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Density-Dependent Parasitism of *Delphacodes kuscheli* Eggs by *Anagrus flaveolus*: Influence of Egg Patchiness and Density

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Many herbivorous insects display a marked tendency to aggregate and previous work has shown that the parasitoids likely to be more effective for pest control programs are those that concentrate their attacks on denser host patches. However, as herbivore density changes different spatial patterns usually emerge in their distribution. In Tucumán province, Argentina the mymarid Anagrus flaveolus *is a native egg parasitoid of* Delphacodes kuscheli, *which oviposits endophitic eggs and is the only demonstrated vector of the MRCV virus that seriously affects maize (*Zea mays*). Winter is the critical period for maize colonization from oat (*Avena sativa*) crops where* D. kuscheli *overwinters. We analyzed, under field conditions and during the winter critical period, percentage parasitism by* A. flaveolus *when host patch density increases following two different patterns: an increase in the batch size, and an increase in the number of infested plants with similar mean batch size. In order to generate a heterogeneous egg patchiness, 144 oat plants were arranged in 36 groups of four plants each, and four types of groups were created by placing one, two, three or four infested plants per group. Each group was characterized by the number of infested plants as well as by the number of eggs. If one, two, three or all four plants were infested, the group was denominated G1, G2, G3 or G4, respectively. Considering only G1, the number of eggs per group increased only if the batch size increased. On the other hand, considering all G1, G2, G3 and G4 groups, the increase in patch density from G1 to G4, was essentially due to an increase in the number of infested plants. The groups were symmetrically distributed in the field in a homogeneous 200-m² area (the position of each group was randomly assigned), and allowed for oviposition for 48 h since* A. flaveolus *only attacks eggs that have three or less days of development. We found that almost all infected plants were parasitized by* A. flaveolus *but parasitism never surpassed 64% of the available eggs, suggesting that the parasitoid selectively attacks eggs inserted in particular places of the oat plant, and/or never saturates a batch. We also found that parasitism was spatially direct density dependent when only G1 was considered, as well as when G1, G2, G3 and G4 were considered together. In*

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the first case, an increase in the number of eggs in a group of four plants represents an increase in the batch size, and higher batch size received higher parasitism. In the second case, it represents an increase in the number of infested plants, and higher patch density received higher parasitism. Although the proportion of infected plants parasitized was similar, infected plants with similar number of eggs received higher parasitism when placed in denser groups (G3 and G4) than when placed in the less dense groups (G1 and G2). Behavioral mechanisms leading to a restriction on re-dispersal, like an area-restricted search behavior, as well as supernormal stimulus of contiguous host egg batches in certain places that may require a higher threshold before mutual interference has an effect, could be explained these results.

INTRODUCTION

Many herbivore insects display a marked tendency to aggregate, generating patches of different density that create a resource for their natural enemies (Begon *et al.*, 1999), and as herbivore density changes different spatial patterns usually emerge in their distribution.

In host–parasitoid systems, spatial variation in host density can lead to heterogeneity in the risk of parasitism to which individual hosts are exposed (with important effects on dynamics), if parasitoids respond behaviorally to local host density (Chesson & Rosenzweig, 1991; Hassell, 2000). It has been suggested that parasitoids likely to be more effective for pest control programs are those that concentrate their attacks on denser host patches (Huffaker, 1969; De Bach, 1974; Beddington *et al*., 1978; Hassell, 1978; Murdoch & Briggs, 1996), generating greater risk in dense patches and lower risk in less dense patches (Hassell & May, 1974; Hassell, 2000). Notwithstanding, Paccala and Hassell (1991), inferring the distribution of searching parasitoids from the pattern of parasitism (assuming the two are linked by a linear functional response), found that aggregation in patches of high host density seems far from being the most commonly observed behavior in nature.

