Spatial Distribution of Scale Insects: Comparative Study Using Taylor's Power Law

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ABSTRACT   Spatial distribution (quantified by Taylor's power law) and population densities of three scale insect species (Homoptera: Coccoidea) were investigated. The olive scale, *Parlatoria oleae* (Colvee), was studied on young and old twigs, and on the spurs of apple trees. The Israeli pine bast scale, *Matsucoccus josephi* Bodenheimer et Harpaz, was studied on the stem, branches, and crown of *Pinus halepensis* Miller. The effect of fruit phenology on the spatial distribution of the citrus mealybug, *Planococcus citri* (Risso), was studied on grapefruit trees. The highest density of the olive scale was registered in the spurs, whereas the Israeli pine bast scale was more abundant on the stem. The citrus mealybug was more abundant during October. There was no effect of the host section or phenology on the within-species distribution of the three scales, supporting previous claims that the species level of aggregation is a species constant. The species index of aggregation for the three scale insects was 1.3 for the olive scale, 1.9 for the bast scale, and 1.6 for the citrus mealybug. It is suggested that the observed spatial patterns are the result of the intrinsic behavior of the scales (e.g., thigmotaxis and negative phototaxis during crawlers dispersal), the morphological characteristics of the host-plant tissue, and the differential activity of natural enemies. The relatively low level of aggregation of the olive scale is probably related to the activity of an efficient natural enemy, a factor which is negligible in the other two scale species.

KEY WORDS   *Parlatoria oleae*, *Matsucoccus josephi*, *Planococcus citri*

THE SPATIAL DISTRIBUTION OF organisms is an intrinsic characteristic of the species, and it is shaped by behavioral and environmental factors (Taylor 1984). Thus, knowledge on the spatial distribution patterns of insect populations may provide information on the behavioral traits of the insect species and on the effects of environmental factors on the population. Additionally, knowledge of the spatial distribution of insects has been applied in agricultural entomology and insect ecology to design reliable and efficient sampling schemes (e.g., Shaw et al. 1983, Ekbom 1985, Thistlewood 1989, Steiner 1990, Yaninek et al. 1991, Ho 1993).

Taylor's power law was first proposed in 1961 to describe the spatial patterns of dispersion in populations of organisms (Taylor 1961). The power law suggests that the mean (X) and variance (S^2) of spatially distributed populations are related by a power equation of the form $S^2 = aX^b$. Since then, Taylor and coworkers have substantiated this relationship with many studies ranging from protozoa to human populations and a variety of sampling programs (Taylor 1961; Taylor et al. 1978, 1980;

Taylor & Woiwod 1980; Taylor 1984). Taylor (1984) also contends that the slope (b) is an index of the spatial distribution characteristic of the species, and that the intercept (a) is the sampling factor that affects the variance to mean ratio. Although this relationship between the mean and the variance holds for most of the populations investigated, some studies have shown that b is not always a characteristic trait of the species, and that behavioral patterns and environmental factors affect the value of the index (Banerjee 1976, Davis & Pedigo 1989).

The aim of the current study was to investigate and contrast the spatial distribution of three scale insects: the olive scale, *Parlatoria oleae* (Colvee) (Diaspididae), the Israeli pine bast scale, *Matsucoccus josephi* Bodenheimer et Harpaz (Matsucoccidae), and the citrus mealybug, *Planococcus citri* (Risso) (Pseudococcidae). In addition, we investigated the effect of the host-tree section (e.g., the microenvironment) and fruit phenology (in the case of the citrus mealybug) on the within-species distribution pattern. The studied species represent three families in the insect superfamily of Coccoidea. The olive scale is a polyphagous insect that feeds on parenchymal tissue of its hosts. The Israeli pine bast scale, endemic to the east Mediter-

ranean, feeds on the parenchymal tissue of two closely associated pine species (stenophagous). The citrus mealybug is a polyphagous insect that feeds on the phloem of its hosts. Scale insects differ from other insect taxa because their distribution pattern is shaped by first instars (the crawler stage). The adult females display neoteny, and are sessile or move very short distances. We suggest that the typical thigmotactic behavior of the crawler (Bodenheimer 1951) is the major factor determining the distribution of the scale population. Thus, based on their common thigmotactic behavior, we hypothesize that the primary spatial distribution patterns of the three scales (displayed by Taylor's power law) should be alike, and that differences between the three scale insect species are the result of distinct environmental factors (e.g., host genotypic resistance, parasitization efficiency) acting on the scale population (Hanks & Denno 1993).

