1988

Analyzing population dynamics of the cabbage aphid, Brevicoryne brassicae L., and its parasitoid Diaeretiella rapae (McIntosh) using simultaneous measurement of host and parasitoid recruitment rates in the field.

E. Rolando Lopez-Gutierrez
University of Massachusetts Amherst

ANALYZING POPULATION DYNAMICS OF THE CABBAGE APHID, *Brevicoryne brassicae* L., AND ITS PARASITOID *Diaeretiella rapae* (McIntosh) USING SIMULTANEOUS MEASUREMENT OF HOST AND PARASITOID RECRUITMENT RATES IN THE FIELD.

A Thesis presented

by

E. ROLANDO LOPEZ-GUTIERREZ

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

September, 1988

Department of Entomology

ANALYZING POPULATION DYNAMICS OF THE CABBAGE APHID, *Brevicoryne brassicae* L., AND ITS PARASITOID *Diaeretiella rapae* (McIntosh) USING SIMULTANEOUS MEASUREMENT OF HOST AND PARASITOID RECRUITMENT RATES IN THE FIELD.

A Thesis presented

by

E. ROLANDO LOPEZ-GUTIERREZ

Approved as to style and content by:

John Edman, Chairperson of committee

Joseph Elkinton, member

Roy G. Van Driesche, member

Dave Ferro, member

John Edman, Department Head
Department of Entomology

DEDICATION

To my parents and my ten brothers and sisters and to Linda. I'm only the peak of the iceberg. Without their unified material and spiritual support not only my thesis but my whole life would not be possible.

ACKNOWLEDGMENTS

Muchisimas gracias, thank you very much to Dr. Roy Van Driesche for teaching me science, biocontrol, and a strong commitment to excellence. To Linda for her love. To Professors: Dr. Peters, Dr. Leonard, Joe, Dave, Chih, Ron, Dr. Edman from the Entomology Department, and Dr. Patrick Sullivan from the Education Department for offering me the best of themselves as scientists and as friends during the hard times here at UMASS which helped me a lot to endure the war that was taking place at the same time in my country, Nicaragua. I also extend thanks to my sponsors at LASPAU (Latin American Scholarship Program of American Universities) whose efficient economic and spiritual support through Miss Judith Adler was a key factor in the accomplishment of this thesis and to my technicians, Eileen, Steven, Peter, Doug, Christopher, Tony, Tom, Pamela, Dave, Chris, Tony, Krista, and my dear friends, Martin y Yolanda, Jorge y Marta Andrea and family... Arturo Tuttle, Sandy Liebhold and Genevieve Bardwell, Ron Mack, Ruth Hazzard with Ethan and Jesse, Craig Hollingsworth, Don Weber, Kathy Murray, Joe Argentine, Karen Idoine, Sue Opp and Sue B., Anne, Juli, Judy, Paula, Joanne, Jacques, and Ralph. I'll miss all of you.

ABSTRACT

ANALYZING POPULATION DYNAMICS OF THE CABBAGE APHID, Brevicoryne brassicae L., AND ITS PARASITOID Diaeretiella rapae (McIntosh) USING SIMULTANEOUS MEASUREMENT OF HOST AND PARASITOID RECRUITMENT RATES IN THE FIELD.

SEPTEMBER, 1988

E. ROLANDO LOPEZ-GUTIERREZ, B.S., UNIVERSIDAD DEL VALLE DE GUATEMALA

M.S., UNIVERSITY OF MASSACHUSETTS

Directed by: Prof. Roy G. Van Driesche

An assessment of total losses due to parasitism in a continuously breeding insect system was made using the cabbage aphid, Brevicoryne brassicae, L. and its braconid parasitoid Diaeretiella rapae (McIntosh) as a model.

The direct measurement of host and parasitoid recruitment was found to be an effective tool in this endeavor. Colony formation in the cabbage aphids was also found to be an important factor acting against parasitoid efficiency and hence reducing aphid losses.

1. RELATION OF COLONY FORMATION AS A LIFE HISTORY TRAIT TO FITNESS IN THE CABBAGE APHID, Brevicoryne brassicae L.

(1) Colony formation is a common, but not universal, life history trait in aphid species. The significance of this trait to the fitness of Brevicoryne brassicae L., the cabbage aphid, was investigated.

(2) Per capita progeny production by female aphids increased 40-50% as the group size increased from 3 or fewer to 5 or more adult females. This effect was observed on both potted plants under greenhouse conditions and on newly mature leaves on field grown plants under warm temperatures (ave. 22°C), but not under cool (ave.15°C) conditions.

(3) Under field conditions, aphids separated from colonies experienced 2-3 times greater levels of parasitism from Diaeretiella rapae (McIntosh), than aphids in either large or small colonies.

(4) Colony formation in Brevicoryne brassicae L. is thus promoted by both enhanced mid-season fecundity in colonies of five or more adults per colony and enhanced survival from the aphid's principal parasitoid.

2. DIRECT MEASUREMENT OF HOST AND PARASITOID RECRUITMENT FOR ASSESSMENT OF TOTAL LOSSES DUE TO PARASITISM IN THE CABBAGE APHID, Brevicoryne brassicae L., A CONTINUOUSLY BREEDING INSECT.

(1) Aphid population density was measured for the life span of two different groups of leaves taking into consideration aphid spatial pattern (in colonies or as isolated aphids) and aphid life stage as large (adults), medium (instars 2-4), or small (first instar) nymphs. Total aphid densities per leaf in both leaf groups, showed a similar pattern of initial increase followed by a decrease as leaves aged. Aphid densities reached peak values of 8.14 and 8.64 aphids per leaf for the two leaf groups studied and 65-67% of all aphids observed occurred in colonies.

(2) Host and parasitoid recruitment to the aphid and to the parasitoid immature populations were measured. Total host recruitments per leaf were 43.7 and 64.6 aphids for the first and second leaf groups. Parasitoid recruitment was 6.8-8.1 for the first leaf group and 8.2-15.8 for the second.

(3) Recruitment values indicated 15.6- 18.6% parasitism for the aphid cohort on the first leaf group and 12.7-24.4% for that on the second leaf group.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I.

RELATION OF COLONY FORMATION AS A LIFE HISTORY TRAIT TO FITNESS IN THE CABBAGE APHID, Brevicoryne brassicae L.

A. Introduction

Colony formation is a common, but not universal, life history trait in aphid species. Life history traits can enhance fitness by increasing fecundity, developmental rate, survival, or any combination of these.

The effect of density on total and daily fecundity in insects varies greatly among species. Most frequently, high densities of mixed-sex populations are correlated with lower total and daily fecundity (e.g. the alfalfa weevil Hypera postica Gyll.,LeCato and Pienkowski 1972; grasshoppers, Smith 1970, and Drosophila melanogaster L., Lints & Lints 1969). In some species, density has no apparent effect on fecundity, e.g., the house fly, Musca domestica L. (Osborn et al. 1970). For certain insect groups such as cockroaches and aphids, in which at least some species have life histories characterized by high density aggregations, positive effects from increased densities have been reported. Typically this has been in the form of more rapid developmental rates of immatures, e.g., the cabbage aphid (Way & Cammell 1970); the cockroach, Periplaneta americana (L.) (Wharton et al. 1968). Reports of insects with positive effects of density on fecundity are rare. One example is the greenhouse whitefly reared in the laboratory (Xu 1983). Among aphids, crowding is frequently associated with alate production (Lamb & White 1966; Sutherland 1969; Lees 1967). Way & Cammell (1970) reported that the initial reproductive rate of adult cabbage aphids developing from

grouped nymphs increased when group size increased from 5 to 20 and then declined. However, this cannot be taken as evidence for enhancement of daily per capita fecundity because females in high density groups reached sexual maturity earlier and thus had more time to reproduce than those in low density groups.

Effects of density on survival are highly variable (Morrison & Strong 1980; Jones & Turner 1987). Among species that form compact colonies (e.g., some aphids, caterpillars, sawflies, etc.), predation or parasitism rates may be reduced by lowered vulnerability of individuals at the center compared to those exposed at the periphery (Morrison & Strong 1980; Griffiths & Lyons 1980). The two advantages provided by group effect (decreased mortality and accelerated development) were studied by Lockwood & Story (1986) in Nezara viridula (L.) when attacked by Podisus maculiventris (Say) and Solenopsis invicta Buren. Aggregated nymphs of N. viridula experieced lower rates of predation than isolated nymphs. The effectiveness of host defensive movements and secretions (wax, powder or glue) may be enhanced by group formation e.g., larvae of Neodiprion swainei Middleton against the predator Podisus modestus (Dallas) (Tostowaryk 1972).

We report here on the effect of colony formation on both daily per capita fecundity and losses due to parasitism by Diaeretiella rapae McIntosh for the cabbage aphid, Brevicoryne brassicae L. and we discuss our findings in light of the value of this life history characteristic to fitness in the cabbage aphid.

B. Materials and Methods

1. Measurement of per capita recruitment of caged females

The effect of colony size (in terms of numbers of adult females per colony) on the per capita recruitment rate of female cabbage aphids under greenhouse and field conditions was determined using 3.4 cm dia. plastic leaf cages constructed from disposable petri dishes ventilated top and bottom with fine screen and held in place on leaves by wooden clips. Unparasitized adult cabbage aphid females were taken from a greenhouse colony maintained on potted collard plants (Brassica oleracea var.acephala c.v. "Vates",a flat leafed form) under greenhouse conditions. Colonies of various numbers of adult females were created by transfering aphids into leaf cages with a fine-tipped brush. Aphids moved by themselves onto leaves after cages were secured to leaves.

