THE WHITE PEACH SCALE, *PSEUDAULACASPIS PENTAGONA* (TARGIONI-TOZZETTI) (HOMOPTERA: DIASPIDIDAE): LIFE HISTORY IN MARYLAND, HOST PLANTS, AND NATURAL ENEMIES

Lawrence M. Hanks and Robert F. Denno

(LMH) Post-doctoral Fellow, Department of Entomology, University of California, Riverside, California 92521; (RFD) Professor, Department of Entomology, University of Maryland, College Park, Maryland 20742.

Abstract.—The white peach scale, *Pseudaulacaspis pentagona* (Targioni Tozzetti), is a severe pest of woody ornamentals and fruit trees throughout the world. In this paper we review information on the life history, host plant relationships, and natural enemies of *P. pentagona*. Also, we present new data on the life history (fecundity and primary sex ratio), population biology (seasonal development, dispersal, dispersion and host plant range), and natural enemies (parasitoids, hyperparasitoids and predators) of *P. pentagona*.

Key Words: Biological control, host plants, natural history, natural enemies, *Pseudaulacaspis pentagona* (Targioni Tozzetti), white peach scale

The white peach scale, *Pseudaulacaspis pentagona* (Targioni Tozzetti), is one of the most damaging armored scale pests of woody ornamentals and fruit trees in the world (Beardsley and Gonzalez 1975, DeBach and Rosen 1976, Johnson and Lyon 1988, Miller and Davidson 1990). By killing mulberry trees, *P. pentagona* threatened the Italian silk industry (Howard 1916), and the widespread ornamental oleander was nearly eradicated from Bermuda (Simmonds 1958, Bennett and Hughes 1959). *P. pentagona* was first recorded in the United States in Florida in the early 1900s (Gossard 1902) where it devastated the peach industry (Gossard 1902, Van Duyn 1967) and continues to be a severe pest throughout the southeastern United States (Johnson and Lyon 1988).

P. pentagona is native to China (Gossard 1902, Howard 1916, Murikami 1970), but is presently distributed throughout western Europe, Asia, Australia, Africa, the Carib-

bean and Pacific Islands, and the Americas where it feeds on a tremendous diversity of host plants (Davidson et al. 1983). In the United States, it occurs from Florida west to Texas and north to Maryland and Tennessee (Davidson et al. 1983).

P. pentagona has long been confused with its sibling congener, the white prunicola scale, *P. prunicola* (Maskell). Both species are broadly sympatric, share many host plant species and occur abundantly throughout Maryland and Virginia (Davidson et al. 1983, Rhoades et al. 1985). Despite the confusion of these two taxa in the early literature, they can be easily separated by taxonomic characters and also the color of their eggs (Davidson et al. 1983). Because eggs of *P. pentagona* are conspicuously white or coral in color, while those of *P. prunicola* are pink, the species can be identified where this characteristic is reported (Davidson et al. 1983). Also, differences in host plant utilization exist between these two armored
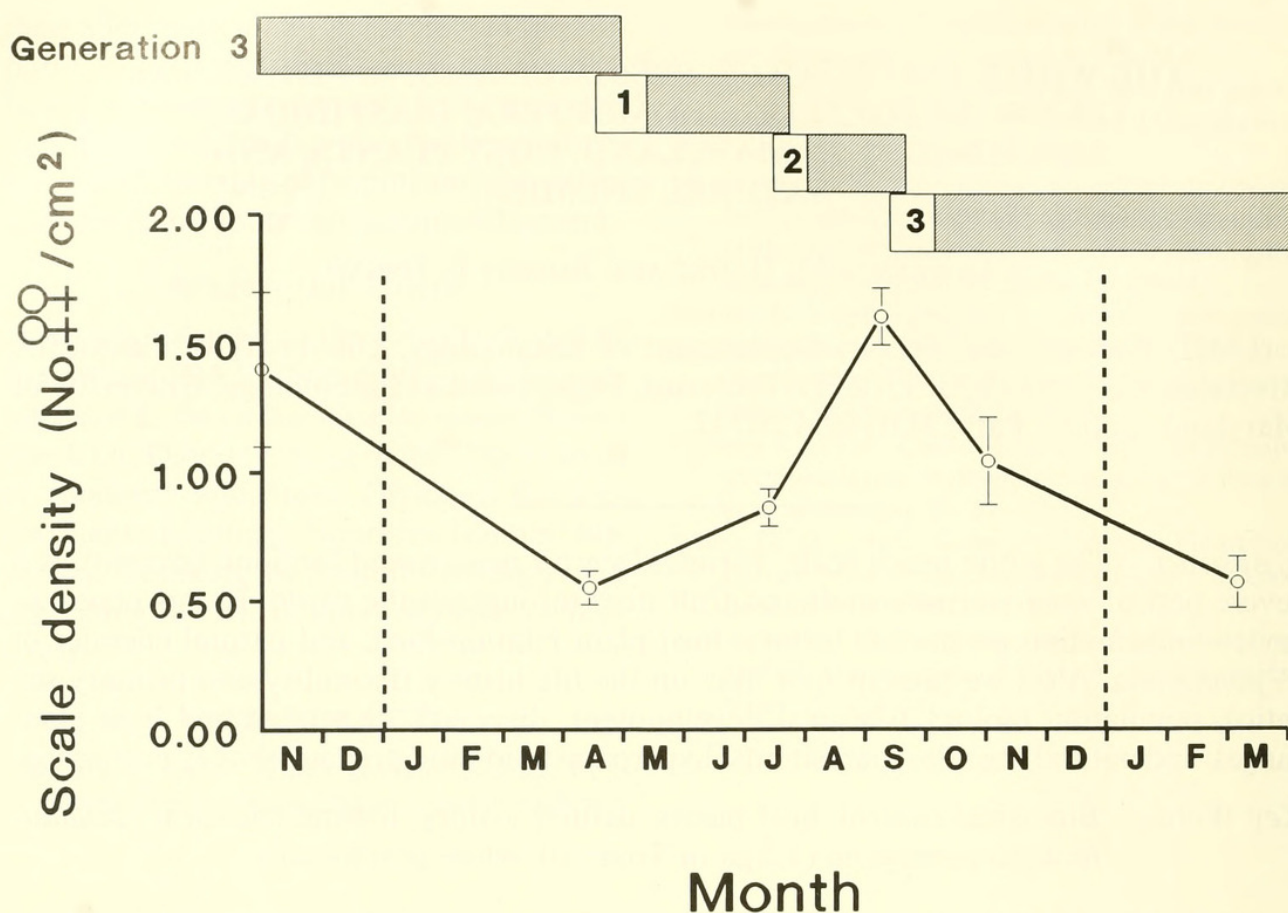
Fig. 1.   Average density (±SE) of female *P. pentagona* (No./cm²) on mulberry trees in the urban landscape of College Park, MD. Means are based on 20 samples (cuttings) taken from 5 field trees in April, July, September and November 1986, and March 1987. Samples taken during the first, second, and third scale generations were when most females were second instars (see Hanks 1991 for detailed methods). Bars at the top indicate the 3 annual generations. The occurrence of the crawler stage (unshaded bars) and the second instar + adult stage (shaded bars) are shown for each generation.

scales. *P. pentagona* can be readily cultured on potatoes, while *P. prunicola* survives poorly on this host (LMH unpublished data).

In this paper we review information on the life history, host plant relationships, and natural enemies of *P. pentagona*. We also present new data on the life history (fecundity and primary sex ratio), population biology (season development, dispsersal, dispersion and host plant range), and natural enemies (parasitoids, hyperparasitoids and predators) of this important economic pest.

LIFE HISTORY

Seasonal development

In the equatorial climate of Trinidad, *P. pentagona* reproduces year round (Bennett 1956), while at more temperate latitudes, 2 to 5 discrete generations per year occur depending on the regional climate (Bennett and Brown 1958, Yonce and Jacklin 1974, Kozarzevskaja and Mihajlovic 1983, Davidson et al. 1983). In Maryland, there are three generations per year with highest densities of adults in August–October (Fig. 1). Successful overwintering takes place only as fertilized adult females (Bennett and Brown 1958, Kuitert 1967, Bobb et al. 1973, pers. obs.). Some females deposit eggs prior to the onset of winter, but these eggs usually fail to survive (Yonce and Jacklin 1974, Nalepa and Meyer 1990, pers. obs.). Development time from egg through adult ranges from 35 to 90 days (Bennett and Brown 1958, Hughes 1960, Van Duyn 1967, Kuitert 1967, Kozarzevskaja and Mihajlovic 1983). Development time for the spring and

summer generations in Maryland is 60 and 50 days respectively and is inversely temperature dependent (LMH unpublished data).