Materials and Methods

Sampling. *Olive Scale.* Sampling of the scale was conducted at two apple orchards in the Golan (≈800 m above sea level). One orchard, Ein Ziwan, consisted of 20-yr-old trees and was characterized by high population levels of the scale. The heavily infested trees in this orchard were concentrated mainly in single half-hectare plots. In the second orchard, Keshet, which consisted of 11-yr-old trees, the infestation was low and the scale was conspicuous only on a few trees located in different sectors of the plantation. In both cases the spacing between trees was 4.5 by 3.0 m, and tree height ranged between 2.5 and 5.0 m. In both orchards, the main apple variety was 'Orleans'. No pesticides were used throughout the study.

In Ein Ziwan, five trees infested with the scale were selected at random (progressive numbers were assigned to all the infested trees in the plot). These trees were used throughout the study. In Keshet, four trees were selected arbitrarily. These trees were sampled only twice (May and July 1991) because, as a result of high parasitization rates, olive scale populations were decimated at the beginning of the study. The canopy of the nine trees was split into upper and lower divisions, and into north–east and south–west directions. In addition, branches were divided into old twigs (twigs >1 yr), young twigs (twigs <1 yr), and spurs (fruit-bearing twigs). Sampling consisted of arbitrarily removing one twig of each type (5 cm long) per division and direction (a total of four twigs of each type per tree) per sampling date. Samples were then examined under magnification, and the number of adult females per square centimeter was determined. Samples in Ein Ziwan were taken during the spring and summer of 1991 (mid-May, early July, mid-August and early October) and during the summer of 1992 (mid-June and mid-August). Thus, in Ein Ziwan, 20 twigs of each type were sampled on each date, and in Keshet, 16 twigs of

each type were sampled on each one of the two dates. Data derived from the two orchards were used for Taylor's spatial distribution analysis, whereas only the data of Ein Ziwan were used to analyze the effect of twig type and division-direction on the population load of the scale insect.

Israeli Pine Bast Scale. Two *Pinus halepensis* stands (Eshta'ol and Massu'a, 23 and 30 yr old, respectively), located in the Judean foothills, were selected. Both study sites are located at an elevation of 300 m above sea level, and stock density was ≈700–800 trees per hectare. Both stands displayed typical symptoms of injury by the scale. Pesticides were not used in any of the stands during the study period.

Forty pine trees were sampled at random (20 pines per forest), by numbering all the pines located within an area of half hectare in the center of the stands. Sampling was performed during a 2-yr period. At each sampling date (winter 1984, spring 1985, autumn 1985, and early spring 1986), five pines per forest were cut and examined in the laboratory. Each pine was divided into three different sections: stem (tree trunk), branches (woody growth emerging from the stem and bearing the twigs), and crown (a term referring to the twigs in the canopy). The stem was divided into 10 segments of approximately the same bark area and in each segment the total amount of larvae per 1,000 cm^2 was determined. The scale population on the branches was sampled as follows: one-third of all the branches in each pine (between five and eight branches of 4 m long per tree) were arbitrarily selected. Branches were then subdivided into three segments according to the distance from the stem (proximal, middle, and distal). From each segment, 1,000 cm^2 were examined and the total number of larvae were recorded. The scale population on the crown was sampled as follows: from each of the above sampled branches, each third twig along the branch was cut (between 10–20 twigs per branch). The total number of larvae along 25 cm of twig growth was determined. The results were then converted to amount of scales per 1,000 cm^2 surface of crown.

