Mortality dynamics and population regulation in *Bemisia tabaci*

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Abstract

Natural mortality is an important determinant of the population dynamics of a species, and an understanding of mortality forces should aid in the development of better management strategies for insect pests. An in situ, observational method was used to construct cohort-based life tables for *Bemisia tabaci* (Gennadius) Biotype B (Homoptera: Aleyrodidae) over 14 generations on cotton in central Arizona, USA, from 1997 to 1999. In descending order, median marginal rates of mortality were highest for predation, dislodgment, unknown causes, egg inviability, and parasitism. The highest mortality occurred during the 4th nymphal stadium, and the median rate of immature survival over 14 generations was 6.6%. Predation during the 4th nymphal stadium was the primary key factor. Irreplaceable mortality was highest for predation and dislodgment, with the absence of these mortality factors leading to the greatest increases in estimated net reproduction. There was little evidence of direct or delayed density-dependence for any mortality factor. Wind, rainfall, and predator densities were associated with dislodgment, and rates of predation were related to densities of *Geocoris* spp., *Orius tristicolor* (White), *Chrysoperla carnea* s.l. Stephens, and *Lygus hesperus* Knight. Simulations suggest that immigration and emigration play important roles in site-specific dynamics by explaining departures from observed population trajectories based solely on endogenous reproduction and mortality. By a direct measurement of these mortality factors and indirect evidence of adult movement, we conclude that efficient pest management may be best accomplished by fostering greater mortality during the 4th stadium, largely through a conservation of predators and by managing immigrating adult populations at their sources.

Introduction

Multiple abiotic and biotic mortality forces act on insect populations. These forces may be naturally occurring, as in the case of predators, parasitoids, pathogens, host-plant effects, and weather, or man-made such as cultural manipulations, and the use of insecticides. Understanding of the timing, spatial distribution, and magnitude of these mortality factors is central to the study of population dynamics. It is also central to predicting pest outbreaks and in developing better pest management systems that take advantage of, and build upon, existing mortality forces. The construction of life tables is a robust method for describing and quantifying mortality in a population. Many life tables have been developed for insects (see reviews by Podoler & Rogers, 1975; Stiling, 1988; Cornell & Hawkins, 1995), and their analyses have provided important insights into the dynamics and regulation of insect populations in many ecological systems (e.g., Morris, 1957, 1959; Varley et al., 1973; Southwood & Reader, 1976; Royama, 1981b; Carey, 1989; Hawkins et al., 1999).

Bemisia tabaci (Gennadius) biotype B (= *B. argentifolii* Bellows and Perring) (Homoptera: Aleyrodidae) is a key pest of many field and horticultural crops world-wide (Oliveira et al., 2001). *Bemisia tabaci* is multivoltine and highly polyphagous. Following its initial invasion into the USA in the mid-1980s (Brown et al., 1995), *B. tabaci* has

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been a key pest of cotton, cantaloupe, and various vegetables in the low desert production areas of Arizona and southern California since the early 1990s (Ellsworth & Martinez-Carrillo, 2001). The insect has no quiescent stage and persists by moving among cultivated and wild hosts throughout the year. In the south-western USA, populations of *B. tabaci* are extremely low during winter months, begin to increase in the spring, and typically reach outbreak levels during summer months on cotton (Watson et al., 1992; L. Cañas, S.E. Naranjo & P.C. Ellsworth, unpubl.).

Despite this insect's pest status and the generalized observations of others, the mechanisms of population change have not been extensively investigated nor well understood. Abiotic effects such as extremes in temperature, low humidity, rainfall, and severe wind storms have been reported to be associated with declines in *B. tabaci* populations (Khalifa & El-Khidir, 1964; Avidov & Harpaz, 1969; Gameel, 1970; Sharaf, 1982; Naranjo et al., 2003). Biotic factors such as host-mediated effects are also known to influence many aspects of *B. tabaci* biology, including survival (reviewed by van Lenteren & Noldus, 1990). A large and diverse assemblage of predators, parasitoids, and pathogens are also known to attack *B. tabaci* (Faria & Wraight, 2001; Gerling et al., 2001; Naranjo, 2001). While many mortality factors are likely to influence populations of *B. tabaci*, there is a dearth of comprehensive data on the specific causes of death in the field, the quantitative rates of mortality associated with these causes, and the impact of these mortalities on population dynamics.

The objective here was to develop comprehensive life tables for *B. tabaci* in order to estimate specific mortality factors affecting each immature developmental stage in the cotton system. A direct, in situ method was used that consisted of identifying and following cohorts from natural populations of *B. tabaci*. Marginal mortality, key factor, density-dependence, irreplaceable mortality, and simulation analyses were used to interpret the effects of this mortality on whitefly population dynamics. This information supports our overall goals to gain insights into the basic population ecology of *B. tabaci* and to identify opportunities for more efficient population regulation leading to improved management of this world-wide pest.

Materials and methods

All studies were conducted at the University of Arizona, Maricopa Agricultural Center, Maricopa, AZ, USA. Cotton, *Gossypium hirsutum* L. (cv. Deltapine NuCOTN 33B), was planted in early to mid-April each year and grown according to standard agronomic practices for the area. Life table data were collected from insecticide-free plots within a 2–3 ha site. Plots were 12 rows (1 m center-to-center) by 45.7 m (0.055 ha) each in 1997 and 18 rows by 36.6 m (0.065 ha) in 1998 and 1999. Separate cohorts (see below) were identified in each of four plots on 4 to 6 different dates throughout each season; however, to improve the sample size, data for any one date were combined across all plots for all analyses presented here.

Cohort establishment

The multivoltine nature of *B. tabaci* leads to broadly overlapping generations throughout the year. Thus, an in situ observational method that took advantage of the sessile nature of the immature stages was used. Cohorts of eggs were identified in natural populations on the undersides of cotton leaves with the aid of an 8X Peak® loupe (Light Impressions, Brea, CA, USA). Newly laid eggs (<1 day old) were identified by their creamy-white color and their location on leaves near the terminal or other new growth of the cotton plant. A small circle was drawn around individual eggs or small clusters of no more than 2–3 eggs using a non-toxic, ultra-fine-point black permanent marker (Sanford, Bellwood, IL). A small slot was cut in the side of the plexiglass hood of the loupe so that the marking pen could be inserted and manipulated within the field of view. A small numbered tag was placed around the petiole of the marked leaf, and flagging tape was tied around the mainstem of the plant to facilitate relocation. No more than five eggs were marked on a single leaf, and the main leaf sectors were used to facilitate the identification of each egg. Only a single leaf was used per plant. Plants were evenly spaced along the central 2–3 rows of each plot. A minimum of 50 eggs was marked in each plot for each date for a total of ≥200 eggs per cohort. The total number of plants used per plot varied depending on insect density and ranged from 20 to 40.

An identical procedure was used to locate and mark the position of newly settled 1st instar nymphs, with the exception that marked circles never contained more than one nymph. Crawlers were readily distinguished from settled 1st instars, which have a slightly more translucent color and are flush with the leaf surface. Crawlers typically settle in a few minutes to 1–2 h after eclosion. To verify that settled nymphs and not mobile crawlers were marked, the leaves were re-examined 1–2 h later. A minimum of 50 nymphs was marked per plot (≥200 per cohort). Eggs and 1st instar nymphs were marked on different plants, and cohorts were established on a single day during morning hours. Cohorts were established on 27 June, 31 July, 11 and 29 August in 1997, 29 June, 17 July, 6 and 25 August, and 1 and 25 September in 1998, and 5 and 26 July, and 9 and 31 August in 1999 (14 cohorts total). These dates cover the breadth of the insect's occurrence on cotton in central Arizona. We use the terms 'cohort' and 'generation' interchangeably in

this paper, because each cohort measures the total mortality from egg to adult and is consistent with the concept of generational mortality.

