*Bulletin of Entomological Research* (2005) **95**, 621–634 DOI: 10.1079/BER2005394

# Phenology and demography of *Homalodisca coagulata* (Hemiptera: Cicadellidae) in southern California citrus and implications for management

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## Abstract

Populations of *Homalodisca coagulata* (Say) were sampled from citrus orchards in southern California, USA to characterize and quantify seasonal occurrences of nymphs and adults with the goal of identifying management opportunities through well-timed treatments and/or natural enemy releases. Higher densities of *H. coagulata* in 2001 contributed to a complete seasonal profile that began in early spring with the emergence of first instar nymphs and their progression through five nymphal instars lasting until mid-August. Adult emergence began in mid-June with peak adult densities attained from mid to late August followed by a gradual decline through autumn. A persistent and significant male bias was observed in the adult sex ratio from the time of first emergence through mid-October in oranges; the same trend was present in lemons, but with more variability. Adult densities gradually declined through the winter months into the following spring before rapidly increasing again in June as the 2002 spring generation of nymphs began emerging as adults. The seasonal timing of nymphs and adults in 2002 was nearly identical to that observed the previous year. Phenology data from both years were incorporated into a stochastic, temperature-dependent model that predicts the occurrences of *H. coagulata* stages through time. Applications of imidacloprid early in the spring generation of nymphs proved very effective at reducing nymphs and sustaining lower densities of adults through summer.

**Keywords:** citrus, USA, *Homalodisca coagulata*, imidacloprid, control, seasonal dynamics, sex ratio, phenology

## Introduction

Effective pest management is often realized through timely control actions initiated at a critical point in the growth and development of pest populations. For many pests, targeting a specific stage at a certain threshold density is necessary not only to avoid economic injury to the crop, but also to most effectively limit population growth. For example, early stage larvae of Lepidoptera and Coleoptera are frequently targeted (Shelton *et al*., 1986; Hare, 1990; Fitt, 1994; Torres-Vila *et al*., 2003) because of their greater susceptibility to chemical treatments. But a cohort of early instars may also represent a significant proportion of a crop infestation that can be reduced through well-timed control measures to suppress population growth. In practice, this idea has proven most successful at preventing late season

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outbreaks of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) in central Arizona cotton. Treatments with insect growth regulators that target early instars at the critical time when populations are beginning to expand have worked effectively to reduce population growth and avoid the injurious infestations that were prevalent prior to first implementation of the insect growth regulator-based integrated pest management in 1996 (Ellsworth & Naranjo, 1999; Ellsworth & Martinez-Carrillo, 2001).

Knowledge of the phenology of a pest organism can increase awareness of infestation patterns and help identify periods of crop vulnerability. In the Arizona programme, a clear understanding of the phenology of *B. tabaci* has contributed to success by improving vigilance in scouting and detection of early infestations during the time that *B. tabaci* regularly begins to increase in cotton. But for many invasive species and perhaps secondary pests that seldom require control action, important data on seasonal occurrence in crops may not be available, leaving some uncertainty about when to be most vigilant with scouting or when to exercise control measures to achieve effective management. Development of a better understanding of the ecology of a pest species towards more effective pest control includes learning seasonal patterns of abundance and scarceness. Further refinement of a management strategy can be obtained by characterizing the demographic structure of a target population to enable more expert targeting of particular developmental stages. Pest managers are better able to make correct treatment decisions when they are aware of the relative prevalence of various demographic groups in a population, e.g. eggs, early or late stage larvae, or adults, especially in the context of greater selectivity that is now possible with many newer insecticides.

The invasion of the glassy-winged sharpshooter *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae) into California is an example of an insect that was initially tolerated in both urban and agricultural settings, even as its range expanded and its infestations grew more conspicuous each year. Various perspectives concerning what action, if any, should be taken to curtail *H. coagulata* populations were quickly galvanized into a unified course of action when the wine-grape vineyards of Temecula in Riverside County, California, USA began dying off (Blua *et al*., 1999). The afflicted grapevines displayed the symptoms of Pierce's disease and the causal bacterium *Xylella fastidiosa* Wells was quickly identified from diseased plants. The Pierce's disease epidemic in Temecula was attributed to the spread of *X. fastidiosa* by *H. coagulata* based on its known vectoring capability (Purcell & Saunders, 1999; Purcell *et al*., 1999; Almeida & Purcell, 2003) and high-density populations that built-up in the area during the mid- to late 1990s. Previously, *H. coagulata* had been identified as the insect vector responsible for the oleander leaf scorch epidemic in southern California (Purcell *et al*., 1999), a new disease caused by a different strain (oleander leaf scorch) of *X. fastidiosa*.

The demonstrated ability of *H. coagulata* to rapidly establish over a large geographical area coupled with the Pierce's disease epidemic in Temecula heightened fears that the major wine and table grape areas of central and northern California lay vulnerable to further expansion of *H. coagulata*. Although Pierce's disease epidemics have occurred periodically in California ever since the late 1800s when the disease was first identified and held responsible for destroying the fledgling grape industry, the expansion by *H. coagulata* represented a grave new threat as a vector of *X. fastidiosa*. Consequently, the *H. coagulata*/Pierce's disease crisis in California has become the focus of massive public funding and intensive research efforts with the comprehensive goal of preventing additional epidemics by targeting both the pathogen and the vector.

Although certain aspects of *H. coagulata* ecology have been well studied, notably its nutritional ecology (e.g. Anderson *et al*., 1992; Brodbeck *et al*., 1990, 1995), there is otherwise relatively little published information on the life history of *H. coagulata* in Florida, California, or elsewhere. As an exclusive xylem-feeder, *H. coagulata* has a wide host range that consists of both herbaceous and woody dicotyledonous plants, but also some monocots on occasion, and involves frequent shifts among available hosts. In California, early observations suggested that *H. coagulata* has two generations per year (Blua *et al*., 1999) and that individuals persist throughout the year without entering diapause. However, many questions remain concerning the time of year of maximum and minimum population size, generation time, and the demographic structure within generations, especially in regard to when various stages might be most effectively targeted by specific control actions. The objective of this study was to study a natural population of *H. coagulata* to characterize and quantify its phenology over a two-year span while also defining the changing demographic structure of that population, then incorporate into a phenology model to assist in future decision making. Concurrent with this investigation, a systemic insecticide treatment was applied to test the impact of targeting a specific stage in the development of *H. coagulata* populations in southern California.

## Materials and methods

### *Field site*

Monitoring of *H. coagulata* populations was carried out at the University of California's Agricultural Operations in Riverside, California during 2001 and 2002. Observations over the few years previous to this study had established that large populations of *H. coagulata* were present on the university farm and in the general vicinity of Riverside. A wide assortment of different citrus species and cultivars grow on slightly more than half of the 204 ha farm with the highest concentrations of *H. coagulata* occurring on the north side. Evidence of heavy colonization within this area of concentrated citrus plantings was evident from the abundance of oviposition scars on the abaxial surface of many leaves throughout all trees that were examined, as well as the conspicuous presence of *H. coagulata* adults. No other crop vegetation on the university farm, nor ornamental vegetation off the farm, displayed the level of colonization that was present in the north section of the university farm. Therefore, it was determined that a stand of citrus from this area should be used for monitoring *H. coagulata* populations that would permit replicated observations throughout the year, but also be free from unplanned insecticide treatments.

An allotment of trees for experimental use in 2001 was granted in field 5 near the centre of a 40-acre tract divided equally among oranges (var. Frost Valencia grafted on Troyer citrange) and lemons (var. Lupe grafted on Cook) with 6.4 m spacing between all rows. This study area was situated in blocks D, E, and F and consisted of five rows of

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oranges (rows 27–31) with 18 trees per row for a total of 85 orange trees (five missing) and five rows of lemons (32–36) with 12 trees per row for a total of 55 lemon trees (five missing). In 2002, two additional sets of orange trees in field 5 were used to monitor *H. coagulata* phenology and demography. One set consisted of 10 rows (17–26) in blocks D and F, the other set consisted of 20 rows (1–20) in blocks F and G.

