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Spatial Dynamics of an Acarine Predator-prey System: Responses of *Amblyseius ovalis* (Evans) to Its Egg-laying Behavior and Density and Aggregation of *Tetranychus urticae* Koch (Acarina: Phytoseiidae: Tetranychidae) 【Research report】

蟎類捕食者食餌系統之空間動態卵形捕植蟎(*Amblyseius ovalis* (Evans))對其產卵行為及二點葉蟎(*Tetranychus urticae* Koch) (Acarina: Phytoseiidae: Tetranychidae)密度與聚集之反應【研究報告】

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Abstract

Stage specific spatial distribution pattern of *Amblyseius ovalis* on carambola fruit orchards was evaluated by the index of dispersion (ID), Green's coefficient of dispersion (Cx), Lloyd's mean crowding index (mc) and patchiness index (mc/m), Taylor's power law ($\log a$ and b), and Iwao's patchiness regression (a , b) from 250 sets of sampling-date data during 1990-1995. All stage-specific populations of *A. ovalis* distributed intensively in random to uniform pattern; however, eggs, females, and overall stages were contagious. The degree of contagiousness of the eggs and the females was the highest among all stage-specific populations according to the results of Taylor's power law analyses of $\log a$ and b . Density-independence of contagiousness of *A. ovalis* was found from their low correlation coefficients between the calculated indices and prey *Tetranychus urticae* or predator densities, but the eggs exhibited a high relationship to its prey density. From the estimated a and b values, we found the basic component units (patches) of the eggs were formed by single egg, but two or more females aggregated in the patch. The female exhibited single-egg-laying behavior within the contagiously-distributed prey cohort which resulted in the egg-aggregation among the prey patch. However, the egg and larval aggregates were due to the prey-aggregation among the patches. The species character, a high degree of uniform distribution and repulsive mechanism of egg and larva, was interpreted as the results of female egg-laying behavior in the prey cohort.

摘要

楊桃上卵形捕植蟎 (*Amblyseius ovalis* (Evans)) 之五年 (1990~95) 250組族群資料依分布指數 (ID) · Green's 分布係數 (Cx) · Lloyd平均聚集指數 (mc) 及聚落度指數 (mc/m) · Taylor乘冪定律迴歸 ($\log a$ 及 b) · 及Iwao聚落度迴歸 (α · β) 等分析結果評估齡別差之空間分布型。卵形捕植蟎各齡期之空間分布傾向隨機至均勻，但是卵、雌成蟎及全部齡期總合之族群則傾向聚集分布。依Taylor乘冪定律迴歸分析所獲得之截距 $\log a$ 及斜率 b 評估各期之聚集度，捕植蟎卵及雌成蟎的聚集度 (degree of contagiousness) 為各期中最高。卵形捕植蟎之分布指數或係數值與其食餌二點葉蟎 (*Tetranychus urticae* Koch) 密度間呈極低相關關係，顯示卵形捕植蟎之聚集度為低食餌密度依變。依Iwao迴歸分析所測得的截距 α 及斜率 β 值，評估得卵在小聚落 (patch) 中之組成單位為“單一個體”，但多個體的雌成蟎則為小聚落之構成單元。雌成蟎產單卵於聚集分布之葉蟎小聚落內的行為，顯然是構成捕植蟎卵聚集之主因。該等小聚落內捕植蟎卵或幼蟎之單一均勻分布及斥拒機制 (另一卵或幼蟎同時出現或存在同一小聚落內之機制) 應為雌成蟎在食餌聚落內之產卵行為特性所致，亦為構成該卵形捕植蟎種空間分布特性之主因。

Key words: spatial distribution, predator-prey system, density, egg-laying behavior.

關鍵詞: 空間分布、捕食者食餌系統、密度、產卵行為。

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ABSTRACT

Stage specific spatial distribution pattern of *Amblyseius ovalis* on carambola fruit orchards was evaluated by the index of dispersion (ID), Green's coefficient of dispersion (Cx), Lloyd's mean crowding index (mc) and patchiness index (mc/m), Taylor's power law (log a and b), and Iwao's patchiness regression (α , β) from 250 sets of sampling-date data during 1990-1995. All stage-specific populations of *A. ovalis* distributed intensively in random to uniform pattern; however, eggs, females, and overall stages were contagious. The degree of contagiousness of the eggs and the females was the highest among all stage-specific populations according to the results of Taylor's power law analyses of log a and b. Density-independence of contagiousness of *A. ovalis* was found from their low correlation coefficients between the calculated indices and prey *Tetranychus urticae* or predator densities, but the eggs exhibited a high relationship to its prey density. From the estimated α and β values, we found the basic component units (patches) of the eggs were formed by single egg, but two or more females aggregated in the patch. The female exhibited single-egg-laying behavior within the contagiously-distributed prey cohort which resulted in the egg-aggregation among the prey patch. However, the egg and larval aggregates were due to the prey-aggregation among the patches. The species character, a high degree of uniform distribution and repulsive mechanism of egg and larva, was interpreted as the results of female egg-laying behavior in the prey cohort.

Key words: spatial distribution, predator-prey system, density, egg-laying behavior

Introduction

Spatial distribution of tetranychids and phytoseiids were reported to determine the optimal sampling size through the adjustment of the fidelity and the cost of the estimates (Croft *et al.*, 1976; Grout, 1985; Herbert and Butler, 1973a, b; Ho, 1993; Jones, 1990; McGroarty and Croft, 1978; Nachman, 1984; Nyrop, 1988a, b; Schoenig and Wilson, 1992; Stephen and Kinn, 1980). The predacious mite is usually high density dependent on its prey population (Croft *et al.*, 1976; Herbert and Butler, 1973a; McGroarty and Croft, 1978; Nachman, 1981a, 1981b, 1984; Wilson *et al.*, 1991). Shih and Wang (1996) and Ho (1993) reported *Tetranychus urticae* and *T. kanzawai* were contagiously distributed in Taiwan with patchy components. Seasonal survivals, variation in distribution, and densities of phytoseiids are associated with its prey density and leaf-structure domatia, although the evidence is limited (Holtzer *et al.*, 1984; Walter and O'Dowd, 1992). The tendency or the degree of aggregation and patchiness of prey density varied with the efficiency of predation and reproduction of predator so that the magnitudes of aggregation of predator might be influenced (Kaiser, 1983; Kuchlein, 1966; Takafuji and Deguchi, 1980). Bernstein (1984) and Sabelis (1981) demonstrated the protraction of arrestment time or emigration response of *Phytoseiulus persimilis* depended upon the density of *Tetranychus urticae* in the patch, while Kuchlein (1966), Takafuji (1977) and Takafuji and Chant (1976) reported that emigration tendency of *Typhlodromus longipilus* was a feed-back response of the density or the interaction of predator-prey system. The protracted arrestment time and orientation

responses of the predatory mites were demonstrated to vary with the amount of kairomone produced in the universe besides the spider mite density (Johnson and Croft, 1976; Nyrop, 1988a; Schmidt, 1976). Consequently, the distribution pattern of phytoseiid mites may vary and be superimposed by the protraction of arrestment time in the prey patch or the prey aggregates (Hanna and Wilson, 1991). The variation of arrestment time of the predator may be the results of behavioral responses to the prey density, kairomone concentration, micro-habitat structure, predator host experience, hunger and age, and interaction between the predator and the prey in the patch. Therefore, the contagiousness and patchiness of the predator depend not only on the density of prey but also on the responses of the individual behavior of the predatory mites to the prey. The distribution pattern of predaceous mites was the consequence of their behavioral changes from time to time due to the interaction and/or the indirect physiological reaction through the contact between the predators of the same species or the interaction between the predators and the prey. In this study, we estimated the dispersion statistics and the contagiousness of the stage-specific populations of *Amblyseius ovalis* and the calculated statistics were used to correlate to the prey and predator density. The results were also used to interpret the female egg-laying behavior of *A. ovalis* associated with the prey patches.