Determination of mortality factors

Following cohort establishment, each nymph was examined every 2–3 days (three times per week) in the field with the aid of a 15X Peak® loupe (Light Impressions, Brea, CA) until that individual died or emerged as an adult. It was difficult to determine the fate of the eggs, even with a lens (15 × magnification); thus, leaves containing eggs were collected after 8–10 days and examined under a dissecting microscope in the laboratory. Eggs complete their development in 5–7 days under typical summer conditions in central Arizona. At each observation, the instar of each live nymph and the instar and cause of death of each dead nymph were recorded. Mortality due to dislodgment, predation, parasitism, inviability (eggs only), and unknown causes was recorded – no cases of infection by pathogens were observed, as indicated by obvious color changes, bloating, or hyphal growth. The instar of dislodged nymphs was estimated by the average instar of other dead nymphs on the same observation date. 'Predation' was mortality primarily due to sucking predators that had evacuated the contents of the whitefly body leaving a deflated and transparent nymphal cuticle or egg chorion on the leaf. On rare occasions, the effects of chewing predation could be seen as partially intact cadavers. Aphelinid parasitoids can successfully attack all nymphal stages of *B. tabaci* (Foltyn & Gerling, 1985; Headrick et al., 1995; Liu & Stansly, 1996), but parasitism can only be observed in 4th instar nymphs by the displacement of mycetomes or by the presence of parasitoid larvae or pupae within the host. Inviable eggs appeared normal, but failed to eclose. To maintain uniformity in determining causes of death, only five people made all the field observations over the 3 years of study, and they frequently consulted one another. A single observer determined the causes of death for all eggs. Once all marked individuals on a leaf had either died or emerged, the leaf was collected and returned to the laboratory to verify the cause of death with a dissecting microscope. Given the method of cohort establishment, the mortality of first instar crawlers was not explicitly measured. However, the duration between eclosion and settling averages less than 3–6 h (Price & Taborsky, 1992; Simmons, 2002), and greenhouse studies indicate that crawler mortality on cotton is negligible (S.E. Naranjo, unpubl.).

Arthropod density

Densities of *B. tabaci* eggs, nymphs, and adults were estimated each week from late June through to at least late September each year. Nymph and egg densities were estimated by counting individuals under a dissecting microscope on a 3.88 cm^2 disk taken from the 5th mainstem leaf below the terminal (Naranjo & Flint, 1994). Nymphs were categorized as either small (1st or 2nd instar) or large (3rd or 4th instar). The densities of adults were estimated by counting individuals, in situ, on the underside of leaves from the 5th mainstem node below the terminal (Naranjo & Flint, 1995). Ten to 30 sample units were randomly collected for immature and adult stages in each plot on each sample date. Arthropod predators were sampled each week with a standard 38 cm diameter sweep net from early June through to late September each year. Two sets of 25 sweeps (50 total) were collected in each plot using a random starting point, frozen, and later sorted in the laboratory with the aid of a dissecting microscope. The densities of immature aphelinid parasitoids (*Eretmocerus* spp. and *Encarsia* spp.) within hosts were estimated from whole leaf samples (20–30 per plot) from the 7th mainstem node below the terminal. Samples were collected weekly from early July through to mid to late September. All larval and pupal parasitoids were counted in the laboratory. There are no known egg parasitoids of *B. tabaci*.

Life table analyses

Standard methods (Varley et al., 1973; Southwood, 1978; Carey, 1993) were used to construct life tables of *B. tabaci* for 14 separate generations. For comparative purposes, net reproductive rates, R_0, were estimated for each generation as the product of temperature-dependent fertility from the data of Wagner (1994) and immature survival. Fertility was estimated from mean daily air temperatures from an on-site weather station (AZMET, 2003) for the 20-day interval following adult emergence, and assuming no adult mortality. A 50 : 50 sex ratio was assumed.

Estimation of mortality rates. At least three mortality factors operated during each of the five immature developmental periods and acted in a contemporaneous fashion. That is, there is no obvious sequence of mortality agents affecting each stage such that mortality from one agent might obscure the action of another. The concepts proposed by Royama (1981a), and later elaborated by Buonaccorsi & Elkinton (1990) and Elkinton et al. (1992), were used to estimate stage-specific, marginal rates of mortality for each factor based on observed (i.e., apparent) stage-specific mortalities. The marginal rate estimates the level of mortality arising from a single factor as if that was the only factor operating. 'Dislodgment' is the only mortality factor for which the apparent rate of death is equal to the marginal rate of death, because this cause of death cannot be obscured by any other contemporaneous factor. For all

other mortality factors, marginal rates of death, M_B, were estimated from the standard equations

$$M_B = d_B/(1 - cM_A), \quad (1)$$

$$M_A = (b - (b^2 - 4cd_A)^{0.5})/2c, \quad (2)$$

$$b = c(d_A + d_B) + 1 - d_B, \quad (3)$$

where the subscripts A and B denote competing contemporaneous mortality factors, d_B is the apparent rate of mortality from factor B, d_A is the sum of apparent mortalities from all other relevant contemporaneous factors, c is an index that describes the outcome of competition between mortality factors A and B, and equation 2 is the quadratic solution for M_A. The probability that factor A obscures factor B is c, while the probability that factor B obscures A is 1 – c. For purposes here c = 1, because factor A, as defined, always obscures factor B when both affect the same insect. Thus, by algebraic manipulation equation 1 simplifies to

$$M_B = d_B/(1 - d_A). \quad (4)$$

Table 1 outlines the apparent rates of mortality needed to estimate marginal rates for each factor of interest within each developmental stage of *B. tabaci* based on equation 4. Buonaccorsi & Elkinton (1990) showed that equations 1–4 were approximate in cases when there was more than one interacting mortality factor. Furthermore, the level of error is related to the probability that individuals are attacked by three or more agents. This probability was likely to be very low for *B. tabaci*, given the short developmental periods of each life stage and the frequent observation intervals. Comparing measured generational mortality to that estimated from stage-specific, marginal death rates resulted in an average error of 0.07% over 14 generations. For most subsequent analyses, mortalities were expressed as k-values ($k = -\ln[1 - M]$), where M is the marginal rate of mortality for a given factor in a given developmental stage. The use of k-values is convenient, because they are additive across stages and mortality factors (Varley & Gradwell, 1960). k-values can be converted back into proportional mortality rates by $1 - e^{[-k]}$.

Key factor and density-dependence analyses. Key factor analysis was conducted using the graphical approach of Varley & Gradwell (1960), which compares patterns of total mortality (total $K = \Sigma k$) to that of individual k-values. The method of Podoler & Rogers (1975) was then used to quantitatively evaluate key factors by regressing individual k-values on total K. This method identifies the key factor as that associated with the largest regression coefficient (i.e., slope). Finally, the method proposed by Smith (1973) was used to examine the relative importance of all factors by sequentially eliminating each key factor in an iterative fashion. Smith (1973) suggested that this approach is useful for discerning the relative importance of factors that may be correlated with the key factor, and hence obscured. After determining the key factor (Podoler & Rogers, 1975), its k-value was then subtracted from K and regressions were calculated for the remaining factors. This step-wise process continued until all but the last two factors had been eliminated.