Trial 1 was conducted on potted plants in a greenhouse during a warm period (ave.$35^{o}\pm4.5^{o}$C). Densities of 1, 3, 5 and 7 adults per cage were tested between 16 June, 1986 - 7 July, 1986. Aphids were allowed to reproduce on the undersides of leaves for three days and the resultant numbers of offspring and surviving females counted. The trial was repeated 5 times with 30 replicates per density each time placing two leaf cages/leaf on each of 4 leaves, using two replicates of each treatment for each plant. Trial 2 was conducted in a collard field at South Deerfield, Massachusetts, between 5 September, 1986 - 26 September, 1986, under cool conditions (ave.$15^{o}\pm2.3^{o}$C), using 1, 3, 5, 7, 9, 11, 13 and 15 females per cage. Aphids from the same greenhouse colony as used in Trial 1 were placed in cages and cages were then placed on the undersides of recently fully-expanded leaves

on field plants and allowed to reproduce for a three day period. Ten replicates were used for each density and the trial was repeated four times. During each repetition treatments were randomly assigned to plants, using five leaves each of 16 plants, with one cage per plant. Trial 3 was conducted between 15 July, 1987 - 18 July, 1987 on plants in a similar collard field in the same location as was used for trial two. The trial was run under warm conditions (ave.$22^{o}\pm3.8^{o}$C). Using aphids from the same greenhouse colony as in previous trials, groups of 1, 3, 5, 7, 9, 11, 13, 15, 20, 25, and 30 adult aphids were placed in cages which were attached to leaves as in previous trials except that 48 plants were used due to a higher number of replicates. Thirty replicates of each density were established at the same time and the trial was conducted once. Because some aphids in trials two and three died during field exposure, treatment values were redefined from single densities to narrow ranges of density; for instance, colonies with 14 and 15 surviving adult females per colony were grouped in lieu of the original targeted density of 15 adults per cage and so on.

2. Distribution of females per colony in the field

A plot of Vates collards was established the first week of May, 1987, at the University Research Farm at South Deerfield, Massachusetts, with 60 cm inter-plant and 120 cm inter-row spacings. Weeds were partially suppressed during the season by hand pulling and cutting. Five leaves of similar age were chosen from each of 1000 similar sized plants, excluding the first four rows at each end of the plot. The leaves were numbered 1-5 on tags stapled directly on the leaves. Leaves were young but fully expanded at the time of selection. Tagged leaves turned senescent after four weeks and were replaced with

a second set of 5000 leaves on new plants selected in the same manner as for the first group. Three times each week tagged leaves were selected as samples to determine aphid density per leaf within the defined cohort of 5000 leaves, using random number coordinates for row, plant and leaf. Samples were selected on each date until a total of 30 leaves containing aphids were encountered. Numbers of leaves encountered that contained no aphids were also recorded. On each leaf with aphids, areas with aphids were cut out with razor blades and placed on moist paper towels in 15 cm dia plastic petri dishes, with ventilated tops. Dishes with aphids were sealed with parafilm in the field and the number and categories of aphids observed were recorded on each dish. Aphids were classified either as isolated, if they occurred in groups of four or fewer, or as colonies if in groups of five or more immediately adjacent aphids. Aphids in colonies were further classified in the field as adults, nymphs or mummies (i.e. parasitized aphids after aphid death). Aphids judged to be in colonies were placed in one petri dish and isolated aphids in another to prevent mixing. Samples were immediately placed in coolers with ice packs to minimize aphid mortality from overheating and to retard movement. Samples were then returned to the laboratory where aphids were further classified into three size categories, i.e. small (first instars), medium (2-4th instars) and large (adults) and any errors in the field classifications were corrected. Aphids were classified by size, but these groups were not physically segregated. In general, handling was avoided wherever possible to minimize mortality. The number of adults in each colony was recorded for each sample and then these data were pooled for the entire eight week sampling period and

the proportion of adults living in colonies with various numbers of adults per colony determined.

3. Use of trap-hosts to assess parasitism of isolated and clustered aphids

To determine if the spatial arrangement of aphids on the leaves in the field (in colonies or scattered) influenced the probability of attack by Diaeretiella rapae, potted collard plants infested with unparasitized aphids from a greenhouse colony were exposed in the same collard field in which the previously described observations on aphid recruitment were made. There were two trials, one using large colonies (average of 132 aphids each) and one using small colonies (12-13 aphids each). For the trial with large colonies, 5 leaves on each of 20 plants were inoculated with 20 adult females for a two day period in a greenhouse. After two days, each leaf contained approximately 130 first instar cabbage aphids. Aphids were restricted to an area of 9.1 cm^2 because females were confined in leaf cages during the infestation process. Plants were then taken to the collard field. Immediately before placing the plants in the field, 10 plants were randomly selected and, after removing the leaf cages, fine-tipped brushes were used to disperse aphid colonies and to produce a distribution of predominantly isolated aphids. Potted plants were then randomly placed among field plants and exposed to parasitoids for four days. During exposure, aphids were mostly second instar nymphs. At the end of the exposure period, plants were returned to the laboratory and placed for two days in an outdoor cage covered with a fine screen. Within the cage, plants with colonies were physically separated from the ones with isolated aphids to prevent mixing. Post-exposure incubation was

required to allow parasitoid eggs within aphids time to hatch, as the first instar parasitoid larva was the smallest stage that could be reliably detected by dissection. After incubation, aphids were washed from leaves with alcohol and random samples of 100 aphids were selected for dissection from each plant. The level of parasitism for each plant in each treatment and the total number of aphids per plant were determined. The experiment was repeated two weeks later in the same field in the same manner as for the first trial but using a smaller colony size of (12-13 aphids per colony) that more closely matched colony sizes observed in the field population.

C. Results

Per capita reproduction of female cabbage aphids was significantly influenced by colony size on potted plants held in a greenhouse at 35^{o}C (significant at =0.001, one-way ANOVA, F=24.4, 346 df) (Fig.1A). The reproduction rate of females in colonies with either one or three adult females per cage was smaller than that of females in colonies of five or seven per cage (Tukey's test, significant at =0.05). On field plants under warm conditions (ave. 22^{o}C), per capita reproduction of female cabbage aphids was also significantly influenced by colony size (Fig.1B) (significant at =0.05, one-way ANOVA, F=2.79, 128 df.), but under cold conditions (ave. 15^{o}C) in the field on leaves of the same age, aphid density has no effect on reproduction (Fig.1B) (one-way ANOVA, with F=0.16, 195 df.). Sixty two percent of adult females observed in samples from the field population under study occurred in colonies containing one to three adult females (Fig.2).

FIG. 1. Per capita recruitment per three-day interval for cabbage aphids, Brevicoryne brassicae, in groups of varying numbers of initial females under greenhouse conditions (A) and field conditions (B) at a collard field in South Deerfield, Massachusetts, in 1986-1987. (Error bars are S.E.M.).

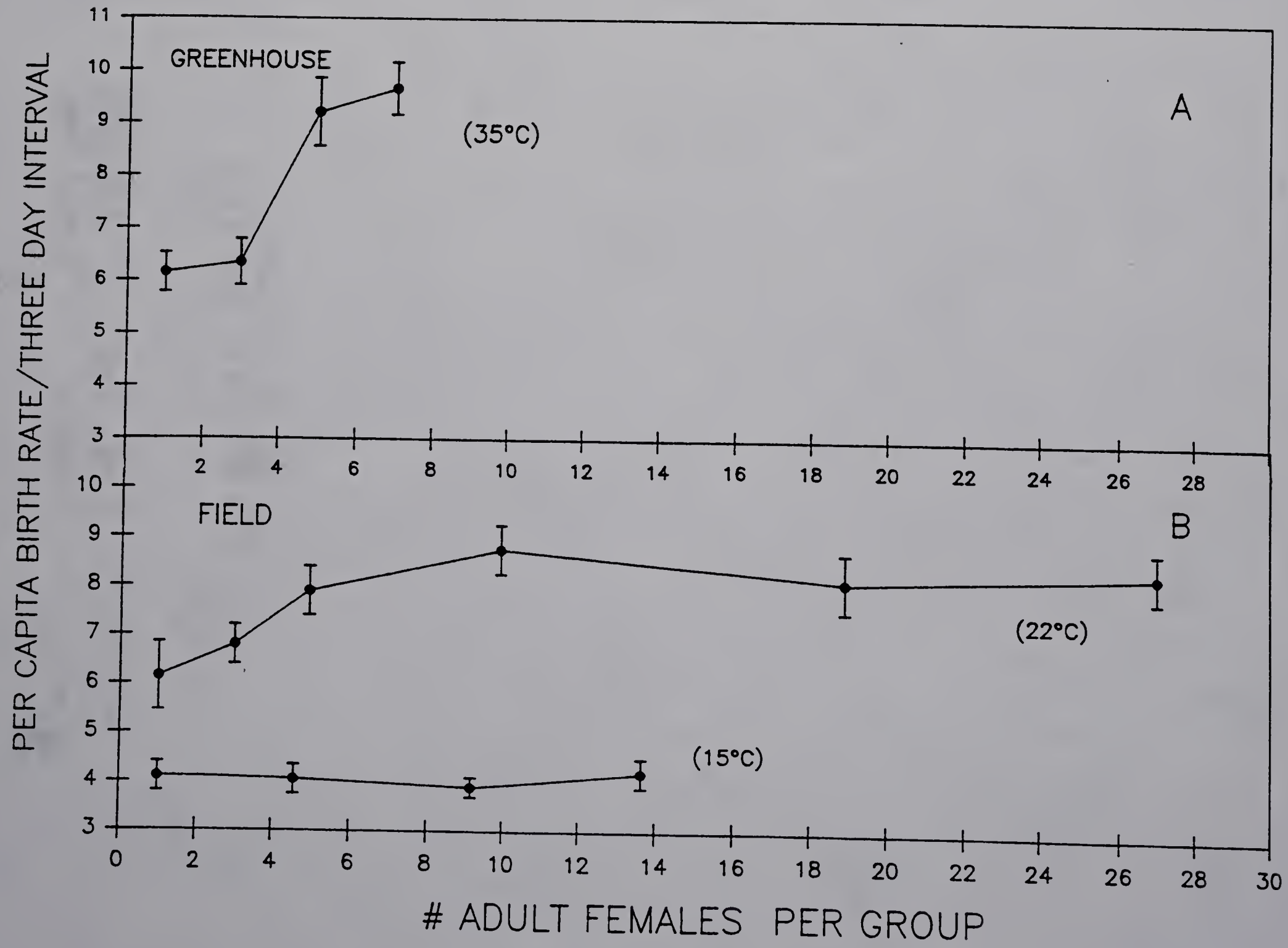
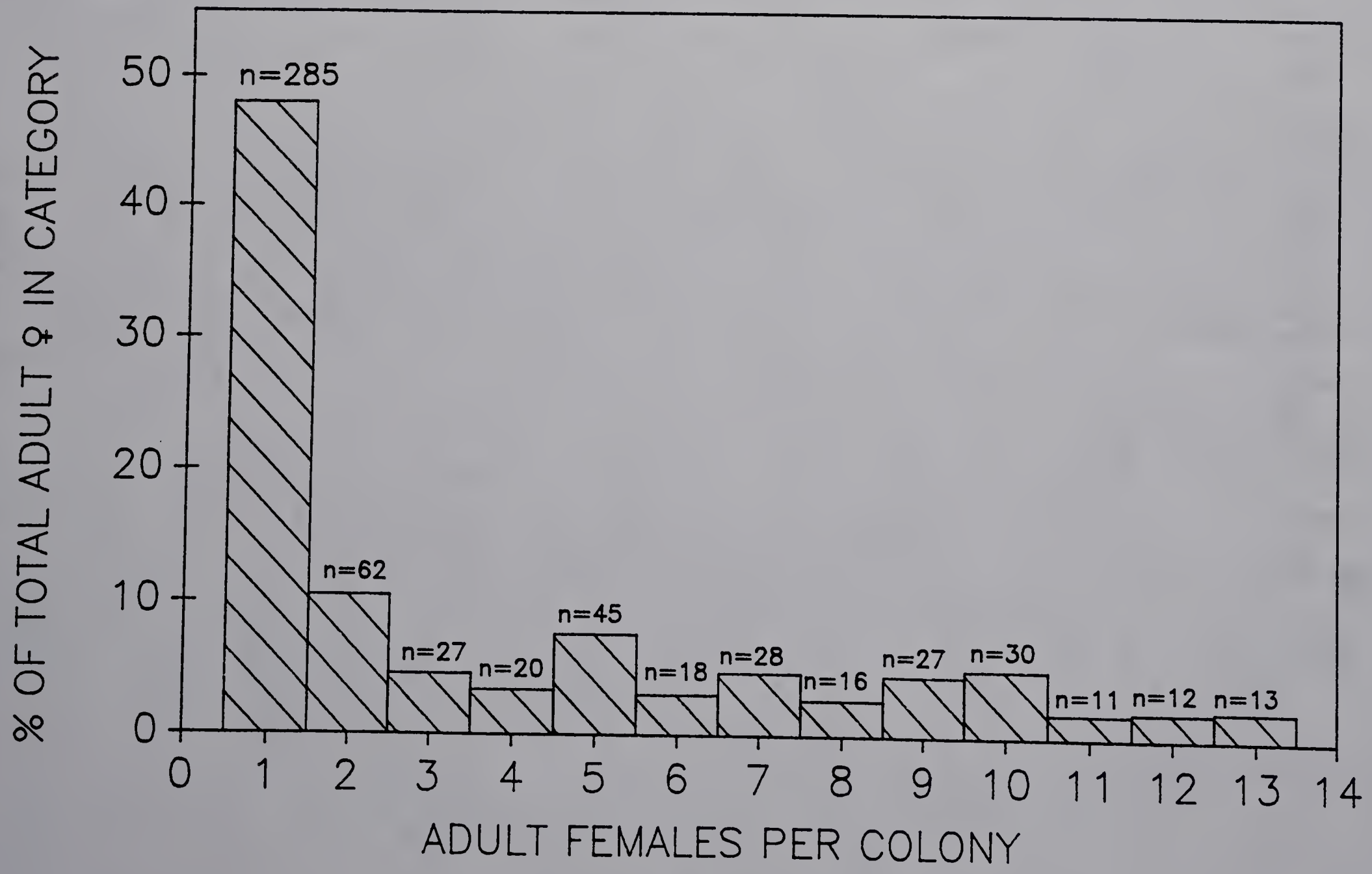