### *Imidacloprid treatment*

Two rows in the block of orange trees were treated on 10 April 2001 with imidacloprid (Admire 2; $240\,g\,l^{-1}$ SC) applied at the rate of $2.34\,l\,ha^{-1}$ ($32\,fl\,oz\,acre^{-1}$) through the irrigation system equipped with two micro-emitter sprinklers per tree (Castle *et al*., 2005). The chemigation treatment to the selected rows permitted systemic uptake of imidacloprid by 36 orange trees without direct impact to the insect populations in adjacent rows that consisted of 49 orange trees.

### *Sampling*

Insect sampling was conducted year-round in 2001 beginning the second week in April and continued weekly until mid-November, at which time a once or twice per month schedule was sustained through the following March. A bucket sampler attached to a 3.7 m extension pole was used to sample the foliage of mature lemon and orange trees that exceeded 7 m in height. The extended reach of the bucket sampler permitted access to both lower and upper sections of the trees and was operated by making a series of forceful thrusts at five locations around each tree. Thrusting into the foliage dislodged adults and nymphs into a collecting jar fastened to a funnel attached to the bottom of the bucket. The contents collected at all five locations per tree were placed into a labelled ziplock bag and constituted a sample unit. In 2001, a total of 12 untreated orange trees and 12 imidacloprid-treated orange trees were bucket sampled each week. By having a minimum of 36 orange trees in each treatment, it was possible to alternate among three sets of 12 trees in both treated and untreated groups, so that any single tree was sampled only once every 3 weeks. Similarly, three sets of seven lemon trees, treated and untreated, were alternated every 3 weeks so as to minimize the impact of sampling on the infestation in any single tree. Beginning in April, 2002, sampling of *H. coagulata* was initiated in an adjacent block of orange trees that included three sets of eight untreated trees that were alternated weekly until the end of July, at which time *H. coagulata* was sampled every other week until the end of October. In yet another block of oranges, but part of the same orchard used in 2001, two different sampling devices, the bucket sampler and a standard insect beat-net, were compared to see if different sampling methods yielded different results based on the catches of *H. coagulata* nymphs and adults with each device. The beat-net was used to collect dislodged *H. coagulata* from branch terminals beaten with a heavy stick at five different locations around each tree.

Each week's sample was returned to the laboratory and stored in a $-30$°C freezer. Upon removal, the contents of each bag were transferred to labelled 20-dram plastic vials containing 70% alcohol. All nymphs in each bag were identified to instar and adult sex was determined.

### *Phenology model*

A stochastic, temperature-dependent phenology model (Dennis *et al*., 1986; Dennis & Kemp, 1988) was developed to provide a more generalized and quantitative representation of the occurrence of nymphal and adult *H. coagulata* stages through time. The model is based on a logistic probability distribution that changes as a function of time $t$, here measured physiologically through the use of accumulated degree-days. The proportion of insects in developmental stage $i$ at time $t$ is given by:

$$\begin{gathered} 1/\{1+\exp[-(a_1-t)/\sqrt{vt}]\} \quad \text{for } i=1 \\ 1/\{1+\exp[-(a_i-t)/\sqrt{vt}]\}-1/\{1+\exp[-(a_{i-1}-t)/\sqrt{vt}]\} \\ \text{for } i=2\ldots5 \\ 1/\{1+\exp[-(a_5-t)/\sqrt{vt}]\} \quad \text{for } i=6 \end{gathered}$$

where $a_1 \ldots a_5$ (units of accumulated degree-days) and $v$ are fitted parameters. Biologically, the parameter $a_i$ is the amount of time needed for an insect to complete the $i$th moult. The model describes a total of six developmental stages including five nymphal instars and adults in a single generation. At any point in time $t$, the $a_i$ values partition the logistic probability density function into six portions. Thus, the probability that an insect will be in stage $i$ at time $t$ is measured by the area under the density function between $a_{i-1}$ and $a_i$. So that the total probability = 1, the model implicitly assumes that $a_0$ and $a_6$ are $-\infty$ and $+\infty$, respectively. The distribution has mean $t$ and variance = $(\pi^2/3)vt$. The parameter $v$ is dimensionless and proportional to this variance. The model further assumes that mortality rates are equal among the developmental stages and that developmental rates are homogeneous among individual insects. Parameters were estimated using a maximum likelihood procedure programmed in SAS (Statistical Analysis System, Cary, North Carolina, USA). Degree-days were estimated using Allen's (1976) method, lower and upper developmental thresholds for *H. coagulata* egg development of 11.9 and 32.9°C (Al-Wahaibi & Morse, 2003), and on-site maximum and minimum temperature data were recorded by a CIMIS weather station (California Department of Water Resources) and reported (http://www.ipm.ucdavis.edu/WEATHER/wxretrieve.html). Developmental thresholds for nymphal stages of *H. coagulata* are not currently available. However, studies on other cicadellid species (Hogg, 1985; Sedlacek *et al*., 1990) indicate that differences in developmental thresholds between eggs and nymphs are $<1$°C, thus, thresholds for eggs should provide reasonably accurate estimates for modelling nymphal development. All degree-day values were based on accumulated heat units from 1 January of each year. Separate models were parameterized for each of four data sets in oranges and lemons in 2001 and 2002 (see above). Based on the resampling methods of Jones & Carberry (1994), a jackknife approach was then used to parameterize a single model over all four sites-years, and a cross-validation method was used to validate the performance of this overall model. Briefly, jackknife estimates of each of the six parameter values above were estimated for a combined model by

$$\hat{P}_* = r\hat{P} - (r-1)\bar{\hat{P}}_{(.)}$$

where $\hat{P}_*$ denotes the parameter value of interest, $\hat{P}$ is the parameter value based on all the data, and $\bar{\hat{P}}_{(.)}$ is the

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average of $r$ partial parameter estimates from all possible combinations (=4) of three site-year data sets out of four total. That is, a single data set is dropped in each partial estimation. A conservative estimate of the standard error of $\hat{P}_*$ is given by

$$\left[\frac{(r-1)}{r}\left(\sum_{i=1}^{r}\hat{P}_{(i)}^{2}-r\bar{\hat{P}}_{(.)}^{2}\right)\right]^{0.5}$$

Similarly, the cross validation procedure involves comparing actual observations for any single data set against a model parameterized with the remaining three data sets. This ensures an independent assessment of the model while taking advantage of the full, but limited, data set (Jones & Carberry, 1994). Model performance was assessed by comparing observations and predictions of six phenological events; the time of peak occurrences of second through fifth instar nymphs and the time when at least 75% and 25% of the insects were either first instars or adults, respectively (Dennis & Kemp, 1988).

## Results

### *Phenology and demography*

During the initial surveys of the field experiment site in late March and early April 2001, very few *H. coagulata* could be detected or observed on the citrus trees designated for monitoring or in the orchard at large. The first sampling of both lemon and orange trees on 10 April yielded a total of 11 adults. By 25 April, young nymphs were emerging on both lemon and orange trees and continued to increase to a seasonal peak in mid-May on oranges (fig. 1a) and slightly later on lemons (fig. 1b) while adults remained scarce. A total of only 30 adults were collected on oranges over seven consecutive sampling dates beginning 25 April until 8 June compared to a total of 3598 nymphs; on lemons, only 16 adults were collected compared to 1293 nymphs during the same interval. Then, on 15 June, 32 and 17 adults were collected on orange and lemon respectively, marking the beginning of adult emergence from the spring generation of nymphs. Adult densities on oranges increased rapidly to a mean >20 per tree by 6 July and remained at this level through the end of August with the exception of one rainy day, 13 July (fig. 1a). In lemons, mean adult densities reached a level of >20 per tree on 3 August and exceeded 30 per tree on two dates in late August before falling back to mean densities >15 per tree through September and October (fig. 1b).