The density-dependence of the mortality factors was examined by regressing individual k-values on logarithmic densities of the various life stages at the beginning of the generation. Delayed density-dependence was tested by estimating insect densities at the beginning of the prior generation. Because insect densities (independent variables) were measured with error, ranged-major axis regression analysis (Legendre, 2001) was used to quantify and test the strengths of the density-dependence. Sample permutation was used to determine if the slope of this relationship was different from zero (Legendre, 2001).

Irreplaceable mortality analysis. Irreplaceable or indispensable mortality is that portion of total generational mortality that would not occur if a given mortality factor was eliminated

Table 1 Matrix for estimating marginal rates of mortality of *Bemisia tabaci* from apparent rates of relevant competing contemporaneous factors

Marginal rate (M_B)	Apparent rate (d_B)	Apparent rate (d_A)	Stage
Inviability	Inviability	Predation + dislodgment	Egg
Parasitism	Parasitism	Predation + dislodgment	4th stage nymphs[a]
Predation	Predation	Dislodgment	Egg and all nymphal stages
Unknown	Unknown	Predation + dislodgment	All nymphal stages

[a]Aphelinid parasitoids can successfully attack all nymphal stages of *B. tabaci* (Foltyn & Gerling, 1985; Headrick et al., 1995; Liu & Stansly, 1996), but parasitism can only be observed in 4th stage nymphs in the field; thus d_A is the sum of predation and dislodgment from all nymphal stages combined.

(Southwood, 1978). Following Carey (1989), irreplaceable mortality was estimated for each mortality factor and each developmental stage. The general form of this calculation is:

$$(1 - \prod_{1}^{j}[1 - M_i]) - (1 - \prod_{1}^{j-1}[1 - M_i]), \quad (5)$$

where M_i is the marginal mortality rate for factor or stage i, and j is the total number of all mortality factors or developmental stages. The first product includes all mortality factors or stages, while the second product includes all mortality factors or stages except for the factor or stage of interest. This method does not take into account any density-dependent compensation in mortality. The effect of irreplaceable mortality on R_0 was estimated as the difference between R_0 without the irreplaceable mortality in question, and with all mortality.

Identifying specific causes of death

To further examine the potential causes of insect dislodgment, step-wise multiple regression (PROC REG, SAS, 1988) was used to quantify the relationship between marginal rates of dislodgment on a given observation date with weather variables and densities of predators. Independent variables included maximum wind speed (m s^{-1}), total precipitation (cm), and cumulative densities (arthropod-days per 50 sweeps) of spiders, predatory beetles, predatory heteropterans, and *Chrysoperla carnea* s.l. Stephens lacewings over each observation interval. Standardized regression coefficients were calculated for the final model (SAS, 1988), in order to directly compare the strength of the respective responses independently of the numerical scales of the independent variables.

Similar analyses were conducted to quantify the relationship between stage-specific marginal rates of predation on each observation date with cumulative densities (per 50 sweeps) of nine taxa of sucking predators during each observation interval. Only sucking predators were examined, because direct chewing predation was observed in only a few instances over the 3 years of this study. A final regression analysis examined the relationship between marginal rates of egg inviability and unknown nymphal mortality with temperature, relative humidity, crop phenology, and cumulative densities of aphelinid parasitoids [as an indicator of host feeding or unsuccessful parasitism (Gerling, 1990; Hoddle et al., 1999)] during each observation interval. Crop phenology was characterized by the accumulated degree-days (base 12.8/30 °C) since planting.

Simulation analyses

In examining patterns of change in population density and associated rates of mortality and net reproduction, inconsistencies were observed during several years (see Results). These discrepancies may be related to errors in the estimation of net reproductive rates, the fact that the life tables are only point estimates of overall survival, or insect dispersal. To examine the effect of these potential factors, census data were compared to simulated population trajectories using estimated rates of mortality. The simulation model was a deterministic, temperature-dependent, stage-structured model based on temperature-dependent rates of immature development and reproduction published by Wagner (1994, 1995) (G. Degrandi-Hoffman & S.E. Naranjo, unpubl.). For each year, the model was initiated with egg, nymph, and adult sample data from the date of first cohort establishment and associated egg and nymphal mortalities for this cohort. The model was run until the date of the second cohort establishment, at which point the model was re-initiated with new sample data and mortality rates from the second generation. This pattern was continued for all subsequent cohorts using on-site weather data.

Results

Characterizing mortality

Complete life tables for all 14 generations are provided in the Supplementary Appendix S1. When pooled over all immature life stages, median rates of mortality were in ranked order: predation (0.532), dislodgment (0.453), unknown factors (0.369), egg inviability (0.109), and parasitism (0.100) (Figure 1A). When pooled over all factors, the highest median marginal rates observed were during the egg stage (0.531) and the 4th nymphal stadium (0.687), and rates during the first three nymphal stadia ranged from 0.167 to 0.226 (Figure 1B). In general, patterns of mortality during each individual developmental period followed the distribution shown in Figure 1A. Based on identifications from an associated study (Naranjo et al., 2004b), parasitism was primarily due to the natives *Eretmocerus eremicus* Rose and Zolnerowich and *Encarsia meritoria* Gahan. Pooled over all generations, the highest levels of mortality were clearly associated with predation, dislodgment, and unknown factors (Figure 1C).

Maximum windspeed, precipitation, and densities of several taxa of predators were associated with dislodgment (Table 2). Maximum windspeed was generally the most important factor associated with dislodgment in the majority of life stages. Rainfall was associated with dislodgment, especially for eggs and 1st instar nymphs. The densities of predaceous beetles [*Collops vittatus* (Say), *Hippodamia convergens* Guérin-Méneville, anthicids, and other coccinellids] and immature green lacewings (*C. carnea* s.l.) were associated with the dislodgment of nymphs. Beetles were comparatively more important as a source of dislodgment in 3rd