Concerning mymarid parasitoids, Broadhead and Cheke (1975) studied the interaction between *Alaptus fusculus*, an oophagous parasitoid, and two species of psocoptera in larch trees. The authors considered a hierarchical spatial pattern of one host species: eggs together in batches, contiguity between batches, particular sites with a high density of contiguous batches, and the patchiness of the batches between trees. Iwao (1968) suggested that changes in the overdispersed distribution of a species may be due to either that the mean size of clumps tends to be larger at higher densities, or that the females lay eggs as small clumps (having a fixed mean) in a slightly aggregated fashion. Therefore, Broadhead and Cheke (1975) expressed the dispersion pattern of parasitoid attacks as a function of parasitoid density and host mean crowding, defined by Lloyd (1967) as the mean number per individual of other individuals in the same sample unit. They found that a parasitoid's attack efficiency declined with increasing parasitoid density, but the supernormal stimulus of contiguous host egg batches in certain places may require a higher threshold before mutual interference has an effect: the greatest density of contiguous host batches occurred on the terminal section of the branches, and it was precisely in these sites where the highest parasitization frequency occurred.

With respect to the interaction between mymarid parasitoids and Auchenorrhyncha hosts, in a review of the existing literature at different spatial scales, Cronin and Strong (1994) found that 62% of the studies showed spatial density -independent parasitism, while the rest of them showed spatial density dependence (24% direct and 14% inverse density dependence).

Delphacodes kuscheli Fennah (Homoptera: Delphacidae) is the only demonstrated vector of the Mal de Río Cuarto Virus (MRCV) in Argentina (Presello *et al*., 1997). This *Fijivirus*,

included in the family Reoviridae, is closely related to Maize Rough Dwarf Virus (MRDV) that seriously affects maize (*Zea mays*) in different provinces in the country, causing significant losses (Lenardón & March, 1983; Lenardon *et al.*, 1998). The vector is commonly associated with maize, oat, wheat (*Triticum aestivum*), sorghum (*Sorghum saccharatum*) and barley (*Hordeum vulgare*), as well as with many natural grass species growing in the vicinity of these crops (Remes Lenicov *et al.*, 1991); in some areas population abundance varied significantly through different years (Ornaghi *et al.*, 1993).

In the province of Tucuman, late winter is a critical period for the planthopper to spread from oat crops to maize crops. Under laboratory conditions and considering oat plants in V5 phenological stage, *D. kuscheli* oviposits endophitic eggs (95 eggs/female during a 6-day period) preferentially in the leaf sheath and basal portion of the fourth leaf blade. The number of eggs, inserted together as a group, varies from one up to six, but 90% of the eggs are laid as one to two per incision (Brentassi & Marino de R. Lenicov, 1999). Under field conditions empirical evidence suggests that in oat crops both isolated plants as well as a number of contiguous plants carrying *D. kuscheli* eggs may be found, and different spatial aggregation of eggs may occur when population density changes. *Anagrus flaveolus* Waterhouse (Hymenoptera: Mymaridae) parasitizes eggs of *D. kuscheli* (Triapitsyn, 1997), and the parasitoid only attacks eggs 3 days old or less (De Santis *et al.*, 1992). One question that arises is how changes in host aggregation, due to changes in population density, affect density-dependent egg parasitism.

The aim of this work is to analyze, during the winter critical period, percentage parasitism when host density increases following two different patterns: an increase in batch size, and an increase in the number of infested plants in a patch.

METHODS

The study area was situated in San Miguel de Tucumán, Argentina (26°49′S, 65°14′W). The regional climate is humid subtropical, the mean annual temperature is 19.6°C and the mean annual rainfall is 947 mm, with 662 mm concentrated in the summer, between December and March (Minetti, 1999). In the region the main annual crops are sugarcane (*Saccharum officinarum*), soybean (*Glycine max*), corn and bean (*Phaseolus* spp.).