Nymphal densities gradually declined through July as the last late instars were collected on 17 August in oranges and 3 August in lemons (fig. 1). A second generation of nymphs did not materialize in citrus following the emergence of adults from the spring generation of nymphs. Consequently, there was no additional recruitment to the summer and autumn adult population, at least none that appeared to be generated in our study orchard. Adult densities declined severely in oranges after November, but remained at modest levels in lemons into February 2002. At this point, adult densities reached a minimum in oranges and lemons comparable to the beginning of the *H. coagulata* phenology survey 1 year earlier.

The first of the 2002 spring generation of nymphs was detected on 4 April and numbers gradually increased, but overall densities were drastically lower than in 2001 (fig. 1). This was also the case in the new study area for 2002 where the first emergence of nymphs also was recorded on 4 April, but mean densities never increased higher than three nymphs per tree (fig. 2). Adults were once again extremely rare through May and early June 2002, but began to increase rapidly beginning 21 June (fig. 2). Adult mean densities in late June and early July quickly exceeded the earlier nymphal densities as recruitment from neighbouring trees such as those used in the 2001 study oranges (fig. 1a) probably contributed to disproportionately higher adult numbers relative to nymphs in 2002 (fig. 2).

The data obtained by both beat net and bucket samplers yielded similar phenology profiles for nymphs and adults as those observed in the other 2002 study blocks and from the 2001 study even though sampling intervals were every 2 weeks. Nymphs predominated in the samples taken from 19 April through 14 June 2002 before the appearance of adults in higher densities on 28 June (fig. 3). Three sampling dates in autumn 2001 conformed to the pattern observed at the other study areas by yielding only adults (fig. 3). Quantities obtained by the beat net were significantly greater ($F_{1,118}=121$, $P<0.0001$) than for the bucket sampler, but the essential point is that each device yielded only adults during the autumn sampling.

The progression of first instar nymphs to adults during the spring of each year occurred as a series of overlapping distributions that extended approximately 4 months between the time that the first and last nymphs were collected (fig. 4). In the 2001 oranges, the peak mean density of each nymphal instar was relatively constant and extended into the adult stage at nearly the same level (fig. 4a). The duration of each instar varied between 6 and 9 weeks, the shortest interval occurring for first instars and the longest for fifth instars. Approximately 12 weeks were spanned from the time that the first nymphs and then first adults were collected. Although the temporal pattern of instar occurrence and duration observed in lemons was similar to oranges, the peak densities of each instar were more variable in lemons (fig. 4b). Fifth instar nymphs were collected one week earlier in lemons than in oranges, but the first appearance of newly emerged adults occurred on the same date in both citrus species. Despite much lower densities in 2002, a similar temporal progression of nymphal instars was observed as in 2001, with the exception that first instar nymphs were collected as early as 4 April. However, the first record of new adult emergence still did not occur until 20 June (fig. 4c).

### *Phenology model*

The stochastic phenology models based on the logistic probability distribution fitted the observed occurrence of the five nymphal instars and adults of *H. coagulata* during a single generation reasonably well for most individual data sets as evidenced by the small asymptotic standard errors of the parameters (table 1). Representative fits of the models to observed data are shown in fig. 5 for two orange data sets in 2001 and 2002. The combined jackknife model estimated from data at all four site-years had intermediate parameter values and 95% confidence intervals around these values generally encompassed those based on individual data sets. Variable parameter values across sites and years imply variability in the timing of occurrences for the six developmental stages as noted above (fig. 5). There was considerable

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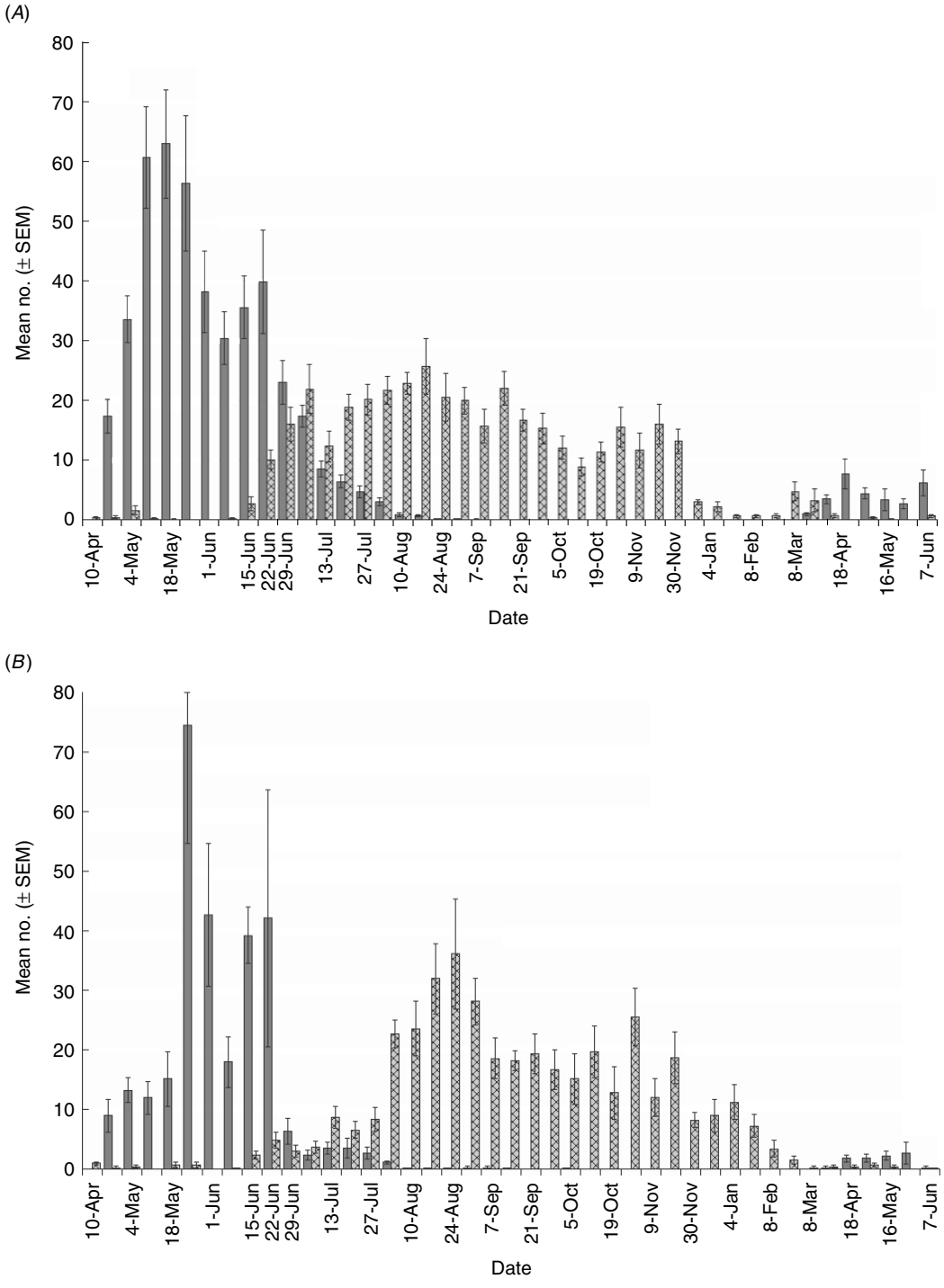


Fig. 1. Mean (±SEM) numbers of *Homalodisca coagulata* nymphs (■) and adults (▨) obtained by the bucket sampler on untreated (a) orange trees ($n = 12$) and (b) lemon trees ($n = 7$) in 2001–2002.