Mating, Sex Determination, Oviposition and Fecundity

Males begin searching for mates immediately after emergence from the pupal case (LMH pers. obs.). Males locate mates in response to a pheromone emitted by females (Heath et al. 1979, Einhorn et al. 1983). Both sexes commonly mate with several individuals and during mating the male stands on top of the female's cover (Van Duyn and Murphey 1971, pers. obs.).

Sex determination in *P. pentagona* as well as other armored scales is haplodiploid (Bennett and Brown 1958). The chromosome number for *P. pentagona* females (2N = 16) and males (N = 8) is twice that of most other diaspidids suggesting a tetraploid origin (Brown and Bennett 1957, but see Nur 1990). In male eggs, paternal chromosomes become condensed during mitotic development and all functional chromosomes are maternal in origin, while female eggs contain functional chromosomes from both parents (Bennett and Brown 1958). Yeast-like symbionts are transmitted transovarially and may play a role in scale nutrition (Brown and Bennett 1957, Miller and Kosztarab 1979, Tremblay 1990).

Adult females usually deposit eggs for periods less than 10 days, but oviposition may be extended in warmer climates (Kuitert 1967, Yonce and Jacklin 1974). The eggs and first instar crawlers of *P. pentagona* are both sexually dichronic and dimorphic (Bennett and Brown 1958). First-deposited eggs are female and are coral in color, which are followed by white male eggs. Generally, the primary sex ratio is 1:1 (Brown and Bennett 1957, Van Duyn and Murphey 1971) and average lifetime fecundity ranges from 50 to 200 eggs per female (Bennett and Brown 1958, Kuitert 1967, Van Duyn and Murphey 1971, Bobb et al. 1973, Ball 1980, Yasuda 1983a). Unmated females do not produce eggs, but can live as long as 60–75 days (Bennett and Brown 1958, Van Duyn and Murphey 1971, LMH unpublished data).

We estimated the fecundity and primary sex ratio of *P. pentagona* from 110 infested cuttings taken from 25 mulberry trees in College Park, MD in February 1986 (see Hanks 1991 for detailed methods). Each cutting was placed in a petri dish and ringed with Vaseline®, and all dishes were maintained in an incubator at 26°C and 70% RH. Average fecundity and sex ratio were estimated at 76.7 and 0.96:1 (M:F) by counting and sexing (by color) the emerging crawlers entrapped in the vaseline and dividing the count for each cutting by the number of adult females/cutting.

Fecundity can be increased by raising *P. pentagona* under warm temperature conditions (Yasuda 1983a) or on preferred host plant species (Hughes 1960, Kozarzevskaja and Mihajlovic 1983). Host plant condition can also influence fecundity. For example, we examined the effect of host plant water deficit on the fecundity and survivorship of *P. pentagona* by raising them on mulberry trees subjected to low water and high water treatments (see Hanks 1991 for methods). Fecundity was significantly lower on drought-stressed trees (26.4 ± 4.8 eggs/female) than on watered trees (36.5 ± 2.3) (ANOVA, $F_{1,18} = 12.01$, $P = 0.003$). Similarly, scale survivorship was significantly lower on drought-stressed trees (69 ± 8%) compared to well-watered trees (84 ± 4%) (ANOVA, $F_{1,18} = 5.88$, $P = 0.02$).

While the primary sex ratio averages 1:1 in most populations (Brown and Bennett 1957, Van Duyn and Murphey 1971), it can be altered by a variety of factors. Delayed fertilization of females may result in a strong male bias in the eggs (Brown and Bennett 1957). A female-biased sex ratio results when scales are raised on fertilized host plants or under warm rearing conditions (Yasuda 1983a, b).

Some females of *P. pentagona* produce only male eggs under certain conditions
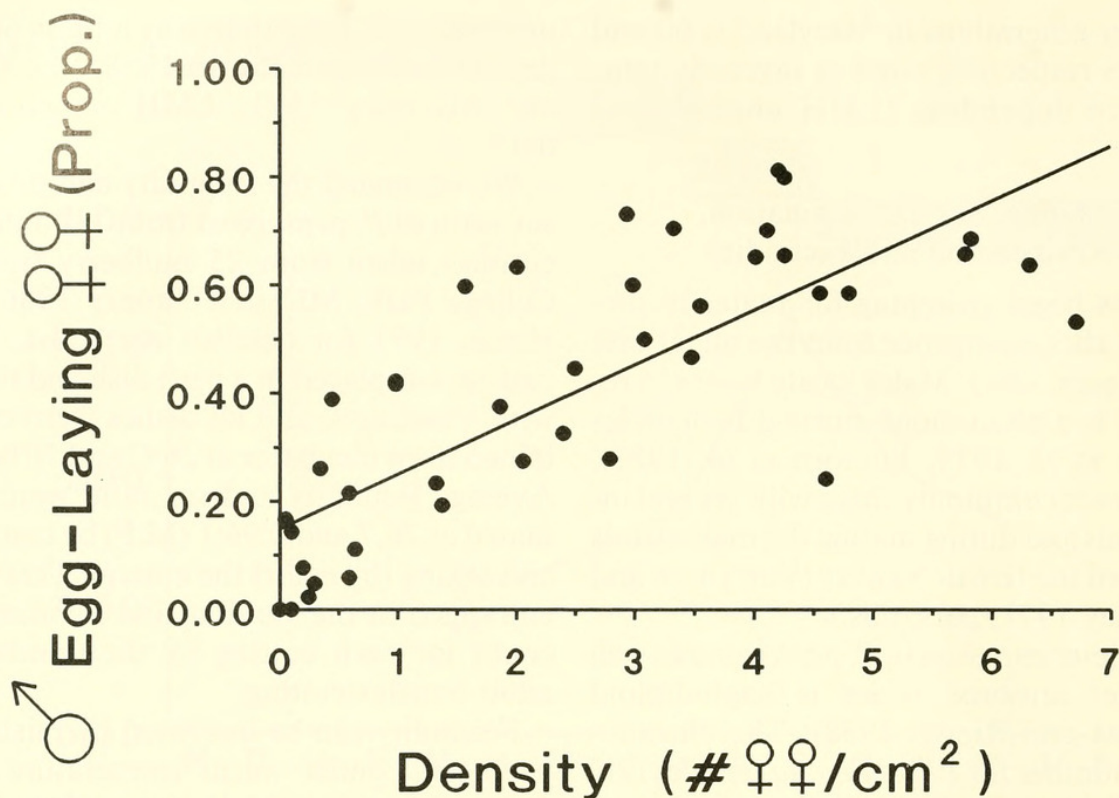
Fig. 2. Relationship between the proportion of female *P. pentagona* laying only male eggs and the density of female scales on mulberry trees. Mulberry trees (34 2-year-old clones in the greenhouse) were artificially infested with scale eggs yielding a range of adult densities from 0.2 to 7.0 adult females/cm²). Subsequently, the number of females producing only male eggs as well as those producing eggs of both sexes was determined by removing scale covers and sexing the offspring (see Hanks 1991 for methods). Best fit regression: $Y = 0.093X + 0.18$, $r^2 = 0.55$, $P < 0.001$.

(Hughes 1960, Bennett and Brown 1958). In Maryland populations of *P. pentagona*, there was a positive relationship between the proportion of females laying only male eggs and the density of female scales on the trees (Fig. 2). Male bias in the offspring at high population densities may have resulted from mate availability and delayed fertilization (Brown and Bennett 1957), because in heavy infestations male pupal cases form a dense mat over females which interferes with mate location and mating (LMH pers. obs.). Also, high concentrations of female pheromones are known to disrupt the searching behavior of the males (Heath et al. 1979).