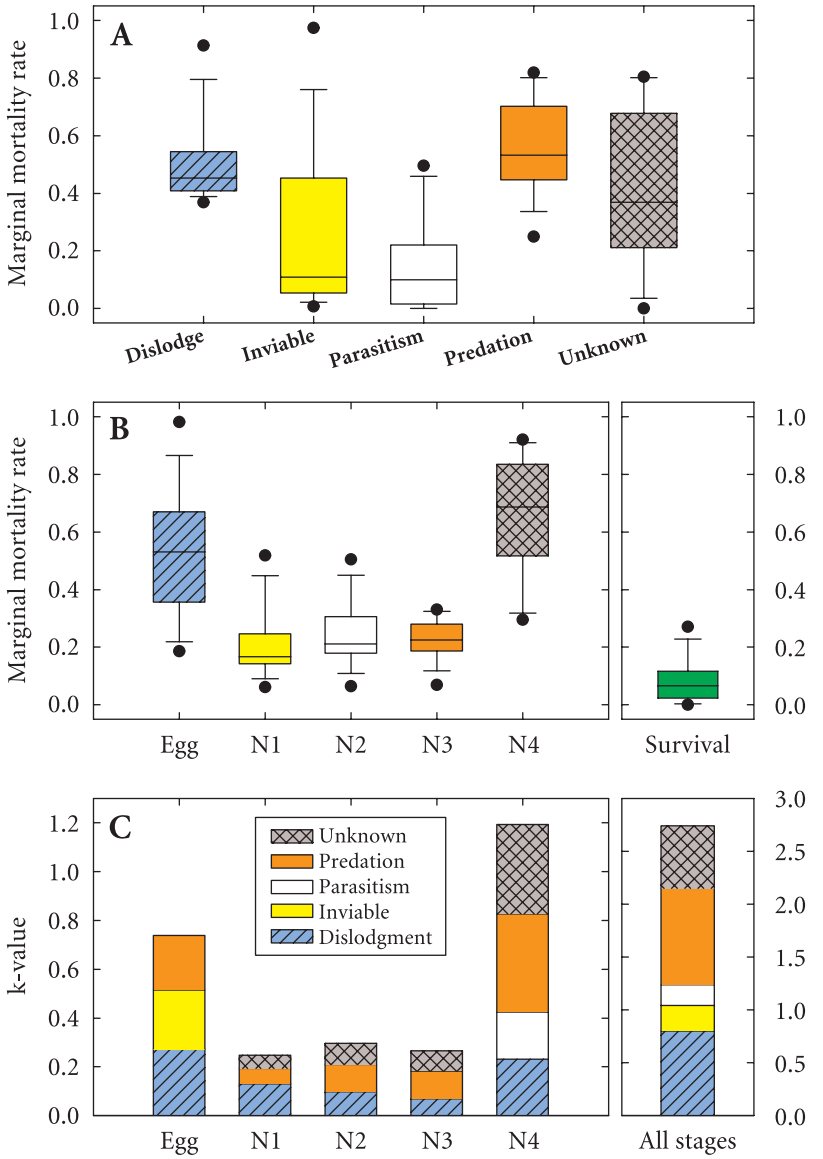

Figure 1 (A) Box plots of marginal rates of mortality for *Bemisia tabaci* in cotton by mortality factors pooled over all preimaginal stages; (B) box plots of marginal rates of mortality during each developmental period pooled over all mortality factors; (C) mean levels of mortality factors within each life stage and all preimaginal stages combined expressed as k-values. For box plots, the line within each box represents the median, the box bounds the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles, and points denote the range. All results based on 14 life tables, Maricopa, Arizona, USA, 1997–99. N1 = 1st instar nymph, etc.

and 4th instar nymphs. Patterns of weather and predator densities over each year (not shown) indicated that predaceous beetles were generally associated with dislodgment during the early portion of the season, while windspeed was more consistently associated with dislodgment during the mid- to late-season.

Predation on eggs and 1st instars appeared to be most closely associated with densities of *Geocoris punctipes* (Say), *Orius tristicolor* (White), and *C. carnea* s.l., with the strongest relationship indicated for *G. punctipes* (Table 3). Densities of *G. punctipes*, *G. pallens* Stål, and especially *O. tristicolor* were associated with predation on 2nd instar nymphs. Rates of predation on 3rd and 4th instar nymphs were related to densities of a larger number of predator taxa, including the species noted above and the omnivore *Lygus hesperus* Knight.

Rates of egg inviability and unknown nymphal mortality were only weakly associated with environmental parameters and parasitoid density (Table 4). Egg inviability was negatively associated with minimum relative humidity; however, the overall regression was marginally significant ($P = 0.08$). Minimum temperature was negatively associated with the unknown mortality of 2nd instar nymphs. The densities of immature parasitoids were positively related to rates of unknown mortality of 3rd instar nymphs. No factor was related to the unknown mortality of 4th instar nymphs (Table 4).

Prior greenhouse studies both with and without artificial wind showed that rates of mortality during the short

Table 2 Multiple regression of marginal rates of dislodgment (per observation interval) of preimaginal stages of *Bemisia tabaci* on various weather variables and densities of predatory arthropods, Maricopa, Arizona, USA 1997–99. N1 = 1st instar nymph, etc.

	Standardized coefficients				
Variable[a]	Egg	N1	N2	N3	N4
Maximum windspeed (m s^{-1})	0.658	0.833	0.805	0.650	0.287
Precipitation (cm)	0.383	0.387	0.206	0.154	0.205
Spiders	ns	ns	ns	ns	ns
Beetles	0.081	0.244	0.131	0.659	0.588
Heteropterans	ns	ns	ns	ns	ns
Chrysoperla carnea s.l.	0.097	0.572	ns	0.279	0.416
F-value	23.6	9.1	47.8	8.2	11.5
P	<0.01	<0.01	<0.01	<0.01	<0.01
R^2	0.92	0.78	0.93	0.77	0.64
n	13	15	15	15	31

Step-wise multiple regression; ns indicated that the variable failed to meet the 0.5 significance level for entry into the model; standardized coefficients weight the relative contribution of each variable independent of their original numerical scale.
[a]Maximum windspeed, total precipitation, and predator density (measured as cumulative density per 50 sweeps) during the observation interval.

Table 3 Multiple regression of marginal rates of predation (per observation interval) of preimaginal stages of *Bemisia tabaci* on densities of various sucking predators, Maricopa, Arizona, USA, 1997–99. N1 = 1st instar nymph, etc.

	Standardized coefficients				
Variable[a]	Egg	N1	N2	N3	N4
Geocoris punctipes	1.724	0.974	0.523	0.639	0.479
Geocoris pallens	ns	ns	0.336	0.609	ns
Orius tristicolor	1.037	0.049	1.097	0.246	0.312
Zelus renardii	ns	ns	ns	ns	ns
Nabis alternatus	ns	ns	ns	ns	ns
Lygus hesperus	ns	ns	ns	0.357	0.564
Spanogonicus albofasciatus	ns	ns	ns	ns	ns
Rhinacloa forticornis	ns	ns	ns	ns	ns
Chrysoperla carnea s.l.	0.411	0.104	ns	0.290	0.301
F-value	15.1	6.7	7.6	5.2	3.2
P	<0.01	<0.01	<0.01	<0.01	0.022
R^2	0.83	0.71	0.69	0.77	0.59
n	13	19	29	34	46

Step-wise multiple regression; ns indicated that the variable failed to meet the 0.5 significance level for entry into the model; standardized coefficients weight the relative contribution of each variable independent of their original numerical scale.
[a]All predator densities measured as cumulative density (arthropod-days) per 50 sweeps during the observation interval.

crawler stage were consistently around 10% (S.E. Naranjo, unpubl.). Applying an additional 10% mortality for this stage would have caused the generational survival to decline by only 0.8% on average. This would not have materially changed the results of any of our analyses below.

Mortality relationships to population dynamics

The population dynamics of *B. tabaci* varied over the years of study, but in general, population densities increased significantly, exceeding established economic threshold levels of five adults per leaf, in late July to early August (Figure 2B). Population densities were highest in 1997, and lowest in 1998. There were no consistent patterns in the dynamics of mortality over time in any year, with the exception that rates of egg mortality, mainly from inviability, were highest in early to mid-August (Figure 2A,C). Although low overall, parasitism was highest in 1997 and essentially absent in 1999. Predation was highest in 1997, and dislodgment was consistently high across all years. Mortality from unknown causes was higher in the latter half of the growing season in 1998 and 1999. During the third cohorts in both 1998 and 1999, a large portion of

Variable[a]	Standardized coefficients				
	Egg	N1	N2	N3	N4
Max. temperature (°C)	ns	ns	ns	ns	ns
Min. temperature (°C)	ns	ns	−0.425	ns	ns
Max. r.h. (%)	ns	0.310	ns	ns	ns
Min. r.h. (%)	−0.482	ns	ns	ns	ns
Degree-days after planting (12.8/30 °C)	ns	ns	ns	ns	ns
Parasitoids per leaf[a]	–	ns	ns	0.356	ns
F-value	3.6	2.9	8.1	5.1	–
P	0.08	0.10	<0.01	0.03	–
R^2	0.23	0.10	0.18	0.13	–
n	14	29	39	37	43

Table 4 Multiple regression of marginal rates of *Bemisia tabaci* egg inviability and unknown nymphal mortality (per observation interval) on various weather variables and densities of aphelinid parasitoids, Maricopa, Arizona, USA 1997–99. N1 = 1st instar nymph, etc.

