

## DISPERSION ANALYSES AND RESOURCE UTILIZATION OF APHID PARASITOIDS IN A NON-DEPLETABLE ENVIRONMENT

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### INTRODUCTION

Resource utilization by parasitoids is affected by the spatial dispersion patterns of both the host and the parasitoid (CHEKE, 1974; MONRO, 1967; MYERS, 1978). Overdispersed populations which deplete most or all of the available resources may suffer serious reductions in subsequent generations (BIRCH, 1971). In addition, the stability of parasitoid/prey/plant systems can be influenced by the spatial distribution of each component (MURDOCH and OATEN, 1974); HASSELL and MAY (1974) have suggested that stability decreases as randomness of prey increases. Our study was designed to examine the resource utilization of parasitoids in a system where host dispersion varies with time.

Unfortunately, many of the commonly used dispersion indices have questionable value for explaining biological events or are influenced by insect density. IWAO (1970) reported that some theoretical models of dispersion, including Poisson, negative binomial, and Neyman Type A, may be fitted to the same count data depending on the frequency classes chosen or the method of fitting the model. MYERS (1978) determined that a density dependent relationship existed between some indices of dispersion and mean insect density, resulting in publication of statistical artifacts as opposed to biologically significant effects. Of the indices tested, only GREEN's coefficient of dispersion,  $C_x$ , the standardized MORISITA's coefficient,  $I_p$ , and the variance/mean ratio,  $s^2/\bar{x}$ , were not seriously affected by density. LLOYD's patchiness index was found to be correlated with density; increasing density led to increasing randomness. Although the regression of mean crowding on the mean suggested by IWAO (1968) and IWAO and KUNO (1971) was not included in MYER's (1978) analysis, this technique has proven effective in both theoretical and empirical situations, and was considered valid by MYERS. An additional objective of our study was to compare the dispersions generated by selected indices, and relate these to the field biology of the naturally occurring aphid-parasitoid community.

In strawberry (*Fragaria chiloensis* (L.)) fields, temporal variations in the spatial dispersion patterns of aphids result in an interesting system which is suitable for investigating the utilization of resources by parasitoids. High aphid reproduction rates and low levels of parasitism (<6%) during peak aphid populations provide primary

parasites with an essentially unlimited host resource. Also, since changes in aphid density per plant are not related to changes in aphid dispersion patterns (TRUMBLE et al., 1983), dispersion indices of parasitoids can be contrasted with fluctuations in either host density or host dispersion.

#### METHODS

Individual plants were used as the primary sampling unit throughout this study. Since each strawberry field was basically a continuum, the "natural habitat unit" for sampling described by PATIL and STITELER (1974) was clearly an individual plant. Selection of individual plants as the sampling unit also agreed with the "unit area" concept of HASSELL and MAY (1974), which specifies that samples should not be collected from areas either so large that a single predator could not exploit several units during its lifetime, or so small that only a portion of a natural clump of prey is present.

Our studies were conducted in winter plantings of "Tufts" strawberries in Orange County, California, which consisted of 15 and 12 double-row beds of plants during 1981 and 1982, respectively. Each bed contained 23 sub-beds with 17 plants per sub-bed. Both plantings were drip irrigated and mulched with transparent plastic. In 1981, weekly counts of parasitized aphids were made from 144 plants selected with a stratified-random sampling design from 15 January to 28 May, except on 21 May when no data were collected. In 1982, counts were recorded from 118 plants per week selected in a similar fashion from 12 January until 2 March, and then parasitized aphids on 72 plants per week were counted from 9 March through 11 May. No data were collected on 16 March or 3 May.

Relative abundances, spatial dispersion and within-plant distributions of the aphid species present during this study were previously reported (TRUMBLE et al., 1983). Due to difficulty in determining the identity of the hosts of both primary parasitoids and hyperparasitoids in the field, count data for parasitized aphids were analyzed as a system, rather than considered for each species individually. Similar analyses were used by KRING and GILSTRAP (1983). In order to document the parasitoid species involved in the system, voucher specimens were collected weekly, reared in the laboratory, and subsequently identified.