variation among the four data sets based on both physiological and chronological time (table 2). The physiological time when most of the population consisted of first instar nymphs varied from 377 to 501 degree-days. There was similar variability in the peak occurrence of second and fifth instar nymphs and the time when adults first begin to appear. In contrast, the difference in the physiological time of the peak occurrence of third and fourth instar nymphs was relatively small across the four site-years. Due to variable temperature profiles between 2001 and 2002, primarily a warmer winter in

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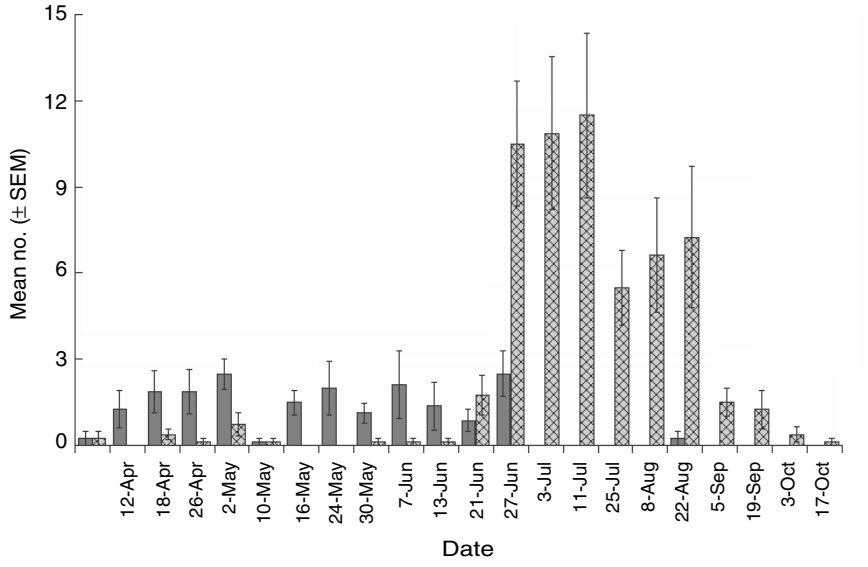


Fig. 2. Mean (±SEM) numbers of *Homalodisca coagulata* nymphs (■) and adults (▩) obtained by the bucket sampler on untreated orange trees ($n = 8$) in 2002.

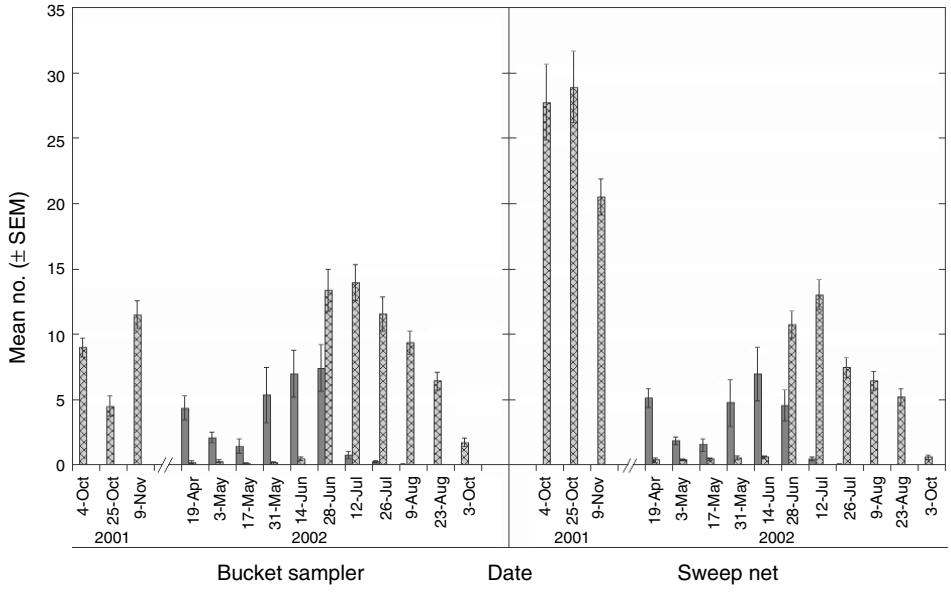


Fig. 3. Mean (±SEM) numbers of *Homalodisca coagulata* nymphs (■) and adults (▩) obtained by using a bucket sampler or a sweep net in 2001–2002. The mean densities of nymphs and adults collected in this study area during 2002 are similar to those reported from the study area represented in fig. 2.

2002, differences in chronological time among data sets ranged from 7 to 14 days depending on developmental stage (table 2). Despite the relatively large differences in physiological and chronological timing for some phenological events, the combined model reasonably predicted the timing of events in each site-years with the exception first instar nymphs. The combined model predicted that most of the population would consist of first instar nymphs 13–15 days too early for the two orange data sets in 2002. All other predictions of the combined model differed from individual observations by less than 8 days (table 2). Predictions were especially good for third and fourth instar nymphs.

### *Sex ratio*

Adult sex ratios exhibited a male bias both years, but with the most consistent bias occurring in the 2001 oranges (fig. 6a). Differences were highest early in the emergence period with significantly greater proportions of males occurring on 29 June, 06 July and 20 July ($\chi^2_1 = 285$,

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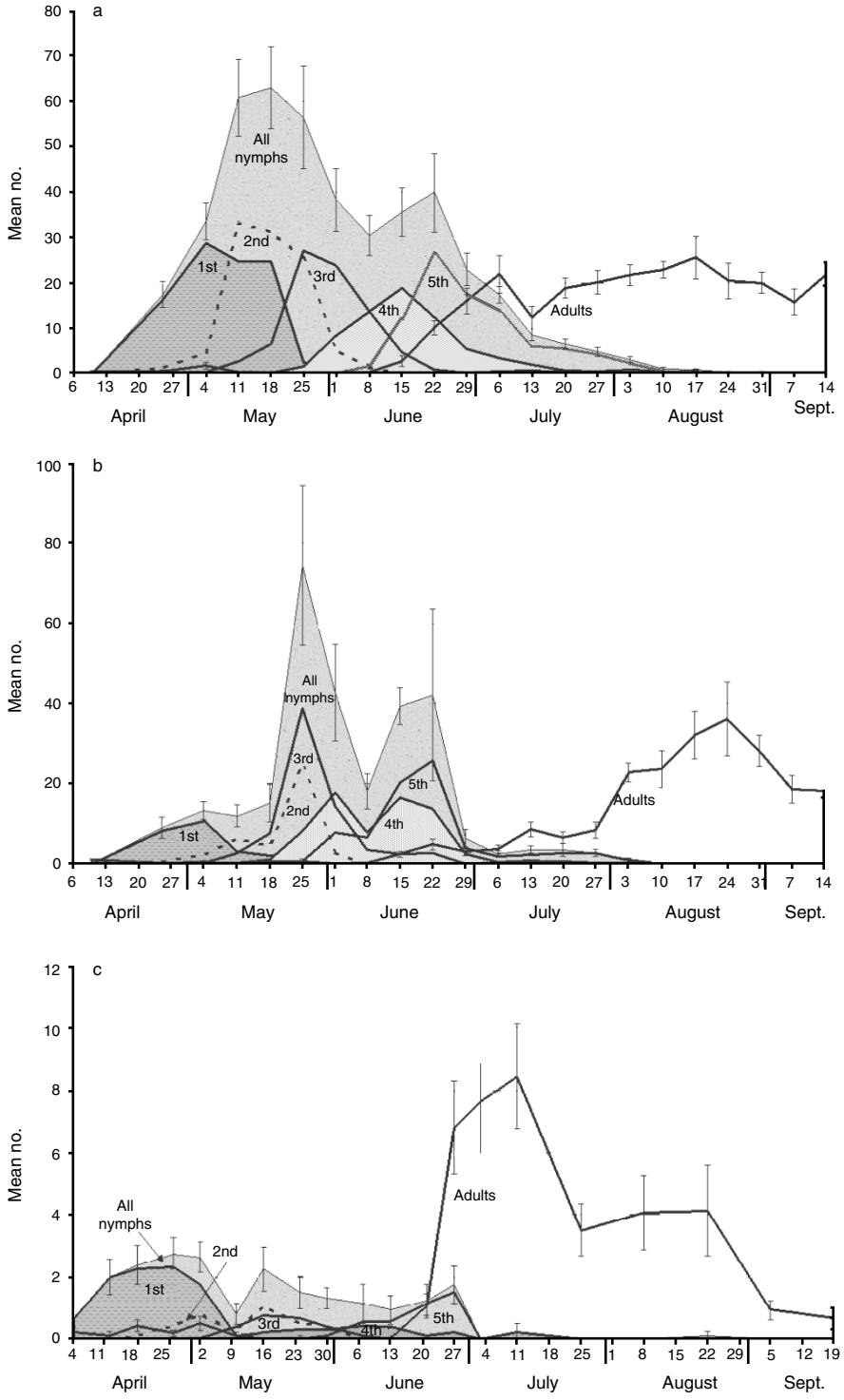


