

# Demographic Analysis of Delayed Mating in Mating Disruption: a Case Study with *Cryptophlebia illepidia* (Lepidoptera: Tortricidae)

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**ABSTRACT** Laboratory-derived life tables were used to determine the effect of delaying mating of adult female koa seedworm, *Cryptophlebia illepidia* (Butler) (Lepidoptera: Tortricidae), 4 and 6 d on population growth rates. Leslie matrices were developed from the life tables and used to project the effects for approximately four generations. Delay of mating caused a decrease in population growth rate and also resulted in asynchronous population cycling between control (1-d delay) and the delayed treatments. By the fourth generation, the control population began to increase 10 and 14 d before the 4- and 6-d delay treatments, respectively. Increasing the mortality of females during the first 7 d of adult life resulted in a greater reduction of the populations where mating was delayed than in the control populations. This result suggests that even at relatively low levels of natural enemy mortality, there is a synergistic effect when mating is delayed. The implications of these effects on mating disruption management programs are discussed.

**KEY WORDS** *Cryptophlebia illepidia*, mating disruption, demography, delayed mating, life tables

MATING DISRUPTION PROGRAMS are becoming an important method for managing insect pests in a wide variety of cropping systems (Cardé and Minks 1995). In the past few years, the requirements of the Food Quality Protection Act (FQPA) and concerns over groundwater pollution and insecticide resistance in certain crop systems have increased the adoption of mating disruption as the control strategy for the future (Brunner et al. 2001). For example, the acreage of apple, *Malus domestica* Borkhauser, and pear *Pyrus communis* L., in Washington under mating disruption for control of codling moth, *Cydia pomonella* (L.), increased exponentially from virtually nonexistent in 1990 to ≈38,000 ha (≈50% state total) in 2000 (Brunner et al. 2001).

One of the biggest obstacles to the use of mating disruption in more systems is the lack of understanding of the exact mode of action of mating disruption (Barclay and Judd 1995, Cardé and Minks 1995). Many theories have been advanced, including habituation, false trail following, altered pheromone ratios, competitive inhibition, and peripheral nervous system effects (Bartell 1982, Cardé and Minks 1995). These theories are important because they help to understand the process by which the insect's mating behavior is affected, but unless mating is completely suppressed, they do not provide a realistic framework that describes the factors that affect population dynamics. For example, several studies have been performed where the percentage of mating between control and

treated areas is compared to help evaluate pest control (Rice and Kirsch 1990, McLaughlin et al. 1994, Agnello et al. 1996, Knight 1996, Lawson et al. 1996). The results from these studies are highly variable with some reporting little or no mating in treated areas and some reporting virtually no differences in the proportion of females mated even when good control is achieved. Clearly, those studies that show no damage in mating disruption-treated areas, with little or no differences in mating success compared with the control (untreated) areas are not directly explainable using predictions from disruption of mate-finding mechanisms alone.

The experiments in the above-mentioned studies estimate the instantaneous percentage of mated females (i.e., at a particular point in time) or the season-long percentage of mated females trapped in control versus areas under mating disruption. Unfortunately, these types of studies are insufficient to evaluate the effect of mating disruption on population dynamics because they typically do not quantify how long after emergence females mate, and the effect of delayed mating on the demography and population dynamics of the pest in question. Studies by Fadamiro et al. (1999) working with the European corn borer, *Ostrinia nubilalis* (Hübner), suggest that delayed mating does occur in mating disruption orchards; they found that the percentage of females mated in mating disruption blocks was lower initially, but increased to the same level as control blocks within ≈10 d.

Examination of the literature on life tables indicates that the time of first reproduction is the most critical factor in determining the growth rate of an expanding population (Carey 1993). Thus, any factor that in-

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creases the time to first reproduction should have marked effects on population dynamics. Barclay and Judd (1995) provide a population model framework that directly addresses mating disruption and specifically the effect of delayed mating, but they provide no data to show the soundness of the model assumptions. A review of 13 studies (Barrer 1976, Ellis and Steele 1982, Proshold et al. 1982, Leather et al. 1985, Lingren et al. 1988, van der Krann and van der Straten 1988, Unnithan and Paye 1991, Walker 1991, Rojas and Cibrian-Tovar 1994, Karalius and Buda 1995, Proshold 1996, Spurgeon et al. 1997, Vickers 1997) addressing the effect of a delay in mating of Lepidoptera shows that four effects are common. As the delay in mating increases, the longevity of the females increases, eggs produced per female decreases, gross percentage fertility of eggs laid decreases, and the period after mating but before egg deposition (preoviposition period) increases. However, it is important to note that the effect of delayed mating was not constant for a particular duration of delay between the different species examined nor did all species exhibit all four effects. In addition, only one of the 13 studies used a demographic framework (and that one only minimally) to determine effects of delayed mating on population dynamics, and the studies typically used a relatively small number of mating pairs.