PER CAPITA BIRTH RATE/THREE DAY INTERVAL
GREENHOUSE
(35°C)
A
FIELD
B
(22°C)
(15°C)
ADULT FEMALES PER GROUP

FIG. 2. Proportion of adult female aphids in groups of various numbers of adult females per group for a population of the cabbage aphid, Brevicoryne brassicae, at a collard field in South Deerfield, Massachusetts, in 1987.


% OF TOTAL ADULT ♀ IN CATEGORY
50
40
30
20
10
0
n=285
n=62
n=27
n=20
n=45
n=18
n=28
n=16
n=27
n=30
n=11
n=12
n=13
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
ADULT FEMALES PER COLONY

Parasitism levels in trap host aphids exposed in the field were twice as large for dispersed versus clustered aphids in large colonies (132 aphids per colony) (Table 1). This difference increased to a threefold level for small colonies (12-13 aphids per colony) (both differences significant in a G-test at =0.05).

D. Discussion

Way and Cammell (1970) postulated that aggregates of phloem-feeding aphids are treated by plants as the equivalents of rapid growth areas. Such 'sinks' cause nutrients to be diverted from distant parts of the plant to the advantage of the aphid colony. Our observations of enhanced per capita recruitment of cabbage aphids under warm conditions in the greenhouse (35°C) and in the field (22°C) can be interpreted as supporting Way and Cammell's (1970) hypothesis, assuming that under warm conditions in the greenhouse and in the field, the factor limiting progeny production is nutrient supply. Possibly, reproduction under cold conditions in the field was not enhanced by larger group size because reproduction rates were too low for the nutrient supply to be limiting.

The reduced level of parasitism from D. rapae experienced by aphids in colonies may have arisen in one of two ways. First, the foraging behavior of D.rapae may have been affected by dispersal of aphids, which would increase the likelihood that some aphids or aphid-derived kairomones would be discovered by foraging parasitoids. Ayal (1987) found that cabbage aphid secretions when dissolved in distilled water and applied to the leaves of potted Brussels sprout plants arrested parasitoids as soon as they encountered treated areas.

Table 1. Percent parasitism in aphids with either dispersed or clustered spatial patterns on potted collard plants exposed for four days in a collard field.

	CLUSTERED	DISPERSED	G-TEST VALUES
LARGE[1] COLONIES	10.3%(300)[2]	23.7%(270)[2]	18.51
$\bar{X}$ APHIDS/PLANT	596	496	
SMALL[1] COLONIES	6.9%(451)[2]	22.2%(343)[2]	39.14
$\bar{X}$ APHIDS/PLANT	41.5	34.3	

[1] Large = 132 aphids/colony; small = 12-13 aphids/colony.

[2] Number of aphids dissected.

Parasitoids spent more time searching treated leaves than clean leaves (Ayal 1987). Wandering aphids would spread such chemical cues as honeydew and wax over wider areas indicating their presence to parasitoids. While the exact influence such modified foraging patterns would have on levels of actual parasitism is unknown, it might, at least in part, account for experimental differences reported here.

An alternate explanation involving aphid defense and the space needed by parasitoids for oviposition also exists. Qualitatively, in the course of the experiments reported here, it was observed that cabbage aphids in colonies exhibited considerable movement. They often kicked in unison when disturbed, especially in large colonies. Such motion was observed to dislodge and otherwise disturb parasitoids with the result that oviposition attempts ceased. In addition, Diaeretiella rapae was noted to require a certain minimum space to ensure that its tarsi were securely attached to the leaf surface in order to be able to bend its abdomen through its legs and oviposit successfully. Parasites could not walk over the backs or between tightly grouped aphids in colonies. Therefore, the combined effects of aphid movement and lack of space in which to assume the needed stance for oviposition may have protected those aphids in the middle of the colony from parasitism. Aphids at the periphery of the colony would be more vulnerable to attack by D. rapae. Isolated aphids or aphids in small groups would on average be more vulnerable to parasitism than those aphids in large groups because of the higher proportion that are exposed to attack at the group's edge. Klingauf & Sengonca (1970) reported that cabbage aphids at the periphery of colonies were more vulnerable to D. rapae attack.

Enhancement of aphid fecundity and protection from parasitism, both promote colony formation in cabbage aphids. A possible deterrent to the over-development of this life history trait may, however, exist. While not part of the work reported here, the cecidomyiid aphid predator, Aphidoletes aphidimyza (Rondani), was observed in the field to be a very common predator attacking cabbage aphids as soon as aphids started to form large colonies. El Titi (1974a) showed that A. aphidimyza can efficiently locate aphid colonies. Adult midges released in a greenhouse succeeded in a single night in finding and ovipositing on a single aphid-infested plant among 75 others that were aphid-free. Honeydew, cornicle secretions and dead aphids seem to be the main factors that help A. aphidimyza find aphid colonies (El Titi 1972/73, 1974b; Ayal 1987). In Myzus persicae, A. aphidimiza lays more eggs if aphids occur in colonies than if they are dispersed (El Titi 1972/73). Assuming then that increasing colony size in cabbage aphids evokes a similar response, predation would act against the trend toward formation of large colonies in Brevicoryne brassicae. Indeed in the B. brassicae population studied here, field samples showed that approximately one third of all aphids occurred as "isolated" individuals (e.g., in groups of 4 or fewer). The occurrence of this high a proportion of aphids not in colonies may reflect the existence of risks as well as benefits of colony formation by cabbage aphids.

CHAPTER II.

DIRECT MEASUREMENT OF HOST AND PARASITOID RECRUITMENT FOR ASSESSMENT OF TOTAL LOSSES DUE TO PARASITISM IN THE CABBAGE APHID, *Brevicoryne brassicae* L., A CONTINUOUSLY BREEDING INSECT.

A. Introduction

Measuring total levels of insect mortality caused by parasitoids is a basic step for life-table construction. Van Driesche (1983) indicated that levels of parasitism seen in samples can be misleading due to relative phenologies of host and parasitoid entry into and advancement out of the sampled stage and differences in mortality rates for healthy and parasitized hosts. Van Driesche & Bellows (1988) presented a method to assess total losses from parasitoids by measurement of total host and parasitoid recruitment. This method was developed for *Pieris rapae* (L.) and *Cotesia glomeratus* (L.), insects with discrete generations. We apply the recruitment method of Van Driesche & Bellows (1988) to the cabbage aphid, *Brevicoryne brassicae* (L.) and its braconid parasitoid *Diaeretiella rapae* (McIntosh), a system without discrete host generations, to determine the relative power of the recruitment method to reveal the impact of parasitoids on continuously breeding hosts, in comparison to conventional practices based on percentage parasitism values seen in samples.