Fig. 4. Demographic structure of *Homalodisca coagulata* in (a) oranges and (b) lemons in 2001, and in oranges in 2002 (c). Area curves for each nymphal instar (first to fifth), all nymphs (±SEM) and adults (±SEM) are based on mean numbers collected with a bucket sampler on each sampling date.

$P = 0.0041$; $\chi^2_1 = 280$, $P < 0.0001$; $\chi^2_1 = 285$, $P = 0.0041$, respectively). Proportions of males remained steadily higher than females thereafter with only slight oscillations about the seasonal means of $0.569 \pm 0.008$ for males and $0.431 \pm 0.008$ for females through mid-October (fig. 6a). Thereafter, near equal proportions of males and females were observed

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Table 1. Parameters for the phenology model fitted to *Homalodisca coagulata* data from oranges and lemons in 2001 and 2002, field 5, University of California's Agricultural Operations, Riverside, California.

| | Parameter values† (asymptotic SE) | | | | | |
|---|---|---|---|---|---|---|
| Site | $a_1$ | $a_2$ | $a_3$ | $a_4$ | $a_5$ | $v$ |
| 2001 | | | | | | |
| Oranges (D–F; 27–31)* | 482.9 (2.53) | 618.4 (2.55) | 756.1 (3.08) | 896.3 (3.43) | 1081.4 (4.08) | 5.99 (0.17) |
| Lemons (D & E; 32–36) | 433.9 (6.22) | 559.9 (4.52) | 700.0 (4.16) | 845.1 (5.10) | 1093.3 (8.39) | 7.17 (0.32) |
| 2002 | | | | | | |
| Oranges (D & F; 17–26) | 543.7 (11.2) | 653.4 (13.0) | 731.6 (13.6) | 818.1 (13.0) | 930.0 (10.2) | 2.68 (0.38) |
| Oranges (F & G; 1–20) | 543.2 (3.66) | 615.9 (4.40) | 716.9 (3.92) | 857.0 (2.77) | 1000.9 (2.09) | 2.99 (0.10) |
| Combined (jackknife)# | 490.6 (22.1) | 608.7 (14.6) | 727.9 (23.0) | 855.2 (20.4) | 1003.2 (40.5) | 4.56 (1.44) |

† Parameters are measured in degree days calculated using Allen's (1976) method with lower and upper developmental thresholds of 11.9 and 32.9°C; the parameters $a_1$–$a_5$, measured in degree-days, partition the logistic probability density function among the six developmental stages and $v$ is proportional to the variance of the logistic distribution (see text and Dennis *et al*., 1986).
* Location of study sites in field 5 are represented by the blocks (D–G) and row numbers (1–36).
# Combined parameters and SE estimated from a jackknife procedure described by Jones & Carberry (1994). See text for further detail.

through 30 November. Following the decline of adults in oranges after 30 November, total numbers of males and females collected each sampling date remained mostly equal through winter and spring. In lemons, a similar pattern of higher male proportions was observed between July and November 2001 (fig. 6b). The seasonal mean proportion of males was $0.552 \pm 0.012$ compared to $0.448 \pm 0.012$ for females, but with greater fluctuations among sampling dates compared to oranges. By late November, near equal proportions of males and females were observed again through the following spring, but with a slight shift to female bias (fig. 6b). Despite the decline in *H. coagulata* densities in 2002, higher mean proportions of male adults were still apparent from the time of emergence in June through the summer (fig. 7).

### *Management*

The treatment of oranges with imidacloprid had a pronounced impact on *H. coagulata* nymphs and adults (fig. 8). However, differences in nymphal counts were not apparent until 6 weeks after the 10 April application when a substantial drop in nymphal densities occurred on 25 May in the treated oranges. Despite the delayed response, the overall numbers of nymphs produced in treated oranges was significantly lower than those produced in the untreated oranges (fig. 8). Following the emergence of adults, the overall numbers of adults were significantly lower in treated oranges despite early and late-season parity in numbers between treated and untreated oranges. Although the initial equivalent numbers of adults in treated and untreated oranges (fig. 8) suggests equivalent emergence rates, the number of fifth instar nymphs collected in the imidacloprid-treated oranges was almost 14-fold lower than those collected in untreated oranges even though the number of first instar nymphs in treated trees was 20% higher (fig. 9). The proportion of the total nymphal population represented by each nymphal instar was fairly equally divided in the untreated oranges with slightly higher percentages of first and second instars compared to third and fourth instars (fig. 9). In the treated oranges, however, the proportion of the total nymphal population declined with each advancing instar (fig. 9), resulting in a distorted demographic structure of the immature population.

## Discussion

The temporal occurrences of *H. coagulata* adults and nymphs in southern California citrus followed a well-defined pattern over both years of the study. The new generation of nymphs began in April each year with the emergence of first instars occurring over a 6–7 week period. The timings of subsequent instars were also nearly identical each year, with fifth instars first appearing in early June and peaking in late June, then tailing off to nil by mid-August. In oranges, the earliest adult emergence began by mid-June each year, then rapidly increased to peak levels by early July. Adult emergence also began in lemons in mid-June, but peak numbers were not observed until August. The later adult peak in lemons may be more reflective of changing nutritional profiles between lemons and oranges that resulted in part from a shift of *H. coagulata* adults to lemons from oranges (Bi *et al*., 2005). Indeed, there was conspicuous flight activity by adults from the time that the new generation of adults began emerging that resulted not only in shifts between oranges and lemons, but between citrus and surrounding fields of various summer annual crops as well as ornamental shrubs and trees in the urban landscape. Very few *H. coagulata* nymphs or adults were observed outside of citrus prior to adult emergence, but this rapidly changed during the summer emergence from citrus as flight-active adults emigrated from the citrus. The failure of adult numbers to climb to higher levels in citrus through July and August as the remainder of the nymphs matured to adults is likely to be due to seasonal movement out of citrus, possibly governed by nutritional factors (Brodbeck *et al*., 1990).