Dispersal Behavior of Crawlers

Eggs of both sexes hatch 3 to 5 days after oviposition (Fig. 3). The colonization of new host plants occurs primarily by the aerial dispersal of crawlers, while intraplant dispersal results from both aerial displacement and walking (Hanks and Denno 1992a). Following dispersal, crawlers of armored scales in general must settle on the host plant relatively soon or survivorship is drastically decreased (Beardsley and Gonzalez 1975). Crawlers of *P. pentagona* actively move about for up to 12 hours before settling to feed (Hughes 1960, Van Duyn and Murphey 1971). Female crawlers wander further from the parent female before settling than do male crawlers. This behavior results in the spread of the population throughout the host plant; male crawlers usually settle in aggregations not far from the maternal cover (Bennett and Brown 1958, Bénassy 1961, Van Duyn 1967). The longevity of male crawlers in glass containers (21.6 ± 1.6 hours, n = 20) was significantly higher than the longevity of female crawlers (15.8 ± 1.5
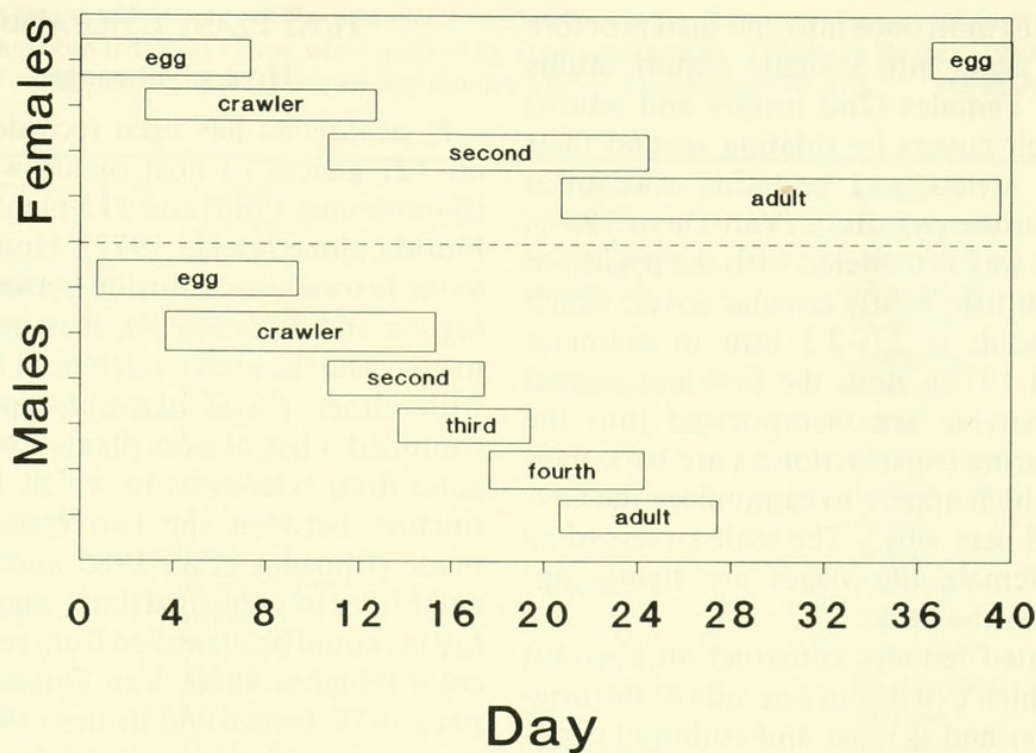
Fig. 3.   Phenology of the life stages of the males and females of *P. pentagona* raised on potatoes in the laboratory at 26°C. Bars represent the duration of each life stage.

hours, n = 20) (ANOVA, $F_{1,18} = 6.03$, $P = 0.03$), suggesting the restricted dispersal of males is not attributable to reduced longevity.

Crawlers of some scale insect species exhibit behaviors (rearing up on their hind legs) in wind currents which increase their chances for aerial transport (Washburn and Washburn 1984). We observed no such behavior in the crawlers of *P. pentagona*. Placed in a directed air flow, crawlers of both sexes taken from high-density cultures clung tenaciously to the substrate. These observations suggest that crawlers do not readily disperse, even though aerial dispersal does occur and is necessary for the colonization of new host plants (Van Duyn 1967).

Crawlers of *P. pentagona* exhibit negative geotaxis, positive phototaxis and thigmotaxis, and tend to settle in cracks and other irregularities in the bark (Bennett and Brown 1958, Hughes 1960, Bénassy 1961, Yonce and Jacklin 1974, Van Duyn and Murphey 1971). Both sexes settle on old bark and rarely colonize new growth (Hughes 1960,

Kuitert 1967). Furthermore, it is quite common for crawlers to settle under existing female covers (Van Duyn and Murphey 1971). For example, in a sample of recently settled crawlers on 3 mulberry trees, 24.7% of female crawlers (N = 81) and 11.8% of male crawlers (N = 85) settled under the covers of adult females from the previous generation. The repeated settling of crawlers under persisting female covers results in an accumulation of scale covers which can encrust the bark of the host (Kuitert 1967).

Growth and Development

After settling, crawlers insert their stylets into the host plant and begin to feed (Beardsley and Gonzalez 1975). To determine the specific mulberry tissues in which *P. pentagona* feeds, we dissected scale-infested cuttings and followed the stylets of 30 adult female scales to their termination. In all cases, the stylets of females terminated in tissues in and around the cambium (primary and secondary xylem). Similarly, Yasuda (1979) reported cambial feeding in *P. pentagona*.

Females molt once into 2nd instars before molting again into sexually mature adults (Fig. 3). Females (2nd instars and adults) form their covers by rotating around their inserted stylets and secreting wax from glands on the pygidium (Van Duyn 1967). Secreted wax is troweled with the pygidium into a whitish, nearly circular cover, which in the adult is 2.0–2.5 mm in diameter (Stoetzel 1976). Both the first and second instar exuviae are incorporated into the cover during construction as are bark fragments which appear to camouflage the cover (LMH pers. obs.). The scale covers of all settled female life stages are tightly appressed to the bark.

Unmated females construct an aberrant cover which extends to one side of the original cover and is loose and cottony in consistency (Bénassy 1958, Bennett and Brown 1958). Unfertilized females partially extend themselves from beneath the extended cover, and may even emerge entirely (Bennett and Brown 1958, pers. obs.). This behavior, also exhibited by other diaspidids (Ezzat 1957, Gentile and Summers 1958), may render females more accessible to males and/or enhance pheromone distribution (Bennett and Brown 1958, Beardsley and Gonzalez 1975).

Males pass through 4 instars (crawlers + 2nd–4th instars) before molting to adults (Fig. 3). As second instars, males begin constructing their distinctive, tubular, white cover (1.5 mm in length for 4th instars). Simultaneously, copious quantities of loose waxy threads are produced which extend beyond the cover (Van Duyn 1967). Adult male emergence is crepuscular (McLaughlin and Ashley 1977). Adult males measure 0.7 mm in length with a 1.4 mm wingspan (Van Duyn 1967). Most males live <1 day and are capable of mating immediately after eclosion (Bennett and Brown 1958, Van Duyn and Murphey 1971). Like males of other diaspidids, *P. pentagona* males are very weak fliers and are incapable of upwind flight in even slight breezes (Rice and Moreno 1970, Moreno et al. 1972).

Host Plant Utilization

Host plant range

P. pentagona has been recorded feeding on 121 genera of host plants world wide (Borchsenius 1966) and 115 plant genera in Florida alone (Dekle 1977). However, due to the taxonomic confusion between *P. pentagona* and *P. prunicola,* it is not possible to associate the above-referenced host plants with either *Pseudaulacaspis* species. We compiled a list of host plants for *P. pentagona* from references in which 1) the distinction between the two congeners was made (Rhoades et al. 1985 and Davidson and Miller unpublished data), and 2) *P. pentagona* could be identified from reported egg color (Hughes 1960, Van Duyn and Murphey 1971, Brown and Bennett 1957). From our survey, 98 genera in 55 families were verified as hosts (Table 1), attesting to the polyphagous nature of this pest. Of those hosts reported, most were angiosperms (not Araucariaceae) and were woody shrubs or trees. However, monocots (e.g. Araceae and Orchidaceae) and primitive (Magnoliaceae) and derived dicot families (Fabaceae) are all recorded hosts.