Citrus Mealybug. The spatial distribution of *P. citri* among grapefruit fruits, *Citrus paradisi* Macfadyen, and its abundance throughout the season (from June to October) was determined by fruit sampling. The study was conducted in two pesticide-free orchards in the Western Galilee (Rosh-Haniqra: 12-yr-old trees ['Sun Rise'] and Regba: 30-yr-old trees ['Marshal']. In each grove, 10–20 trees per sampling date were selected at random. Citrus trees located within an area of a half hectare in the center of the orchard were numbered, and random numbers were used to select trees. Different trees were used in each sampling date. During the 2 yr, 10 fruits per tree were arbitrarily removed from the crown at 1-mo intervals. The fruits were examined in the laboratory and the number of mealybugs per fruit was recorded.

Table 1. Average density of adult female olive scale ± SD per square centimeter in the three sections of the apple tree and during the different sampling dates

Sampling date	Tree section		
	Young twig	Old twig	Spur
May 91	4.51ab ± 1.39	2.21b ± 0.71	6.92a ± 2.16
July 91	1.99b ± 0.34	2.39b ± 0.79	8.56a ± 1.74
Aug. 91	0.50b ± 0.34	1.21b ± 0.51	5.75a ± 0.74
Oct. 91	0.04c ± 0.03	1.61b ± 1.12	7.16a ± 1.43
June 92	0.05c ± 0.02	1.64b ± 1.05	6.82a ± 1.06
Aug. 92	0.04c ± 0.05	0.64b ± 0.83	2.47a ± 0.96
Total	1.19c	1.62b	6.28a

Within row means followed by the same letter are not significantly different ($P > 0.05$; SNK test).

Table 2. ANOVA table on population densities of adult olive scale

Source	df	SS	F	P
Block	4	3.7143	5.18	<0.01
Section (twig type)	2	80.2972	224.09	<0.01
Direction	3	1.7802	3.31	0.03
Section × Direction	6	0.9187	0.85	0.54
Error (between subjects)	44	7.8833		
Date	5	15.0741	3.01	<0.01
Date × Block	20	21.5981	9.99	<0.01
Date × Section	10	15.9428	14.75	<0.01
Date × Direction	15	3.6179	2.23	<0.01
Date × Section × Direction	30	4.2920	1.32	0.15
Error (date)	220	27.7744		

Statistical Analysis and Distribution Indices. Because one of the apple orchards (Keshet) was sampled only during the first two dates, the analysis testing twig type (young twig, old twig, and spur), direction, and date of effects on olive scale density was done only on the data from one orchard (Ein Ziwan). The model used was of a repeated measurements analysis of variance (ANOVA) (SAS Institute 1990) on five trees, each composed of three types of twigs and four directions. The trees were considered blocks, and their interaction with directions and twig type was pooled for the *between subjects* error term. Data were transformed to $Log_{10} + 0.1$ to homogenize the variance. The Student–Newman–Keuls (SNK) test (SAS Institute 1990) was used to separate means. Data on the Israeli pine bast scale were analyzed with a general linear model (SAS Institute 1990). Variability between season and forest was analyzed through the error term of pines within forest and season. For the differences between sections (stem, branches, and crown) we used the within pine error term. Number of bast scales was transformed ($Log_{10} + 1$) to homogenize the variance. The SNK test was used to separate means. Differences in citrus mealybug loads during the four periods (June, July, September, and October), and between orchards, were analyzed with a two-way ANOVA (SAS Institute 1990). Data from the same period on the 2 yr were pooled for the analysis. Data was transformed ($Log_{10} + 0.1$) to homogenize the variance. Replicates represented the average amount of mealybugs per fruit in each sampled tree. The SNK test was used to separate means.