During June 1998, 144 oat plants in phenological stage V5 were planted individually in plastic pots (20 cm diameter and 18 cm height); 84 randomly selected plants were put individually into cylindrical glass cages (12.5 cm diameter and 30 cm height) with two to three *D. kuscheli* adult females collected in the field, which were allowed to oviposit for 24 h. After the oviposition period the plants were inspected, and in all cases it was found that the eggs were deposited between the first and the second leaf sheaths (6 cm apart) and 1 cm above the ground. No clearly defined batches were distinguished in most cases, so all eggs found in an individual plant were considered a single batch. The 144 plants were arranged in 36 groups of four plants each, and the four plants in a given group were separated 4–5 cm from each other. In order to generate a heterogeneous egg patchiness, we created four types of patches by placing one, two, three or four infested plants per group (Figure 1). Each group of four plants was thus characterized by the number of infested plants as well as by the number of eggs. If one, two, three or all four plants were infested, the group was denominated G1, G2, G3 or G4, respectively. Considering only G1 (one infested plant per group), the number of eggs in the group increased only if the batch size increased. So, in order to extend the range of egg density in G1, two plants with the lowest number of eggs (12 and 18) and two with the greatest number of eggs (42 and 50) were assigned to the G1 group, while the other 80 infested plants were assigned randomly among the four groups. On the other hand, considering all G1, G2, G3 and G4 groups, the increase in patch density from G1 to G4, was essentially due to the increase in the number of infested plants, and egg patch density varied from 12 (one group from G1) up to 108 (one group from G4) (Table 1). All 36 groups were randomly assigned in a symmetric arrange of six rows and six columns in a 200-m² area;

TABLE 1. *D. kuscheli* egg density and patchiness: mean number (m), standard deviation (s) and coefficient of variation (CV% = $100s/m$)

Patch (group of four plants)	Number of batches per patch	Mean number of eggs per batch	Number of eggs per patch	Replicates
G1	1	26.08	$m = 26.08$; ($s = 11.06$) CV% = 42.39	12
G2	2	23.56	$m = 47.12$; ($s = 11.50$) CV% = 24.10	8
G3	3	23.37	$m = 70.11$; ($s = 11.11$) CV% = 15.84	8
G4	4	22.85	$m = 91.40$; ($s = 9.71$) CV% = 10.63	8

groups were separated 1.5 m from each other. Except for host egg patchiness, the area was homogeneous in other aspects, as it was only covered with grass *Cynodon dactylon* (L.) Pers. 14–18 cm high.

After 48 h all plants were carried to the laboratory and the number of host eggs per plant (both parasitized and unparasitized) was recorded. Density dependence was analyzed for two different spatial patterns. In the first case only G1 ($n = 12$) was considered, under the null hypothesis that egg parasitism would be directly density dependent. In the second case G1, G2, G3 and G4 ($n = 36$) were considered together, under the null hypothesis that egg parasitism would also be directly density dependent, through an increased parasitism on individual infested plants and not through an increase in the proportion of infested plants parasitized.

Spatial density dependence was analyzed by χ^2-test and by a type II regression model using the Bartlett method (Sokal & Rohlf, 1979) complemented with standard regression, using egg patch density as the independent variable and egg parasitism (as arcsin $\sqrt{\mathbf{p}}$, where $\mathbf{p}$ = number of parasitized eggs in the patch/total number of eggs in the patch) as the dependent variable.

In order to analyze whether parasitism on individual plants was higher if placed in denser patches, two sets of 'homogeneous' plants (individual plants bearing similar number of eggs) were selected. One set, representing a situation of low egg density, had a mean number of 18.2 eggs per plant (extreme values were 17 and 19) and 18 replicates: four placed in G1, four in G2, six in G3 and four in G4. The other set represented a situation of moderate egg density, with a mean number of 30 eggs per plant (extreme values were 25–35) and 22 replicates: three placed in G1, three in G2, eight in G3 and eight in G4. The differences were analyzed by χ^2-test.

RESULTS

The density and patchiness of *D. kuscheli* eggs are shown in Table 1 and Figure 1. Total number of *D. kuscheli* eggs exposed was 2009, of which 755 were parasitized (37.6%). Parasitization in a single batch never exceeded 64%, and 81 out of 84 infected plants (96.4%) were parasitized by *A. flaveolus*.

In G1 (only one infected plant per group of four plants) the batch size ranged from 12 to 50. Eleven plants (91.7% of all infected plants) were parasitized by *A. flaveolus*, and the maximum percent parasitism (62.43 and 41.55) corresponded to the infected plants with higher number of eggs (44 and 50, respectively). The slope of the regression equation was different from 0: Bartlett's method: $y = 0.56 + 0.96x$ ($r = 0.70$; $P < 0.02$); and the standard regression: $y = 0.57 + 0.95x$ ($r = 0.70$; $t_{(10\ df)} = 3.12$; $P < 0.02$) (Figure 2).