B. Materials and Methods

1. Field site description; sampling for aphid density and percent parasitism

A 30 x 33 m plot of collards (*Brassica oleracea* var. *acephala* c.v. "Vates", a flat leafed form) was established at the University

of Massachussetts research farm in South Deerfield, MA, the first week of May, 1987 with 60 cm inter-plant and 120 cm inter-row spacings. Mechanical cultivation and hand hoeing were used to suppress but not eliminate weeds. No pesticides of any kind were applied to the plot. The field was artificially infested with cabbage aphids (Brevicoryne brassicae L.) on 13 July, 1987 with 1500 adult females distributed over 100 plants in groups of various size (1-30 aphids per group). Fifty consecutive plants from each of 21 adjacent rows were selected to monitor development and parasitism of the aphid population. Four peripheral rows on each side of the plot were left unsampled. On each of the 1050 sample plants, five newly-expanded leaves were selected and marked with numbered paper tags. Only aphids on this group of leaves were considered in the study. This limitation was imposed to eliminate leaf age, and hence leaf quality, as an influence on sample variability within dates. This initial set of leaves was used for four weeks (leaf group # 1 July 21 - August 14), after which time a second set (leaf group # 2 August 16 - September 11) of 5250 newly matured leaves was selected and marked in the same manner as previously described and used for sampling for the next four weeks. During each four week period tagged leaves progressed from newly expanded young leaves to senescent leaves at or near the soil level with prominent yellow areas. During the eight-week study period, beginning on 21 July, samples were taken three times a week using random row, plant and leaf coordinates to determine aphid density per leaf. Sample leaves were examined in the field and all aphid-bearing sections of each leaf were excised with a razor blade and immediately placed in ventilated petri dishes on top of a piece of dampened paper towel.

Aphids deemed to be in "colonies" (defined arbitrarily as five or more aphids in immediate physical contact) were placed in separate petri dishes from aphids in smaller groups (designated as "isolated"). All petri dishes for each given plant were marked with the date and plant number. Care was taken to ensure that no parasites entered the petri dishes. In addition to live aphids, all apparently live aphid mummies were collected and placed in the petri dishes of the aphid groups with which the mummies were associated. Dishes were sealed with paraffin film and the plant and leaf numbers as well as the number of adult and nymphal aphids (based on visual estimate of instar in the field) were recorded on each dish. Dishes were then placed in a cooler containing ice packs and kept in the shade until sampling was completed. Sampling was continued on each occasion until thirty aphid-bearing leaves were encountered. Numbers of leaves selected on each sample date that had no aphids were recorded. At the end of the field sampling, leaves were returned to the laboratory and all leaves were immediately (same day) inspected and aphids reclassified into three life stage categories distinguishable with a hand lens: large (adults), medium (instars 2-4), and small (first instar) nymphs. These size groupings times the two spatial aggregation types (colonies, isolated) constituted the six basic categories of aphids recognized in the study for which per leaf densities and percentage parasitisms were determined.

During the reclassification process aphids were not physically disturbed except for adults which were transfered to separate petri dishes so as to avoid confusion with fourth instar nymphs reaching adulthood during the 48 hr incubation period required prior to

dissection. Incubation of samples prior to dissection was required because the smallest stage of the parasitoid that could be successfully detected in aphid dissections was the first instar larva. Parasitoid eggs required approximatly 30 day degrees of development to hatch; thus petri dishes of field collected aphids were held in a growth chamber for 48 hr at 25±2°C to permit any newly-oviposited D. rapae eggs to hatch. At the end of this period the dishes were removed and stored at 1-5°C to prevent any further parasitoid development prior to aphid dissection. Aphids of each of the six categories ("isolated" or "colony" aphids for each of the adult, medium, and small size classes) were then dissected to detect parasitoid immature stages. All aphids from a given day's sample were dissected unless the total for a given aphid category was greater than 50, in which case a randomly selected sub-sample of 50 aphids from the category was used. Dissections were done so that aphids remained grouped by sample leaf. Records were thus made for each leaf within each aphid category of the numbers of aphids originally found in the field on the leaf, the number placed in incubation, the number dissected and the number found to be parasitized. For parasitized aphids, the immature parasitoids were classified as either first, second and "older" instars. Since the sampling procedure involved unequal subsampling between aphid categories, percentage parasitism values for combinations of categories (e.g., "all" or "all aphids in colonies") were calculated with each category's contribution weighted in proportion to the total numbers per leaf in each category.

2. Sampling for reproduction rate and exposure of trap-host nymphs to assess parasitoid attack rates

On each sample date adult aphids were selected from the field population to determine the per capita reproduction rate of the field aphid population. Tagged collard leaves in the plot were searched until 40 adult female aphids were located. Aphids were classified as adults by body size, degree of waxy body secretions, and in some cases, presence of associated nymphs that were obviously progeny of the individual being examined. Each adult was either caged in place or if this was not possible it was moved with a small paint brush and placed in a more suitable location apart from other aphids on the underside of a tagged leaf. Aphids were placed in leaf cages as described in Lopez et al. (1988). On the following sampling date (typically 2-3 days later), each cage was removed and the number of newly produced nymphs in each cage counted. Adults were collected and taken to the laboratory for dissection and examined for evidence of parasitism or of disease.

Nymphs produced by caged adults were left in place on leaves after leaf cages were removed to assess parasitoid attack rates (hereafter referred to as trap-host nymphs). On the next sampling occasion, the number of nymphs remaining in each group was noted and the portions of each leaf bearing these nymphs were cut out and taken to the laboratory where leaves were incubated for 48 h at 25°C, whereafter the nymphs were dissected to detect possible parasitism.

3. Laboratory assessment of developmental rate of the parasitoid

Adult female aphids were isolated in leaf cages attached to potted collard plants within fine mesh sleeve cages in a greenhouse.

Progeny (first- and second-instar nymphs) of these adults were collected and exposed to adult D. rapae females under close observation until 360 nymphs were attacked. All non-parasitized aphids were removed, and plants incubated in growth chambers at 15, 20 or 25°C for varying lengths of time. Within each temperature regime, parasitized nymphs were removed after 40, 50, 60, and 70 degree-days had accumulated utilizing an assumed base temperature of 10°C. Aphids were immediately placed in alcohol and dissected to detect immature parasitoids. For each parasitoid, the life stage (egg, larval instar, etc.) was recorded, following the drawings of Spencer (1926).

4. Calculation of composite parameters

Utilizing the directly measured parameters of aphid density, parasitism, birth rates of caged adult aphids, and parasitoid attack rates on trap-host nymphs, host and parasitoid recruitment rates (as numbers per leaf per period) were calculated. Two independent techniques were used to calculate parasitoid recruitment.

a. Host recruitment. The number of new aphids entering the population (by birth) per leaf per interval (2-3 days) in general terms may be calculated by the following equation:

$$HI = D \times R \qquad (1)$$

where HI is host recruitment/leaf/interval, D is the average density of adult females per leaf in the interval and R is the reproduction rate of adult females during the interval. However, several distinctions were required to separate groups of individuals reproducing at different rates. Adult females were divided into three categories, healthy, parasitized and diseased, based on their observed

conditions at the time of dissection, either in density samples from the field population or in dissections of adults used to assess per capita birth rates in the field in leaf cages. Both density and reproduction records were separated for each sample into these groups, designed as: Dh= density of healthy aphids per leaf per interval, Dp= density of parasitized aphids per leaf per interval, Dd= density of diseased aphids per leaf per interval, Rh= per capita birth rate of healthy aphids, Rp= per capita birth rate of parasitized aphids, and Rd= per capita birth rate of diseased aphids. The original general equation can now be revised to include separate records for each of these categories as follows:

$$HI = (Dh \times Rh) + (Dd \times Rd) + (Dp \times Rp) \qquad (2)$$

Finally, within the category of healthy aphids, a distinction was made between densities of healthy aphids in colonies containing three or fewer adults (Dh) and those found in colonies with more than three adults (Dh*). This distinction was required because of a positive enhancement of per capita reproduction in larger groups (Lopez et al. 1988). A correction factor (F=1.28) was then applied to adjust the reproduction rate of the later category (large colonies) utilizing data of Lopez et al. (1988). The final equation for B. brassicae recruitment thus becomes:

$$HI = (Dh \times Rh) + (Dh^* \times Rh \times F) + (Dd \times Rd) + (Dp \times Rp) \qquad (3)$$

b. Parasitoid recruitment. Two methods were used to measure parasitoid recruitment. It was assessed either by multiplying the daily attack rate seen in trap-host aphids by the density of non-

parasitized aphids per leaf in the field ("trap-host" method) or by identifying hosts seen in the dissections of field aphids in which parasitoids were sufficiently juvenile (based on parasitoid instar) to have arisen within the interval between field samples ("marker- stage" method).

i. Method 1. ("Trap-host" Method). Parasitoid recruitment per leaf was calculated by multiplying the numbers of "available" (i.e. unparasitized) hosts per leaf by the attack rate experienced in each interval by trap-host nymphs. To correct for differences in attackability of adult versus small or medium aphids to parasitoid attack, a correction factor of 0.63 was applied in calculating parasite recruitment rates for the adult aphid categories, using literature values of parasitoid preference between adult and nymphal aphids (Hafez 1961).

ii. Method 2. ("Marker-Stage" Method). Results of a parasitoid development rate experiment and records of degree days accumulated in the field for each interval were used to define the maximize sizes of immature parasitoids that could denote within-interval parasitoid recruitment for each interval. Typically only first instar parasitoid larvae were sufficiently juvenile to be counted as recruitment except for one period when a sample date was missed because of rain, for which interval sufficient day degrees accumulated to allow parasitoids to reach the second instar. This size criterion was then applied to dissection data used to determine percentage parasitism in the field population. Parasitoid recruitment per leaf per interval was thus determined for each of the six aphids categories: colonies and isolated times small, medium,and adult size classes.

C. Results

Total aphid densities per leaf in both leaf groups showed a similar pattern of initial increase when young leaves were being colonized, followed by decrease as leaves aged (Fig. 3). Total aphids per leaf peaked at 8.14 for the first group of leaves on 29 July and at 8.64 for the second group of leaves on 26 August. Aphids in colonies consistently outnumbered isolated aphids on all sample dates (Fig. 3). In pooled samples, aphids in colonies constituted 65.4% of all aphids for the first leaf group and 67.7% for the second leaf group. Isolated aphids were predominantly in the medium size class for both leaf groups, whereas for colony aphids the small and medium-sized aphids were more nearly equal in abundance (Table 2, Fig. 4).