Counts of parasitized aphids were analyzed with a variety of dispersion indices. GREEN's coefficient (GREEN, 1966),  $C_x$ , was calculated separately for each week's data using the formula:

$$\frac{[s^2/m]-1}{\Sigma x-1}$$

where  $m$ =mean number of parasitized aphids per plant,  $s^2$ =variance, and  $\Sigma x$ =total number of parasitized aphids observed each week.

LLOYD's patchiness index,  $m^*/m$ , was determined by solving LLOYD's (1967) formu-

la for  $\bar{m}^*$ , where  $\bar{m}^* = m + (\sigma^2/m - 1)$ , and substituting the  $s^2$  and  $\bar{x}$  from our field counts. This value was then divided by the mean number of parasitized aphids per sample date, providing  $\bar{m}^*/m$  values for each week samples that were collected.

Spatial dispersions calculated by the regression method proposed by IWAO (1968) and IWAO and KUNO (1971) were generated by solving the formula:  $\bar{m}^* = \alpha + \beta m$ , where  $\alpha$ , which is estimated by  $a$ , is the intercept on the ordinate, and  $\beta$ , which is estimated by  $b$ , is the slope of the regression line formed when  $\bar{m}^*$  was regressed on the mean. The  $\bar{m}^*$  value was calculated as described previously for LLOYD's patchiness index. Students  $t$ -tests were used to test the hypotheses that  $a=0$  or  $b=1$ . The Proc GLM procedure of Statistical Analysis Systems (SAS) (HELWIG and COUNCIL, 1979) was used to generate the regression lines. Comparisons between slopes of temporally stratified populations were made using  $t$ -tests.

The parameters  $a$  and  $b$  of Taylor's Power Law (TAYLOR, 1965),  $s^2 = am^b$ , were estimated from the regression equation:  $\log(s^2) = \log(a) + (b) \log(m)$ , where  $a$  and  $b$  = the intercept and regression coefficient, respectively. Regression lines and related parameters were ascertained using the Proc GLM procedure of SAS.

## RESULTS

Four aphid species, four species of primary parasites and seven species of hyperparasitoids were present during this study (Table 1). *Chaetosiphon fragaefolii* (COCKERELL) was the dominant aphid (>60%), but early season populations of *Aphis gossypii* GLOVER were as large or larger. *Lysiphlebus testaceipes* CRESSON was the most common primary parasitoid, and *Dendrocerus aphidum* (RONDANI)

Table 1. Species of aphids, primary parasites and hyperparasites collected from strawberry plantings in Orange County, California, during 1981 and 1982.

Aphid species	Primary parasitoid species <sup>1)</sup>	Hyperparasitoid species
A. <i>Chaetosiphon fragaefolii</i> (COCKERELL)	<i>Lysiphlebus testaceipes</i> CRESSON [A, B, C]	<i>Dendrocerus aphidum</i> (RONDANI) [A, B, C, D]
B. <i>Aphis gossypii</i> GLOVER	<i>Aphelinus semiflavus</i> HOWARD [A, B, C, D]	<i>Alloxysta megourae</i> "complex" [B]
C. <i>Macrosiphum euphorbiae</i> (THOMAS)	<i>Aphidius urticae</i> HALIDAY [C, D]	<i>Asaphes californicus</i> GIRAULT [A, B]
D. <i>Myzus persicae</i> (SULZER)	<i>Ephedrus californicus</i> BAKER [C, D]	<i>Aphidencyrus aphidivorus</i> (MAYER) [A, B, C] <i>Phaenoglyphis americana</i> BAKER [A, B] <i>Pachyneuron siphonophora</i> (ASHMEAD) [A, B] <i>Alloxysta schlingeri</i> ANDREWS [A, B]

<sup>1)</sup> Letters in brackets refer to the aphid species from which primary parasitoids and hyperparasitoids emerged.