Materials and Methods

Sampling methods

A total of 44 (5-y-old) carambola trees planted in a 4-by-11 array at 5.5 m intervals was encircled by 2 rows of

wind breakers. Every carambola tree was assigned a coordinate number to which Legg and Yeargan's (1985) random selection and path routes were adopted to determine each individual sampled tree in the orchard. One leaf with 10-13 leaflets in each selected tree was cut and labeled, and put into a plastic bag with absorbent cotton paper strips. The numbers of mites of *A. ovalis* and its prey *T. urticae* of each stage from every weekly sample were counted and recorded in the laboratory under the dissection binocular microscope.

Analyses of data for dispersion indices and coefficients

Distribution of *A. ovalis* in the habitat is only valid when the population exists for a certain duration on the carambola tree. Those populations containing 0 densities were not considered either in analyzing dispersion indices or coefficients, nor in estimating distribution patterns. Therefore, we deleted the data-set with zero counts. The detection of distribution patterns of *A. ovalis* using the values of means and variances to estimate the indices or coefficients were made according to the following models: 1. Index of dispersion, ID (Patil and Stiteler, 1974); 2. Green's coefficient of dispersion, Cx (Green, 1966); 3. Lloyd's mean crowding index, mc (Lloyd, 1967); 4. Lloyd's patchiness index, mc/m (Lloyd, 1967); 5. Taylor's power law, log a and b (Taylor, 1961; 1984; Taylor *et al.* 1978); and 6. Iwao's patchiness regression, α and β (Iwao, 1968; 1977). These calculated values of indices or coefficients were used to detect the spatial distribution pattern of each stage-specific and overall-stage groups of *A. ovalis* in the carambola on different sampling dates. The significance of distribution of overall and stage-specific populations of *A.*

ovalis in contagious patterns were tested with the assumption that the population distributed either in aggregate or random to uniform. In other words, the contagious distribution pattern of *A. ovalis* was determined by the frequency of the dispersion index or coefficient which was significantly larger than 0.5 with a binomial distribution.

The estimated stage-specific indices and coefficients were also used to analyze the correlation coefficients between ID, Cx, mc and mc/m values of *A. ovalis* and the corresponding densities of *T. urticae* and *A. ovalis* (Table 1). The relationship of contagiousness of predators associated with prey and their own densities was discussed. However, when the sum of individuals in the samples is 1, $\sum x_i$, it makes denominator equal to zero and the results are undefined. The analyses of data for the Cx's excluded those data sets with sum equal to one.

Since *A. ovalis* does not exhibit territorial behavior but long protraction of residency in the habitat, we assume that most of individuals of *A. ovalis* aggregate in "patch" with a character of random distribution and the patch-density is higher than the population mean. Thus, Lloyd's mean crowding index (mc) was adopted and the mc's of the equation using means and variances were estimated. We also evaluated the population distribution of *A. ovalis* including "mean number per individual of other individuals in the same quadrat", i.e., Lloyd's patchiness index (mc/m) besides the population mean (Lloyd 1967). Therefore, the mc's and m's calculated were used to estimate the "patchiness indices". The frequency of the contagious distribution of *A. ovalis*, in all sampled populations determined by $mc / m > 1$, was tested for

the significance of the predator distributing in aggregation.

Regression analyses of Taylor's power law and Iwao's patchiness

The calculated means and variances were adopted to fit the Taylor's power law model (Taylor, 1961; 1984) to estimate the intercepts $\log a$ and the slopes b 's from the estimated regression equations. The linear regression model of mean crowding (mc 's) as a function of the means was also adopted to fit the regression models to estimate the intercepts α 's and slopes β 's from the obtained regression equations (Iwao, 1968; 1977). The estimated $\log a$ and b , and α and β were used to estimate the tendency of the populations distributed in aggregation or random to uniform, and the characters of the patch components including single or multiple individuals. Besides the estimation of dispersion statistics and their interpretation of *A. ovalis* aggregation, the influences of the females behavior on the contagiousness of eggs in the patch, i.e., the number of individuals within the patches and the patch aggregation was inferred to the patch-character of *A. ovalis*.

Results

Index of dispersion

A total of 250 sets of weekly samples was collected and estimated for the means and variances of *A. ovalis* and the means of *T. urticae*. Most of ID values estimated from means and variances were equal to or not significantly different from 1, which showed that *A. ovalis* populations were expected to distribute mostly in random (Table 1, Fig. 1). According to the estimated values of Green's coefficient (Cx), Lloyd's mean crowding index (mc) and patchiness index (mc/m), *A. ovalis* popu-

lation also distributed mostly in random or random to uniform, but Cx of eggs and females showed a high frequency to distribute in aggregate (Table 1, Fig. 2-4). The overall evaluation of distribution pattern from the four estimated indices and coefficients indicated that *A. ovalis* retained a very high intensity to random distribution in the field (Table 1, Fig. 1-4). However, most of ID values of eggs (90.91%) and females (80.00%) at high density (mean ≥ 0.3 individuals/leaf) were larger than 1 (Shih and Wang, unpublished) which indicated *A. ovalis* might distribute from random to aggregation because of the stage-specificity and density variation (Fig. 1). The estimated frequencies of ID distributed in aggregate for eggs, larvae, nymphs, females and males were 39.13%, 5.00%, 22.02%, 36.09% and 14.81%, respectively, which were lower than the expected 0.5 frequency when the *A. ovalis* was expected to be distributed in either aggregation or random to uniform with binomial distribution (Table 1). Therefore, the stage-specific populations were random to uniform (Table 1). The overall population of all stages of *A. ovalis*, the frequency of ID was 71.17% which showed that overall-predator population were significantly contagious. Those contagious behavior was due to the different stage-specific individuals taken to estimate the dispersion indices or coefficients. The results of correlation coefficient analyses between the values of ID of *A. ovalis* and the corresponding prey densities of *T. urticae* showed that the ID's of egg and larvae were significantly and positively correlated with its prey density, but neither the other stage-specific nor the overall-stage populations were (Table 2). ID values of eggs, nymph, females, and overall stages of *A. ovalis*

were significantly correlated with the corresponding predator densities, but larvae and male were not (Table 2).