This study examines the effect of delayed mating on the demography of the koa seedworm, *Cryptophlebia illepidia* (Butler), a major pest of macadamia nuts and certain tropical fruits in Hawaii (Jones 1994a, b). The work presented here is based on life tables constructed from laboratory-reared moths. The life table parameters were used to construct Leslie matrices (Leslie 1945, 1948). These matrices were then used to simulate the effect of delayed mating on population growth over a 180-d period. This period corresponds to approximately the time when nut protection is needed in macadamia nut production (Jones 1994b).

### Materials and Methods

A colony of *C. illepidia* was collected from a macadamia nut orchard in the Kau area of the island of Hawaii in 1997. This colony was augmented several times during the period of spring to fall 1998 and fall 1999 by adding field-collected larvae. *C. illepidia* were reared using the methods and diet described by Jones et al. (1997).

To examine the effects of delayed mating on reproduction, cohorts of female moths were placed in oviposition jars (3.7 liter, 26 cm tall, 14 cm diameter) and treated one of three ways. The treatments consisted of withholding males for 1, 4, or 6 d after female emergence (the normal preoviposition period for *C. illepidia* is 1 d [Jones et al. 1997]). Each day, the eggs laid were circled with a fine-point marker of a different color so that eclosion could be determined later. Oviposition jars were changed whenever counting eggs became difficult. Each day, all dead moths were removed and their sex determined to allow us to determine life table statistics. All studies were run at

22°C and a photoperiod of 14:10 (L:D) h in temperature cabinets. The experiments were replicated eight times, twice in 1999 and six times in spring 2000. The number of females per jar varied between replicates depending on colony production, but was never >30 or less than 8. The sex ratio in the jars was started at 1:1.

**Life Table Statistics.** Life table statistics were calculated according the methods of Carey (1993). Our studies did not generate complete life tables, but instead generated adult fertility tables. We used the data from Jones et al. (1997) on immature mortality, and developmental times to calculate demographic parameters for the life table. The parameters calculated included  $l_x$  (survivorship curve),  $h_x$  (daily hatch rate),  $L_x m_x h_x$  (mortality corrected production of daughters), gross and net fecundity rates, mean age of gross and net fecundity, gross reproductive rate, population doubling time, and age of first reproduction. The adult fertility table was calculated by pooling the replicates to give cohort sizes of 177, 178, and 176 females for the 1-, 4-, and 6-d delay treatments, respectively.

Differences in the mean adult lifespan of females and males between the different delay treatments were tested using analysis of variance (ANOVA) followed by the Tukey honestly significant difference (HSD) test to generate mean separations (SAS Institute 2000) performed on the pooled data set. Data were checked for normality and transformed using  $\sqrt{x}$  before ANOVA was performed (SAS Institute 2000). Homogeneity of variance was tested using Bartlett's test (Bartlett and Kendall 1946).

**Leslie Matrices.** The life tables were used to construct Leslie matrices (Leslie 1945, 1948) for each treatment using the methods described by Carey (1993). A Leslie matrix is the exponential growth model converted to matrix algebra, which allows the user to specify daily survival and reproduction rates and can provide age structure at any point in time (Leslie 1945, 1948). The Leslie matrix predictions are not intended to provide an accurate estimate of absolute population levels; however, they can be useful for studying the relative performances of populations with different growth and mortality schedules and additionally, they can provide useful insights into population dynamics (Pielou 1977, Carey 1993).

Briefly, a Leslie matrix is a square matrix that describes the transition of the population over a single time period (1 d in our case) (Southwood and Henderson 2000). It consists of a top row with daily birth elements and a subdiagonal with period survival elements (Carey 1993). The Leslie matrix is multiplied by an age vector containing the stage structure of the population to achieve a new age vector with the new stage structure (advanced 1 d in our case). The population level is projected into the future by an iterative process where the new age vector is multiplied by the Leslie matrix. The initial stage distribution in these studies was initiated by a single newly emerged adult female (actual age 40 d old from hatch) in all three treatments. The birth elements in the top row of the matrices were modified to incorporate the daily fer-

tility function and were thus calculated using  $h_x m_x$  rather than only  $m_x$ . All matrix multiplication was performed using Minitab 10extra (Minitab 1995).