Table 2. Temporal variation in the occurrence and spatial dispersion patterns of parasitized aphids in strawberries during 1981 as measured by GREEN's coefficient,  $C_x$ , and LLOYD's Patchiness Index,  $m^*/m$ .<sup>1)</sup>

Date	$\bar{x} \pm$ s. e. parasitized aphids/plant	$C_x$ aphids <sup>2)</sup>	$C_x$ parasitized aphids	Patchiness index $m^*/m$
15 Jan.	0	0.53	— <sup>3)</sup>	—
22 Jan.	0	0.29	—	—
29 Jan.	0	0.14	—	—
5 Feb.	0	0.21	—	—
12 Feb.	0	0.12	—	—
19 Feb.	0.01 ± 0.01	0.12	—	—
26 Feb.	0.02 ± 0.01	0.13	0.33	32.33
6 Mar.	0.03 ± 0.01	0.07	0.16	16.67
12 Mar.	0.25 ± 0.07	0.03	0.05	8.52
19 Mar.	0.09 ± 0.03	0.01	0.01	1.77
26 Mar.	0.17 ± 0.05	0.02	0.04	6.05
2 Apr.	0.67 ± 0.15	0.03	0.04	6.60
9 Apr.	0.20 ± 0.05	0.02	0.03	5.21
16 Apr.	0.16 ± 0.05	0.01	0.04	6.60
23 Apr.	0.24 ± 0.05	0.01	0.01	2.37
30 Apr.	0.18 ± 0.04	0.02	0.02	3.88
7 May	0.12 ± 0.04	0.01	0.07	10.08
14 May	0.08 ± 0.03	0.01	0.07	9.67
21 May	—	—	—	—
28 May	0.08 ± 0.03	0.01	0.03	4.87

<sup>1)</sup> Data from winter planting in Orange Co., California; 144 plants sampled/week.

<sup>2)</sup> After TRUMBLE et al. (1983).

<sup>3)</sup> Value cannot be calculated or data unavailable.

was the predominant hyperparasitoid.

Counts of parasitized aphids per plant, sampling dates, GREEN's coefficient ( $C_x$ ) and LLOYD's patchiness index ( $m^*/m$ ) have been listed in Tables 2 and 3 for 1981 and 1982, respectively. GREEN's coefficient and LLOYD's patchiness index showed changes in spatial dispersion with time, and both indices generated similar results. GREEN (1966) considered populations to be overdispersed when  $C_x=1$ , while  $C_x$  values of 0 indicated random distributions. LLOYD (1967) stated that a patchiness index of 1 was indicative of a random population, and that the index increased with increasing aggregation. Thus, both indices agreed that parasitoids were highly aggregated initially, but became less aggregated with time. Since the density of parasitized aphids declined to early season levels following peak populations in both years, yet corresponding changes in dispersion were not evident, MYER'S (1978) assertion that LLOYD's patchiness index was dependent on density could not be verified.

IWAO'S (1968) regression of mean crowding ( $m^*$ ) on the mean was not suitable for analyzing count data from populations in which dispersion changes with time. The regression line tends to "average" the data points and, as a result, short term

Table 3. Temporal variation in the occurrence and spatial dispersion patterns of parasitized aphids in strawberries during 1982 as measured by GREEN's coefficient,  $C_x$ , and LLOYD's Patchiness Index,  $m^*/m$ .<sup>1)</sup>