Indices of spatial distribution were calculated for the three scales by regressing the variance as a function of the mean (power law). In the case of the olive scale, the mean and the variance for each one of the tree sections (young twigs, old twigs, and spurs) was calculated for each sampled tree (four samples of each section per tree). For the Israeli pine bast scale, the mean and variance in each one of the sections (stem, branches, and crown) was calculated for each pine (more than 10 samples of each section per pine). Similarly, the

mean loads and variance of citrus mealybug were obtained by averaging the scale density per fruit in each of the sampled trees (10 samples per tree). In the case of the mealybug, the data per period (June, July, September, and October) includes the two sampling seasons (1991–1992). Differences in slope within species were analyzed with a test of homogeneity of regression slopes (Sokal & Rohlf 1981).

Results

Table 1 shows the average number of olive scale per section and sampling date and Table 2 displays the ANOVA table for the olive scale densities. In general, the spur was the tree section with significantly higher olive scale loads during all the sampling dates ($P < 0.01$). Olive scale loads in both the young and old twig were similar, except for some sampling dates in which the old twig supported higher loads of the scale. The olive scale density in the young twig declined steadily with time. This seems to be related to the rapid increase in twig size that takes place during a short period. By August 1992, population loads of the scale were significantly reduced in the three sections because of the buildup of parasitoid populations. The direction within trees had a small and inconsistent effect (over time) on scale loads (data not shown). In general, population loads were significantly lower only on the south–west upper-crown direction ($P = 0.03$).

Average loads of *M. josephi* in the three sections of the pines, and the ANOVA table, are shown in Tables 3 and 4. Significantly higher population loads of the scale were recorded on the stem ($P <$

Table 3. Mean density of the Israeli pine bast scale in the different pine sections

Pine section	Avg scale density ± SD (larvae per 1,000 cm²)
Crown	38.2b ± 35.6
Branches	26.6b ± 27.5
Stem	115.7a ± 55.6

Means followed by the same letter are not significantly different ($P > 0.05$; SNK test).

Table 4. ANOVA table on population densities of the Israeli pine bast scale

Source	df	SS	F	P
Forest	1	1.5842	0.61	0.44
Season	3	25.9867	3.35	0.03
Forest × Season	3	15.5915	2.01	0.13
Error (between pines)	32	90.0530		
Section	2	29.3741	92.60	<0.01
Season × Section	6	14.0675	14.78	<0.01
Error (within pines)	3,034	710.6048		

Table 6. ANOVA table on population densities of the citrus mealybug

Source	df	SS	F	P
Period	3	20.6278	20.52	<0.001
Orchard	1	1.1535	3.44	0.06
Period × Orchard	3	2.9707	2.96	0.03
Error	272	91.1437		

0.01). Average scale density on the branches and crown was similar. No differences were found between forests ($P = 0.44$). Seasonal differences ($P = 0.03$) resulted from the phenology of the scale.

Population loads of the citrus mealybug in October were significantly higher than those in September and June, but similar to that of July ($P < 0.01$) (Tables 5 and 6). Average number of mealybugs per fruit was similar during July and August, and significantly lower in June. No significant differences were found between orchards ($P = 0.06$).

The level of aggregation (b) of the olive scale in the three sections was very similar: young twig, $b = 1.25 \pm 0.09$, $n = 24$; old twig: $b = 1.31 \pm 0.12$, $n = 25$; spurs, $b = 1.39 \pm 0.10$, $n = 26$. No differences were found between the three slopes ($F = 0.22$; df = 2, 68; $P > 0.75$). The combined regression for the three sections is shown in Fig. 1. The common slope was $b = 1.32 \pm 0.08$. The degree of aggregation in the Israeli pine bast scale was in general higher than in the olive scale. The slopes for the three sections of the pines were statistically similar ($F = 2.06$; df = 2, 114; $0.25 > P > 0.10$): stem, $b = 2.05 \pm 0.15$, $n = 40$; branches, $b = 1.86 \pm 0.18$, $n = 40$; crown, $b = 1.81 \pm 0.12$, $n = 40$. The combined regression and slope ($b = 1.90 \pm 0.07$) for the three sections of the pines are shown in Fig. 2. Regarding the citrus mealybug, the index of aggregation was intermediate to that of the olive scale and the pine bast scale at all the dates sampled: June, $b = 1.50 \pm 0.09$, $n = 20$; July, $b = 1.56 \pm 0.05$, $n = 40$; September, $b = 1.63 \pm 0.12$, $n = 40$; October, $b = 1.66 \pm 0.17$, $n = 40$. No differences were found among the four slopes ($F = 0.76$; df = 3, 352; $0.75 > P > 0.50$). The combined index of aggregation for the mealybug was $b = 1.61 \pm 0.09$ (Fig. 3). For the three scale insects, the slope was significantly higher than 1 ($P < 0.05$).