Table 1. Frequency distribution of spatial distribution pattern of *Amblyseius ovalis* estimated by ID, Cx, mc and mc/m

| | Numbers of distribution patterns (%) | | | | | |
|----------------------------|--------------------------------------|------------------|------------------|-------------------|-----------------|---------------------------|
| | Egg No. (%) | Larva No. (%) | Nymph No. (%) | Female No. (%) | Male No. (%) | Overall stages No. (%) |
| ID | | | | | | |
| Uniform | 16 (23.19) | 15 (37.50) | 39 (35.78) | 46 (36.84) | 11 (40.74) | 47 (28.83) |
| Random | 26 (37.68) | 23 (57.50) | 46 (42.20) | 39 (29.32) | 12 (44.44) | 0 (0.00) |
| Aggregate | 27 (39.13) | 2 (5.00) | 24 (22.02) | 48 (36.09) | 4 (14.81) | 116 (71.17) |
| Total valid sample sets | 69 | 40 | 109 | 133 | 27 | 163 |
| Cx | | | | | | |
| Uniform | 16 (37.21) | 14 (82.35) | 39 (61.90) | 45 (46.88) | 11 (73.33) | 47 (34.81) |
| Random | 0 (0.00) | 1 (5.88) | 2 (3.17) | 2 (2.08) | 0 (0.00) | 0 (0.00) |
| Aggregate | 27 (62.79) | 2 (11.76) | 22 (34.92) | 49 (51.04) | 4 (26.67) | 88 (65.19) |
| Total valid sample sets | 43 | 17 | 63 | 96 | 15 | 135 |
| mc | | | | | | |
| Uniform | 16 (23.19) | 15 (37.50) | 39 (35.78) | 46 (36.84) | 11 (40.74) | 6 (3.68) |
| Random | 26 (37.68) | 23 (57.50) | 46 (42.02) | 39 (29.32) | 12 (40.44) | 0 (0.00) |
| Aggregate | 27 (39.13) | 2 (5.00) | 24 (22.02) | 48 (36.09) | 4 (14.81) | 157 (96.32) |
| Total valid sample sets | 69 | 40 | 109 | 133 | 27 | 133 |
| mc/m | | | | | | |
| Uniform | 37 (86.05) | 15 (37.50) | 39 (35.78) | 85 (88.54) | 11 (40.74) | 47 (28.73) |
| Random | 6 (13.95) | 23 (57.50) | 46 (42.20) | 1 (1.04) | 12 (44.44) | 0 (0.00) |
| Aggregate | 0 (0.00) | 2 (5.00) | 24 (22.02) | 10 (10.42) | 4 (14.81) | 116 (71.17) |
| Total valid sample sets | 43 | 40 | 109 | 96 | 27 | 163 |

Table 2. Correlation coefficients between indices or coefficients of stage-specific spatial distribution of *Amblyseius ovalis* and corresponding densities of *Tetranychus urticae*

| Stage | ID (p-values) | Cx (p-values) | mc (p-values) | mc/m (p-values) |
|-------------------|----------------|----------------|----------------|-----------------|
| Egg | 0.497 (0.001) | 0.150 (0.339) | 0.515 (0.001) | 0.497 (0.001) |
| Larva | 0.569 (0.001) | 0.662 (0.004) | 0.515 (0.001) | 0.356 (0.024) |
| Nymph | 0.011 (0.913) | -0.021 (0.871) | 0.024 (0.802) | -0.015 (0.878) |
| Female | 0.002 (0.978) | 0.046 (0.662) | -0.011 (0.896) | 0.003 (0.977) |
| Male | -0.289 (0.144) | -0.419 (0.120) | -0.289 (0.144) | -0.279 (0.158) |
| Overall stages | 0.199 (0.011) | -0.002 (0.986) | 0.207 (0.008) | 0.037 (0.642) |

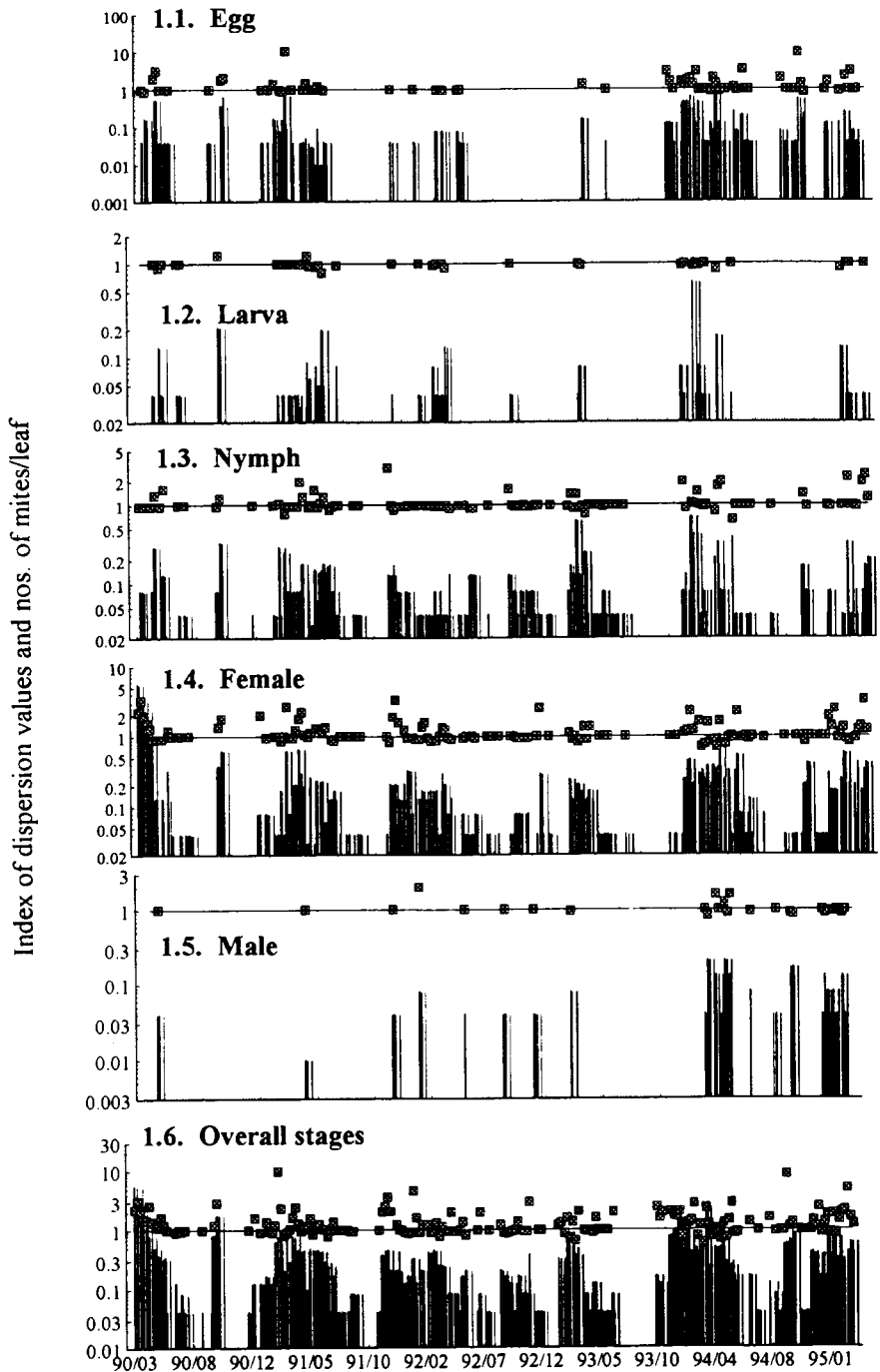


Fig 1. Population densities (bars) and index of dispersion values ($ID=SS/m$) (squares) of *Amblyseius ovalis* in carambola orchard.