Date	$\bar{x} \pm$ s. e. parasitized aphids/plant	$C_x$ aphids <sup>2)</sup>	$C_x$ parasitized aphids	Patchiness index $(m^*/m)$
12 Jan.	0	0.25	— <sup>3)</sup>	—
19 Jan.	0	0.11	—	—
26 Jan.	0.02 ± 0.01	0.10	—	—
2 Feb.	0.06 ± 0.02	0.06	0.06	6.16
9 Feb.	0.17 ± 0.10	0.04	0.36	37.65
16 Feb.	0.07 ± 0.03	0.05	0.10	10.20
23 Feb.	0.56 ± 0.19	0.04	0.10	11.74
2 Mar.	1.70 ± 0.52	0.04	0.09	10.63
9 Mar.	7.35 ± 1.60	0.03	0.05	4.28
16 Mar.	—	—	—	—
23 Mar.	7.14 ± 0.98	0.02	0.02	2.21
30 Mar.	3.64 ± 0.50	0.01	0.02	2.14
6 Apr.	1.42 ± 0.23	0.01	0.02	2.27
13 Apr.	0.76 ± 0.12	0.01	0.01	1.07
20 Apr.	0.47 ± 0.09	0.12	0.01	1.28
27 Apr.	0.19 ± 0.06	0.06	0.04	3.79
4 May	—	—	—	—
11 May	0.01 ± 0.01	0.05	0.00	1.00

<sup>1)</sup> Data from winter planting in Orange Co., California; 118 plants sampled weekly until 2 Mar., and 72 plants/week thereafter.

<sup>2)</sup> After TRUMBLE et al. (1983).

<sup>3)</sup> Value cannot be calculated or data unavailable.

or initial dispersions, such as those reported by SHIYOMI and NAKAMURA (1964) or SYLVESTER and COX (1961) can be obscured by data from subsequent observations. However, this problem can be solved by temporally stratifying data (TRUMBLE, 1983), or by segmenting data into patterns suggested by other dispersion indices. The regression lines presented in Table 4 include data from counts stratified temporally into increasing and decreasing populations, as well as full season counts.

According to IWAO (1968), each regression line has two basic components which are related to the dispersion of populations. The intercept is the "index of basic contagion" ( $a$ ) which describes an individual as the basic unit of a population when  $a=0$ , or a group of individuals when  $a>0$ . The regression coefficient ( $b$ ) is the "density contagiousness coefficient," which distinguishes how the basic components of a population are distributed within their habitat; values of  $b$  greater than 1 indicate an aggregated population. All of the regression lines presented in Table 1 show values of  $a$  which are not significantly greater than 0, and values of  $b$  which are significantly greater than 1. Thus, regardless of the segmentation of the data, the basic distributional unit of our populations was the individual parasitized aphid, and these individuals were dispersed in an aggregated manner. However, a comparison of slopes

Table 4. Summary of data generated by Iwao's regression of  $\bar{m}^*$  on the mean for increasing, decreasing and entire season counts of parasitized aphids per plant in strawberries.

Population status	Regression line ( $a+bm$ )	$r^2$ value	$t$ values <sup>1)</sup>	
			$a=0$	$b>1$
1981				
Increasing	$-0.16 \pm 3.58m$	0.53	0.48 ns	4.30*
Decreasing	$-0.07 \pm 2.38m$	0.43	0.57 ns	3.02*
Full season	$-0.21 \pm 3.41m$	0.52	1.29 ns	6.32*
1982				
Increasing	$0.37 \pm 2.40m$	0.90	0.49 ns	10.18*
Decreasing	$0.54 \pm 1.28m$	0.93	1.82 ns	4.80*
Full season	$0.18 \pm 1.88m$	0.82	0.32 ns	8.39*

<sup>1)</sup> ns=not significant at the  $p<0.05$  level, \*=significant at the  $p<0.01$  level.

for increasing and decreasing populations in 1982 indicated that early season (increasing) populations were significantly more aggregated ( $p=0.01$ ,  $t=3.11$ ,  $df=32$ ). Lower densities in 1981 produced a similar, but less significant, trend ( $p=0.12$ ,  $t=1.63$ ,  $df=41$ ). Therefore, results analogous to those of  $C_x$  and  $\bar{m}^*/m$  were produced only when count data were stratified.

Analyses of counts using TAYLOR's Power Law (TAYLOR, 1967) generated results similar to those from IWAO's regression. When the power law,  $s^2=am^b$ , was illustrated as a regression in logarithms,  $\log(s^2)=\log(a)+(b)\log(m)$ , a regression coefficient or "index of aggregation" significantly greater than unity in both years suggested an aggregated population (Figs. 1 and 2). In spite of a greater than ten-fold difference in maximum density between 1981 and 1982, the regression coefficients remained remarkably similar, supporting TAYLOR's (1967) contention that the index of aggregation should remain constant for a species in a single environment. No comparisons were made for intercepts ( $a$  values), since, unlike IWAO' regression, the intercept for the power law varies with sampling method and population growth rate, and therefore is of no biological significance.