Table 5. Density of citrus mealybugs on grapefruit

Period 1991–1992	Avg amount of mealybugs per fruit ± SD
June	0.09c ± 0.07
July	1.87ab ± 0.32
Sept.	1.58b ± 0.35
Oct.	1.91a ± 0.22

Means followed by the same letter are not significantly different ($P > 0.05$; SNK test).

Discussion

Although the within-species index of aggregation (b) may differ with varying conditions or life stage, there is ample evidence that b remains constant among populations when environmental conditions vary little (Taylor et al. 1988). In the case of the three species of scale insects analyzed in this study, b was not affected by plant gross architecture, nor by tree phenology (in our case fruit development). These findings suggest that the investigated micro-environments (young and old twigs, spurs, crown, stem and branches, and changes over time in fruit development) differ by little or have no marked effect on the spatial distribution of the studied scales. In addition, our results suggest that low sample density—as exemplified by mealybugs in June and the olive scale in young and old twigs—does not affect the spatial distribution of the studied scales. These results demonstrate the within-species constancy of b, and support the use of Taylor's power law in the investigation of the spatial distribution of scale insects.

Five kinds of spatial patterns have been suggested: vectorial (caused by linear environmental gradients), reproductive (producing density gradients), social (caused by the within-species behav-
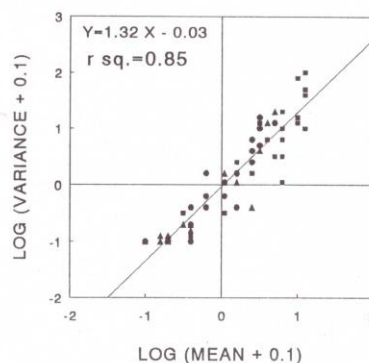

Fig. 1. Combined regression line for the olive scale population mean (scale insects per square centimeter) and variance in the three sections of the apple tree (■, young twigs; ▲, old twigs; and ●, spurs).
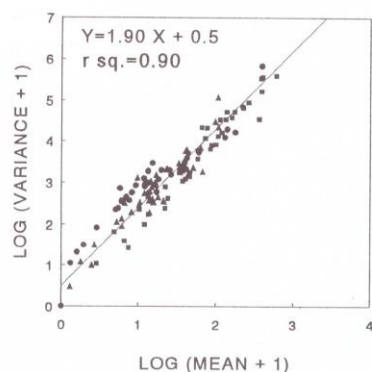
Fig. 2. Combined regression line for the population mean (scale insects per 1,000 cm²) and variance of the Israeli pine bast scale in the three pine sections (■, stem; ▲, branches; and ●, crown).
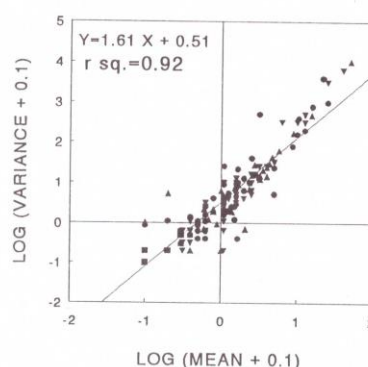
Fig. 3. Combined regression line for the citrus mealybug population mean (mealybugs per fruit) and variance for the four studied periods. ■, June; ▲, July; ●, September; and ▼, October.

