidae] : Relation densité-dépendance entre l'agrégation des parasites adultes et la mortalité de l'hôte.

Des tests réalisés en plein air et en laboratoire sur le choix offert aux adultes d'*Encarsia opulenta* Silvestri, exposés à des densités variables de l'Aleurode des Citrus : *Aleurocanthus woglumi* Ashby indiquent : (1) une relation fonctionnelle directe entre l'agrégation de parasites adultes et la densité-hôte, résultant (2) d'une mortalité directe dépendant de la densité d'*A. woglumi* en l'espace de temps d'une simple génération. Les implications de tels types de recherches non effectuées au hasard de la part d'*E. opulenta* sur la stabilité de l'interaction hôte-parasite sur les Citrus du Texas, sont discutées.

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