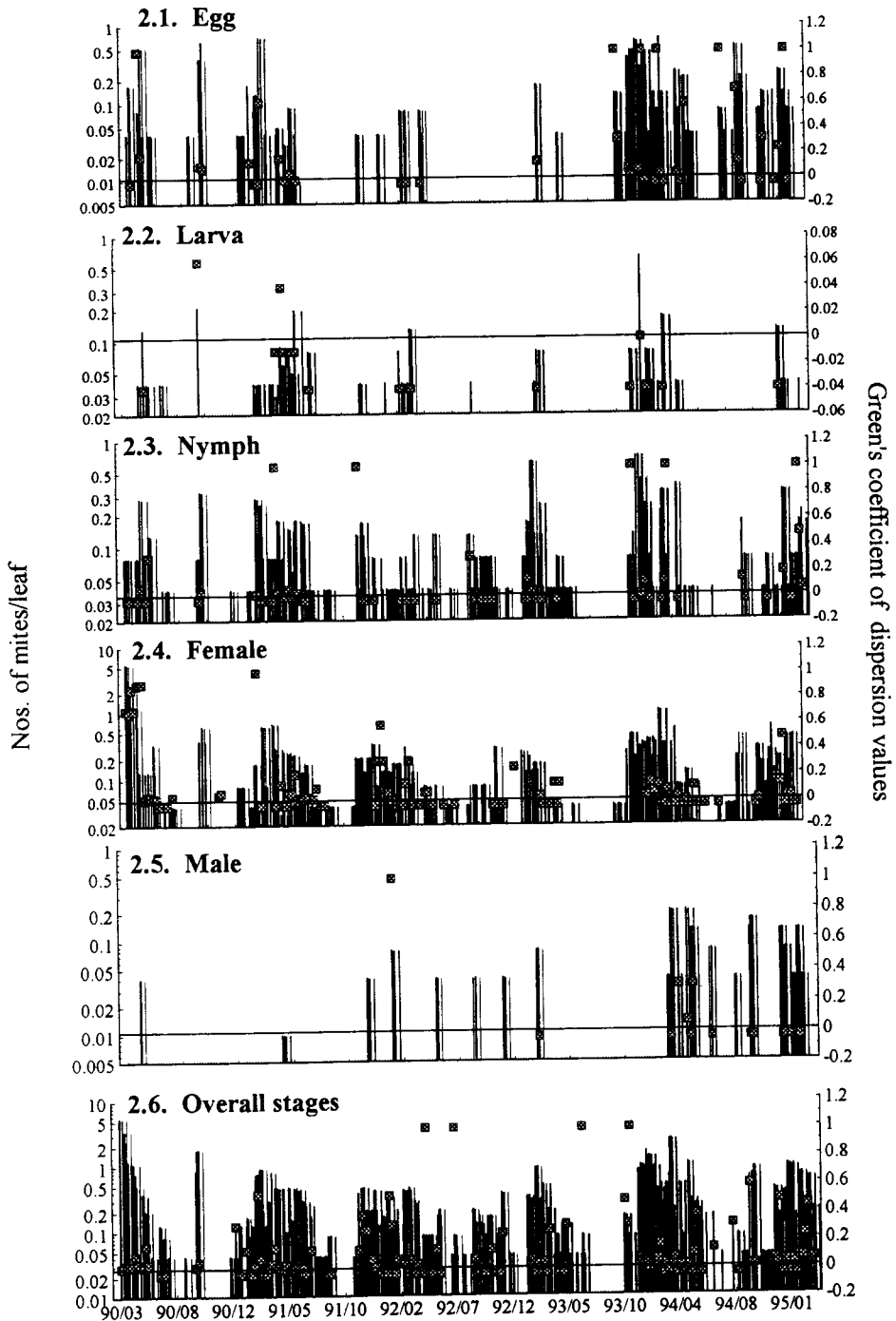


Fig 2. Population mean densities (bars) and Green's coefficient of dispersion values ($C_x = ((SS/m) - 1) / (\sum x_i - 1)$) (squares) of *Amblyseius ovalis* in carambola orchard.