The most commonly reported hosts in the United States are mulberry (*Morus alba* L.), peach (*Prunus persica* L.), persimmon (*Diospyros* spp.), chinaberry (*Melia azedarach* L.), and *Callicarpa* spp. (Davidson et al. 1983). In Maryland, *P. pentagona* occurs most abundantly on *M. alba,* but is found less commonly on *Catalpa* and rarely on *Cornus* and *Juglans* (LMH unpublished data). Our observed pattern of host utilization in Maryland was largely confirmed by extracting host plant records for *P. pentagona* from the museum collection of scale insects at the USDA Systematic Entomology Laboratory, Beltsville, Maryland as well as host species records listed by Rhoades et al. (1985). Records from 7 reported host species showed that *P. pentagona* was collected primarily from *M. alba* (≈30% of samples), *Catalpa speciosa* Warder (≈30% of samples), and *Salix nigra* L. (≈20% of

Table 1. Genera and Families of the host plants of *Pseudaulacaspis pentagona*. Genera are from Davidson and Miller (unpublished data) except when marked by (1) Rhoades et al. (1985), (2) Hughes (1960), (3) Van Duyn and Murphey (1971), and (4) Brown and Bennett (1957). Genera marked with "*" are shared with *P. prunicola.*

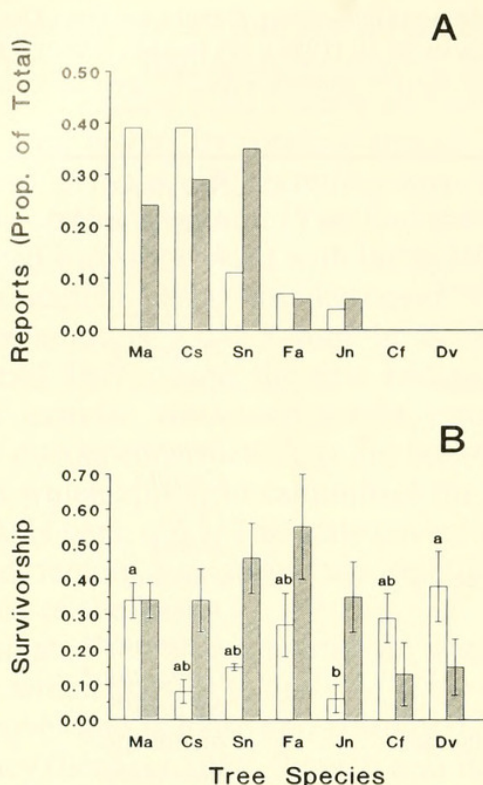|			
Acanthaceae:	*Acanthus*	Lauraceae:	Sassafras
	Crossandra	Lythraceae:	Lagerstroemia[1]
Actinidiaceae:	*Actinidia*	Magnoliaceae:	*Magnolia**
Amaranthaceae:	*Gomphrena*	Malvaceae:	*Gossypium*
Anacardiaceae:	*Mangifera*		*Hibiscus*
	Rhus		*Malachra*
	Schinus	Meliaceae:	*Cedrela*
	Spondias		*Melia*
Apocynaceae:	*Allamanda*	Moraceae:	*Broussonetia*
	*Nerium**		*Castilla*
	Plumeria		*Ficus*
Aquifoliaceae:	*Ilex**		*Morus*
Araceae:	Philodendron	Oleaceae:	*Fraxinus**
Araliaceae:	Aralia		*Jasminium*
	Hedera		*Ligustrum**
Araucariaceae:	Dombeya		*Osmanthus**
Berberidaceae:	Mohonia		*Syringa*[1]*
Bignonaceae:	*Catalpa**	Orchidaceae:	orchid spp.
	Tecoma		*Stanhopea*
Brassicaceae:	*Iberis*	Passifloraceae:	*Passiflora*
Buddleiaceae:	Buddleia	Piperaceae:	*Piper*
Buxaceae:	*Buxus*[1]	Pittosporaceae:	*Pittosporum*
Caricaceae:	Carica	Ranunculaceae:	*Clematis*
Celastraceae:	Euonymus	Rhamnaceae:	*Rhamnus*
Convolvulaceae:	Ipomoea		*Ziziphus*
Cornaceae:	Cornus	Rosaceae:	*Cydonia*
Crassulaceae:	*Bryophylum*		*Persica*
	Kalanchoe		*Prunus**
	Sedum	Rubiaceae:	*Cinchona*
Cucurbitaceae:	*Cucurbita*		*Palicourea*
Cycadaceae:	*Cycas*	Rutaceae:	*Citrus*
Ebenaceae:	*Diospyros*	Salicaceae:	*Salix**
Ericaceae:	*Rhododendron*[1]		*Populus**
Euphorbiaceae:	*Croton**	Sapindaceae:	*Koelreuteria*[2]
	Euphorbia	Solanaceae:	*Solanum*
	Jatrophya		*Capsicum*
	Manihot	Sterculiaceae:	*Firmiana*
	Ricinus		*Sterculia*
Fabaceae:	*Acacia*		*Theobroma*
	Crotolaria	Theaceae:	*Camellia*
	Glycine[1]	Ulmaceae:	*Trema*
	Pueraria[3]		*Ulmus*[3]
Fagaceae:	*Castanea*	Urticaceae:	*Boehmeria*
Geraniaceae:	*Geranium*	Verbenaceae:	*Castoria*
	Perlargonium		*Callicarpa*
Grossulariceae:	*Ribes*		*Lantana*
Hydrangeaceae:	*Hydrangea*		*Stachytarpheta*[4]
Juglandaceae:	*Carya*[1]	Vitidaceae:	*Vitis*
	Juglans		

Fig. 4. (A). Number of host plant records (proportion of total) of *P. pentagona* feeding on *Morus alba* (Ma), *Catalpa speciosa* (Ca), *Salix nigra* (Sa), *Fraxinus americana* (Fa), *Juglans nigra* (Jn), *Cornus florida* (Cf), and *Diospyros virginiana* (Dv). Maryland and Virginia records were taken respectively from: 1) the museum collection of scale insects at the USDA Systematic Entomology Laboratory, Beltsville, Maryland (unshaded bars), and 2) Rhoades et al. (1985) (shaded bars). (B) Crawler (unshaded bars) and postcrawler survivorship (shaded bars) of *P. pentagona* raised on the above seven host plant species. Survivorship was determined by transferring 6 cohorts of 15 female eggs to 3 trees of each plant species and raising the eggs to adulthood (see Hanks 1991 for detailed methods). All cohorts were caged so that host plant effects were not confounded by the actions of natural enemies. Eggs for all transfers were collected on scale-infested cuttings taken from one mulberry tree in College Park, MD. There was no significant host plant effect on postcrawler survivorship. Means for crawler survivorship (±SE) marked with different letters were significantly different (ANOVA, Bonferroni *t*-test, *P* < 0.05).

samples) followed by *Fraxinus americana* L. ($\approx 5\%$), and *Juglans nigra* L. ($\approx 5\%$) (Fig. 4A). Despite their abundance in the Maryland area, there were no records of *P. pentagona* on *Cornus florida* L. or *Diospyros virginiana* L. *M. alba* was probably underrepresented in museum records because the occurrence of *P. pentagona* on this host is

common knowledge and does not often require verification.

We examined the ability of *P. pentagona* to survive on these 7 common tree species by transferring cohorts of female eggs to each plant species and raising the eggs to adulthood (Fig. 4B). Crawler (egg to settled crawler), but not postcrawler survivorship (settled crawler to mature adult) differed significantly among plant species (ANOVA$_{crawler}$, $F_{1,14} = 3.67$, $P = 0.012$; ANOVA$_{postcrawler}$, $F_{1,14} = 1.55$, $P = 0.220$; Fig. 4B). The significant host species effect resulted from the reduced survivorship of crawlers on *J. nigra*. However, survivorship did not differ significantly on 5 tree species (*M. alba*, *C. speciosa*, *S. nigra*, *F. americana*, *C. florida*, and *D. virginiana*) suggesting that *P. pentagona* can colonize and survive on a variety of unrelated host plant species. *P. pentagona* showed high survivorship on some host species which it rarely infests (ash, dogwood, persimmon), suggesting that factors other than the direct effects of the host plant on performance are responsible for the rarity of infestations on these hosts in the field. Despite the evidence for polyphagy, *P. pentagona* does show variation in performance among some host plant species (Simmonds 1958, Hughes 1960), and even among individual mulberry trees (Hanks 1991).