When G1, G2, G3 and G4 were considered together, the number of batches (i.e., infected plants) per group ranged from one (G1) up to four (G4). Infected plants with a low number of host eggs (10–20) were found in all groups: 14.7% in G1; 20.6% in G2; 26.5% in G3; and 35.3% in G4. Infected plants with a moderate number of eggs (21–40) were also found: 10.9% in G1; 15.2% in G2; 32.6% in G3; and 55.9% in G4. Finally, infected plants with a
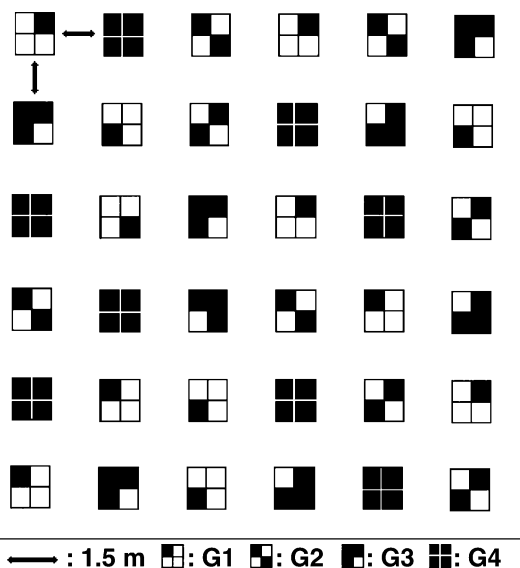
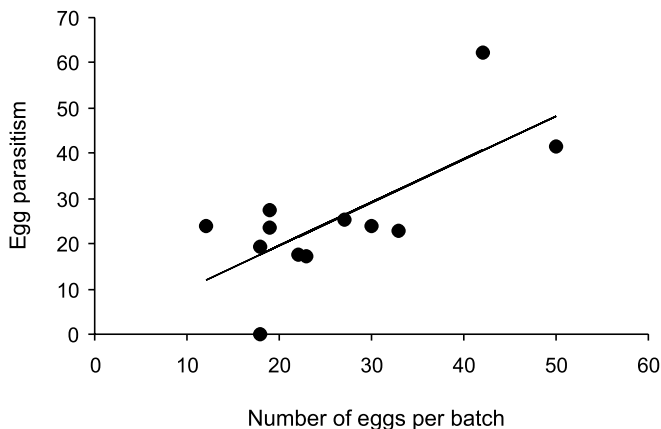FIGURE 1.   The experimental heterogeneous egg patchiness (schematic).

FIGURE 2.   Percent parasitism as a function of egg density per batch, when only G1 were considered. The full line represents the regression equation calculated with the Bartlett's method: $y = 0.57 + 0.95x$; and the dotted line the one calculated with standard regression: $y = 0.56 + 0.96x$.

high number of host eggs (41–50) were placed 50% in G1 and 50% in G2. The mean number of eggs per infected plant exhibited by G1, G2, G3 and G4 (Table 1) did not differ significantly: $\chi^2_{(3\ df)} = 0.26$ (n.s.).

Proportion of parasitized infected plants was: G1 (0.92, $n = 12$ infected plants and 11 parasitized), G2 (1, $n = 16$ infected plants and 16 parasitized), G3 (0.92, $n = 24$ infected plants and 22 parasitized) and G4 (1, $n = 32$ infected plants and 32 parasitized); the difference was not significant: $\chi^2_{(3\ df)} = 0.08$ (n.s.).