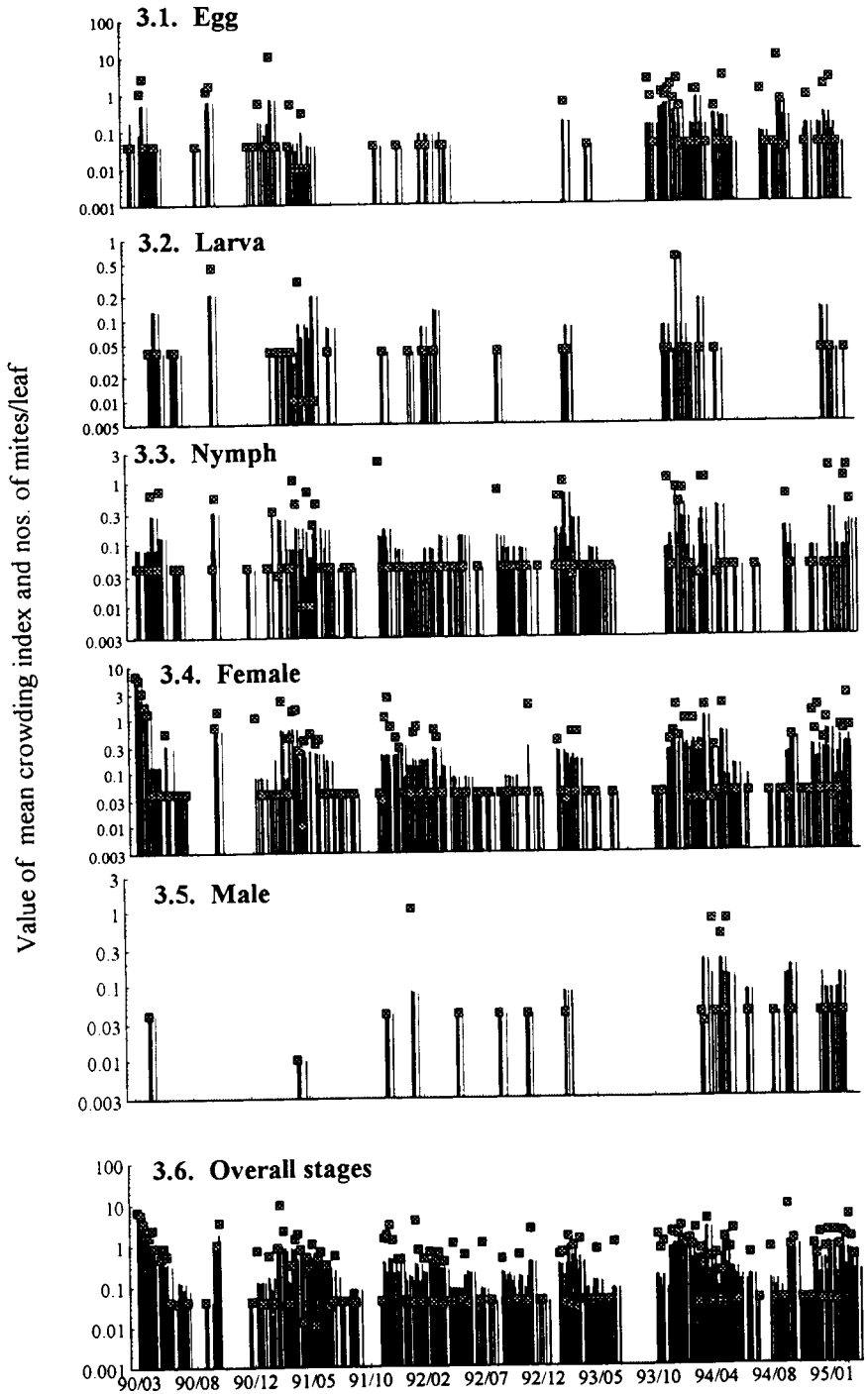


Fig 3. Population mean densities (bars) and values of Lloyd's mean crowding index ($mc=m+(SS/m)-1$) (squares) of *Amblyseius ovalis* in carambola orchard.

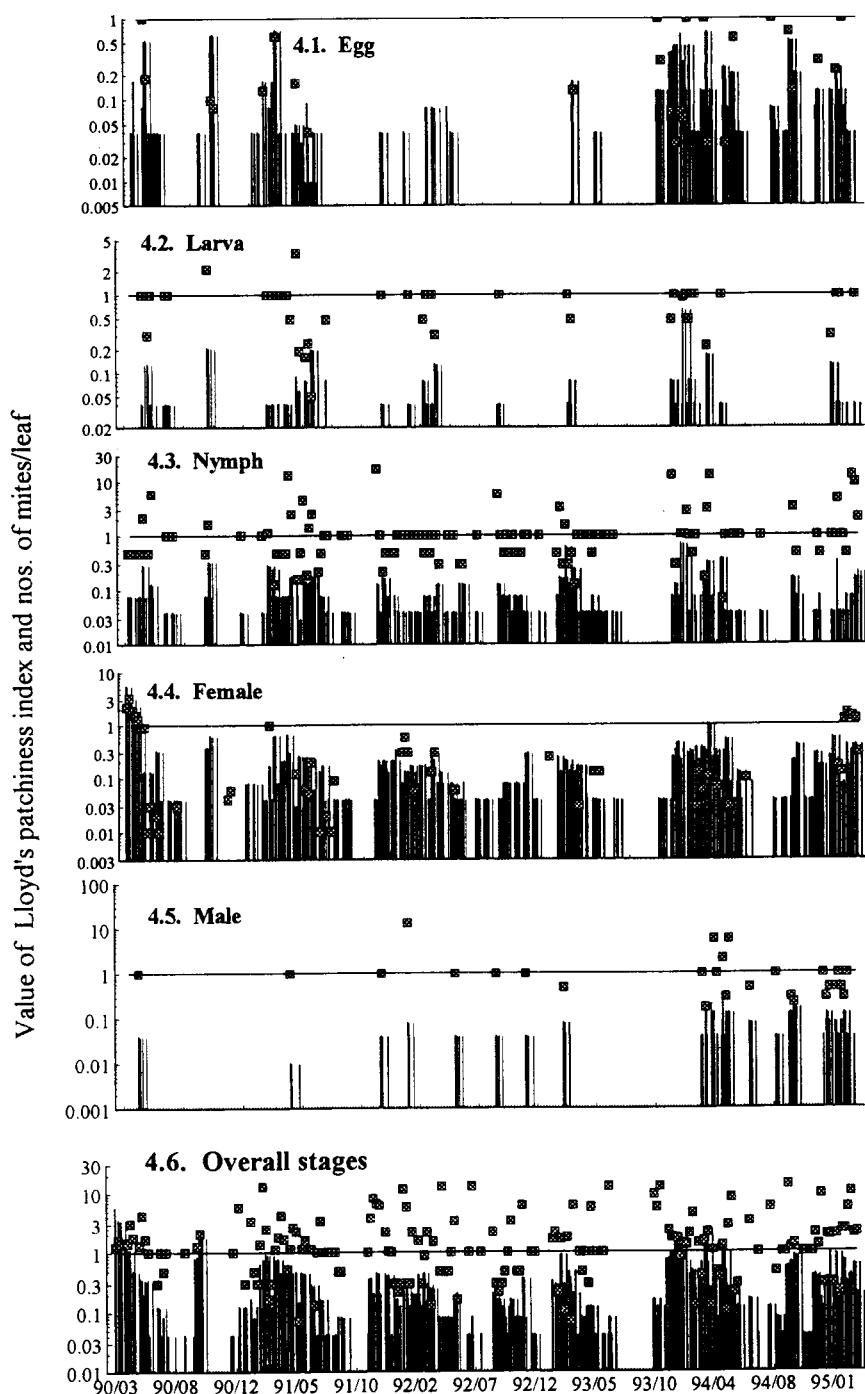


Fig 4. Population densities (bars) and values of Lloyd's patchiness index (mc/m) (squares) of *Amlyseius ovalis* in carambola orchard.

Green's coefficient of dispersion, Cx

Those data collected from the field with total density count of a given sample day equal to 1 ($x_i=1$) were not included in the analyses for Cx due to the undefined results by zero denominator. In February and July of 1990, 1992-1995, the spatial distribution of stage specific *A. ovalis* was random and associated with its low density. Shih and Wang (1996) reported that the density of *T. urticae*, prey of *A. ovalis*, was low at these periods of time in the field. The Cx values of mid-March and mid-August were mostly equal or close to zero, which indicated the *A. ovalis* population distributed mostly in random (Fig. 2). Mayer (1978) reported that the Cx was not density related which means that the independence of Cx from density was due to the estimated coefficient divided by a large denominator ($\sum x_i$) when the population was in high density. In other words, the predator population in the high density with large value of the denominator ($\sum x_i$) produced a low estimation of Cx which would limit the significance of the aggregation behavior of the *A. ovalis* at the high density (Table 1). The large value of $\sum x_i$ also influenced the magnitude of the Cx values to correlate with the corresponding prey and predator densities (Table 2,3). When the *A. ovalis* densities were at increasing phase and peak density, the corresponding Cx values were higher than zero which indicated *A. ovalis* distributed in aggregate pattern (Fig. 2). Although most of stage-specific *A. ovalis* populations were large enough to estimate their distribution, the 15 or 17 available samples of the adult-male or larval samples were not sufficiently enough to evaluate the correlation between Cx and its densities (Fig. 2, Table 2). More than a half of