Levels of percentage parasitism in live aphids ranged from 15.65 - 28.29% for the first leaf group and 12.72 - 36.42% for the second leaf group (Fig. 5). When live mummies on leaves were added to sample counts, levels of apparent parasitism increased an average 7.3% for the first group of leaves and 12.1% for the second. Levels of parasitism in pooled samples were not significantly different between the early and late season leaf groups (19.37 vs. 21.07%, Z test, $p=.16$). Levels of parasitism in isolated aphids, however, were significantly higher than in aphids found in colonies for both leaf groups (Z test, $p<0.001$ for the first leaf group and Z test, $p<0.001$ for the second leaf group). Levels of parastism in pooled samples increased from small to medium aphids and decreased from medium aphids to adults, except for colony aphids in the second leaf group (Table 3). When mummies were retained, differences in parasitism between isolated and colony aphids were even more pronounced (Table 4).

FIG. 3. Densities of cabbage aphids per leaf in a collard field in South Deerfield, Massachusetts, in 1987, for two leaf groups, divided by aphid spatial characteristics. (Error bars are S.E.M.).

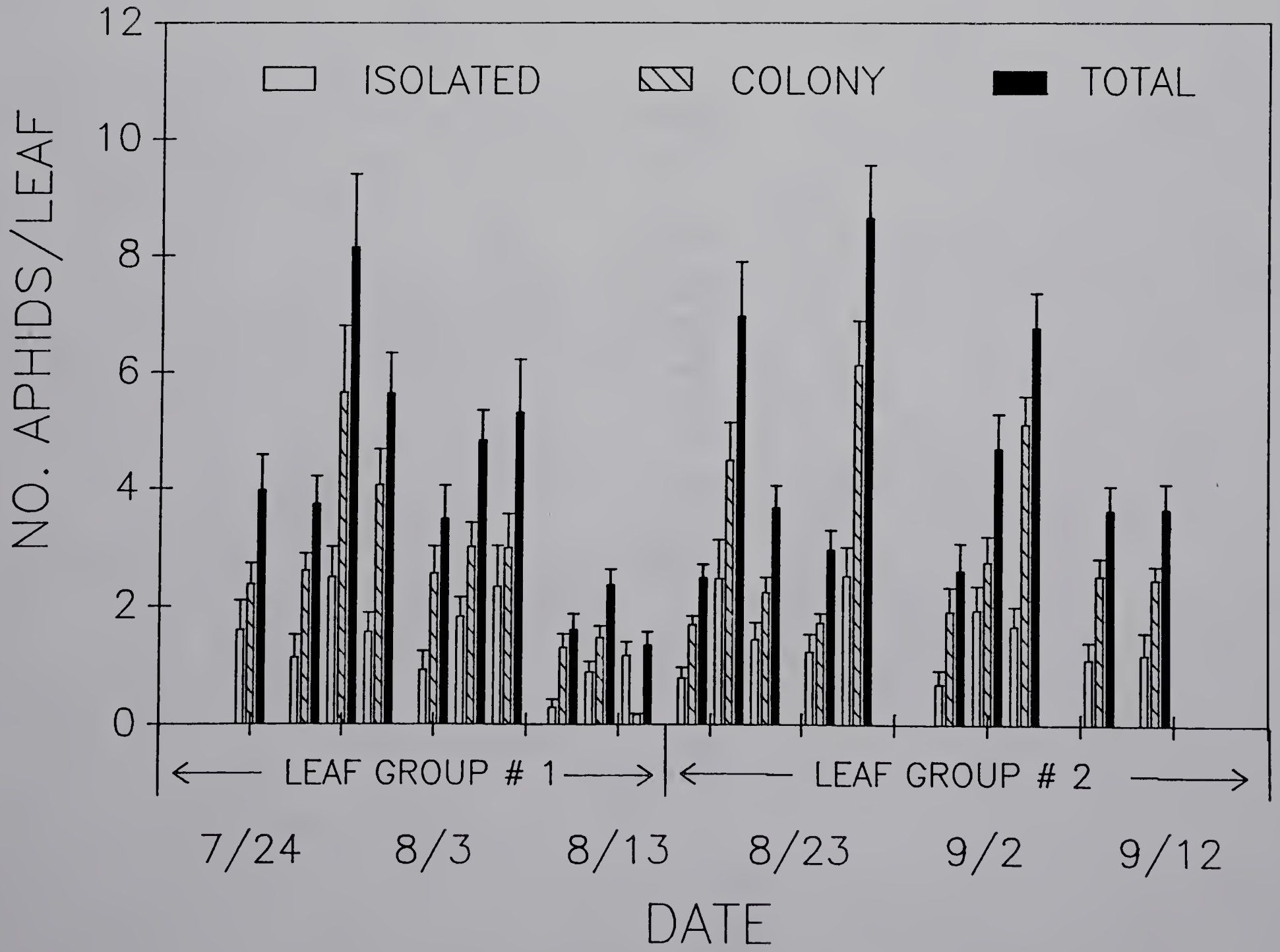

ISOLATED
COLONY
TOTAL
NO. APHIDS/LEAF
12
10
8
6
4
2
0
LEAF GROUP # 1
LEAF GROUP # 2
7/24
8/3
8/13
8/23
9/2
9/12
DATE

FIG. 4. Densities of cabbage aphids per leaf in a collard field in South Deerfield, Massachusetts, in 1987, for two leaf groups, divided by aphid size classes. (Error bars are S.E.M.).

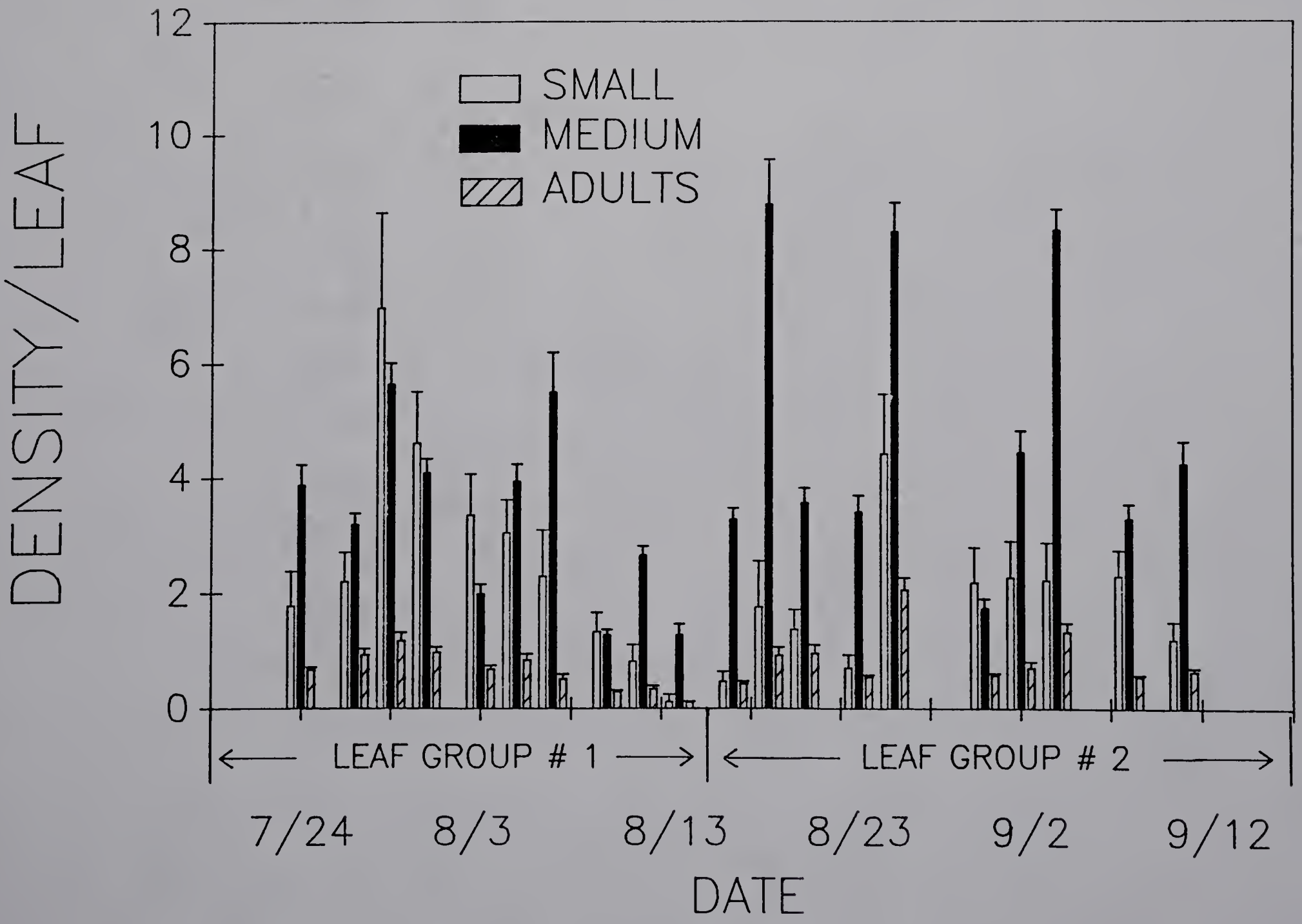

DENSITY/LEAF
12
10
8
6
4
2
0
SMALL
MEDIUM
ADULTS
LEAF GROUP # 1
LEAF GROUP # 2
7/24
8/3
8/13
8/23
9/2
9/12
DATE

FIG. 5. Levels of parasitism of cabbage aphids on collards, seen in samples from two leaf groups, at South Deerfield, Massachusetts, 1987. (Error bars are S.E.M.).