The phenology data presented here is the first empirical data to suggest that the two generation per year observation (Blua *et al*., 1999) may not functionally materialize in all locations. In our particular field plots within a large citrus orchard, the June/July emergence of adults produced a conspicuous number of reproductive females as indicated by the white patches of brochosomes on their forewings (Hix, 2001). Egg deposition in the citrus during July and August was apparent, but so too was the high degree of parasitism that often approaches 100% (Hoddle, 2004) during summer months. Outside of our citrus orchard study site, there may well have been a small proportion of the second egg generation that hatched to nymphs, but as a rule

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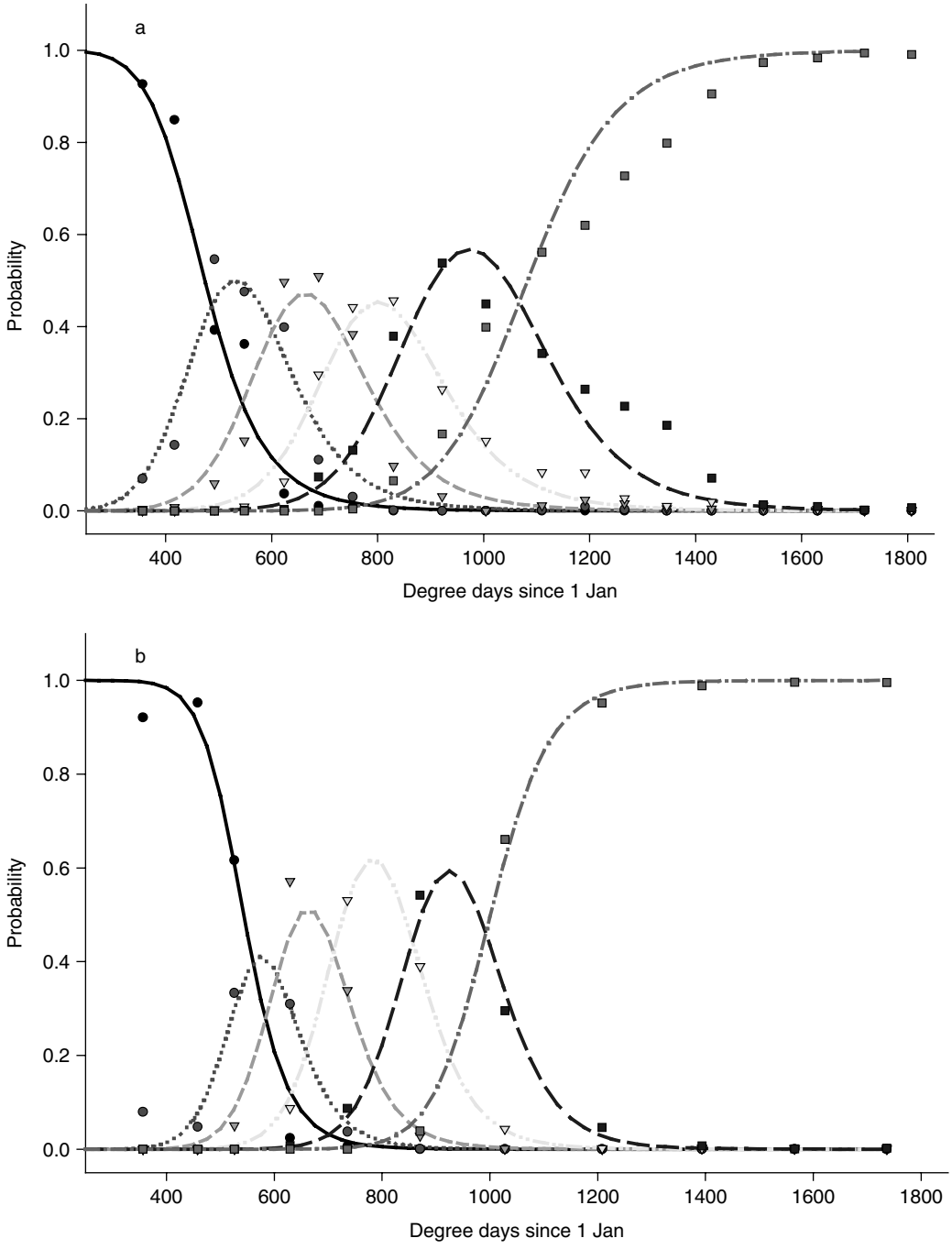


Fig. 5. Comparison of observed data (points) to the Dennis-Kemp phenology model (lines) for nymphal and adult *Homalodisca coagulata* for two representative orchards; (a) oranges in 2001 and (b) oranges (field 5) in 2002, University of California's Agricultural Operations, Riverside, California. —, first instars; ...., second instars; – –, third instars; – –, fourth instars; – – –, fifth instars; - · - · -, adults.

summer egg parasitism in southern California is intensive. In one survey completed in 1996–1997, Triapitsyn *et al*. (1998) observed no parasitism of *H. coagulata* eggs collected in early spring, but up to 80% of eggs collected on July 1997 on various ornamental plants in Riverside, California were parasitized. In another study, parasitism of *H. coagulata* eggs by *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae) in California reached up to 100% (Phillips, 1998). The drastic difference in parasitism between first and second generations of *H. coagulata* led Triapitsyn & Phillips (2000) to conclude that the large numbers of *H. coagulata* in southern California were due in part to poor natural control of the first generation during early spring. The results from both years of our study indicating a very reduced contribution to the

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Table 2. Comparison of observed and predicted phenological events for *Homalodisca coagulata* in oranges and lemons in 2001 and 2002, University of California's Agricultural Operations, Riverside, California.

| Event | Degree-days | | Day of year | | Difference from model (days) |
|---|---|---|---|---|---|
| | Observed | Predicted[a] | Observed | Predicted | |
| 75% first instar | | | | | |
| Orange 2001 | 427 | 453 | 125 | 127 | 2 |
| Lemon 2001 | 377 | 463 | 118 | 128 | 10 |
| Orange 2002 | 503 | 442 | 117 | 104 | −13 |
| Orange F5 2002 | 501 | 420 | 117 | 102 | −15 |
| Peak second instar | | | | | |
| Orange 2001 | 544 | 554 | 137 | 139 | 2 |
| Lemon 2001 | 489 | 547 | 130 | 138 | 8 |
| Orange 2002 | 596 | 544 | 132 | 126 | −6 |
| Orange F5 2002 | 576 | 533 | 131 | 126 | −5 |
| Peak third instar | | | | | |
| Orange 2001 | 681 | 671 | 151 | 151 | 0 |
| Lemon 2001 | 622 | 644 | 144 | 148 | 4 |
| Orange 2002 | 690 | 660 | 146 | 143 | −3 |
| Orange F5 2002 | 663 | 664 | 143 | 143 | 0 |
| Peak fourth instar | | | | | |
| Orange 2001 | 820 | 797 | 165 | 163 | −2 |
| Lemon 2001 | 765 | 768 | 159 | 160 | 1 |
| Orange 2002 | 772 | 788 | 155 | 156 | 1 |
| Orange F5 2002 | 784 | 799 | 155 | 157 | 2 |
| Peak fifth instar | | | | | |
| Orange 2001 | 982 | 937 | 178 | 174 | −4 |
| Lemon 2001 | 961 | 917 | 176 | 173 | −3 |
| Orange 2002 | 871 | 937 | 165 | 170 | 5 |
| Orange F5 2002 | 926 | 962 | 169 | 173 | 4 |
| 25% Adult | | | | | |
| Orange 2001 | 997 | 947 | 179 | 175 | −4 |
| Lemon 2001 | 1000 | 934 | 179 | 174 | −5 |
| Orange 2002 | 877 | 950 | 165 | 172 | 6 |
| Orange F5 2002 | 943 | 979 | 171 | 174 | 3 |

[a] Predicted timing based on a cross-validation approach (Jones & Carberry, 1994) which compares the observed timing of one data set with that predicted from a model based on the remaining three data sets combined.

sustaining population by the second generation corroborates the earlier findings of high parasitism of the second generation of *H. coagulata* eggs.

This raises the question of how *H. coagulata* populations are sustained through the autumn and winter months to give rise to the following spring generation of nymphs if production of the second generation is severely curtailed each year. It must be reiterated that the data from the present study supports the concept of a suppressed second generation based on sampling completed in citrus only and allows the possibility that second generation development occurred outside citrus. However, even if there is only minimal contribution to the sustaining population by the second generation as indicated by the available evidence, the phenology data for adults nevertheless is supportive of the alternative scenario that first generation adults do carry over to the following winter and early spring to give rise to the next spring generation. The data presented for oranges (fig. 1a) showed a gradual attrition of adult numbers through the end of November following the 17 August 2001 peak. From December on, adult numbers are markedly lower but still detectable through the end of February before rising slightly during March and April. A similar pattern of attrition following the 24 August 2001 peak was observed in lemons, except that the gradual decline continued right through the end of February with still detectable numbers represented from March through May. However, in both orange and lemon data sets, a slight rise in adult numbers from mid-October through mid-November may indicate recruitment of adults from outside citrus, possibly representative of second generation adults produced on alternate hosts. On the other hand, putative contraction of the wider landscape population of *H. coagulata* back into citrus during the autumn could represent mostly first generation adults that had emigrated from citrus during the summer before returning in autumn.