ior), coactive (caused by behavioral interactions between species), and stochastic (the result of randomizing environmental processes) (Taylor 1984). Different degrees of aggregation may be obtained by any of these mechanisms. For example, high population densities combined with suitable microhabitats may result in reduced levels of aggregation, whereas social behavior may produce stronger aggregated distributions (Soberon & Loevinsohn 1987). In the case of the three scale insects investigated in the current study, the analysis of their spatial patterns showed a significantly aggregated distribution. Dispersal behavior in scale insects may explain their aggregative distribution patterns. During settlement, crawlers tend to settle close to the parent female (Greathead 1990). In addition, scale insects display high thigmotactic behavior and negative phototaxis, thus, selecting crevices and cracks of the host plant, or the areas of contact between the fruit and sepals (in the case of the citrus mealybug), as preferred feeding sites (Bodenheimer 1951). The tendency to aggregate in the three scale species investigated could, therefore, be explained by the short distance crawlers tend to move away from the mother scale or the ovisac, and by their characteristic thigmotactic behavior. However, the different degree of aggregation between the three species could result from their accessibility to suitable host-feeding tissue. Whereas crawlers of the pine bast scale avoid settling on many portions of the bark area (e.g., bark affected by resinosis and bark with heavy cork layers), the olive scale is able to colonize most of the above-ground woody parts of the apple tree (Huffaker et al. 1962). Hence, pine bast scales tend to aggregate in available patches on those places of

the bark that are more suitable for their development, thus, displaying a strong aggregation pattern, whereas the olive scale will tend to spread more evenly throughout all the woody parts of the tree showing a less-marked aggregative pattern. Regarding the mealybug, once an individual female scale colonizes a fruit, most of her offspring will settle around the stalk and near the mother. Abscission of immature fruit follows after a certain density of scales per fruit is reached and the attachment between the fruit and the stalk weakens (Mendel et al. 1991). Thus, it is expected that the level of aggregation should be high as a result of the mealybug tendency to concentrate around the stalks—at the beginning under the sepals and then in the surrounding tissue.

Level of aggregation in scale insects may also result from coactive factors. The host or prey, patch size, and distance between patches could be affected by the specific foraging behavior of their parasitoids or predators, or both (e.g., functional and numerical response, movement, searching efficiency). Several studies have shown that parasitized hosts can display an aggregated distribution in space (e.g., Carroll & Luck 1984, Casas 1990). However, Rogers (1972) suggested that spatial randomness in the distribution of parasitized hosts may arise when the degree of parasitism is high. Pressure of natural enemies on the host population varies among the three scale insects. *Aphytis maculicornis* (Masi) (Hymenoptera: Aphelinidae) is the dominant enemy in Israel of the olive scale (Applebaum & Rosen 1964, Cohen & Nestel 1993). This parasitoid as well as other congeneric species are known as effective natural enemies of scale insects (Rosen & DeBach 1990). Thus, the

high degree of parasitism exerted by parasitoids may contribute to the observed mild aggregative pattern of the olive scale ($b = 1.32$). In this respect, Murdoch et al. (1984) reported that the spatial distribution of parasitized olive scale by *Aphytis* Howard shows a nonaggregative pattern. In contrast to the above situation, the main natural enemies of the Israeli pine bast scale, *Elatophilus hebraicus* Pericart (Hemiptera: Anthocoridae), and that of the citrus mealybug, *Anagyrus pseudococci* (Girault) (Hymenoptera: Encyrtidae), are considered inefficient regulators of their preys (Carmi 1989, Mendel et al. 1991). Hence, it is expected that host patches of the citrus mealybug and the Israeli pine bast scale will not be cleared by natural enemies as efficiently as those of the olive scale (though populations of the mealybug are attacked by more efficient natural enemies than those of the pine bast scale).

The established spatial distribution patterns of insect populations seem to be the result of their intrinsic behavioral patterns, the morphological traits of the host plant, and the overall effect of their major mortality factors. In the case of the three scale insects investigated in the current study, a similar basic distribution pattern could be expected as a result of their common dispersal behavior (short walking distances of crawlers and thigmotaxis). Deviations from this expected basic distribution pattern, thus, seem to arise from the interaction of the three scales with their different habitats and levels of predation pressure.

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