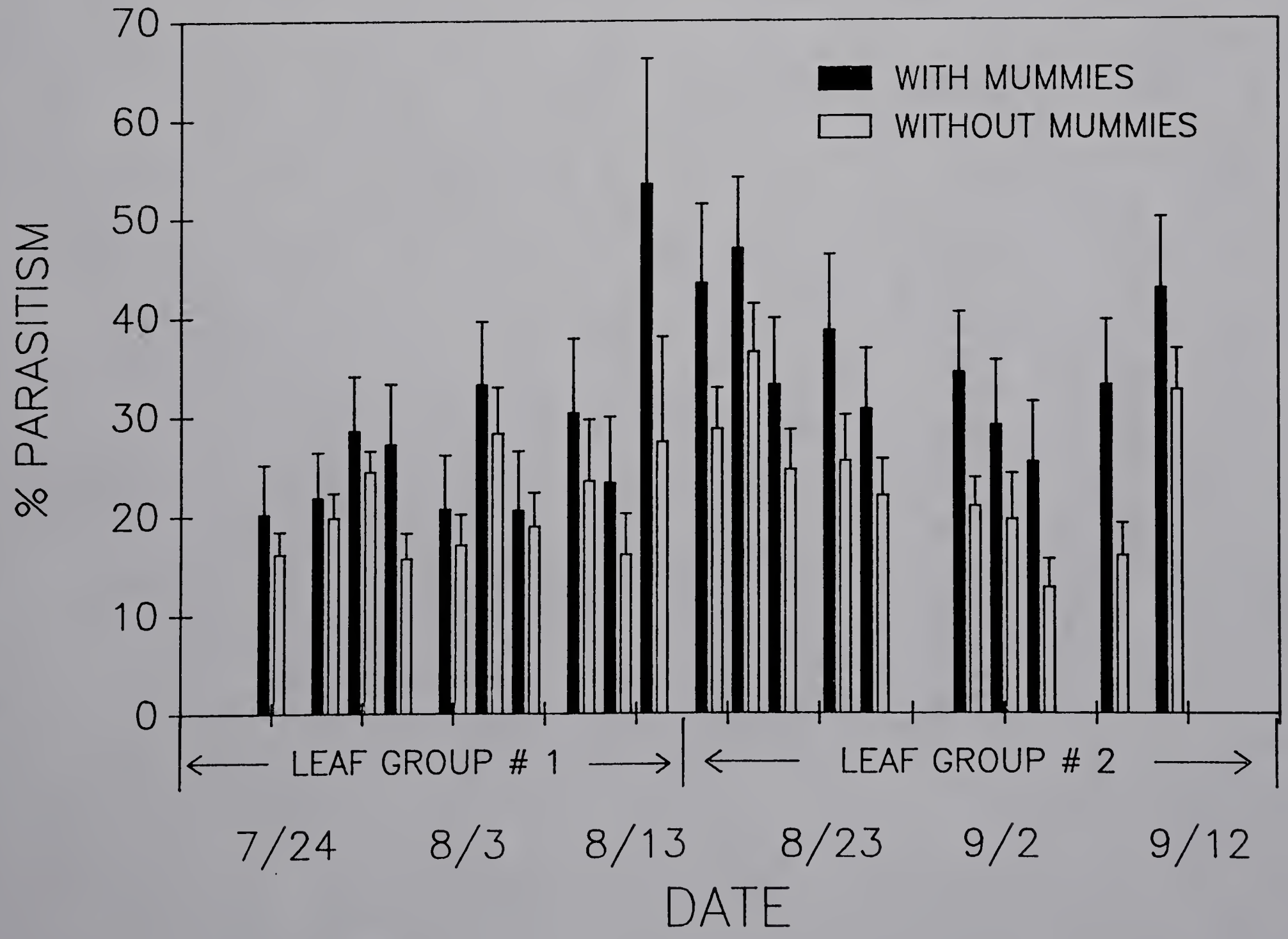

70
60
50
40
30
20
10
0
% PARASITISM
WITH MUMMIES
WITHOUT MUMMIES
LEAF GROUP # 1
LEAF GROUP # 2
7/24
8/3
8/13
8/23
9/2
9/12
DATE

FIG. 6. (A) Daily per capita birth rates of healthy, parasitized and diseased cabbage aphids in a collard field at South Deerfield, Massachusetts, 1987, for two leaf groups, and (B) per capita birth rate per day-degree (base=6.7^{o}C) for healthy cabbage aphids only, for the same population as in (A). (Error bars are S.E.M.).

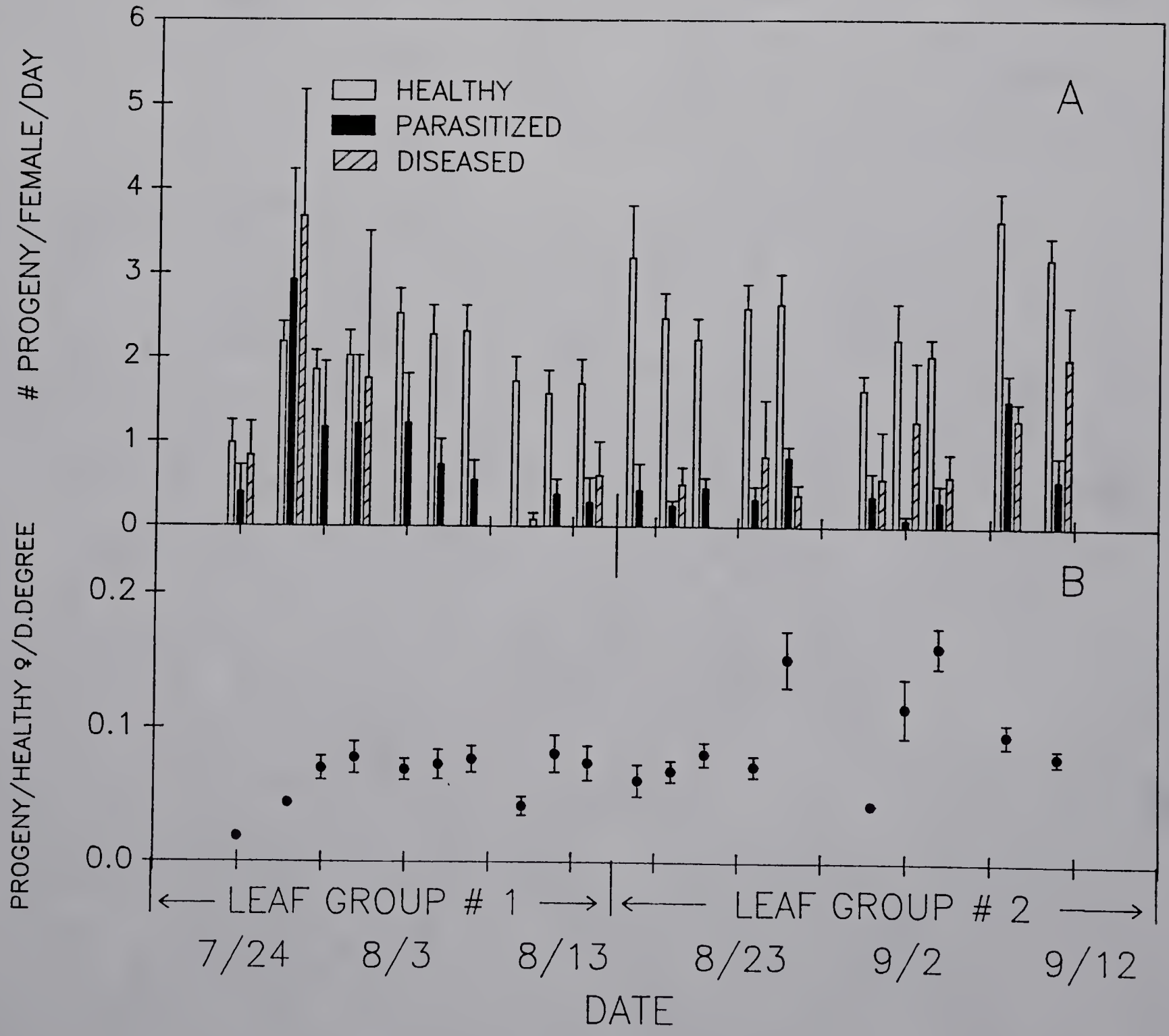

HEALTHY
PARASITIZED
DISEASED
A
B
PROGENY/FEMALE/DAY
PROGENY/HEALTHY ♀/D.DEGREE
6
5
4
3
2
1
0
0.2
0.1
0.0
← LEAF GROUP # 1 →
← LEAF GROUP # 2 →
7/24
8/3
8/13
8/23
9/2
9/12
DATE

FIG. 7. Daily attack rates of Diaeretiella rapae on second or third instar cabbage aphid nymphs exposed as trap-hosts in a collard field at South Deerfield, Massachusetts, 1987, for two leaf groups.

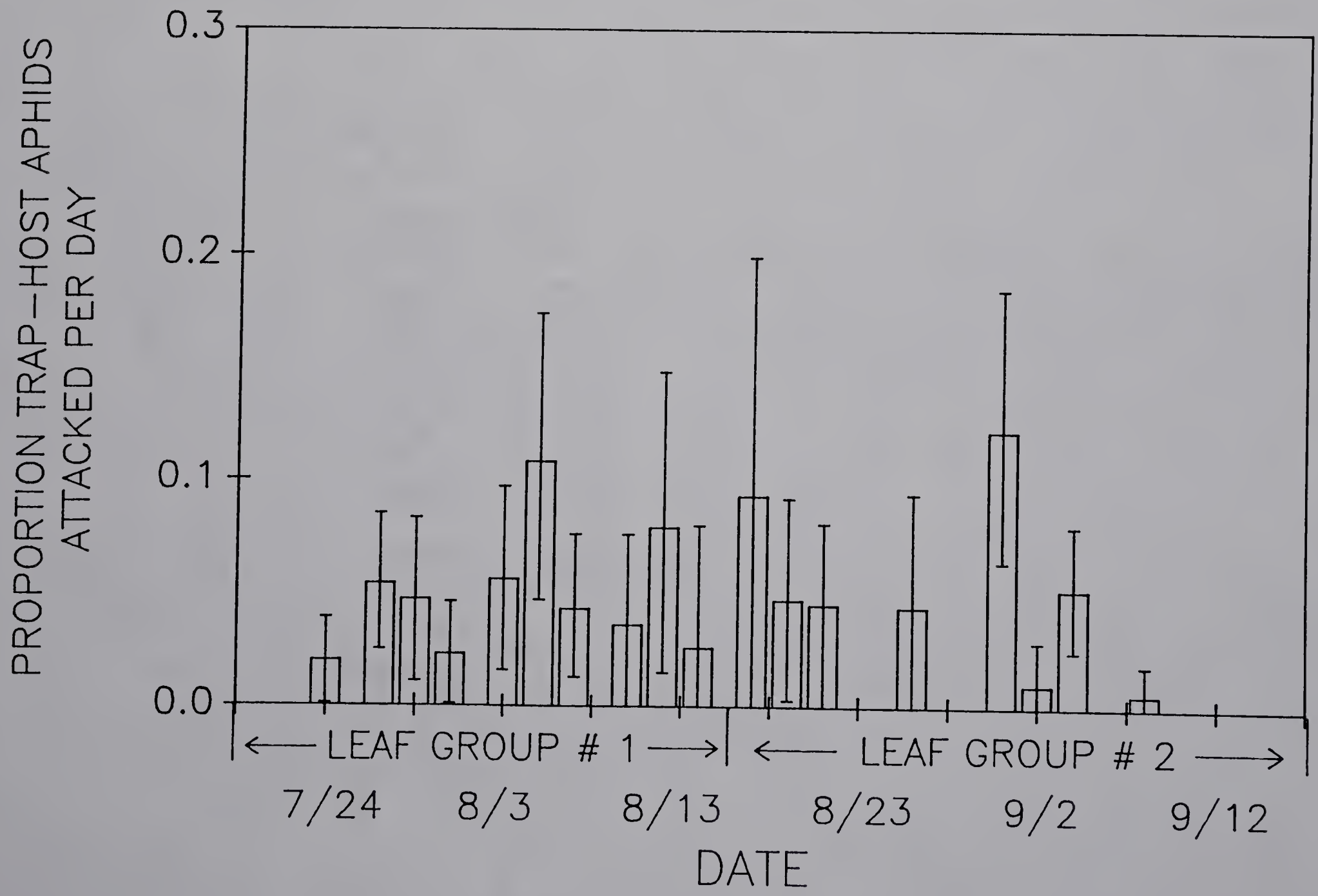

PROPORTION TRAP—HOST APHIDS
ATTACKED PER DAY
0.3
0.2
0.1
0.0
← LEAF GROUP # 1 →
← LEAF GROUP # 2 →
7/24
8/3
8/13
8/23
9/2
9/12
DATE