The abrupt rise in numbers of adult *H. coagulata* beginning in mid-June each year signified the emergence of a new generation of adults. This demarcation is important not only because it represented the imminent release of large numbers of adults to the surrounding landscape where the spread of *X. fastidiosa* could occur, but also because the transition from the few surviving adults from the previous year to the new generation of adults was so complete that demographic data such as sex ratio could be ascribed almost entirely to the new generation. Data sets from lemons and oranges in 2001 and oranges in 2002 indicated a persistent male bias right from the time of first emergence through the summer months and into the autumn. The highest mean proportions of males were observed early in the emergence

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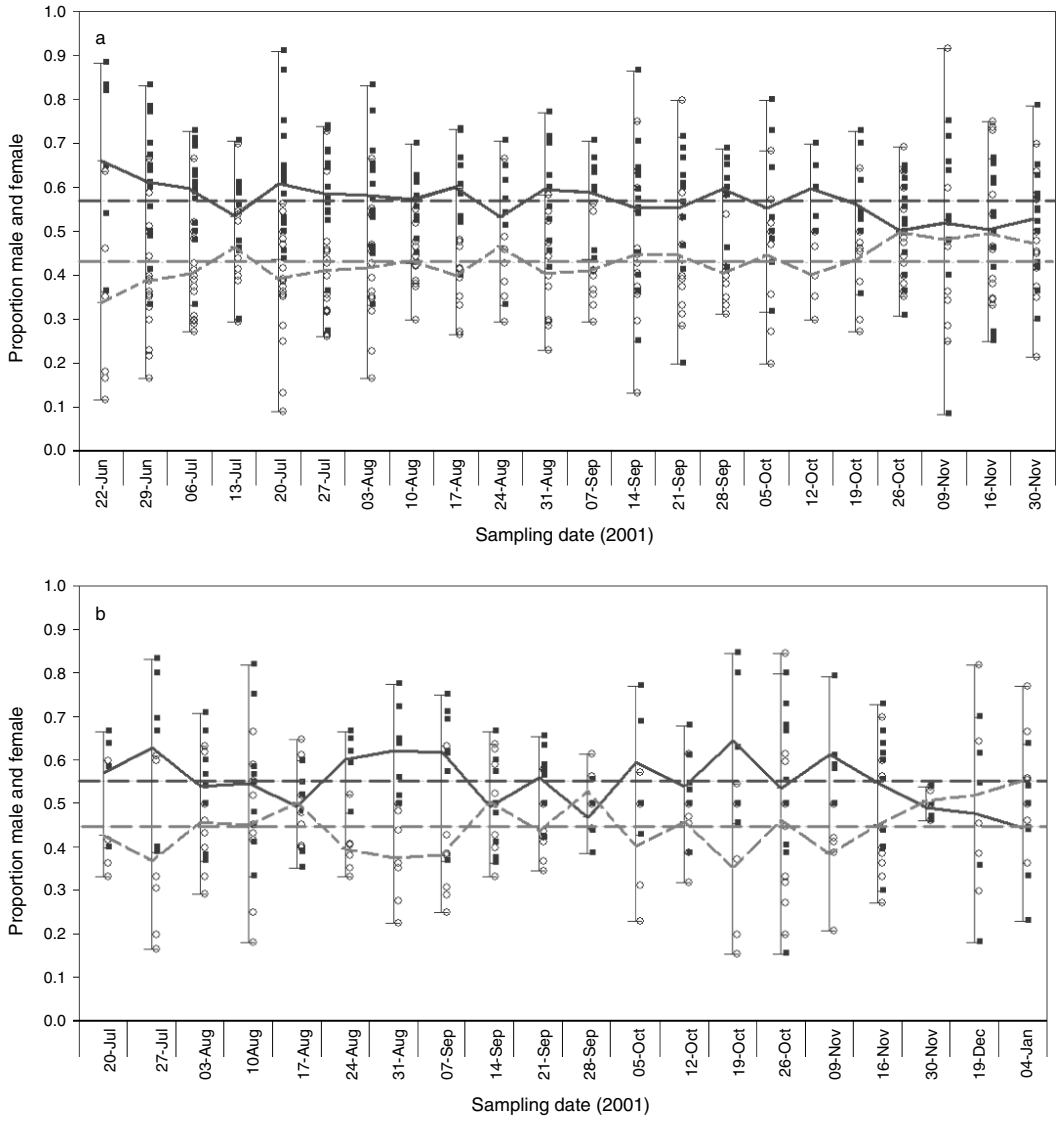


Fig. 6. Mean proportions of adult male (— ■) and female (---○) *Homalodisca coagulata* on (a) oranges and (b) lemons in 2001. A total of 24 orange trees and 14 lemon trees were sampled each date, but proportions of males and females were determined only for trees with ≥10 adults (a). The traversing lines track the mean proportions on each date for each sex, the horizontal dashed lines represent the mean seasonal proportions for each sex (males above). After 30 November, adult densities dropped below the threshold level of 10 per tree in oranges; the same occurred on 8 February in lemons.

period each year, suggesting slightly faster nymphal development for the smaller males compared to females. This effect was most apparent in the 2001 oranges with mean male proportions decreasing from a high of 0.66 on 22 June to 0.61 on 29 June, 0.60 on 6 July, before dropping below the seasonal mean of 0.57 on 13 July. Thereafter, the relative proportions of males and females varied little about the seasonal mean through mid-October. In lemons, the relative mean proportions were not as stable through time even though the overall trend was also male biased. Fewer samples on a weekly basis were collected in lemons compared to oranges, and the canopy of the lemon trees tended to be more uneven and open than the denser and more consistent canopies of the orange trees. Consequently, the relative variability observed in the sex ratios in lemons was more likely to be attributable to sampling error rather than real differences between lemons and oranges. The biological significance of a male-biased sex ratio for *H. coagulata* is unknown at this point. It seems improbable that differential mortality in one or more nymphal instars would account for such differences, but nonetheless is conceivable. Attempts to sex early nymphal instars were unsuccessful due to underdevelopment of genitalia.

Increasing reliance on pest- and stage-specific insecticides will depend upon information concerning when the target pests/stages are present and how they can be most effectively treated. In the present study, the imidacloprid treatment made in early April was quite effective in reducing

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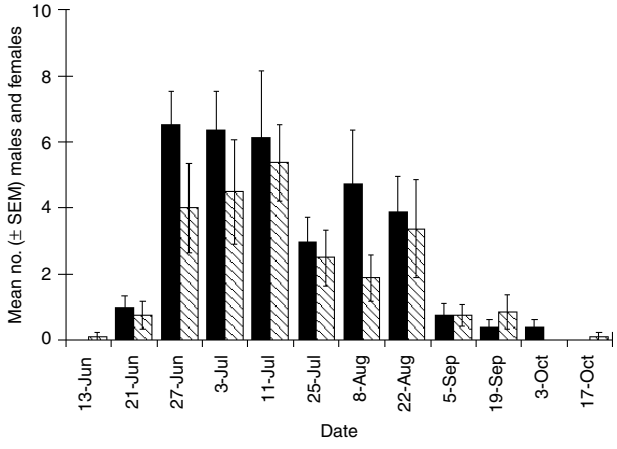


Fig. 7. Mean (±SEM) proportions of adult male (■) and female (▨) *Homalodisca coagulata* on oranges in 2002.