A Leslie matrix provides not only total future population estimates but also the age structure of the population at any point in time (the new age vector). We used the matrices to project the population levels for each stage on a daily basis for up to 180 d into the future. This period corresponds to approximately four generations for koa seedworm. The population projections were used to compare not only the relative population growth rates but also examined for any lags in growth rates. Comparisons among delay treatments were performed by dividing the projected population levels for a given delay treatment by the 1-d (control) population level. The comparisons were performed for all stages combined (total), larval, and adult stages.

After the initial analysis, the Leslie matrices were modified so that we could examine the effect of increased mortality occurring the first week after adult emergence. This effect was examined because it has been speculated that delayed mating may allow natural enemy efficiency to increase by killing females before they reproduce (Barelay and Judd 1995). To accomplish this, the age-specific mortality was uniformly increased over the first 7 d of adult life so that mortality increased by 10, 20, 35, or 50% over the mortality observed in the life table studies. The resultant Leslie matrix was then projected 180 d into the future. The hypothesis examined was whether decreased survival early in the female's life had more of an effect in the delayed mating treatments than on the control (1-d delay) treatment. To test this hypothesis, the population size for a given delay (1, 4, or 6 d) and increased mortality rate (10, 20, 35, or 50%) was divided by the population size for the respective delay, but no additional mortality simulation. For example, the population size of the 1-d delay + 10% mortality simulation was divided by population size of the 1-d delay + 0% additional mortality simulation. This analysis allows the examination of the relative population size for a given amount of additional mortality between the three different delays. If the response of between delays were similar, the lines for a given increased percentage mortality (e.g., 10% additional) would overlap for the three different delays. If the relative population density decreases as the delay in mating increases, it indicates that the mating delay and additional mortality in the first 7 d act in more than a simply additive manner (i.e., synergistically).

The increased mortality simulations also can be used to estimate the level of mortality a population with no delay in mating must experience to reduce it to the size of a population experiencing no additional mortality, but a delay of 4 or 6 d. This can be accomplished by calculating the relative size of the control population (with 10, 20, 35, or 50% mortality) and the 4- and 6-d delay populations (with no additional mortality) over the entire length of the simulation. When the mortality added to the control population is low, the population size of the control will be greater than the delayed population (i.e., relative population size

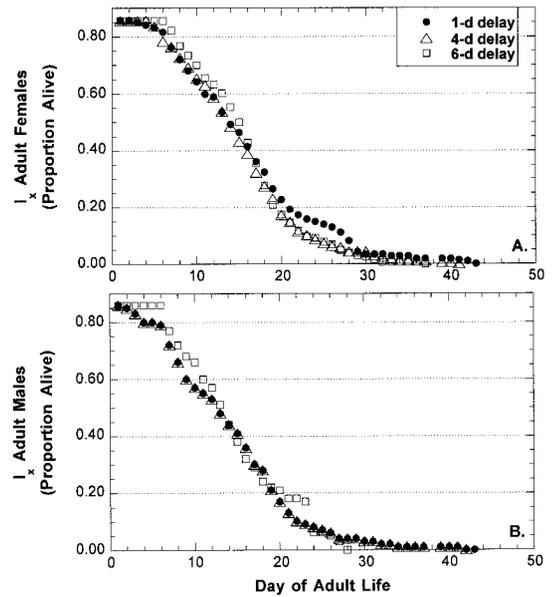


Fig. 1. Survival curves of adult koa seedworm when mating was delayed 4 and 6 d past the normal 1-d preoviposition period. (A) Adult females. (B) Adult males.

>1) and when the mortality added is high, the relative size will be less than the delayed population (i.e., <1). When the relative sizes oscillate around 1, the population sizes will be similar, indicating that the additional mortality applied to the control population has reduced its size to approximately that of the population where mating was delayed.

## Results

**Life Table Study.** Mortality patterns of females in all treatments followed similar patterns (Fig. 1A). All females in the 6-d treatment were dead by 36 d after emergence, whereas the oldest females in the 1- and 4-d treatments survived to 42 and 40 d, respectively. ANOVA revealed no significant difference in the mean longevity between any of the treatments ( $F = 0.91$ ;  $df = 2, 349$ ;  $P = 0.41$ ).