The mean and extreme number of eggs per patch were: G1 = 26.08 (12 and 50); G2 = 47.12 (34 and 62); G3 = 70.11 (54 and 95); and G4 = 91.40 (78 and 108). The standard deviation
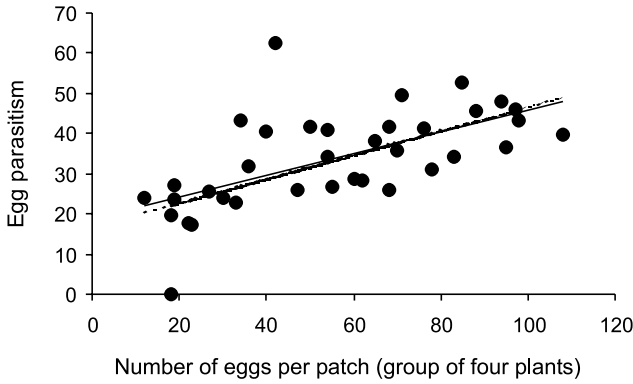
FIGURE 3. Percent parasitism as a function of egg density per patch, when G1, G2, G3 and G4 were considered together. The full line represents the regression equation calculated with the Bartlett's method: $y = 16.87 + 0.30x$; and the dotted line the one calculated with standard regression: $y = 18.83 + 0.26x$.
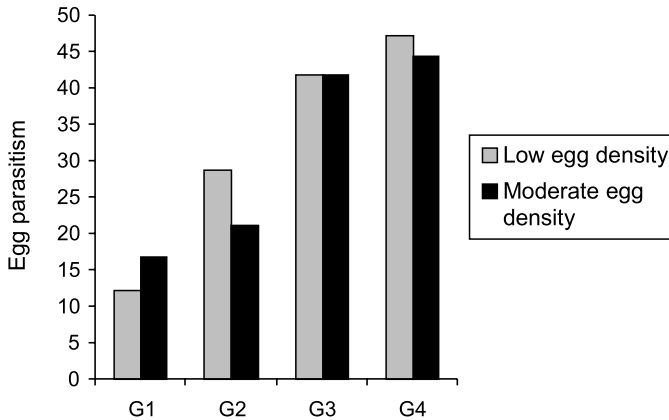

FIGURE 4. Percent parasitism as a function of egg density per batch, when only 'homogeneous' batches (similar egg density) placed in groups of four plants with low (G1 and G2) and high number of batches (G3 and G4) were considered.

and the coefficient of variation were, respectively, $s = 27.68$ and CV% $= 49.59$. The slope of the regression equation was different from 0: Bartlett's method: $y = 16.87 + 0.30x$ ($r = 0.6$; $P < 0.005$); and standard regression: $y = 19.37 + 0.26x$ ($r = 0.6$; $t_{(34\ df)} = 4.37$; $P < 0.001$) (Figure 3).

Parasitism of an individual infected plant, irrespective of whether it had a low ($\chi^2_{(3\ df)} = 25.4$; $P < 0.001$) or a moderate ($\chi^2_{(3\ df)} = 33.9$; $P < 0.001$) number of eggs, was significantly higher if placed in denser patches (Figure 4).

DISCUSSION

The presence of parasitoids and hosts in the same habitat is the result of an active behavior of the parasitoids, unless parasitoid emergence occurs alongside a suitable host. The parasitoids respond to a hierarchy of environmental cues, the most important of which appears to be

chemical, that lead them to the appropriate habitat, host locality and host, and stimulate them to oviposit (Vinson, 1976, 1977).

Mechanisms leading to parasitoid aggregation on patches of higher host density include long range attraction of parasitoids, usually in response to olfactory cues; once in a dense patch, aggregation is maintained through a restriction on re-dispersal (Hassell & May, 1974; Hassell, 1978, 2000). However, only 29% of the examples reviewed by Lessells (1985), Stiling (1987), Walde and Murdoch (1988) and Paccala and Hassell (1991) show spatial direct density dependence, the others being density independent or spatially inverse density dependent. In these latter cases, a possible mechanism preventing aggregation is interference between parasitoids: if parasitoids aggregate, interference could negatively affect the efficiency of parasitoid attacks, as shown in the case of the mymarid *A. fusculus* attacking eggs of a species of *Mesopsocus* (Broadhead & Cheke, 1975).