FIG 8. (A) Daily recruitment per leaf of a cabbage aphid population on collards at South Deerfield, Massachusetts, 1987, and (B), of its parasitoid, Diaeretiella rapae, measured by both the trap-host method (#1) and the marker-stage method (#2). (Error bars are S.E.M.).

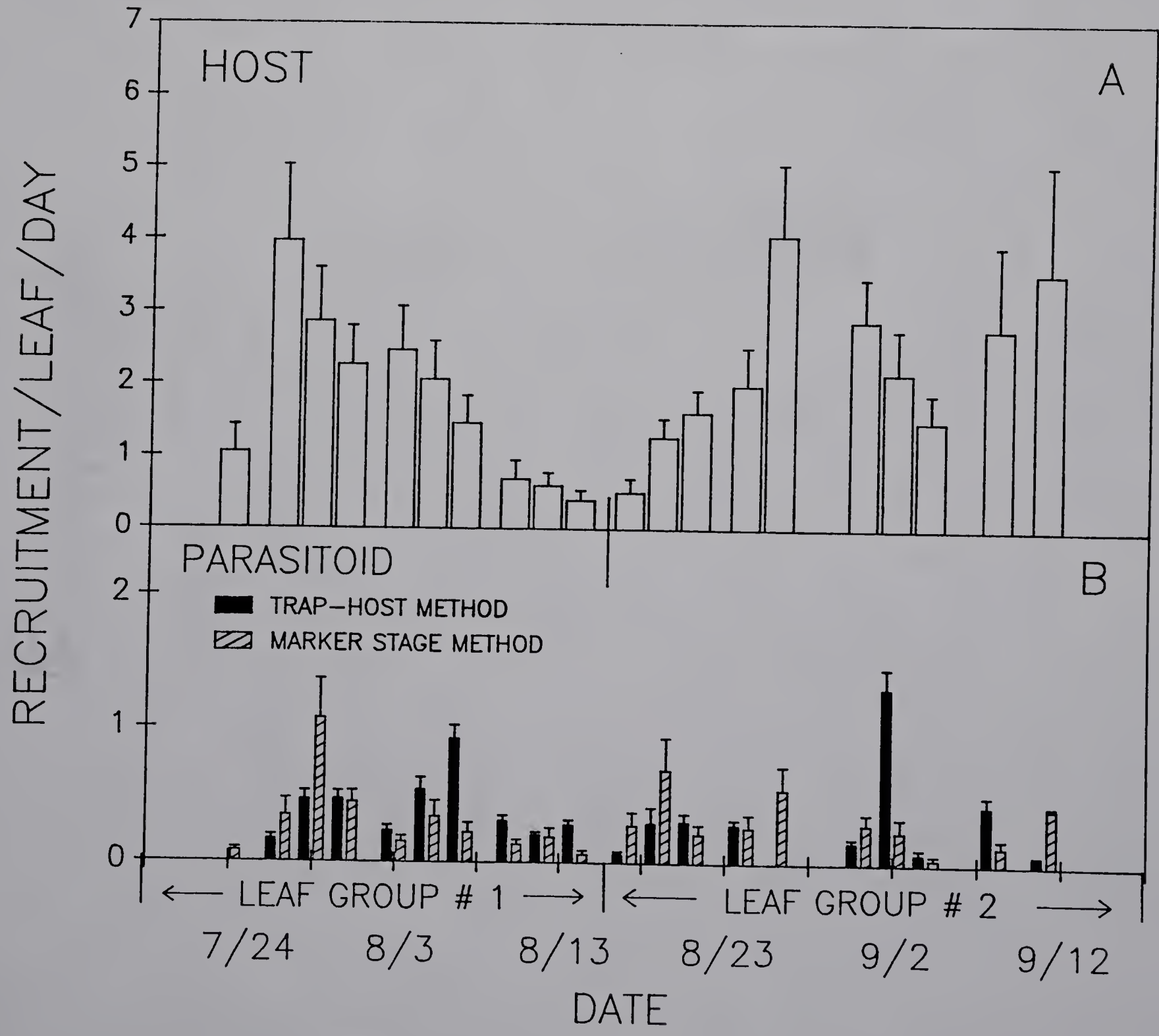

RECRUITMENT/LEAF/DAY
HOST
A
PARASITOID
B
TRAP–HOST METHOD
MARKER STAGE METHOD
0
1
2
3
4
5
6
7
← LEAF GROUP # 1 →
← LEAF GROUP # 2 →
7/24
8/3
8/13
8/23
9/2
9/12
DATE

Table 2. Distribution of cabbage aphids by size and spatial pattern categories for all samples summed within leaf groups at South Deerfield, Massachusetts, 1987.

	Leaf Group #1 (7/21 to 8/14)		Leaf Group #2 (8/16 to 9/11)	
	#	%	#	%
ISOLATED				
SMALL	305	7.86	135	3.25
MEDIUM	929	23.96	1082	26.07
LARGE	107	2.76	124	2.99
TOTAL	1341	34.58	1341	32.31
COLONIES				
SMALL	1115	28.75	856	20.63
MEDIUM	1146	29.55	1620	39.04
LARGE	276	7.12	333	8.02
TOTAL	2537	65.42	2809	67.69
GRAND TOTAL	3878	100	4150	100

Table 3. Percentage parasitism of live cabbage aphids (not including mummies) divided by spatial characteristics of aphids and aphid life stage

	Leaf Group #1 (7/21 to 8/14)		Leaf Group #2 (8/16 to 9/11)	
	%	SEM	%	SEM
ISOLATED				
SMALL	20.32	2.69	28.13	4.48
MEDIUM	33.30	2.06	46.46	2.20
ADULTS	27.59	4.79	37.62	5.00
TOTAL	29.28	1.58	42.24	1.83
COLONIES				
SMALL	4.63	1.05	6.38	1.27
MEDIUM	18.60	1.73	6.90	1.08
ADULTS	13.13	2.16	25.61	2.59
TOTAL	12.94	0.97	9.89	0.83
GRAND TOTAL	19.37	0.87	21.07	0.85
TOTALS BY SIZE				
SMALL	7.94	1.00	8.22	1.19
MEDIUM	26.52	1.39	23.87	1.14
ADULTS	19.43	2.12	29.43	2.29

Table 4. Percentage parasitism of cabbage aphids when live mummies are retained in samples at South Deeffield, Massachusetts, 1987

	Leaf Group #1 (7/21 to 8/14)		Leaf Group #2 (8/16 to 9/11)	
	%	SEM	%	SEM
ISOLATED	39.48	3.06	56.05	2.89
COLONIES	15.70	2.81	20.57	1.58
TOTAL	25.97	2.15	36.27	2.07

Table 5. Cabbage aphid recruitment per leaf group for aphids of different qualities at South Deerfield, Massachusetts, in 1987, in collards

	Leaf Group #1 (7/24 to 8/14)		Leaf Group #2 (8/14 to 9/11)	
TYPE OF APHID	$\bar{X}$	SEM	$\bar{X}$	SEM
HEALTHY	34.71	3.46	55.01	4.92
PARASITIZED	6.86	2.74	5.25	1.27
DISEASED	2.15	1.08	4.34	1.36
TOTALS	43.72	4.54	64.59	5.26

Table 6. Parasitoid recruitment (trap-host method) per leaf for cabbage aphids on collards at South Deerfield, Massachusetts, 1987, divided by leaf group and aphid age class

	Leaf Group #1 (7/21 to 8/14)		Leaf Group #2 (8/16 to 9/11)	
	$\bar{X}$	SEM	$\bar{X}$	SEM
ISOLATED				
SMALL	0.63	0.06	0.89	0.08
MEDIUM	1.51	0.12	2.92	0.19
ADULT	0.10	0.01	0.17	0.02
TOTAL	2.24	0.13	3.98	0.21
COLONIES				
SMALL	3.21	0.31	5.18	0.43
MEDIUM	2.30	0.21	5.82	0.45
ADULT	0.40	0.01	0.80	0.02
TOTAL	5.88	0.37	11.80	0.63
GRAND TOTAL	8.12	0.39	15.78	0.66

Table 7. Parasitoid recruitment (marker-stage method) per leaf for cabbage aphids on collards at South Deerfield, Massachusetts, 1987, divided by leaf group and aphid age class

	Leaf Group #1 (7/21 to 8/14)			Leaf Group #2 (8/16 to 9/11)		
	$\bar{X}$	SEM	%	$\bar{X}$	SEM	%
ISOLATED						
SMALL	1.30	0.31	19.18	0.79	0.20	9.63
MEDIUM	2.10	0.50	30.88	2.76	0.46	33.71
ADULTS	0.07	0.05	1.09	0.12	0.05	1.47
TOTAL	3.47	0.60	51.15	3.65	0.51	44.22
COLONIES						
SMALL	1.64	0.49	24.1	1.92	0.52	23.44
MEDIUM	1.50	0.40	22.00	2.20	0.60	26.92
ADULTS	0.19	0.08	1.16	0.41	0.22	5.02
TOTAL	3.33	0.63	48.99	4.53	0.82	55.45
GRAND TOTAL	6.796	0.86	100	8.17	0.96	100

Table 8. Total host and parasitoid recruitment[1] for each leaf group at a collard field in South Deerfield, Massachusetts, 1987

	Leaf Group #1 (7/21 to 8/14)		Leaf Group #2 (8/16 to 9/11)	
	Total Recruit.	SEM	Total Recruit.	SEM
APHID	43.72	4.54	64.59	5.26
PARASITOID				
-Trap Host Method	8.12	0.39	15.78	0.66
-Marker Stage Method	6.80	0.86	8.17	0.96
Total % Parasitism	%	SEM	%	SEM
-Using Trap Host Method	18.57	1.96	24.43	2.60
-Using Marker Stage Method	15.55	1.79	12.65	1.87

[1]Parasitoid recruitment calculated by each of two independent methods

Birth rates of caged adult aphids drawn on each sample date from the field population ranged from 0.98 to 3.63 progeny per female per day for healthy adults, 0.00 to 2.92 for parasitized adults and 0.00 to 3.67 for diseased aphids (Fig. 6A). For healthy aphids, the birth rate per degree-day was constant for the first leaf group but was more variable in the second leaf group (Fig. 6B).