Step-wise multiple regression; ns indicated that the variable failed to meet the 0.5 significance level for entry into the model; standardized coefficients weight the relative contribution of each variable independent of their original numerical scale.

[a]Parasitoid densities measured as cumulative density (insect-days) of immature parasitoids per leaf during the observation interval.

this unknown mortality was associated with a distinct morphology in which the abdominal area of 4th instar nymphs collapsed and appeared abnormally sunken. Culturing of cadavers, consultations with insect pathologists who examined samples, and preliminary scanning electron microscopy failed to identify a biological cause (S.E. Naranjo & P.C. Ellsworth, unpubl.). The distribution of mortality across different life stages was very consistent with the highest levels of mortality occurring during the egg stage and 4th nymphal stadium (Figure 2C).

Survivorship curves were relatively consistent, with one exception (third cohort in 1998), across the 14 generations observed, where relatively high levels of mortality were seen in egg and later stages (Figure 3). The median survivorship over all generations was 0.066. Despite a low immature survival, the estimated R_0 was less than 1 during only a single generation in each year, and only once (in 1998) did the population densities of all stages decline markedly following this generation – adults did decline somewhat after each of these generations (Figure 2A,B). In the early part of the season, $R_0>1$ was consistent with an increasing population size each year. However, population trends in the latter portion of the season appeared less directly related to estimated R_0. In 1998, the population density increased only slightly after a marked drop in early August, despite a relatively high R_0 in late August through to early October. Likewise, the population density declined from mid to late September 1999 despite an R_0 of 4.2 estimated for the cohort established on 31 August (Figure 2B,C).

A simulation of whitefly population dynamics based solely on endogenous survival and reproduction in 1997 provided relatively good estimates of insect density during the middle portion of the season (Figure 4). There were, however, large discrepancies between the observed and simulated densities in late June to early July, and again in early to mid-September (Figure 4). This same pattern was apparent for 1998. In 1999 the discrepancy at the end of the season was prominent, but the early season departure was less pronounced. The large differences between observed and predicted densities are suggestive of immigration into cotton in the early summer and emigration from this host in the early fall (Figure 4).

Importance and impact of mortality factors

Mortality during the 4th nymphal stadium and egg stage was most closely associated with the observed variation in generational mortality (by graphical method, not shown; and confirmed by regression method, Table 5 top section). The key factor regression method (Smith, 1973; Podoler & Rogers, 1975) confirmed these patterns by stage (Table 5, top section). After removal of mortality during the 4th nymphal stadium and egg stage, mortality during the 1st and 2nd stadia was most closely associated with generational mortality, respectively. A further delineation of mortality factors during each developmental period showed that predation and dislodgment during the 4th nymphal stadium were the top two key factors, followed by egg inviability (Table 5, bottom section). Using this sequential method, the top seven stage-specific key factors were all associated with either the egg or 4th nymphal instar.

There was little evidence of density-dependence for any of the mortality factors observed. Dislodgment of eggs and small nymphs (1st or 2nd instars) was inversely density-dependent, and unknown factors were positively density-dependent for large nymphs (3rd or 4th instars). In all these instances the magnitudes of the significant regression

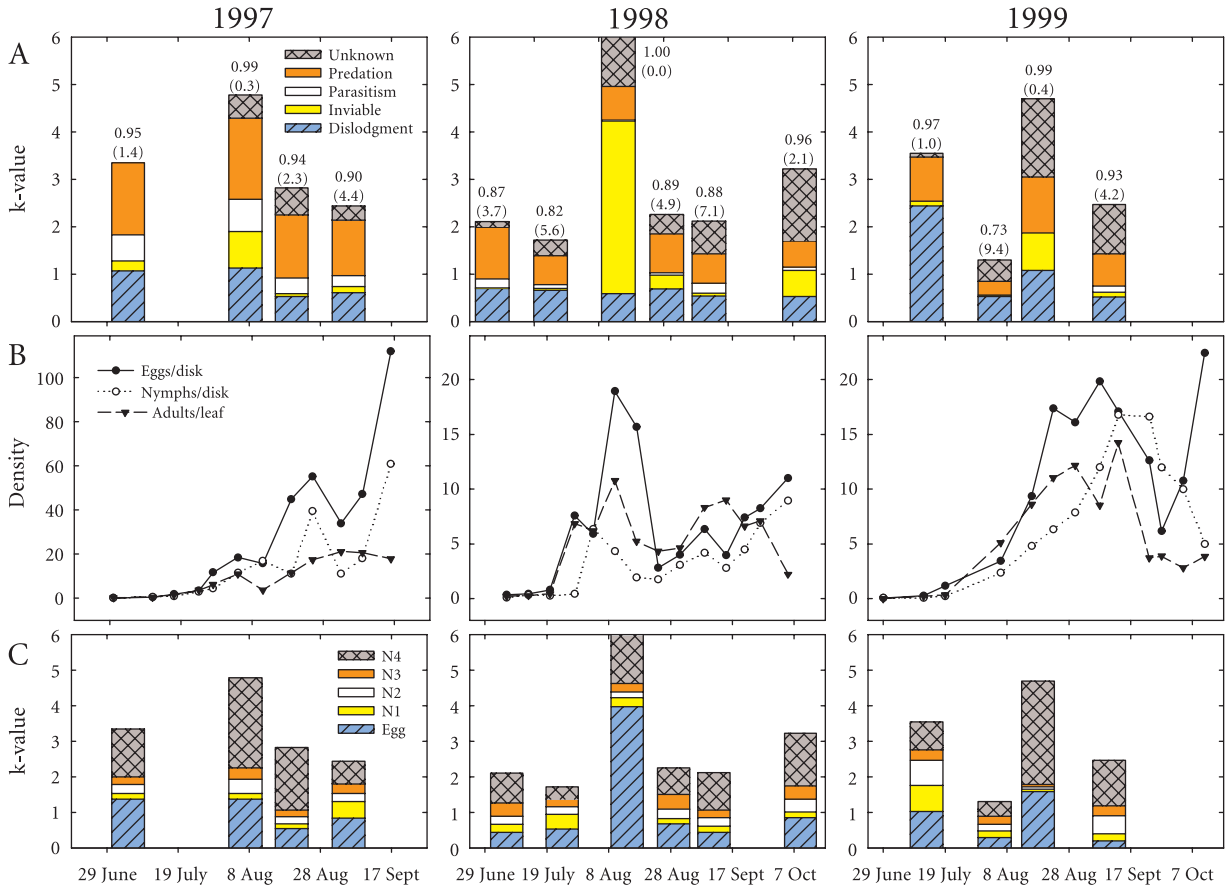

Figure 2 Population dynamics of immature and adult stages of *Bemisia tabaci* (B), and the dynamics of immature mortality (A, C) in cotton over 3 years, Maricopa, Arizona, USA, 1997–99. The stacked bars denote levels of immature mortality by (A) factor, or (C) stage, as k-values, and are plotted at the mid-point of the period during which each cohort was observed. The numbers along the top of each bar in the top panel denote the total generational preimaginal mortality and the estimated R_0 (in parentheses). Note the different scale for insect density in 1997. N1 = 1st instar nymph, etc.