Spatial Distribution of Scales on Mulberry Trees

Scale insects commonly show patchy distributions on their hosts, and it is not uncommon for heavily infested trees to neighbor scale-free trees (Edmunds and Alstad 1978, Miller and Kosztarab 1979, Wainhouse and Howell 1983). Populations of *P. pentagona* also show contagious distributions on their host plants in Bermuda and Florida (Simmonds 1958, Van Duyn 1967). We examined the dispersion of *P. pentagona* in the urban landscape of Maryland by estimating the densities of populations (No. adult females/cm^2 determined by vi-
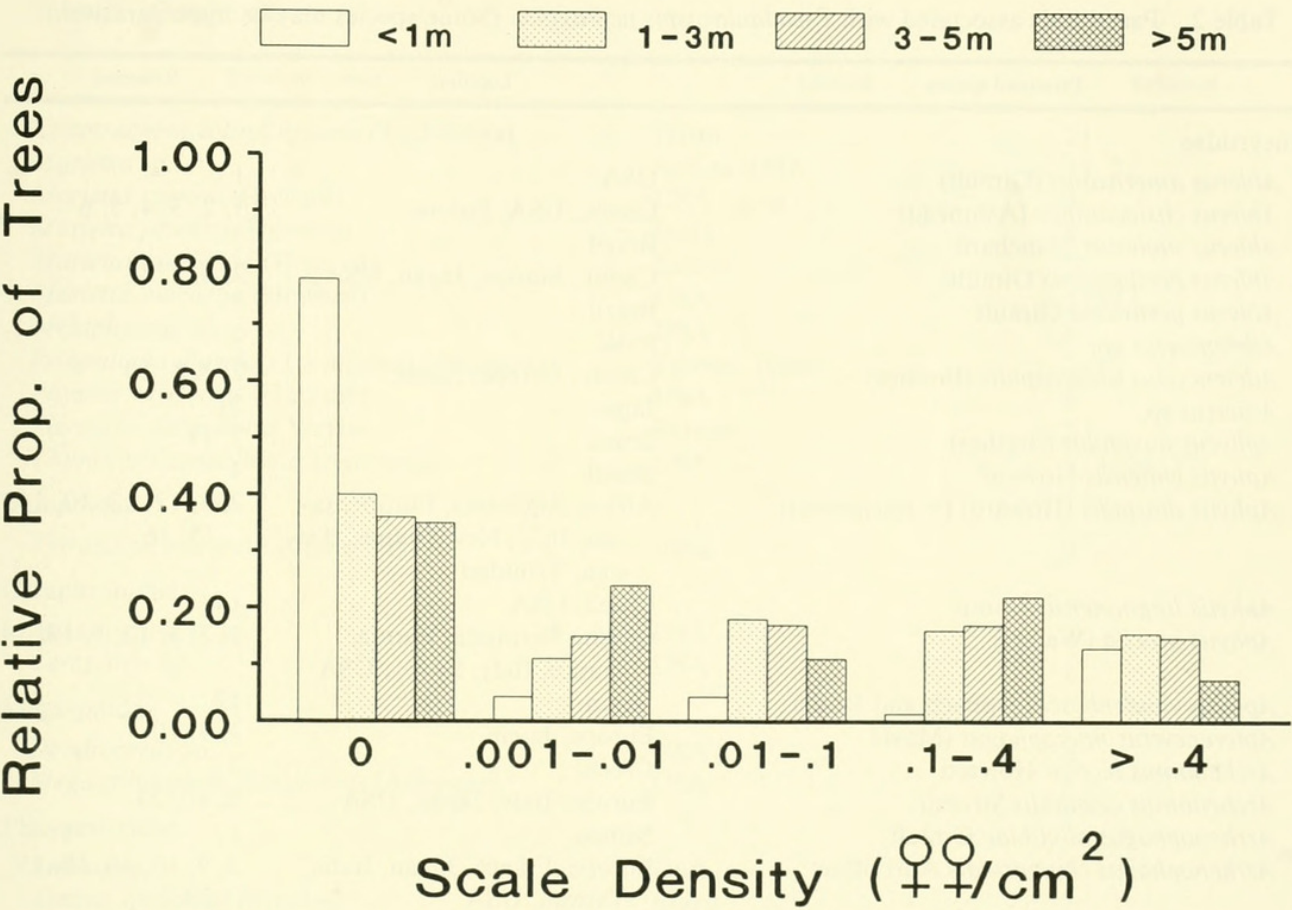
Fig. 5.   Relative proportion of 4 sizes of mulberry trees (<1 m, 1–3 m, 3–5 m, and >5 m in height) in 5 density classes of *P. pentagona* (0, 0.001–0.01, 0.01–0.1, 0.1–0.4, and >0.4 adult females/cm²).

sual counts) on 100 randomly-selected mulberry trees. Dispersion of *P. pentagona* populations was assessed by calculating k-values of the negative binomial model (Southwood 1966). Large values of k (>8) indicate a uniform dispersion of populations across trees, while contagiously distributed populations are indicated by small k values (Southwood 1966). The k value for populations of *P. pentagona* was 0.07, indicating a highly clumped distribution on mulberry trees in Maryland. The contagious distribution of *P. pentagona* in Maryland results from a combination of water-stress and natural enemy attack which relegates scale populations to trees in the urban landscape not suffering from moisture deficit (Hanks and Denno 1992b). Adaptation of *P. pentagona* to individual trees was weak and failed to account for the discrepant infestations which can occur on neighboring trees (Hanks 1991).

We also examined the relative abundance of *P. pentagona* on mulberry trees of differing size. The height and density of scale infestations were determined for 300 randomly-selected mulberry trees in the urban landscape. Trees were segregated by height into 4 classes (<1 m, 1–3 m, 3–5 m, and >5 m) and by scale density into 5 density classes (0, 0.001–0.01, 0.01–0.1, 0.1–0.4, and >0.4 adult females/cm²). Trees in the four size classes differed significantly in their scale densities (Kruskal-Wallis test, $P = 0.0001$; Fig. 5). Of the 300 field trees, 46% were entirely free of scales and 16% carried heavy infestations (>0.4 adult females/cm²). Most trees in the smallest size class were scale-free (78%) while most trees in larger size classes were infested to some extent (>50%) (Fig. 5). Simmonds (1958) also reported that *P. pentagona* was much less abundant on young hosts (oleanders) than older shrubs. The poor dispersal and colo-

Table 2. Parasitoids associated with *Pseudaulacaspis pentagona*. (Some species may be hyperparasites.)

Parasitoid species	Location	Reference
Encyrtidae		
Ablerus americanus (Girault)	USA	1
Ablerus clisiocampae (Ashmead)	Czech., USA, Europe	1, 2, 3, 4, 5, 6
Ablerus molestus Blanchard	Brazil	7
Ablerus perspeciosus Girault	Czech., Europe, Japan, USA	2, 3, 5, 8
Ablerus peruviana Girault	Brazil	7
Adelencyrtus sp.	India	9
Adelencyrtus aulacaspidis (Brethes)	Czech., Europe, Japan	2, 3, 8, 10
Anicetus sp.	Japan	21
Aphycus flavidulus (Brethes)	Brazil	7, 11
Aphytis chilensis Howard	Brazil	4
Aphytis diaspidis (Howard) (= *fuscipennis*)	Africa, Argentina, Europe, Japan, Italy, New Guinea, Taiwan, Trinidad	2, 5, 12, 13, 10, 14, 15, 16
Aphytis lingnanensis Comp.	China, USA	14
Aphytis proclia (Walker)	Czech., Bermuda, Burma, France, Italy, Switz., USA	1, 3, 5, 12, 5, 13, 14
Aphytis vandenboschi DeBach and Rosen	Japan	12
Apterencyrtus microphagus (Mayr)	Europe, Japan	2, 7, 10
Archenomus bicolor Howard	Czech.	3
Archenomus orientalis Silvestri	Europe, Italy, Japan, USA	2, 10, 23
Arrhenophagus albitibiae Girault	Samoa	17
Arrhenophagus chionaspidis Aurivillius	Europe, France, Japan, India, Taiwan, USA	2, 9, 10, 16, 18, 19, 20
Aspidiotiphagus citrinus (Craw.)	Argentina, Bermuda, Colombia, Czech., Europe, Japan, Trinidad, USA	1, 3, 13, 21, 2, 22, 5, 4, 23, 5, 24
Aspidiotiphagus lounsburyi (Berlese and Paoli)	Bermuda, Principe, Sao Tome, USA	1, 2, 13
Azotus capensis (Howard)	Europe, Japan	2, 8
Azotus marchali Howard	USA	6
Azotus platensis (Brethes)	Argentina, Brazil	7, 25
Cales noacki Howard	Argentina, Brazil, Europe, Czech.	2, 3, 7, 25
Cheiloneurus sp.	India	9
Coccobius (= *Physicus*) sp.	India	9
Coccophagioides kuwanae (Silvestri)	Europe, Japan, Italy	2, 8, 9, 10
Comperiella bifasciata Howard	Orient, USA	14
Encarsia sp.	India	9
Encarsia aurantii (Howard)	Brazil, Europe	2, 7, 11
Encarsia (= *Prospaltella*) *berlesei* Howard	Arg., Bermuda, Colombia, France, Hungary, Iran, Italy, Japan, Turkey, USA, USSR,† Yugo.	1, 3, 6, 26, 27, 4, 5, 10, 14, 24, 14, 22, 28, 29, 30
Encarsia citrina (Craw.)	USA	14
Encarsia (= *Prospaltella*) *diaspidicola* (Silvestri)	Africa, Bermuda, Europe, France, Japan, Italy, Taiwan	2, 4, 13, 14, 20, 10, 16
Encarsia lounsburyi (Berlese and Paoli)	Bermuda, New Guinea, Trinidad, USA	1, 5, 13, 23
Encarsia murtfeldtae (Howard)	Argentina, Europe, Italy, USA	2, 5, 23
Encarsia perniciosi (Tower)	China	14
Epitetracnemus sp.	India	9
Epitetracnemus (= *Anabrolepis*) *comis* Nois and Hui	China	31

Table 2. Continued.