## DISCUSSION

The spatial distributions of parasitized aphids among clumps of hosts have some interesting implications for resource utilization by primary parasitoids. Aggregation of offspring has obvious advantages for adults, including reduced searching time, increased oviposition or capture rates, and a more efficient utilization of energy. Aspects of predator or parasitoid searching behavior which would lead to aggregated distributions have been discussed in detail (ROYAMA, 1970; HASSELL and MAY, 1974; EVANS, 1976). Thus, parasitoids in our system would be most efficient if they oviposited in all aphids within a clump or patch, and then proceeded to another

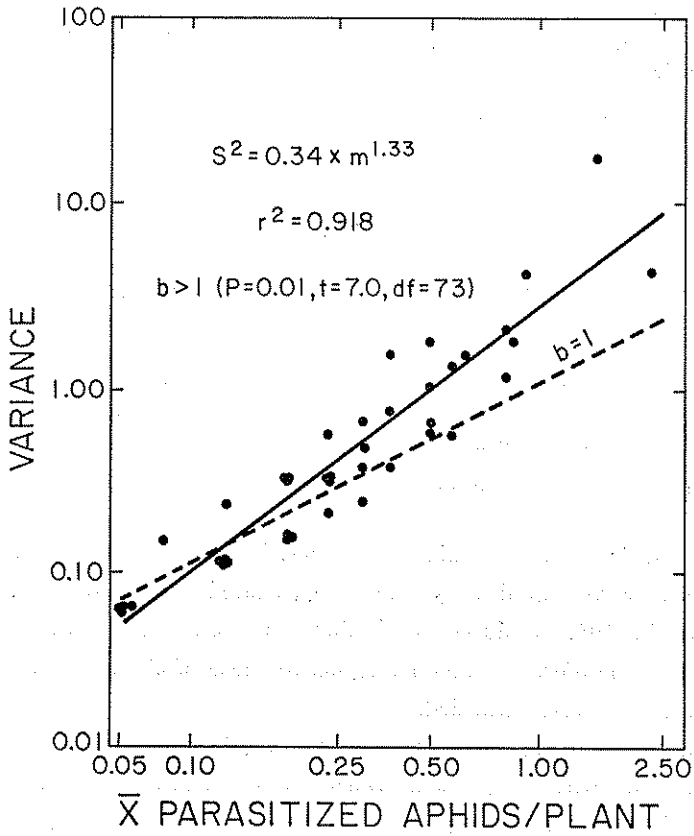


Fig. 1. TAYLOR's power law illustrated as a linear regression of  $\log(\text{variance}) \times \log(\text{mean})$  for counts of parasitized aphids per plant in 1981.

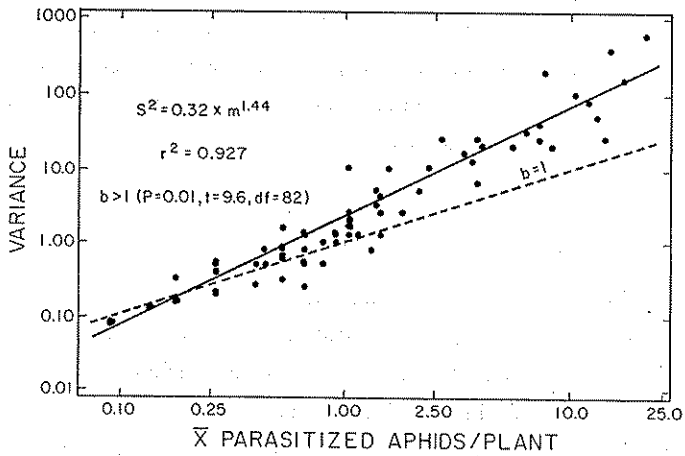


Fig. 2. TAYLOR's power law illustrated as a linear regression of  $\log(\text{variance}) \times \log(\text{mean})$  for counts of parasitized aphids per plant in 1982.