the numbers of nymphs and adults on oranges. However, a lag period of about 6 weeks occurred before peak concentrations were detected in xylem fluid of the treated orange trees (Castle *et al*., 2005). Consequently, very little impact, if any, was measured on first instar nymphs based on the higher total number collected on treated trees compared to the untreated trees. Progressive reductions in the numbers of each subsequent instar began only with the second instars on the treated trees. Perhaps an earlier treatment of imidacloprid prior to the 10 April date used in this study would have allowed the time needed for imidacloprid to reach a sufficiently high titre and distribution throughout the mature orange trees so as to impact all nymphal instars including the first instar. The potential problem with this approach, however, is that an application made well before the emergence of the first instars would be anticipatory in nature, and therefore possibly unnecessary if an infestation failed to materialize. Adult *H. coagulata* were too few during the spring of 2001 and 2002 to monitor reliably and to serve as a gauge of whether the *H. coagulata* nymphal population was likely to increase, although an alternative approach might depend upon sampling *H. coagulata* eggs on citrus leaves. Other chemical treatments effective against specific instars of *H. coagulata* could be planned more easily and used with greater confidence so long as pest managers were aware of the relatively discrete occurrence of *H. coagulata* instars. For example, applications of the chitin synthesis inhibitor buprofezin could be directed at first and second instars during the time window in late April and early May when they predominate in citrus. Treatment with a broad-spectrum insecticide could be made over a wider time period than for buprofezin, although younger nymphs may still prove more vulnerable to treatments than older nymphs and adults. The essential point is that knowledge of the phenology of particular stages known to be vulnerable to specific treatments provides pest managers with the capability to anticipate and plan their course of action along with a basic understanding of why they are doing so.

The combined phenology model may serve as a useful pest management tool in predicting the occurrence of particular *H. coagulata* stages in southern California citrus. Although the timing of the initial occurrence of first instar nymphs proved to be highly variable, the combined model predictions of the timing of second to fifth instar nymphs and adults were comparatively good. The combined model in some cases predicted an earlier occurrence of a particular stage, but in other cases predicted a later occurrence. Differences that are positive (last column of table 2) are potentially more detrimental to management decisions than those that are negative. This is because the timing of a

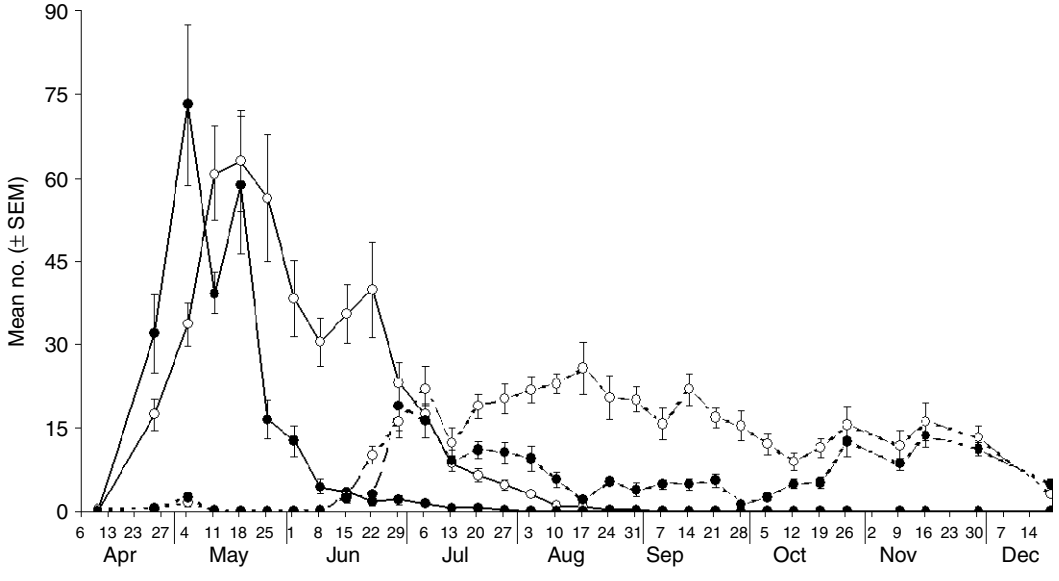


Fig. 8. Effect of a systemic treatment of imidacloprid on *Homalodisca coagulata* nymphs (—) and adults (---) on 2001 oranges. Mean (±SEM) numbers of nymphs and adults were obtained by sampling 12 trees each per date in both treated (●) and untreated (○) oranges.

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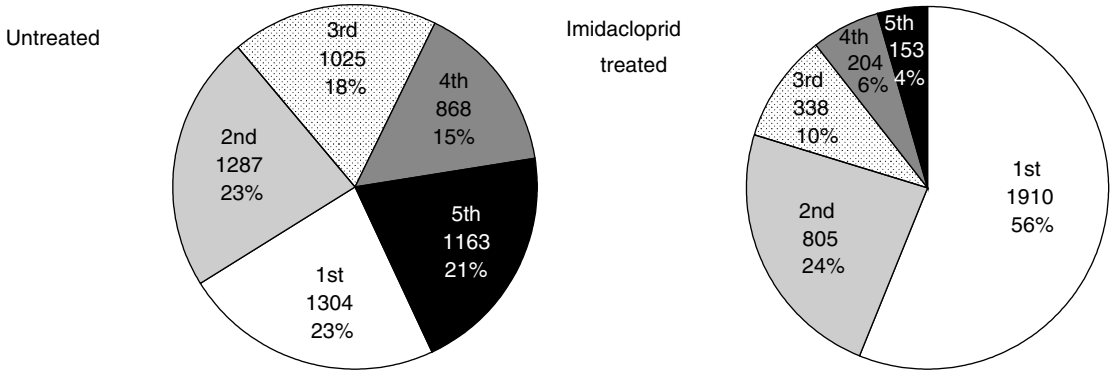


Fig. 9. Comparison of the total number of nymphs and percentage of total nymphs of *Homalodisca coagulata* represented by each nymphal instar (first to fifth) in imidacloprid-treated and untreated oranges in 2001.

sampling or spraying would occur after the peak occurrence of a target stage and may prove less effective than if it had been conducted earlier. In contrast, negative differences mean that the particular operation is carried out too early, i.e. before peak occurrence. A sampling operation conducted too early would be likely to yield none or too few individuals of a particular stage to warrant a control action, and would therefore require repeated sampling at later times until an action threshold was reached. Because the combined model predicted an earlier occurrence of stages in most cases where differences were observed it is generally conservative, erring on the side of taking action to soon rather than too late. However, caution would have to be exercised in those cases where the combined model predicted a later occurrence. Overall, further refinement and broader validation of the phenology model is needed and this will be possible as additional data sets on the seasonal occurrences of *H. coagulata* stages are realized.

Ultimately, the task for pest managers will be to determine what effect control actions taken against *H. coagulata* populations have on the spread of *X. fastidiosa* and the occurrence of Pierce's disease. The number of *H. coagulata* and other leafhopper vectors that feed upon *X. fastidiosa*-infected plants, the proportion that attain *X. fastidiosa* through feeding, and the proportion that visit and ultimately inoculate uninfected host plants play a critical role in the spatial and temporal dynamics of Pierce's disease and other vector-borne diseases (Anderson, 1981). In the absence of specific knowledge concerning vector-specific parameters of *X. fastidiosa* epidemiology, the most obvious course of action is to proceed with efforts to reduce *H. coagulata* populations. Incorporating the phenology data and model into decision-making may help to improve management for *H. coagulata* through better-timed and more effective control actions.

## Acknowledgements

We are grateful to Mac Learned, Greg Ballmer and Paul Merten for their assistance, and William Kemp for advice on developing the phenology model. This study was partially supported by funds from the University of California Pierce's Disease Research Grant Program.

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(Accepted 22 August 2005)