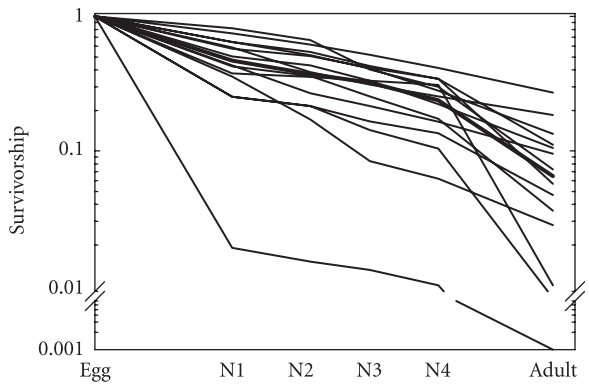

Figure 3 Survivorship curves for immature *Bemisia tabaci* in cotton over 14 generations, Maricopa, Arizona, USA, 1997–99. The bold line denotes median survivorship. N1 = 1st instar nymph, etc.

slopes were small (<0.14). There was no evidence of delayed density-dependence. Because parasitoids may attack all nymphal instars, separate regressions were run for small nymphal hosts, large nymphal hosts, and all nymphal hosts combined. Again, there was no evidence of direct or delayed density-dependence (Table 6). Further examination of the individual data plots showed no indication of direct or delayed density-dependence over narrower subsets of whitefly density.

Pooled over all developmental stages, the highest rates of irreplaceable mortality were consistently associated with predation (median = 0.097) and dislodgment (median = 0.071) (Figure 5A). Irreplaceable mortality from unknown causes was relatively high during certain generations (median = 0.048), while that due to egg inviability (0.009) and parasitism (0.012) was very low across all generations.

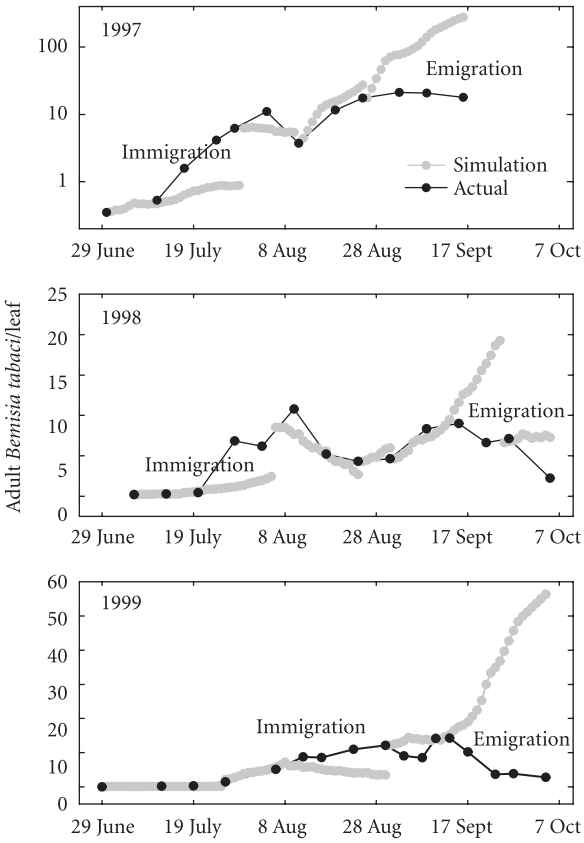

Figure 4 Comparison of simulated and actual population trajectories for adult *Bemisia tabaci* in cotton, Maricopa, Arizona, USA. Simulations are based on a temperature-dependent, stage-structured model that was initiated with actual insect densities (eggs, nymphs, and adults) and observed rates of immature mortality at the establishment of each of four (1997, 1999), or six (1998) cohorts. These discrepancies during early and late season likely reflect the important impact of immigration and emigration to site-specific dynamics.

Patterns of change in R_0 were similar to those observed for mortality factors; however, relatively small changes in irreplaceable mortality sometimes led to large changes in potential population growth (Figure 5B). For example, median rates of irreplaceable mortality (ca. 0.07–0.10) for dislodgment and predation were associated with absolute increases in the median R_0 of 3.5–4. In an extreme case, removal of irreplaceable mortality from dislodgment of 0.30 during a single generation was associated with a 12-fold increase in R_0.

Pooled across developmental stages, the highest rates of irreplaceable mortality were associated with the egg (median = 0.067), and especially 4th instar nymphs (median = 0.126) (Figure 5C). Patterns in irreplaceable mortality relative to stage were reflected in R_0, but again, relatively small levels of irreplaceable mortality were often associated with large changes in potential population growth (Figure 5D). This was most striking for 4th instar nymphs, where median rates of irreplaceable mortality (≈ 0.13) led to a median absolute change in net reproduction >4. In an extreme case, the removal of an irreplaceable mortality of 0.22 during the 4th stadium led to an absolute change in net reproduction of 14.4.

Discussion

A four-part analytic approach was used with the objective of developing, understanding, and interpreting comprehensive life tables for *B. tabaci* in cotton: marginal mortality, key factor, irreplaceable mortality, and simulation analyses. Marginal mortality analyses properly characterized each mortality factor in the context of all other contemporaneous mortalities. Key factor analyses provided an ordination of all factors and stages to identify the relative importance of each to variations in generational mortality. Irreplaceable mortality analyses allowed us to understand and quantify the impact of each factor on potential reproduction. Finally, with our data on mortality and the existing information about reproduction, simulation helped to explain observed population dynamics in contrast to expected growth trajectories.

Despite the flaws in the key factor analysis outlined by Royama (1996), these analyses were revealing in our system. Key factor analysis identified mortality occurring during the fourth nymphal stadium as the most important for describing generational mortality and predation during this developmental stage as the primary key factor. In turn, predation, which could be explained by densities of several common sucking predators, also provided the highest level of irreplaceable mortality, and the removal of this mortality source consistently led to the largest changes in net reproduction. Dislodgment of 4th instar nymphs, which was largely explained by the combined effect of wind, rain, and the action of chewing predators capable of removing insects from the plant, was the secondary key factor and in turn contributed the next largest level of irreplaceable mortality and associated change in net reproduction. These are the first quantitative estimates of predation on this insect in the field, and are consistent with qualitative studies based on gut content analyses (Hagler & Naranjo, 1994a,b; Naranjo & Hagler, 1998). By contrast, Horowitz et al. (1984) developed life tables for *B. tabaci* by repeated destructive sampling of artificial cohorts in cotton fields and determined mortality during the first nymphal stadium to be the key factor. No specific causes of this mortality were identified.

Detailed study and comprehensive analyses derived from our direct in situ method of quantifying the mortality

Table 5 Key factor analysis of *Bemisia tabaci* over 14 generations in cotton, Maricopa, Arizona, USA, 1997–99, based on the methods of Smith (1973), and Podoler & Rogers (1975). N1 = 1st instar nymph, etc. N1 = 1st instar nymph, etc.