Anagrus are proovigenic solitary egg parasitoids. Despite the fact that they are minute ($<$1mm), delicate in structure and relatively short-lived (survivorship is of about 2–3 days) (Stiling *et al.*, 1991; Corbett & Rosenheim, 1996a,b), the adults are capable of dispersing several kilometers (Antolin & Strong, 1987). Although dispersal distance probably depends on many factors such as behavior and meteorology, oriented movement towards host patches is likely based on chemical cues (Corbett & Rosenheim, 1996a,b). In our study, we suspect the orientation of parasitoids towards the 200-m^2 experimental area is likely to explain the general results. Despite the short duration of the field experiment, only 48 h, 81 (96.4%) of all egg batches exposed were parasitized, and overall egg parasitism was 38%.

Concerning parasitism at smaller spatial scales, different behaviors exist. *Anagrus delicatus* deposits only a small fraction of eggs in a clutch of *Prokelisia marginata* before dispersing (Cronin & Strong, 1990). Denno (1994) presented examples from a review of the existing literature: *Paranagrus optabilis* oviposits into every egg in the clutch of *Perkinsiella saccharicida*; *Anagrus atomus* selectively oviposits in eggs of *Javesella pellucida* deposited in leaf blades rather than in those inserted in stems; and *Paustenon oxylus* preferentially oviposits into eggs found in the thin walled stems of wheat and oat. Possibly the best known relationship is that established between the grape leafhoppers (some species of *Erythroneura*) and the mymarid wasps formerly known as *Anagrus epos* Girault in California (Doutt & Nakata, 1965, 1973; Doutt *et al.*, 1966; Seyedolesami & Croft, 1980; Wilson *et al.*, 1989; Pickett *et al.*, 1989; Settle & Wilson, 1990; Corbett & Rosenheim, 1996a,b; Corbett *et al.*, 1996; Murphy *et al.*, 1996). When studying *A. epos* attacking two leafhopper hosts (*Erythroneura elegantula* and *E. variabilis*) in a laboratory microhabitat (a grape leaf), Settle and Wilson (1990) found that the parasitoid exhibited an 'area-restricted search' behavior. When initially searching for hosts, the parasitoid moved rapidly, exhibiting small turning angles, whereas, upon finding a host cue, the parasitoid immediately slowed down increasing the turning angles.

In the case of *A. flaveolus*, when a parasitoid finds an infested plant, it displays the following behavior: it first walks up and down the stem for some minutes. Then it begins ovipositing, going downwards along the stem from the upper portion of the batch. At times the parasitoid stops oviposition to rest and preen, reassuming oviposition after a few minutes (Virla, obs.).

In this study we found that in presence of sufficiently varied host patch density, parasitism by *A. flaveolus* was directly density dependent for the two spatial patterns analyzed: when an increase in egg density essentially represented an increase in batch size, or an increase in the number of batches of similar mean size.

When the increase in patch density implies an increase in batch size, possible explanations to directly density-dependent parasitism are the behavioral mechanisms of the parasitoids leading to a restriction on re-dispersal, like an area-restricted search behavior.

When the increase in patch density represented an increase in the number of batches, directly density-dependent parasitism was due to an increased number of eggs parasitized if

the batch of eggs was placed in denser patches. This could be due to a supernormal stimulus of contiguous host egg batches in certain places that, if mutual interference exists, may require a higher threshold before interference has an effect, as in the case with *A. fusculus* (Broadhead & Cheke, 1975).

We also found that almost all batches were parasitized. However, parasitism only once affected more than 64% of the available eggs, suggesting that the parasitoid selectively attacks eggs inserted in particular places of the oat plant and/or never saturates a batch. Possible interference between parasitoids cannot be discarded.

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REFERENCES

ANTOLIN, M.A. & STRONG, D.R. (1987) Long distance dispersal by a parasitoid (*Anagrus delicatus* Mymaridae) and its host. *Oecologia (Berlin)* **73**, 288–292.

BEDDINGTON, J.R., FREE, C.A. & LAWTON, J.H. (1978) Modeling biological control: on the characteristics of successful natural enemies. *Nature* **273**, 513–519.

BEGON, M., HARPER, J.L. & TOWNSEND, C.R. (1999) *Ecology*, 3rd edition. Blackwell Science, pp. 1068.

BRENTASSI, E. & LENICOV, A.M. DE R. (1999) Oviposición de *Delphacodes kuscheli* (Homoptera: Delphacidae) sobre plantas de cebada en condiciones de laboratorio. *Revista de la Facultad de Agronomía de La Plata* **104**, 67–74.