Daily parasite attack rates (as proportions) on second and third instar aphid nymphs exposed as trap-hosts under field conditions ranged from 0.02 to 0.11 for the first leaf group and from 0.00 to 0.12 for the second leaf group (Fig. 7).

Total aphids recruited to the population per leaf per day ranged from 0.40 to 3.97 for the first leaf group and from 0.51 to 3.53 for the second group (Fig. 8A). Healthy aphids accounted for 79.39% of the total recruitment for the first leaf group and 85.17% for the second leaf group (Table 5). Parasitized aphids contributed modestly to the total recruitment (15.69% for the first leaf group and 8.13% for the second leaf group), whereas only low levels of recruiment were from diseased adults (Table 5).

Parasitoid recruitment differed as measured by the trap- host and short marker-stage method, with higher levels estimated by the trap-host method (Tables 6,7). Isolated aphids received a disproportionately higher percentage of parasitoid recruitment (as seen in the marker-stage method) than their percentage in pooled samples (51% of recruitment vs. 35% of aphids for the first leaf group and 44% of recruitment vs. 32% of aphids for the second leaf group). Aphids in colonies, in contrast, experience disproportionately lower parasitoid recruitment compared to their frequency in pooled sample

counts (49% of recruitment vs. 65% of aphids for the first group and 55% of recruitment vs. 68% of aphids in the second leaf group) (Tables 2,7).

Seasonal trends in host and parasitoid recruitment showed a non-continuous pattern in the first leaf group. In the second leaf group, the pattern was more erratic (Fig. 8). Summed across leaf group lifetimes, levels of parasitoid and host recruitment indicated 15.55 - 18.57% losses by aphids cohorts to parasitoids for the first leaf group and 12.65 - 24.43% for the second, depending on which measure of parasitoid recruitment was used (Table 8).

D. Discussion

Observations of disproportionately higher parasitoid recruitment in isolated versus colony aphids was consistent with both higher levels of parasitism seen on isolated aphids in field samples and the higher attack rates in laboratory aphids exposed in the field for short intervals on potted collard plants (Lopez et al. 1988). Direct observation of disproportionate recruitment into isolated aphids as a class makes it reasonably certain that the higher levels of parasitism of isolated aphids in field samples are due to higher parasitoid attack rates on aphids that have already become isolated, and not, as might be postulated, due to selective movement of parasitized aphids away from colonies after being parasitized.

Parasitoid recruitment levels in adult aphids were lower than would have been expected in view of adult aphid abundance as a percentage of total aphids, especially for the first group of leaves in which adults constituted 10% of all aphids but received only 2% of all parasitoid attacks. This supports the idea that adult aphids are

not a "preferred" host stage for this parasitoid (Hafez 1961, Klingauf and Sengonca 1970, Bahana and Karuhize 1986). This may reflect either non-preference on the part of the parasitoid or more effective defensive mechanisms (kicking, rotational movements, etc.) by this larger life stage.

In spite of initial expectations to the contrary, birth rates of healthy aphids per day-degree across the season did not suggest any decline in plant quality as leaves within study groups aged. This implies that the decline in over all host recruitment at the population level was likely due to factors affecting aphid densities, either higher mortality or higher emigration rates. The later is not a likely explanation as densities observed in this study were always low (4-8 aphids per leaf).

The marker-stage method to measure parasitoid recruitment seems a better choice than the trap-host method for aphid systems because parasitoid recruitment events could be directly observed and hence could be reliably associated with the type of aphids in which they occurred, which was not true for the trap-host method. Also, the marker-stage method was not affected by parasitoid host instar or host spatial pattern preferences.

We conclude that the recruitment method for assessing total lossess to parasitoids, can be succesfully applied to insects with aphid-type life histories. The observed total losses in B. brassicae from D. rapae parasitism were modest (12-25%) supporting the generally held view that D. rapae has only limited effectiveness in controlling population growth of B. brassicae in the field.

BIBLIOGRAPHY

Ayal, Y. (1987). The foraging strategy of Diaeretiella rapae. I. The concept of the elementary unit of foraging. J. An. Ecol., 56,1057-1068.

Bahana, J. & Karuhize, G. (1986). The role of Diaeretiella rapae (McIntosh) (Hymenoptera:Braconidae) in the population control of cabbage aphid, Brevicoryne brassicae L. Hemiptera:aphididae) in Kenya. Insect Sc. Applic. 7, 605-609.

El Titi, A. (1972/73). Einfl sse von Beutedichte und Morphologie del Wirtspflanze auf die Eiablageuvon Aphydoletes aphidimyza (Rond.) (Diptera: Itonididae). Zeit. fur Ange. Ent., 72, 400-415.

El Titi, A. (1974a). Auswirkung von der rauberischen Gallmucke Aphidoletes aphidimyza (Rond.) (Itonididae: Diptera) auf Blattlauspopulatione unter Glas. Zeit. fur Ange. Ent., 76,406-417.

El Titi, A. (1974b). Zur Auslsung der Eiablage bei der aphidophagen Gallmucke Aphidoletes aphidimyza (Rond.) (Diptera: Cecidomyiidae). Ent. Exp. et Appl., 17, 9-21.

Griffiths, K.J. & Lyons, L.A. (1980). Further releases of Lophyroplectus luteator (Hymenoptera: Ichneumonidae), an introduced parasite of Neodiprion sertifer (Hymenoptera: Diprionidae). Can. Ent., 112, 421-26.

Hafez, M. (1961). Seasonal fluctuations of the population density of the cabbage aphid, Brevicoryne brassicae L. in the Netherlands, and the role of its parasite Aphidius (Diaeretiella) rapae (McIntosh). Tijdschr. PlZiekr. 67, 445-548.

Jones, T.H. & Turner, B.D. (1987). The effect of host spatial distribution on patterns of parasitism by Nasonia vitripennis. Ent. Exp. et Appl., 44, 169-175.

Klingauf, F. & Sengonca, C. (1970). Koloniebildung von Rohrenblattlausen (Aphididae) unter Feindeinwirkung. Entomophaga, 15, 359-377.

Lamb, K. P. & White, D. (1966). Effect of temperature , starvation and crowding on production of alate young by the cabbage aphid (Brevicoryne brassicae). Ent. Exp. et Appl., 9,179-184.

Lees, A.D. (1967). The production of the apterous and alate forms in the aphid Megoura viciae Buckton, with special reference to the role of crowding. J.Insect Physiol., 13,289-318

LeCato, G. L. & Pienkowski, R. L. (1972). Fecundity, egg fertility, duration of oviposition, and longevity of alfalfa weevils from eight matings and storage conditions. An. Ent. Soc. Am., 65,319-23.

Lints, F. A. & Lints, C. V.(1969). Respiration in Drosophila. III. Influence of pre-imaginal environment on respiration and aging in Drosophila melanogaster hybrids. Exp. Geront., 4,81-94.

Lockwood, J.A. & Story, R.N. (1986). Adaptive functions of nymphal aggregation in the southern green stink bug, Nezara viridula (L) (Hemiptera: Pentatomidae). Env. Ent., 15, 739-749.

Lopez, E.R., Van Driesche, R.G. & Elkinton, J.S. (1988). Relation of colony formation as a life history trait to fitness in the cabbage aphid, Brevicoryne brassicae L. (in preparation)

Morrison, G.M.& Strong,Jr. D. R. (1980). Spatial variations in host density and the intensity of parasitism: some empirical examples. Env. Ent., 9, 149-52.

Osborn, A. W., Shipp , E. & Rodger, J. C. (1970). House fly fecundity in relation to density. J. Ec. Ent., 63,1020-21.

Smith, D. S. (1970). Crowding in grasshoppers. I. Effect of crowding withing one generation on Melanoplus sanguinipes. An. Ent. Soc. Am., 63,1775-76.

Spencer, H. (1926). Biology of the parasites and hyperparasites of aphids. An. Ent. Soc. Am. 19, 119-157.

Sutherland, O. R. W. (1969). The role of crowding in the production of winged forms by two strains of the pea aphid, Acyrtosiphon pisum. J. of Insect Physiol, 15,1385-1410.

Tostowaryk, W. (1972). The effect of prey defense on the functional response of Podisus modestus (Hemiptera: Pentatomidae) to densities of sawflies Neodiprion swainei and N. pratti banksianae (Hymenoptera: Neodiprionidae). Canadian Ent., 104, 61-69.

Van Driesche, R. G. 1983. The meaning of "percentage parasitism" in studies of insect parasitoids. Environ. Entomol. 12, 1611-1622.

Van Driesche, R.G. & T.S. Bellows. (1988). Host and parasitoid recruitment for quantifying losses from parasitism, with reference to Pieris rapae and Cotesia glomeratus. Ecol. Ent. (in press).

Wharton, D. R. A., Lola, J.E. & Wharton, M. L. (1968). Growth factors and population density in the American cockroach, Periplaneta americana. J.of Insect Physiol., 14,637-53.

Way, M. J. & Cammell, M.E. (1970). Aggregation behaviour in relation to food utilization by aphids. In: Animal Populations in Relation to Their Food Resources, ed. A. Watson, Brit. Ecol. Soc. Symp.N°10, 229-47.

Xu, R. M. (1983). Density effect on fecundity and mortality on greenhouse whitefly populations. Bulletin SROP, 6, 101-107.