	Step						
Stage/factor1	1	2	3	4	5	6	7
Egg	0.342	**0.532**					
N1	−0.008	0.220	**0.436**				
N2	0.069	0.202	0.416	**0.681**			
N3	0.001	0.049	0.148	0.319			
N4	**0.597**						
Egg							
Inviable	0.155	0.171	**0.210**				
Dislodgment	0.129	0.101	0.141	**0.219**			
Predation	0.067	0.106	0.125	0.168	0.167	0.241	**0.312**
N1							
Dislodgment	0.007	0.039	0.010	0.116	0.014	0.149	0.184
Predation	0.002	0.006	0.063	0.025	0.027	0.052	0.051
Unknown	−0.017	−0.021	−0.019	−0.023	−0.023	−0.009	0.006
N2							
Dislodgment	0.049	0.092	0.109	0.159	0.105	0.162	0.277
Predation	0.041	0.056	0.070	0.076	0.068	0.112	0.100
Unknown	−0.021	−0.036	−0.032	−0.063	−0.026	−0.057	−0.044
N3							
Dislodgment	0.008	0.018	0.019	0.033	−0.004	0.044	0.076
Predation	0.022	0.029	0.030	0.032	0.042	0.073	0.062
Unknown	−0.029	−0.042	−0.038	−0.058	−0.038	−0.044	−0.024
N4							
Dislodgment	0.148	**0.214**					
Parasitism	0.131	0.178	0.195	0.203	0.261	**0.277**	
Predation	**0.222**						
Unknown	0.163	0.087	0.115	0.111	**0.408**		

Values represent the slope of the regression of individual k-values on total K (–ln of generational survival). The factor with the highest slope (key factor; in bold type) is eliminated in each subsequent step in order to estimate the relative effect of each factor on overall variation in generational survival. The top portion of the table examines all mortality factors pooled by stage; the bottom portion examines stage- and factor-specific mortalities.

of *B. tabaci* in unmanaged Arizona cotton provide an understanding of this pest's population dynamics that have implications for management. We can show through simulation modeling that the endogenous production of *B. tabaci* is responsible for their in-season population dynamics, but that adult movement is the likely source of change at or near economic infestation (i.e., immigration), and at the end of the season as the crop matures (i.e., emigration). Management is ultimately dependent on human-influenced and natural mortality factors that collectively influence a pest's population relative to economically tolerable levels. By direct measurement of these mortality factors and indirect evidence of adult movement, we conclude that efficient pest management may be best accomplished by fostering greater mortality during the 4th stadium, largely through predation, and by managing immigrating adult populations at their sources.

The impact of predation on potential population growth rates (see Figure 5) bolsters the conclusion that preservation of this mortality component may be the key to management. Companion life table studies conducted in fields receiving selective and non-selective insecticides support our key factor and irreplaceable mortality analyses, and the important contribution of predation to the regulation of *B. tabaci* populations. These studies show that the conservation of predators permits a continued suppression of *B. tabaci* populations in fields treated with selective insecticides, whereas this natural suppression is diminished or lost in fields treated with broad-spectrum materials (Ellsworth & Martinez-Carrillo, 2001; Naranjo, 2001; Naranjo et al., 2004b; S.E. Naranjo & P.C. Ellsworth, unpubl. data). Prior to this, much of our understanding of the role of predators in *B. tabaci* population dynamics was anecdotal, and based on correlative analyses and observations of pest resurgence following the use of broad-spectrum insecticides (see reviews by Gerling et al., 2001; Naranjo, 2001).

Table 6 Density-dependent analyses of mortality factors affecting various life stages of *Bemisia tabaci* over 14 generations in cotton, Maricopa, Arizona, USA, 1997–99

	Within generation		Lag-1 generation[a]	
Stage/factor	Slope[b]	P	Slope	P
Egg				
Inviability	0.195	0.179	−0.244	0.319
Dislodgment	−0.094	0.008	0.007	0.489
Predation	−0.072	0.289	0.071	0.311
Small nymphs[c]				
Dislodgment	−0.138	0.020	−0.117	0.397
Parasitism[d]	0.281	0.417	0.099	0.189
Predation	−0.179	0.422	0.065	0.208
Unknown	0.071	0.081	0.067	0.165
Large nymphs[e]				
Dislodgment	0.039	0.119	−0.182	0.075
Parasitism[d]	0.009	0.479	−0.161	0.122
Predation	0.033	0.335	−0.186	0.155
Unknown	0.114	0.002	−0.084	0.233
All nymphs				
Parasitism[d]	0.124	0.399	0.079	0.202

[a]Marginal mortality (k-value) regressed on ln insect density at the beginning of the prior generation.
[b]Ranged major-axis regression (Legendre, 2001); P-value tests if regression coefficient >0 determined by 500 random permutations; n = 14 for within generation, n = 11 for lag-1 generation.
[c]Combined 1st and 2nd instar *B. tabaci*.
[d]Parasitoids may attack all nymphal instars but parasitism is only evident in 4th instar hosts.
[e]Combined 3rd and 4th instar *B. tabaci*.

In contrast, parasitism was a relatively minor component of mortality, a conclusion shared by Horowitz et al. (1984) in Israeli cotton, and fungi played no role in our studies despite their identification world-wide as *Bemisia* pathogens (Lacey et al., 1996; Faria & Wraight, 2001). In the south-western USA, three native and many exotic aphelinid species potentially attack *B. tabaci* (Hoelmer, 1996; Kirk & Lacey, 1996; Gerling & Naranjo, 1998; Hoelmer & Kirk, 1999; Kirk et al., 2001; Naranjo et al., 2003). The parasitism observed in this study was primarily due to two native species, although in recent years most of the parasitism of *B. tabaci* in cotton and other crops in Arizona has been due to several exotic *Eretmocerus* and *Encarsia* species (Goolsby et al., 2005; L. Cañas, S.E. Naranjo & P.C. Ellsworth, unpubl.; S.E. Naranjo, unpubl.). Very little of this mortality was irreplaceable (≈ 1% on average). Despite the use of marginal rate analyses, much of the mortality initially imposed by parasitoids may subsequently be replaced by predation and other factors. Census-based data have reported high rates of parasitism in cotton and other crops, but these estimates, unlike life table estimates, are poor predictors of the overall impact of parasitoids on *B. tabaci* population dynamics (Naranjo, 2001).

Dislodgment was associated with several climatic variables, including monsoon-associated, high winds or haboobs (similar to the khamsins in the Middle-East), and rainfall. Observations on several occasions clearly showed that disappearance was caused by high winds, blowing dust, and sometimes rain, the previous night. Several authors have also suggested that weather factors play an important role in *B. tabaci* survival and population dynamics. In the Sudan, Khalifa & El-Khidir (1964) noted that *B. tabaci* populations declined dramatically following heavy rain storms (>10 mm), and Gameel (1970) reported a high mortality among immature stages associated with high temperatures and low relative humidities. Similarly, in the Jordan Valley, Avidov & Harpaz (1969) noted that outbreaks of *B. tabaci* were delayed by low relative humidities and khamsins (hot and dry winds loaded with sand particles), and Sharaf (1982) also found that immature survival declined rapidly during periods characterized by high temperature, low relative humidity, and khamsins. Similar declines in population density in cotton were observed near our study site in 1996, that were associated with a severe thunderstorm (Naranjo et al., 2003).