nearby colony to repeat the process. As populations of parasitized aphids were aggregated, our data substantiated a tendency of parasitoids to oviposit in adjoining host groups, but IWAO's regression indicated that an individual rather than a clump was the basic unit of the population. We believe that utilization of an individual as the basic unit of the population is an evolutionary response that has occurred in reaction to pressure from hyperparasitoids.

Clearly, oviposition of a few individuals within a host group, rather than oviposition in an entire host clump, would provide primary parasitoids with several avoidance or defense mechanisms which would require increased energy expenditure and evolutionary fitness by hyperparasitoids. Not only would hyperparasites be faced with the difficulty of locating an individual amongst a group (as discussed by WEIN (1976) for other predator-prey systems), but they also would need to adapt to defense mechanisms of aphids including sticky exudates (EDWARDS, 1966) and the mechanical and physical defenses listed by STARY (1970). If all aphid hosts in a clump were parasitized, hyperparasitoids would avoid these difficulties, and the primary parasitoids would risk losing a considerable number of progeny if the clump were discovered. Thus, oviposition of "individuals" in an aggregated fashion represents a "trade-off" for the primary parasitoids, with energy utilization, searching effectiveness and oviposition rate balanced against the potential losses associated with hyperparasitism. The initial aggregations in populations of parasitized aphids (Tables 1 and 2) could be explained, in part, by the highly aggregated host dispersions and by a tendency for parasites to oviposit more intensively in host groups when low host density and high host aggregation increased the probability of prolonged periods of unsuccessful searching.

#### SUMMARY

Dispersions and resource utilization of primary and secondary parasitoids developing in non-depletable primary host populations were determined for an aphid-parasitoid community occurring on strawberries. Analyses of dispersions based on GREEN's coefficient and LLOYD's Patchiness Index indicated parasitized aphids were highly aggregated initially, became less aggregated as density increased, and remained aggregated following collapse of the aphid populations. The "index of aggregation" values calculated using TAYLOR's Power Law concurred with results from the other indices, and the similarity of the regression coefficients from both seasons suggests that the index of aggregation may be characteristic for communities as well as species. Analysis with IWAO's regression of mean crowding on the mean generated similar results when population data were stratified temporally, and also indicated that the individual was the basic unit of the population.

In a non-depletable environment, oviposition of individuals exhibiting an aggregated dispersion pattern within clumps of hosts provides primary parasitoids with a



suitable trade-off between energy utilization or genetic potential, and losses associated with hyperparasitism.