Mortality of male moths was similar between all the treatments (Fig. 1B). All males were dead by 41, 40, and 28 d in the 1-, 4-, and 6-d delay treatments, respectively. ANOVA showed no significant differences in longevity existed between treatments ( $F = 1.18$ ;  $df = 2, 338$ ;  $P = 0.31$ ).

Fertile eggs were laid the day after males were introduced in each treatment, so preoviposition period appeared to be unaffected by delay in mating. Female fertility in all treatments decreased at approximately the same rate, regardless of the delay in mating (Fig. 2). By 26 d after female emergence, none of the eggs laid in any treatment were fertile. The net fertility rate decreased from 135.8 to 114.8 to 71.2 as mating was delayed 1, 4, and 6 d, respectively (Table 1). Likewise, the gross hatch rate decreased from 0.71 to 0.69 to 0.58

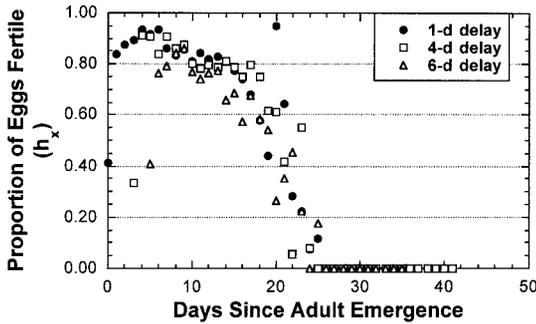


Fig. 2. Fertility curves of adult koa seedworm females when mating was delayed 4 and 6 d past the normal 1-d preoviposition period.

as the delay in mating increased from 1, 4, and 6 d (Table 2).

The cumulative production of daughters ( $\Sigma L_x m_x$ ) showed a marked increase as the delay in mating decreased (Fig. 3A). The total production of daughters is the net reproductive rate ( $R_0$ ); it decreased from 78.1 to 66.5 to 46.0 as the delay increased from the control to the 4- and 6-d delays, respectively (Table 2). However, given the high infertility rates, the  $\Sigma L_x m_x h_x$  statistic gives a more accurate picture of the reproductive rate (Fig. 3B). Incorporating the fertility rate, the net reproductive rates are 66.5, 56.3, and 34.9 females produced per female for the 1-, 4-, and 6-d delay treatments, respectively (Table 2).

Examination of the life table statistics shows that the largest differences were between the 6-d delay treatment and the other two treatments (Tables 1-3). It is particularly noticeable in the net and gross fecundity, fertility, and reproductive rates, population doubling times, and the generation times. The control and 4-d treatments tend to show differences mostly in the net statistics (net fecundity rate, net fertility rate, net reproductive rate). These differences are probably because the female mortality rate in the 4-d delay treatments was slightly higher than in the 1-d delay treatment and the net hatch rate of the 4-d delay treatment was slightly higher than in the 1-d delay treatment.

The mean age of gross and net fecundity and fertility tended to increase as the delay went from the 1-

Table 1. Fecundity and fertility rates for koa seedworm where mating was delayed 1 (control), 4, or 6 d after female emergence

Population Parameter	Control	4-d delay	6-d delay
Gross fecundity rate <sup>a</sup>	282.8	271.4	211.4
Net fecundity rate <sup>b</sup>	159.5	135.6	94.0
Gross fertility rate	200.4	186.7	121.7
Net fertility rate	135.8	114.8	71.2
Eggs/female/day	12.1	10.9	7.3
Fertile eggs/female/day	10.3	9.3	5.5

<sup>a</sup> Gross schedules assume no mortality occurs (i.e., the female lives to the last possible day of the cohort).

<sup>b</sup> Net schedules assume mortality occurs at the average rate (i.e., the female dies as the average point for the cohort).

Table 2. Reproductive parameters of koa seedworm when mating was delayed 1 (control), 4, or 6 d after female emergence

Population Parameter	Control	4-d delay	6-d delay
Proportion female	0.49	0.49	0.49
Gross hatch rate <sup>a</sup>	0.71	0.69	0.58
Net hatch rate <sup>b</sup>	0.85	0.85	0.76
Net reproductive rate	78.1	66.5	46.0
Gross reproductive rate	138.6	133.0	103.6
Generation time ( <i>T</i> )	47.6	49.2	51.2
Population double time	7.6	8.1	9.3
<i>r</i>	0.092	0.085	0.075

<sup>a</sup> Gross schedules assume no mortality occurs (i.e., the female lives to the last possible day of the cohort).