BROADHEAD, E. & CHEKE, R.A. (1975) Host spatial pattern, parasitoid interference and the modelling of the dynamics of *Alaptus fusculus* (Hym.: Mymaridae), a parisotoid of two *Meopsocus* species (Psocoptera). *Journal of Animal Ecology* **44**, 767–789.

CHESSON, P. & ROSENZWEIG, M. (1991) Behavior, heterogeneity, and the dynamics of interacting species. *Ecology* **72**, 1187–1195.

CORBETT, A. & ROSENHEIM, J.A. (1996a) Quantifying movement of a minute parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), using fluorescent dust marking and recapture. *Biological Control* **6**, 35–44.

CORBETT, A. & ROSENHEIM, J.A. (1996b) Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. *Ecology & Entomology* **21**, 155–164.

CORBETT, A., MURPHY, B., ROSENHEIM, J. & BRUINS, P. (1996) Labeling an egg parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), with Rubidium within an overwintering refuge. *Environmental Entomology* **25**, 29–38.

CRONIN, J.T. & STRONG, D.R. (1990) Biology of *Anagrus delicatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Prokelisia* spp. (Homoptera: Delphacidae). *Annals of the Entomological Society of America* **83**, 846–854.

CRONIN, J.T. & STRONG, D.R. (1994) Parasitoid interactions and their contribution to the stabilization of Auchenorrhyncha populations, in *Planthoppers, their Ecology and Management* (DENNO, R.F. & PERFECT, T.J., Eds.). Chapman & Hall, New York, pp. 400–428.

DE SANTIS, L., VIRLA, E. & MARAGLIANO, R. (1992) Presencia de *Anagrus flaveolus* en la República Argentina, parasitoide de un insecto dañino del trigo y el maíz (Insecta-Hymenoptera-Mymaridae). *Revista de la Facultad de Agronomía (Buenos Aires)* **13**, 19–23.

DE BACH, P. (1974) *Biological Control by Natural Enemies*. Cambridge University Press, Cambridge, pp. 323.

DENNO, R.F. (1994) Life history variation in planthoppers, in *Planthoppers, their Ecology and Management* (DENNO, R.F. & PERFECT, T.J., Eds.). Chapman & Hall, New York, pp. 163–215.

DOUTT, R. & NAKATA, J. (1965) Overwintering refuge of *Anagrus epos* (Hymenoptera: Mymaridae). *Journal of Economic Entomology* **58**, 586.

DOUTT, R. & NAKATA, J. (1973) The *Rubus* leafhopper and its egg parasitoid: an endemic biotic system useful in grape-pest management. *Environmental Entomology* **2**, 381–386.

DOUTT, R., NAKATA, J. & SKINNER, F. (1966) Dispersal of grape leafhopper parasites from a blackberry refuge. *California Agriculture* October, 14–15.

HASSELL, M.P. (1978) *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, pp. 237.

HASSELL, M.P. (2000) *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions*. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, pp. 200.

HASSELL, M.P. & MAY, R.M. (1974) Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology* **43**, 567–594.

HUFFAKER, C.B. (1969) *Biological Control*. Plenum Press, New York & London, pp. 511.

IWAO, S. (1968) A new regression method for analyzing the aggregation pattern of animal populations. *Researches in Population Ecology* **10**, 1–20.

LENARDÓN, S. & MARCH, G. (1983) Estado actual del 'Mal de Río Cuarto' en cultivos de maíz. *Revista CREA* **104**, 22–42.

LENARDON, S., MARCH, G., NOME, S. & ORNAGHI, J.A. (1998) Recent outbreak of 'Mal de Río Cuarto' virus in corn in Argentina. *Plant Disease* **82**, 448.

LESSELLS, C.M. (1985) Parasitoid foraging: should parasitism be density dependent?. *Journal of Animal Ecology* **54**, 27–41.

LLOYD, M. (1967) Mean crowding. *Journal of Animal Ecology* **36**, 1–30.