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#### REFERENCES

- BIRCH, L. C. (1970) The role of environmental heterogeneity and genetical heterogeneity in determining distribution and abundance. 190-123. In P. J. den BOER and G. R. GRADWELL (eds.) *Dynamics of populations*. Proceedings of the Advanced Study Institute on "Dynamics of numbers in populations." Wageningen: Centre for Agricultural Publishing and Documentation.
- CHEKE, R. A. (1974) Experiments on the effect of host spatial distribution on the numerical response of parasitoids. *J. Anim. Ecol.* 43: 107-114.
- EDWARDS, J. S. (1966) Defense by smear: supercooling in the cornicle wax of aphids. *Nature* 211: 73-74.
- EVANS, H. F. (1976) The searching behavior of *Anthocoris confusus* (REUTER) in relation to prey density and plant surface topography. *Ecol. Entomol.* 1: 163-169.
- GREEN, R. H. (1966) Measurement of nonrandomness in spatial distributions. *Res. Popul. Ecol.* 8: 1-7.
- HASSELL, M. P. and R. M. MAY (1974) Aggregation of predators and insect parasites and its effect on stability. *J. Anim. Ecol.* 43: 567-594.
- HELVIG, J. T. and K. A. COUNCIL (eds.) (1979) *SAS User's Guide, 1979 ed.* SAS Institute Inc., Cary, North Carolina. 494 pp.
- IWAO, S. (1968) A new regression method for analyzing the aggregation pattern of animal populations. *Res. Popul. Ecol.* 10: 1-20.
- IWAO, S. (1970) Problems of spatial distribution in animal population ecology. 117-149. In G. P. PATIL (ed.) *Random counts in scientific work*, Vol. 2. The Pennsylvania State University Press, University Park, Pennsylvania.
- IWAO, S. and E. KUNO (1971) An approach to the analysis of aggregation pattern in biological populations. 461-513. In G. PATIL, E. PIELOU and E. WATERS (eds.) *Statistical Ecology*, Vol. 1. The Pennsylvania State University Press, University Park, Pennsylvania.
- KRING, T. J. and F. E. GILSTRAP (1983) Within-field distribution of green-bug (Homoptera: Aphididae) and its parasitoids in Texas winter wheat. *J. Econ. Entomol.* 76: 57-62.
- LLOYD, M. (1967) Mean crowding. *J. Anim. Ecol.* 36: 1-30.
- MYERS, J. H. (1978) Selecting a measure of dispersion. *Environ. Entomol.* 7: 619-621.
- MONRO, J. (1967) The exploitation and conservation of resources by populations of insects. *J. Anim. Ecol.* 36: 531-547.
- MURDOCH, W. W. and A. OATEN (1975) Predation and population stability. *Adv. Ecol. Res.* 9: 1-125.
- PATIL, G. P. and W. M. STITELER (1974) Concepts of aggregation and their quantification: a critical review with some new results and applications. *Res. Popul. Ecol.* 15: 238-254.

- ROYAMA, T. (1970) Evolutionary significance of predator's response to local differences in prey density: A theoretical study. 344-357. In P. J. den BOER and G. R. GRADWELL (eds.) *Dynamics of populations*. Proceedings of the Advanced Study Institute on "Dynamics of numbers in populations." Wageningen: Centre for Agricultural Publishing and Documentation.
- SHIYOMI, M. and K. NAKAMURA (1964) Experimental studies on the distribution of aphid counts. *Res. Popul. Ecol.* 6: 79-87.
- STARY, P. (1970) *Biology of aphid parasites*. Series Entomologica, Vol. 6. Dr. D. W. JUNK, The Hague, 643 pp.
- SYLVESTER, E. S. and E. L. COX (1961) Sequential plans for sampling aphids on sugar beets in Kern County, California. *J. Econ. Entomol.* 54: 1080-1085.
- TAYLOR, L. R. (1965) A natural law for the spatial distribution of insects. *Proc. XII Internat. Cong. Entomol.* 12: 396-397.
- TRUMBLE, J. T., E. R. OATMAN and V. VOTH (1983) Temporal variation in the spatial dispersion patterns of aphids (Homoptera: Aphididae) infesting strawberries. *Environ. Entomol.* 12: 595-598.
- WIENS, J. A. (1976) Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7: 81-120.

資源が十分にある条件下におけるアブラムシの寄生蜂の  
分布解析と資源利用パターン

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イチゴに発生するアブラムシとそれらの寄生蜂との相互作用系において、一次及び二次寄生蜂の空間分布および資源利用について調べた。GREEN の示数および LLOYD の集中度示数に基づいて分布解析を行うと、寄生を受けたアブラムシの分布は最初きわめて集中していたが、密度が増えるにつれて集中度が低くなった。TAYLOR の示数を用いても同様な傾向がみられ、密度が著しく異なった2年間の調査での回帰係数は同様な値を示した。IWAO の  $m^*$ - $m$  解析でも、データを時間的に小分けして解析すると同様な結果が得られ、個体が分布の基本単位であることが示された。

資源(寄主)が十分にあるとき、一次寄生蜂が寄主のコロニーの中で集中的なパターンに従って産卵する性質はエネルギー効率の点では不利だが、二次寄生回避の面からは有利であろう。