Parasitoid species	Location	Reference
Epitetracnemus lindingaspis (Tachikawa)	Japan	21
Marietta sp.	Samoa, USA	17, 27
Marietta carnesi (Howard)	USA	1
Marietta javensis (Howard)	India	9
Marietta mexicana (Howard)	Europe	2
Marietta pulchella (Howard)	USA	5, 32
Metaphyscus sp.	USA	6
Prospaltella diaspidis (= *niigata*) Nakagama	Europe, Japan	2, 13
Physcus varicornis (Howard)	USA	6
Pteroptrix dimidiatus Westw.	Europe	2
Thysanus flavopalliatus (Ashmead)	USA	1, 4, 22, 27
Eulophidae		
Tetrasticus pupureus (Cameron)	India	9
Ceraphronidae		
Aphanogmus n. sp.	USA	1
Ceraphron sp.	USA	6
Megaspilidae		
Dendrocerus sp.	USA	6
Megaspilus prob. *fuscipennis* (Ashmead)	USA	6
Platygasteridae		
Amitus sp.	USA	6
Amitus spiniferus (Brethes)	Brazil	7
Signiphoridae		
Chartocerus pulcher (Girault)	USA	5
Signiphora aspidioti Ashmead	Europe	2
Signiphora bifasciatus Ashmead	Brazil	4, 11
Signiphora caridei Brethes	Brazil, Europe	2, 4, 11
Signiphora endophragmata Blanchard	Argentina	25
Signiphora flavopalliatus Ashmead	USA	4, 27
Signiphora platensis Brethes	Brazil, Europe	2, 7

References: 1) Collins and Whitcomb (1975), 2) Kosztarab and Kozár (1988), 3) Kozarzevskaja and Mihajlovic (1983), 4) Hughes (1960), 5) Peck 1963, 6) Nalepa and Meyer (1990), 7) Silva et al. (1968), 8) Murakami (and references therein, 1970), 9) Sankaran (1984), 10) Yasumatsu and Watanabe (1965), 11) Davidson and Miller (in prep.), 12) Rosen and DeBach (1979), 13) Simmonds (1958), 14) Cock (1985), 15) Mercet (1932), 16) Yen (1973), 17) Liebregts and Sands (1989), 18) Ball and Stange (1979), 19) Tachikawa (1959), 20) Quilici et al. (1987), 21) Yasuda (1981), 22) Kuitert (1967), 23) Clausen (1978), 24) Posada and Garcia (1976), 25) DeSantis (1941), 26) Darvas and Zsellér (1985), 27) Van Duyn and Murphey (1971), 28) Habibian (1981), 29) Kózar et al. (1982), 30) Howard (1912), 31) Noyes and Hui (1987), 32) Present study.
† Locations cited as USSR indicate territories encompassed by former USSR.

nizing ability of armored scales (Beardsley and Gonzalez 1975) probably contributes to their rarity on young and/or small hosts.

NATURAL HISTORY

Parasitoids and hyperparasitoids

A total of 60 species of parasitoids and hyperparasitoids have been associated with P. pentagona world wide (Table 2), although some of these records are probably confounded with the enemies of P. prunicola. Approximately 75% of the parasitoids were wasps in the family Aphelinidae. Similarly, 6 species of aphelinid wasps dominated the community of parasitoids attacking populations of P. pentagona at our study site in College Park, MD. The aphelinids included
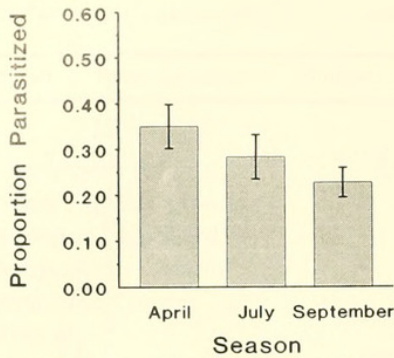
Fig. 6. Proportion of *P. pentagona* females parasitized by *E. berlesei, A. proclia*, and *A. bicolor* on mulberry trees in the urban landscape of College Park, MD. Parasitoids were sampled by taking scale-infested cuttings from mulberry trees during the first, second, and third scale generations when most females were second instars. Twenty cuttings were collected from 5 field trees in April, July and September 1986. Cuttings were returned to the laboratory, placed in plastic bags and stored in an incubator (21–24°C). The emerging parasitoids were identified to species and counted. Rates of parasitism for each cutting were determined by dividing the number of parasitized females by the total number of female scales (see Hanks 1991 for detailed methods).

3 primary parasites, *Encarsia berlesei* (Howard), *Archenomus bicolor* Howard (Gordh), and *Aphytis proclia* (Walker) and 3 hyperparasitoids, *Ablerus clisiocampae* (Ashmead), *A. perspeciosus* Girault and *Marietta pulchella* (Howard) also emerged from scales on the cuttings. Only female scales were attacked and males remained free of parasitoids.

E. berlesei is a parthenogenetic endoparasitoid which attacks only two other host species, *P. prunicola* and *Melanaspis obscura* (Comstock), in the United States (Howard 1912, Krombein et al. 1979, Stimmel 1982). The parthenogenetic ectoparasitoid, *A. proclia,* is polyphagous attacking a variety of armored scales in the United States (Krombein et al. 1979, but see Rosen and DeBach 1979 for possible taxonomic confusion). *A. bicolor* is a bisexual endoparasitoid which attacks only *P. pentagona* and an *Aspidiotus* species in the United States (Krombein et al. 1979). Multiple parasitism is unknown in *E. berlesei* and *A. bicolor*, but *P. pentagona* is occasionally
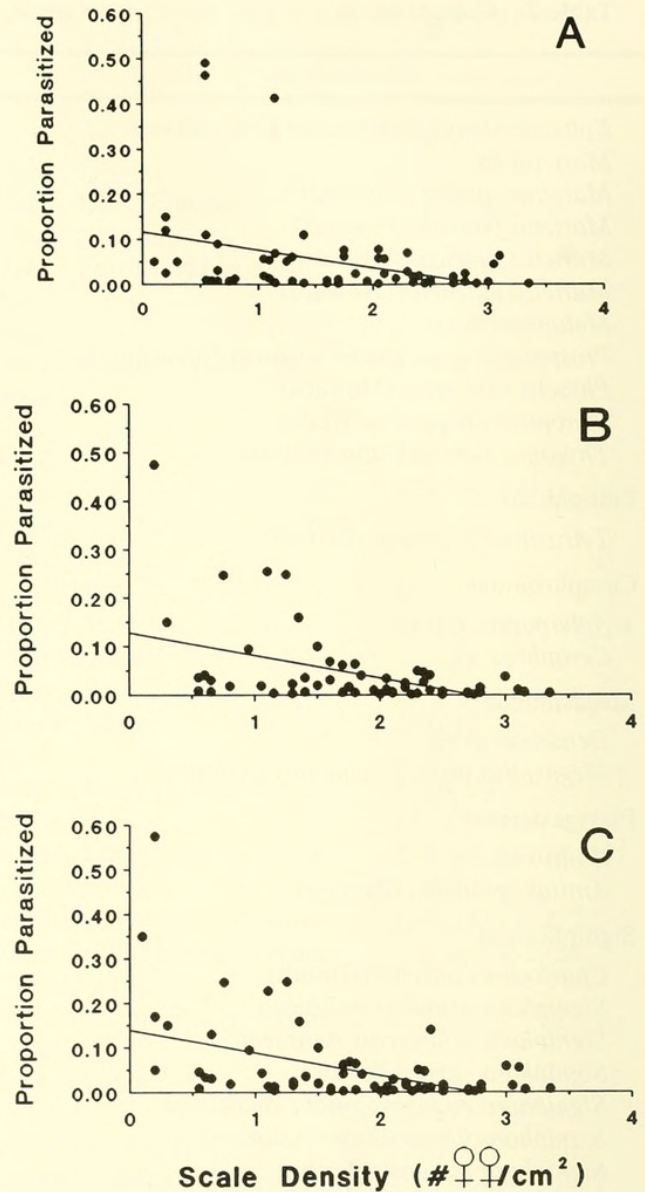

Fig. 7. Relationship between parasitism rate (proportion of scales parasitized by *E. berlesei* [A], *A. proclia* [B], and *A. bicolor* [C]) and the density of *P. pentagona* (No. adult females/cm²) on 50 mulberry trees in the urban landscape of College Park, MD (see Hanks 1991 for detailed methods).

multiply parasitized by *A. proclia* (at most 2 parasitoids/host) (LMH unpublished data).