the egg and the female populations distributed in aggregate (Table 1). The total valid samples of overall stage populations for Cx analyses were less than those of other tested indices (Table 1). The distribution of the overall stages of *A. ovalis* was significantly contagious with 65.19% of the population distributing in aggregate (Table 1). Correlation coefficients (r) of Cx values to the corresponding prey *T. urticae* densities were 0.150 ($p=0.339$), 0.662 ($p=0.004$), -0.020 ($p=0.871$), 0.046 ($p=0.662$), and -0.419 ($p=0.120$) for eggs, larvae, nymphs, females and males of *A. ovalis*, respectively, and 0.002 ($p=0.986$) for the overall stages (Table 2). Therefore, the Cx values of *A. ovalis* of larvae were significantly correlated with the density of *T. urticae* but other stages and overall stages were not. The Cx values of stage-specific predators (egg: $r=-0.043$, $p=0.782$; larva: $r=0.230$, $p=0.374$; nymph: $r=-0.083$, $p=0.520$; female: $r=-0.019$, $p=0.853$; male: $r=-0.175$, $p=0.534$) and overall stages ($r=-0.098$, $p=0.256$) were also not positively nor significantly correlated with their own densities (Table 2).

Lloyd's mean crowding index and patchiness index (mc, mc/m)

Mean crowding indices of *A. ovalis* and its contagiousness varied with stages (Fig. 3, Table 1). The contagiousness of *A. ovalis* evaluated with mean crowding, 39.13% and 36.09% of the eggs and females populations, respectively, showed *A. ovalis* were contagious and the numbers of individuals existing in the same patches were higher than the corresponding means, while the other stage-specific populations were distributed from random to uniform (Fig. 3, Table 1). However, 96.32% of the overall-stage populations distributed contagiously and the sum numbers of individuals of all different stages were

higher than the means (Table 1). Therefore, the basic component of the overall-stage population was patch while the stage-specific populations were not. Tested statistics of mc for the stage-specific of *A. ovalis* showed that 60.87%, 95.00%, 77.98%, 63.91% and 85.19% of eggs, larvae, nymphs, females, and males, respectively, distributed in random to uniform (Table 1). Correlation coefficients between the estimated mc values to the densities of *T. urticae* were 0.515 ($p=0.001$), 0.515 ($p=0.001$), 0.024 ($p=0.802$), -0.011 ($p=0.896$), -0.289 ($p=0.144$), and 0.207 ($p=0.008$) for egg, larvae, nymph, female, male, and overall-stages, respectively (Table 2). Consequently, the egg and larval mc values of *A. ovalis* were significantly correlated with the prey density, but the other stages and overall stages were not (Table 2). The correlation coefficients of mc values of each stage-specific and overall-stage predators to their own densities were all significant except the males (Table 2).

All estimated Lloyd's patchiness indices mc/m of stage-specific *A. ovalis* were equal to 1 or less than 1 (Fig. 4). Table 1 shows the probabilities of patchiness indices related to the dispersion criterion of distribution, i.e., $mc/m > 1$ for aggregate, $mc/m = 1$ for random and $mc/m < 1$ for uniform. None of eggs, but very a few of larvae (5.00%), nymphs (22.02%), females (10.42%) and males (14.81%) were contagiously distributed to form patches. Those of estimated values of patchiness indices which were larger than 1 were related to their high densities (Fig. 4). However, most of estimated mc/m values of stage-specific population of *A. ovalis* were equal or less than 1, but a 71.17% of mc/m values of the overall-stage was large than 1 (Table 1). The overall-stage of *A. ovalis* formed patches and the indi-

viduals of the different stages aggregated in the patches. The correlation coefficients of mc/m values of nymph, female, male and overall-stage were not significantly related with their prey densities, but the egg and larvae were weakly but significantly correlated (Table 2). All the stage-specific mc/m values of *A. ovalis* were not significantly correlated with their own predator density but the mc/m values of eggs were (Table 3). No significant correlation between the mc/m and density of *A. ovalis* was owing to the large value of the denominator of the mean when the predators at high density might distribute in aggregate.

Taylor's power law

The calculated logarithmic values of variances and means of eggs, larvae, nymphs, female and male adults of *A. ovalis* were fitted to estimate the regression equations with the intercepts ($\log a$) and the slopes (b) (Table 4). The estimated b 's were either significantly larger than 1 for eggs (1.2963), nymphs (1.0894), females (1.1627) and males (1.0289) or less than 1 for larvae (0.9723] (Table 4). The estimated values of $\log a$ of eggs, nymphs and females were significantly larger than 0, but the larval $\log a$ was not (Table 4). The estimated $\log a$ and b 's show that all the stage-specific *A. ovalis* expected to distribute in an aggregate pattern but larvae in a uniform one ($b < 1$) (Table 4). However, overall-stage populations of *A. ovalis* were contagious in the field.

Iwao's patchiness regression

The results of regression analyses by Iwao's patchiness model of mc 's to the means, the estimated α 's of eggs, larvae, nymphs, females and males are -0.207, -0.006, 0.036, 0.106, and 0.023, respectively, while β 's are 5.978, 0.899, 1.628, 1.380, and 1.425 (Table 5).

Table 3. Correlation coefficients between indices or coefficients of stage-specific spatial distribution and corresponding densities of *Amblyseius ovalis*

| Stage | ID (p-values) | Cx (p-values) | mc (p-values) | mc/m (p-values) |
|----------------|----------------|----------------|---------------|-----------------|
| Egg | 0.563 (0.001) | -0.043 (0.782) | 0.633 (0.001) | 0.563 (0.001) |
| Larva | -0.142 (0.383) | 0.230 (0.374) | 0.786 (0.001) | -0.038 (0.815) |
| Nymph | 0.199 (0.038) | -0.083 (0.520) | 0.467 (0.001) | 0.068 (0.480) |
| Female | 0.458 (0.001) | -0.019 (0.853) | 0.881 (0.001) | 0.028 (0.747) |
| Male | 0.085 (0.672) | -0.175 (0.534) | 0.276 (0.163) | 0.063 (0.754) |
| Overall stages | 0.259 (0.001) | -0.099 (0.256) | 0.648 (0.001) | -0.023 (0.775) |

Table 4. Estimated values of intercepts (log a) and slopes (b) of stage specific *Amblyseius ovalis* by regression analyses of variance to the means with Taylor's power law model

| Stage | log a (SE) | b (SE) | R-square | p-values |
|----------------|----------------|----------------|----------|----------|
| Egg | 0.420 (0.056)* | 1.296 (0.051)* | 0.907 | 0.001 |
| Larva | -0.041 (0.021) | 0.972 (0.017)* | 0.989 | 0.001 |
| Nymph | 0.126 (0.035)* | 1.089 (0.031)* | 0.920 | 0.001 |
| Female | 0.200 (0.023)* | 1.163 (0.023)* | 0.952 | 0.001 |
| Male | 0.049 (0.072) | 1.029 (0.061)* | 0.920 | 0.001 |
| Overall stages | 0.237 (0.024)* | 1.184 (0.028)* | 0.917 | 0.001 |

* The intercept log a and slope b values followed by an asterisk are significantly different from 0 and 1, respectively, according to Student t-test ($p=0.05$).