The balance of reproduction, mortality, immigration, and emigration controls population dynamics, and our studies implicate the important role of adult movement in determining the dynamics of this pest in Arizona cotton. *Bemisia tabaci* is a highly polyphagous, multivoltine insect that moves among a number of cultivated and non-crop host plants over the year (Watson et al., 1992). Thus, population growth patterns in cotton during the summer months are dependent, in part, on sources and sinks for adult *B. tabaci*. Our simulation analyses, which accounted for mortality from this study and reproduction from other studies, but not for immigration or emigration, clearly show a pattern that is indicative of an influx of adults into our cotton system, at or near the time of economic infestation, and then an efflux of adults towards the end of the season. For the period between this influx and efflux, the model predictions closely mimicked observed populations during the bulk of the growing season, when population dynamics are governed almost entirely by endogenous reproduction and mortality. Adult *B. tabaci* are moderately mobile (Byrne, 1999), and anecdotal evidence suggests that large numbers of this insect immigrate into cotton in late June to early July in central Arizona, often associated with the end of spring cantaloupe production, and then begin to emigrate with declining cotton host quality in the early fall as irrigation of the crop is terminated. Clearly, immigration and emigration are strong

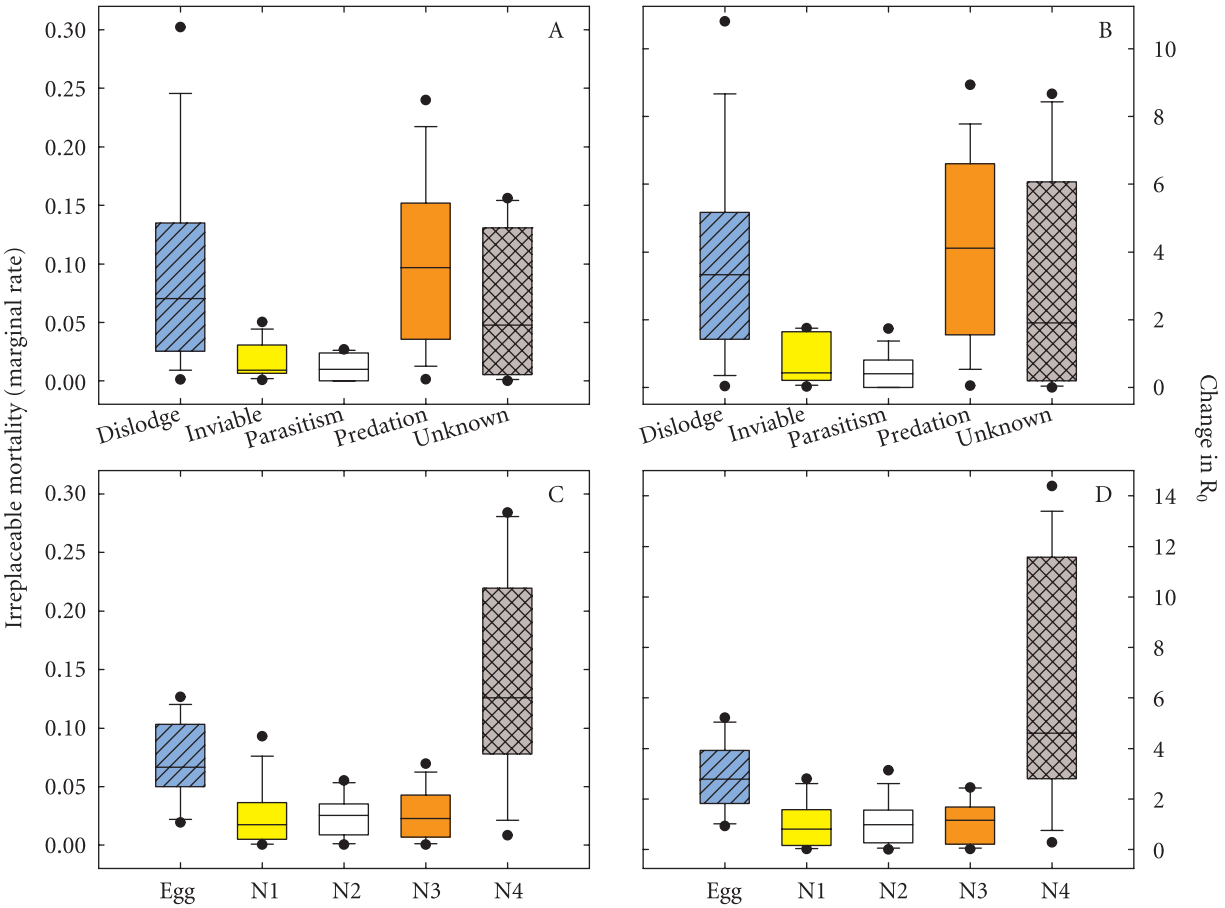

Figure 5 Box plots of marginal rates of irreplaceable mortality for *Bemisia tabaci* in cotton by mortality factors pooled over (A) all life stages, and (C) life stages pooled over all mortality factors, for 14 generations, Maricopa, Arizona, USA, 1997–99. (B) and (D) show the change in estimated net reproduction, R_0, associated with elimination of factor and stage-specific irreplaceable mortalities, respectively. The line within each box represents the median, the box bounds the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles, and points denote the range. N1 = 1st instar nymph, etc.

determinants of site-specific population dynamics, and a better understanding of the population dynamics of this insect will require more comprehensive study of populations over both space and time. On-going studies are beginning to address this issue by examining the year-round population and mortality dynamics of *B. tabaci* from a broader ecosystem perspective (Naranjo et al., 2004a; L. Cañas, S.E. Naranjo & P.C. Ellsworth, unpubl.).

Cotton is the principal summer host for *B. tabaci* in the low desert of the south-western USA, and during the summer months population densities of this insect and the potential for economic damage are greatest. Thus, this work provides an important basis for understanding basic population regulation and potential changes in the system for improved management of this insect. As noted above, once established in cotton, populations are residential and ostensibly subject to the forces described here. On average, natural enemies (i.e., predators), along with a host of other factors, inflict nearly 94% mortality on a generation of *B. tabaci*; however, consistent mortality >99% is probably needed to effectively control its populations. Thus, on average, at least another ca. 5% of irreplaceable mortality is required to achieve the economic suppression of large colonizing populations. In the absence of any direct or delayed density-dependent mortality – which would appear to be the case in our system – the application of additional mortality to a factor that is already large will have a disproportionately greater impact on generational survival (Morris, 1957). For our system, mortality would be most influential if added during the 4th nymphal stadium. For example, ca. 30% more total mortality would be required in the 4th stadium to reach 99% generational mortality, but >66% additional mortality would be needed during earlier stadia. Similarly, adding predation

would be more useful to pest management than adding an equal amount of parasitism or dislodgment to the 4th stadium. Parasitoids would need to contribute >75% additional mortality in order to have an equivalent impact as adding just 30% more predation of 4th instars. Thus, conservation activities focused on the predator complex would be likely to be more beneficial in terms of suppression of *B. tabaci* than those focused on parasitoids for our system. Additional mortality from other sources such as host-plant resistance, irrigation and nitrogen management, and other managed (e.g., selective insecticides) and natural inputs would change the absolute levels of natural enemy-induced mortality needed. Nonetheless, a greater effort should focus on adding mortality to factors (i.e., predation) and stages (i.e., the 4th instar) that already have relatively large levels of mortality, and therefore have the greatest opportunity to impact population regulation. Our studies have yielded new insights into *B. tabaci* mortality and population dynamics, and represent a novel approach to identifying opportunities for more efficient pest management.

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Supplementary material

The authors have provided the following supplementary material, which can be accessed at http://www.blackwellpublishing.com/products/journals/suppmat/EEA/EEA297/EEA297sm.htm.

Appendix S1 Life tables for *Bemisia tabaci* populations in cotton at Maricopa, Arizona, USA 1997–99.

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