Parasitism rate (combined mortality from all three primary parasitoid species) declined gradually over the course of the season dropping from 35% in the spring to 25% in the fall generation of scales (Fig. 6). The seasonal decrease in parasitism rate occurred despite a threefold increase in scale population size from spring to fall (Fig. 1). This pattern is strongly suggestive of tem-

porally inverse density-dependent parasit-
ism (Hanks 1991). Also, spatial patterns of
inverse density-dependent parasitism by *A.
proclia, E. berlesei,* and *A. bicolor* were ob-
served among populations of *P. pentagona*
on different mulberry trees (Fig. 7). Thus,
patterns of inverse density-dependent par-
asitism in the parasitoids of *P. pentagona*
are evident at both temporal and spatial
scales (Hanks 1991). Explanations for in-
verse density-dependent parasitism include
parasitoid egg depletion, interference among
parasitoids at high host densities, and fail-
ure of parasitoids to aggregate in patches of
high host density (Hanks 1991).

The three primary parasitoids differed in
their proportional contribution to total par-
asitism from one scale generation to the next
(Fig. 8). *A. proclia* was the most abundant
species emerging from scales in the third
(April) and first (July) generations, while *E.
berlesei* was the most prolific parasitoid at-
tacking second generation scales in fall.

Also, the three primary parasitoid species
showed marked differences in their patterns
of spring emergence within one scale gen-
eration (overwintering females) (Fig. 9). *E.
berlesei* and *A. proclia* were the first para-
sitoids to emerge in spring followed one week
later by *A. bicolor.* Both *E. berlesei* and *A.
proclia* showed a distinct second peak of
emergence, as has been observed for these
two parasitoids of *P. pentagona* in Japan
(Yasuda 1981). Similarly, Simmonds (1958)
observed a double peak of emergence for an
Aphytis species attacking *P. pentagona* in
Bermuda. These data suggest that by emerg-
ing earlier in the scale generation, *E. berlesei*
and *A. proclia* can complete two genera-
tions, while *A. bicolor* by emerging late is
restricted to a single generation. That *E. ber-
lesei* and *A. proclia* can complete 2 gener-
ations on a single generation of *P. pentagona*
may explain why these two species are the
most abundant parasitoids in the system.
The proportion of total parasitism attrib-
utable to *A. proclia, E. berlesei,* and *A. bi-
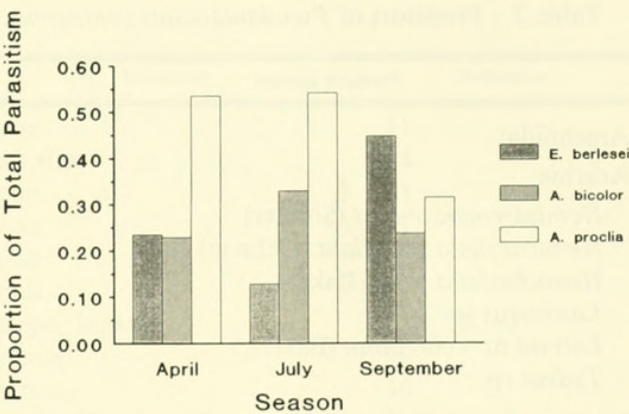color* was 41, 35, and 24% respectively.

Fig. 8. Relative proportion of total parasitism of
P. pentagona attributable to *E. berlesei, A. proclia,* and
A. bicolor during the first, second and third scale gen-
erations (see Fig. 6 caption for methods).

Even though parasitized females of *P.
pentagona* were invariably killed, they oc-
casionally managed to deposit a fraction of
their eggs. For example, 9.7% of female *P.
pentagona* (n = 396) that were parasitized
by *A. proclia* succeeded in laying 28 ± 14
eggs, while 9.2% (n = 131) of the scales were
parasitized by the endoparasites *E. berlesei,*
and *A. bicolor* deposited 25 ± 9.9 eggs. In
Maryland populations of *P. pentagona,* the
hyperparasitoids *A. clisiocampae, A. per-
speciosus,* and *M. pulchella* were not com-
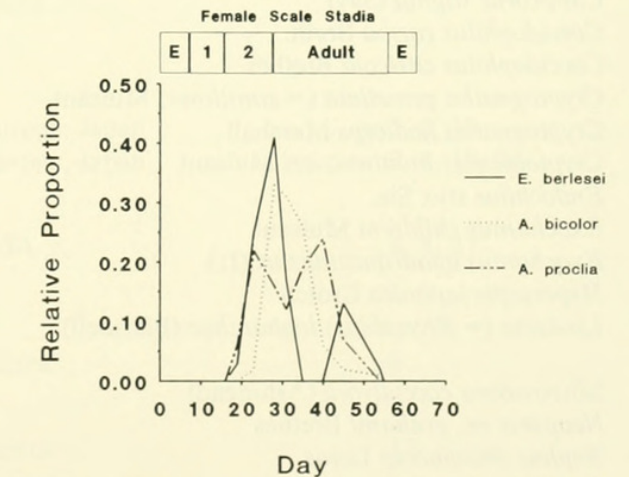mon and accounted for 1.2, 0.7, and 0.1%

Fig. 9. Relative proportion of individuals of *E. ber-
lesei, A. proclia,* and *A. bicolor* (expressed as a propor-
tion of the total number of conspecifics collected)
emerging each day from overwintering females of *P.
pentagona* on mulberry cuttings (see Fig. 6 caption for
methods). Bar illustrates the phenology of the life his-
tory stages of *P. pentagona* (egg, first instar crawlers,
second instars and adults).

Table 3.   Predators of *Pseudaulacaspis pentagona*.

Predator species	Locations	Reference
Arachnida:		
Acarina		
Hemisarcoptes malus (Shimer)	Principe, Sao Tome, USA	1, 13, 32
Hemicheyletia scutellata (DeLeon) 1	USA	1
Hemicheyletia wellsi Baker	USA	1
Lasioseius sp.	Principe, Sao Tome	13
Lorryia nr. *cobremani* (Baker) 1	USA	1
Tydeus sp.	Bermuda	13
Insecta:		
Orthoptera		
Periplaneta americana L.	Bermuda	13
Periplaneta australasiae (Fabr.)	Bermuda	13
Thysanoptera		
Karnyothrips flavipes (Jones) 1	USA	1
Halothrips nr. *americanus* (Hood) 1	USA	4
Coleoptera		
Coccinellidae		
Callicaria superba Mulsant	Europe, Japan, Taiwan	2, 8, 10, 16, 30
Chilocorus bipustulatus L.	Europe, Italy	2, 11, 13, 20, 33
Chilocorus bivulnerus Mulsant	USA	35
Chilocorus cacti L.	Cuba, Puerto Rico, Trinidad	13, 14, 38
Chilocorus circumdatus (Gylh.)	Ceylon, India	14, 33
Chilocorus kuwanae Silvestri	China, Europe, Japan, USA	2, 8, 10, 13, 14, 30, 33
Chilocorus nigritus (Fabricius)	Mauritius, Reunion	34, 36
Chilocorus politus Mulsant	Mauritius, Reunion	34, 36
Chilocorus rubidus Hope	Europe, Japan	2, 8, 10
Chilocorus similis (Rossi)	Japan	33
Chilocorus stigma (Say)	USA	1, 4, 27, 32
Coccidophilus cariba Breth.	Antigua, Montserrat	14
Coccidophilus citricola Brethes	Argentina, Colombia, Trinidad	14, 24, 33
Cryptognatha gemellata (= *simillima*) Mulsant	Trinidad	14
Cryptognatha nodiceps Marshall	Principe, Sao Tome, Trinidad	13, 37
Cryptolaemus montrouzieri Mulsant	USA, Reunion	4, 36
Endochilus styx Sic.	Sao Tome, Principe	13
Exochomus childreni Mulsant	USA	4
Exochomus quadripustulastus (L.)	Europe	2, 11
Hyperaspis japonica Crotch	Europe, Japan	2, 9, 10, 30
Lindorus (= *Rhyzobius*) *lophanthae* (Blaisdell)	Argentina, Australia, Bermuda, Brazil, Europe, Italy, USA	1, 2, 4, 7, 13, 14, 20, 32, 33
Microweisea coccidivora (Ashmead)	USA	1
Neaporia nr. *grahami* Brethes	Bermuda	13
Nephus phosphorus Lewis	Japan	21
Orculus sp.	Principe, Sao Tome	13
Pentilia insidiosa Mulsant	Puerto Rico, Trinidad	13, 14
Pharosymnus sp.	Bermuda	11
Pharosymnus horni Gorh.	India	9
Prodilis nr. *gorhami* (Brethes)	Trinidad	14
Pseudoscymnus hareja Weise	Europe, Japan	2, 10, 14, 30
Rodalia cardinalis (Mulsant)	Brazil	7
Rodalia concolor Lewis	Europe, Japan	2, 8, 10, 30

Table 3. Continued.