The statistical tests of 5 fitted regression equations showed that all α 's were not significantly different from zero except the female's (Table 5). It indicated the basic component units of the patches of the stage-specific populations were formed by single individual, but two or more females aggregated in the patch (Iwao, 1968; 1977). The α of egg and larva were less than 0, evidently, whenever the existence of an individual of egg and larva of *A. ovalis* would repulse another egg and larva, respectively, to coexist in the same patch. Those α and β values of male are not significantly larger than 0 and 1, respectively, showed that male population eventually distributed in random (Table 5). The β of the female was significantly larger than 1 and α was significantly larger than 0, the basic

component units of the females was patchy and the females in the patch were contagious (Table 5) (Iwao, 1977). In addition, the α 's is not significantly larger than 0 and β 's is significantly larger than 1, the nymph of *A. ovalis* formed patch but the patch included only one individual (Table 5) (Iwao, 1977). Since β was larger than 1 and α fell between 0 and -1, *A. ovalis* eggs and larvae formed patches and patches were distributed contagiously but eggs or larvae in the patch were single in number. Consequently, the presence of an individual of egg or larva in the patch reduced the probability of the presence of another individual in the same patch.

Discussion

Table 5. Estimated values of intercepts (α) and slopes (β) of stage specific *Amblyseius ovalis* by regression analyses of mean crowding to the means with Iwao's patchiness regression model

| Stage | α (SE) | β (SE) | R-square | p-values |
|----------------|----------------|----------------|----------|----------|
| Egg | -0.207 (0.212) | 5.978 (0.893)* | 0.401 | 0.001 |
| Larva | -0.006 (0.015) | 0.899 (0.115)* | 0.618 | 0.001 |
| Nymph | 0.036 (0.047) | 1.628 (0.298)* | 0.218 | 0.001 |
| Female | 0.106 (0.042)* | 1.380 (0.065)* | 0.777 | 0.001 |
| Male | 0.023 (0.099) | 1.425 (0.990) | 0.076 | 0.163 |
| Overall stages | 0.287 (0.099)* | 1.461 (0.135)* | 0.420 | 0.001 |

* The α and β values followed by an asterisk are significantly different from 0 and 1, respectively, according to Student t-test ($p=0.05$).

Distribution behavior of *A. ovalis* evaluated with ID, Cx, mc and mc/m

The random to uniform distributions of the stage-specific *A. ovalis* were evaluated with ID, Cx, mc and mc/m indices or coefficient except those of the egg's and female's evaluated by Cx (Table 1). The large values of denominators at the high densities of eggs and females produced the low frequencies of Cx values which were significantly larger than 0 among all the tested populations (Table 1). The high frequencies of 71% to 96% of the overall-stage populations evaluated by mc or ID or mc/m indices showed that *A. ovalis* distributed contagiously in the field (Table 1). A 65.19% of the distribution patterns of the overall-stage populations of *A. ovalis*, evaluated by Cx coefficients was also contagious (Table 1). From the aggregate tendency evaluated by the frequencies of the mc/m > 1, the stage-specific predatory populations performed differently due to the individual behavioral influences and the component characters or "patchiness" formation of the species (Lloyd, 1967). From the distribution patterns, evaluated by ID, Cx and mc, of 36.09%, 51.04%, and 36.09% of the stage-specific female adults, respectively, *A.*

ovalis populations intended to disperse in aggregation (Table 1). The 10.42% of mc/m values of females was larger than 1 (Table 1), which indicated that a few *A. ovalis* females produced "patch" and formed aggregate (Lloyd, 1967). Among all estimated egg dispersion indices or coefficients, frequencies of mc/m of the eggs (86.05%) and females (88.54%) were the highest ones, which indicated that most of *A. ovalis* distributed in uniform. A high degree of uniform distribution of egg and the females is interpreted as the result of the large values of denominators when the populations were in high density and the "mean number per individual of other neighbor individuals in the same quadrat or patch" was reduced.

Correlation between the estimated dispersion indices and prey densities

Very few estimated coefficient or index of *A. ovalis* was significantly ($p > 0.05$) and positively correlated with the prey densities (Table 2). Correlation coefficient between the prey densities and the values of ID's of eggs ($r=0.497$, $p=0.001$) and larvae ($r=0.569$, $p=0.001$), Cx's of larvae ($r=0.662$, $p=0.004$), and mc's of eggs ($r=0.510$, $p=0.515$) and larvae ($r=0.515$, $p=0.001$) were highly

significant. It showed *A. ovalis* exhibited a high tendency of aggregation behavior in egg or larval stages relating to the corresponding density of its prey; however, the other indices and coefficients of stage-specific populations of *A. ovalis* were not significantly correlated with prey densities and the population distributed in random to uniform pattern. Shih and Wang (1996) reported that *T. urticae* population in the field distributed in high aggregate. In addition, the values of the females dispersion indices and coefficients of predators were very low to correlate with their prey densities (ID: $r=0.002$, $p=0.978$; Cx: $r=0.046$, $p=0.662$; mc: $r=-0.011$, $p=0.896$; mc/m: $r=0.003$, $p=0.977$) which indicated the contagiousness of the predator females was not related to the prey densities or the degree of aggregate of the prey in the patches. Consequently, even if the female did aggregate, they would not correlate with the prey aggregate sites or patches. Although the overall stages showed that a very high frequency of population was contagious (Table 1), there was no evidence to prove that the contagiousness of *A. ovalis* was density-dependent to the prey (Table 2).

In conclusion, predatory females would normally lay a single egg in the prey patch and the distribution pattern of the almost-immobile larvae would therefore not aggregate in the egg-hatching sites from the extended influences of the egg-distribution. When the mean densities of the females are higher than one, the *A. ovalis* females might exhibit aggregate distribution (Fig. 1~4), although we find a low frequency of the predatory females with contagious distribution (Table 1).

Correlation between the estimated dispersion indices and predator densities

A. ovalis showed high and significant correlation coefficients between the predator densities and their responding values of ID of egg ($r=0.563$, $p=0.001$), mc of egg ($r=0.633$, $p=0.001$), larvae ($r=0.786$, $p=0.001$), female ($r=0.882$, $p=0.001$) and overall-stage ($r=0.648$, $p=0.001$), while all other indices or coefficients of stage-specific populations did not (Table 3). Consequently, the distribution pattern of *A. ovalis*, in terms of stage-specific, did not exist in a constant state, which varied with its own density or the prey density. The distribution of stage-specific *A. ovalis* was from random to uniform when the density was low in the field.