MINETTI, J.L. (1999) *Atlas climático del Noroeste Argentino*. Ed. Lab. Climatológico Sudamericano, Fund. C. C. Zon Caldenius, CONICET & UNT, Tucumán, pp. 108.

MURDOCH, W.W. & BRIGGS, C.J. (1996) Theory for biological control: recent developments. *Ecology* **77**, 2001–2013.

MURPHY, B., ROSENHEIM, J. & GRANETT, J. (1996) Habitat diversification for improving biological control: abundance of *Anagrus epos* (Hymenoptera: Mymaridae) in grape vineyards. *Environmental Entomology* **25**, 495–504.

ORNAGHI, J., BOITO, G., SANCHEZ, G., MARCH, G. & BEVIACQUA, J. (1993) Studies on the population of *Delpahcodes kuscheli* Fennah in different years and agricultural areas. *Journal of Genetics & Breeding* **47**, 277–282.

PACCALA, S.W. & HASSELL, M.P. (1991) The persistence of host-parasitoid associations in patchy environments. II. Evaluation of field data. *American Naturalist* **138**, 584–605.

PICKETT, C., WILSON, L., FLAHERTY, D. & GONZALEZ, D. (1989) Measuring the host preference of parasites: an aid in evaluating biotypes of *Anagrus epos* (Hym., Mymaridae). *Entomophaga* **34**, 551–558.

PRESELLO, D.A., COSTAMAGNA, A., CONCI, L., DE REMES LENICOV, A.M., GUZMAN, F. & HERRERA, P. (1997) Mal de Río Cuarto del Maíz, estudio de la capacidad vectora de las poblaciones de *Toya propinqua* presentes en el área de Pergamino. *Actas VI Congreso Nacional de Maíz* (Pergamino, Argentina) **2** (II), 1–5.

REMES LENICOV, A.M. DE, VIRLA, E. & DAGOBERTO, E. (1991) Cambios estacionales en la población del vector del 'Mal de Rio Cuarto' (*Delphacodes kuscheli* Fennah, 1955) en cultivos de avena y sus malezas circundantes en Sampacho, Córdoba. (Insecta-Homoptera-Fulgoroidea). *Actas Taller de actualización sobre Mal de Rio Cuarto*, INTA Pergamino, Buenos Aires, pp. 116–129.

SETTLE, W.H. & WILSON, L.T. (1990) Behavioural factors affecting differential parasitism by *Anagrus epos* (Hymenoptera: Mymaridae), of two species of erythroneuran leafhoppers (Homoptera: Cicadellidae). *Journal of Animal Ecology* **59**, 877–891.

SEYEDOLESAMI, H. & CROFT, B.A. (1980) Spatial distribution of overwintering eggs of the white apple leafhopper *Typhlocyba pomaria*, and parasitism by *Anagrus epos*. *Environmental Entomology* **9**, 624–628.

SOKAL, R.R. & ROHLF, F.J. (1979) *Biometría*. H. Blume Ediciones, Madrid, pp. 832.

STILING, P.D. (1987) The frequency of density dependence in insect host-parasitoid systems. *Ecology* **68**, 844–856.

STILING, P.D., THROCKMORTON, A., SILVANIMA, J. & STRONG, D. (1991) Does spatial scale affects the incidence of density dependence? A field test with insect parasitoids. *Ecology* **72**, 2143–2154.

TRIAPITSYN, S. (1997) The genus *Anagrus* (Hymenoptera: Mymaridae) in America South of the United States: a review. *CEIBA* **38**, 1–12.

VINSON, S.B. (1976) Host selection by insect parasitoids. *Annual Review of Entomology* **21**, 109–134.

VINSON, S.B. (1977) Behavioural chemicals in the augmentation of natural enemies, in *Biological Control by Augmentation of Natural Enemies* (RIDGWAY, R.L. & VINSON, S.B., Eds.), Plenum, New York, pp. 237–239.

WILSON, L., PICKETT, C., FLAHERTY, D. & BATES, T. (1989) French prune trees: refuge for grape leafhopper parasite. *California Agriculture* March–April, 7–8.

WALDE, S.J. & MURDOCH, W.W. (1988) Spatial density dependence in parasitoids. *Annual Reviews in Entomology* **33**, 441–466.