Predator species	Locations	Reference
Rodalia limbata Motschulsky	Japan	21
Scymnomorphus sp.	Mauritius	34
Scymnus hareja Weise	Japan	13
Scymnus hilaris Motschulsky	Japan	21
Serangium japonicum Chapin	Japan	21
Stethorus spp.	Japan	21
Stethorus japonicus Kamiya	Europe, Japan	2, 8, 10, 30
Sticholotis gomyi Chazeau	Reunion	36
Sticholotis madagassa Weise	Reunion	36
Sticholotis punctata Crotch	Europe, Japan	2, 8, 30
Sticholotis quadrisignata Weise	Samoa	17
Sukunahikona japonica H. Kamiya	Japan	21
Telsimia nigra (Weise)	Europe, Japan	2, 13, 14, 30
Telsimia nitida Chapin 1	Samoa	17
Nitidulidae		
Cybocephalus sp.	Bermuda, India, Trinidad, USA	1, 9, 14
Cybocephalus binotatus Gouvelle	Reunion	36
Cybocephalus foderi (= *luteipes*) Endrody-Youga	Hungary	26
Cybocephalus gibbulus Erichson	Europe, Japan, USA	2, 13, 30
Cybocephalus nipponicus Endrody-Younga	Japan	21
Cybocephalus pullus Endrody-Younga	Reunion	36
Cybocephalus rufifrons Reitter	Europe, Italy	2, 20, 22
Neuroptera		
Chrysopidae		
Chrysopa sp.	USA	4, 27
Chrysoperla rufilabris (Burmeister)	USA	1
Mallada boninensis (Okamoto)	Europe, Japan, Taiwan	2, 10, 16, 30
Coniopterygidae		
Heteroconis picticornis (Banks)	China	14
Lepidoptera		
Arctiidae		
Eilema griseola (Hubner)	Europe, Japan	2, 8, 39
Lithosia quadradives Butler	Europe, Japan	2, 8, 10, 30
Cosmopterigidae		
Pyroderces rileyi (= *stigmatophora*) (Walsingham) 2	USA	4, 8, 27
Noctuidae		
Eublemma sp.	Africa	8
Stathmopodidae		
Stathmopoda sp. 2	Samoa	17
Diptera		
Dentifibula sp.	Japan	21
Dentifibula viburni (Felt)	USA	1
Lestodiplosis sp.	Japan	21
Cecidomyiidae		
spp.?	India	9
Anthrocnodax diaspidis Kieff.	Italy	33

Table 3. Continued.

Predator species	Locations	Reference
Anthrocnodax moricola Kieff.	Africa	33
Silvestrina silvestrii Kieff.	Africa, Brazil	33
Tricontrarinia ciliatipennis Kieff.	Japan	33
Syrphidae		
Salpingogaster nigriventris Bigot	Argentina, USA	33

References as in Table 2 with the addition of: 33) Thompson and Simmonds (1964), 34) Moutia and Mamet (1947), 35) Gossard (1902), 36) Guyot and Quilici (1987), 37) Bennett (1956), 38) Wolcott (1960), 39) Strickland (1947).

mortality of the primary parasitoids. Our sampling and rearing methods (see caption for Fig. 6) did not allow for the association of hyperparasitoids with specific host species. Hyperparasites were also uncommon in populations of *P. pentagona* elsewhere (Williams 1970, Collins and Whitcomb 1975, Yasuda 1981).

Predators

A total of 80 species of predators have been reported attacking *P. pentagona* throughout the world, most of which (58%) are coccinellid beetles (Table 3). In Maryland, the coccinellids *Lindorus lophanthae* (Blaisdell) and *Chilocorus stigma* Say commonly feed on *P. pentagona*. Adults and larvae of both *C. stigma* and *L. lophanthae* entirely consume first instar scale insects, but when feeding on second instars and adults chew characteristic oblong holes into scale covers (Hanks 1991).

In Maryland populations of *P. pentagona*, coccinellid larvae (*L. lophanthae* and *C. stigma* combined) were scarce during spring and summer, but increased dramatically in density by the end of the summer generation of scales in September (Fig. 10A). Predator density was therefore high when scales began to oviposit in September. Predation rate by the two coccinellids remained low (<5%) through spring and summer, but increased substantially in late fall to 30% (Fig. 10B). Even though these coccinellids aggregated on mulberry trees with high scale densities, their impact on scale populations was rel-

atively low due to their appearance late in the season (Hanks 1991).

Biological Control and Management of *P. pentagona*

P. pentagona is one of 18 diaspidid species which has been successfully controlled using biological agents (DeBach and Rosen 1976). *E. berlesei* is a widely distributed parasite (Table 1.2) that has provided effective control of *P. pentagona* in several areas (Howard 1916, DeBach and Rosen 1976, Greathead 1976, Clausen 1978). The coccinellids *L. lophanthae* and *C. stigma* are polyphagous predators which have proven successful in controlling scale insects (Clausen 1978).

Nevertheless, these enemies failed to suppress populations of *P. pentagona* in the disturbed urban landscape of Maryland where scale populations frequently outbreak and occasionally even kill their mulberry hosts. Reasons for this failure include 1) inverse density-dependent parasitism exhibited by *E. berlesei*, *A. proclia*, and *A. bicolor* (scale insects escape their parasitoids (Hanks 1991)), 2) partial oviposition by female scales despite being parasitized, and 3) the rarity of predaceous coccinellids through summer when *P. pentagona* populations are growing rapidly (Hanks 1991). However, in forest habitats, generalized predators (earwigs, tree crickets, harvestmen) which are less abundant in landscape settings maintain populations of *P. pentagona* at very low densities (Hanks and Den-
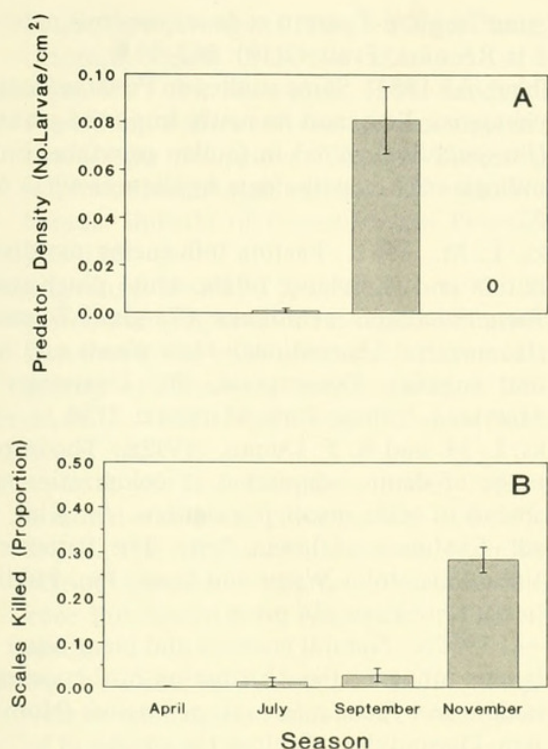
Fig. 10. (A) Density of coccinellid larvae (*L. lophanthae* and *C. stigma* combined) in populations of *P. pentagona* on mulberry trees in the urban landscape of College Park, MD. Predators were sampled by taking 20 scale-infested cuttings from 5 mulberry trees during the first, second, and third scale generations and in the late fall, 1986 (see Fig. 3 for sampling dates and *P. pentagona* phenology, and Hanks 1991 for sampling details). Cuttings were returned to the laboratory and the number of coccinellid larvae and the number of predator-damaged and undamaged adult female scales were counted. (B) Seasonal change in predation rate (proportion of *P. pentagona* killed which showed characteristic feeding damage by *L. lophanthae* and *C. stigma*).

no 1992b). Similarly, hymenopterous parasitoids were reported to suppress densities of *P. pentagona* in undisturbed habitats in Florida (Collins and Whitcome 1975). From a pest management perspective, dense and diverse plantings of ornamental trees encourage generalist predators and provide a better setting for natural control of armored scale pests (Hanks and Denno 1992b).

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