In conclusion, the values of ID, Cx, mc and mc/m were sufficient enough to evaluate the degree of contagiousness and randomness of *A. ovalis*. However, the assessment of contagious or random distribution of *A. ovalis* would be reasonably estimated with a large volume of data sets instead of a single or a limit set of indices or coefficients to show the probability (Tables 1, 2). Prey density and aggregation affects the contagiousness of *A. ovalis* which has been shown by the relationship between the estimated values of coefficients or indices and the prey density while the contagiousness of predatory eggs, larvae and females also exhibited the relation to their own densities (Table 2, 3).

Taylor's power law and Iwao's regression analyses

Evaluating the contagiousness of *A. ovalis* with the coefficient values, b 's, from Taylor's power law regression analyses, we found high degrees of aggregation in eggs ($b (=1.296) > 1$, $p=0.05$), females ($b (=1.163^*) > 1$, $p=0.05$), and overall-stage ($b (=1.184)$, $p=0.05$) (Table 4). When the results were interpreted with Iwao's intercepts α and coeffi-

icients β , the females *A. ovalis* did not produce an aggregate patch of egg in the prey patch ($-1 \leq \alpha (-0.207) < 0$; $\beta (=5.978) > 1$, $p=0.05$), although the female contagiously distributed in a patch ($\alpha (=0.106) > 0$, $p=0.05$; $\beta (=1.380) > 1$, $p=0.05$) (Table 5). Therefore, the females *A. ovalis* exhibited aggregate distribution among and within the patches while the overall stage population also exhibited contagiously in the field ($\alpha (=0.287) > 0$, $p=0.05$; $\beta (=1.461) > 1$, $p=0.05$) (Table 5).

The evidences indicated (1) stage-specific populations dispersed in random and overall-stage distributions were in aggregate evaluated by the 4 indices or coefficients, (2) the degree of aggregate of the egg and the female were higher than those of the other stage-specific populations evaluated by ID, Cx and mc, (3) the high degree of aggregation of all stage-specific populations (slope $b > 1$) and the eggs and the females ($b > 1$, $\log a > 0$) were also contagious by Taylor's power law regression analyses, (4) females aggregated to form patch but each patch contained only 1 egg, evaluated by Iwao's α and β values. Consequently, the eggs, larvae and females of *A. ovalis* are contagiously dispersed among the patches but the eggs in each patch are singularly dispersed. The female egg-laying behavior produced negative coexistence of eggs in the patch, evaluated by ID, Cx, mc, mc/m, and Iwao's α and β values, even the females showed a higher frequency of contagious distribution than those of other stages. Represented by the estimated values of the dispersion indices or coefficients, the degree of contagiousness of the eggs and the larvae except the other stage-specific and overall-stage populations was significantly correlated with their corresponding prey densities. The contagiousness

of the overall-stage population evaluated by the values of ID, Cx, mc, and mc/m was high and retained a high frequency of the population to be contagious, i.e., the population distributed in aggregate. Therefore, *A. ovalis* females seemed to distribute in random or uniform at low density ($r=0.458$, $p=0.001$ for ID; $r=0.881$, $p=0.001$ for mc) (Table 3), and the female egg-laying behavior of producing single-egg in each of the aggregate prey cohort resulted in the aggregation among the egg-patch instead of within the egg-patch, even though the degree of the prey density in the unit and their contagiousness was high. However, the influences of (1) the density-dependent of the female egg-laying behavior from time to time, and (2) the protraction of arrestment time of the females in the patch on the egg-distribution pattern or eggs per patch need further intensive study.

The distribution of the patches of the larvae was uniform ($\alpha (-0.006) \leq 0$, and $\beta (0.899) < 1$) and the number of individuals in the patch was single. The contagiousness of the larvae was significantly correlated with the corresponding density of *T. urticae*. We infer, the contagiousness of the larvae in each patch was the result of extended influences of egg-distribution and the prey density. The basic component of female population was patchy and the individuals in the patches were contagiously distributed ($\alpha (0.106) > 0$, and $\beta (1.380) > 1$); however, the contagiousness of the females was density-independent from prey and predators.

In conclusion, we suggest the spatial distribution of *A. ovalis*, if not all but at least a large proportion of the populations, is stage-specific, density and behavior dependent. The predators at or near the low densities

distributed indistinguishably from random to uniform. The density-dependence of the dispersion indices (or coefficients) or the contagiousness of *A. ovalis* on prey and its own population densities need further study to estimate the progressive and disproportional changes of the range of spacing between individuals. In other words, the contagiousness and evaluated dispersion indices or coefficients depending on their density levels need further intensive study. The density-dependent disproportional changes of dispersion behavior of *A. ovalis*, the populations with large volume of samples containing 0 counts and very low density urged us to develop a present-absent sampling technique to simplify the population studies. The limitation of prey density and patchy size on the arrestment rates and the prolongation of arrestment time of the predators in the patch are vital and require further study to offer the basic information of disproportional changes of dispersion behavior and for mass rearing of *A. ovalis* on *T. urticae*.

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蟎類捕食者—食餌系統之空間動態：卵形捕植蟎 (*Amblyseius ovalis* (Evans)) 對其產卵行爲及二點葉蟎 (*Tetranychus urticae* Koch) (Acarina: Phytoseiidae: Tetranychidae) 密度與聚集之反應

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摘 要

楊桃上卵形捕植蟎 (*Amblyseius ovalis* (Evans)) 之五年 (1990~95) 250 組族群資料依分布指數 (ID), Green's 分布係數 (Cx), Lloyd 平均聚集指數 (mc) 及聚落度指數 (mc/m), Taylor 乘冪定律迴歸 ($\log a$ 及 b), 及 Iwao 聚落度迴歸 (α, β) 等分析結果評估齡別差之空間分布型。卵形捕植蟎各齡期之空間分布傾向隨機至均勻, 但是卵、雌成蟎及全部齡期總合之族群則傾向聚集分布。依 Taylor 乘冪定律迴歸分析所獲得之截距 $\log a$ 及斜率 b 評估各期之聚集度, 捕植蟎卵及雌成蟎的聚集度 (degree of contagiousness) 為各期中最高。卵形捕植蟎之分布指數或係數值與其食餌二點葉蟎 (*Tetranychus urticae* Koch) 密度間呈極低相關關係, 顯示卵形捕植蟎之聚集度為低食餌密度依變。依 Iwao 迴歸分析所測得的截距 α 及斜率 β 值, 評估得卵在小聚落 (patch) 中之組成單位為“單一個體”, 但多個體的雌成蟎則為小聚落之構成單元。雌成蟎產單卵於聚集分布之葉蟎小聚落內的行爲, 顯然是構成捕植蟎卵聚集之主因。該等小聚落內捕植蟎卵或幼蟎之單一均勻分布及斥拒機制 (另一卵或幼蟎同時出現或存在同一小聚落內之機制) 應為雌成蟎在食餌聚落內之產卵行爲特性所致, 亦為構成該卵形捕植蟎種空間分布特性之主因。

關鍵詞：空間分布、捕食者食餌系統、密度、產卵行爲