<sup>b</sup> Net schedules assume mortality occurs at the average rate (i.e., the female dies as the average point for the cohort).

to the 6-d delay treatments (Table 3). However, the increase is not simply equal to the time for the 1-d delay treatment plus the additional time of delay, because the shape of the  $L_x m_x$  or  $L_x m_x h_x$  curve determines these statistics (Fig. 3). The shapes of the control and 4-d delay treatments are similar, whereas the 6-d delay treatment has a slower rate of increase.

Leslie Matrix Studies. Using the Leslie matrices to model the different treatments showed that the effect of delayed mating can have large and cumulative effects on population development (Fig. 4 A-C). The delay in mating results in an increasingly asynchronous cycling of the three populations. For example, even in the first generation following the initiation of the simulation, the control population (1-d delay)

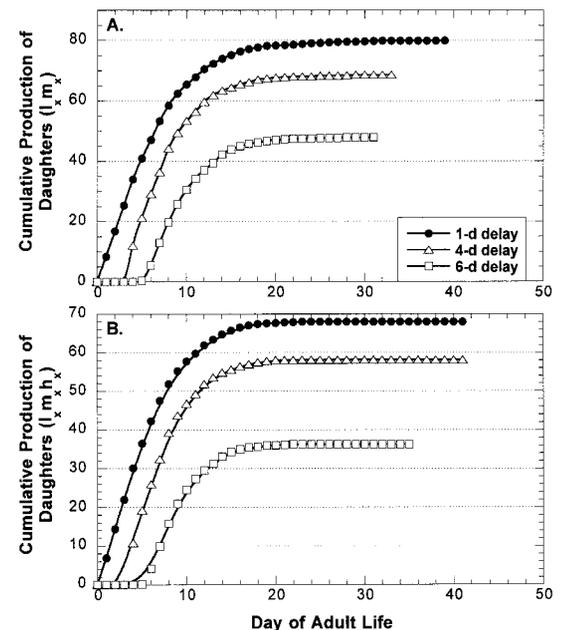


Fig. 3. Cumulative production of daughters by adult koa seedworm when mating was delayed 4 and 6 d past the normal 1-d preoviposition period. (A) Fertility not considered. (B) Corrected by fertility.

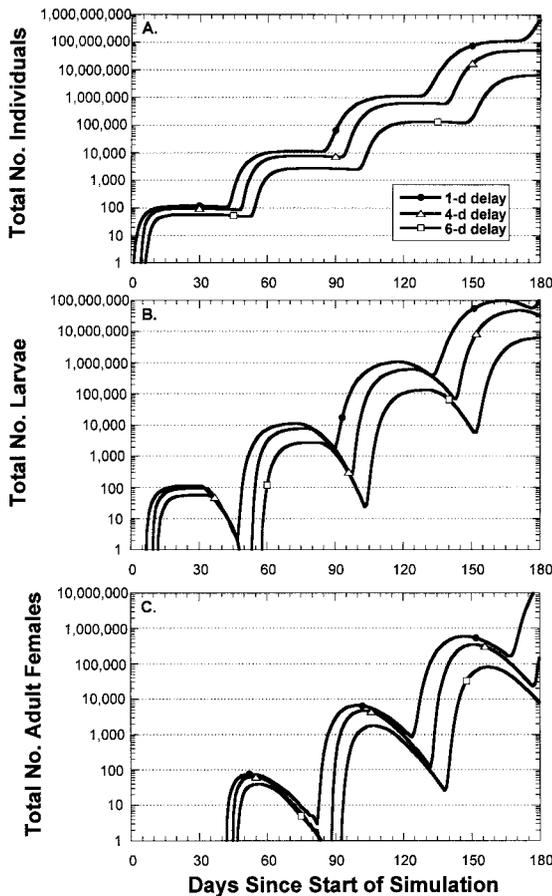
**Table 3.** Mean age of attaining net and gross fecundity and fertility for koa seedworm when mating was delayed 1 (control), 4, or 6 d after female emergence

Population Parameter	Control	4-d delay	6-d delay
Mean age gross fecundity <sup>a</sup>	52.3	54.1	56.2
Mean age net fecundity <sup>b</sup>	47.5	49.1	51.1
Mean age gross fertility	48.3	50.1	51.9
Mean age net fertility	47.0	48.1	50.6
Mean age hatch	51.6	53.1	54.0

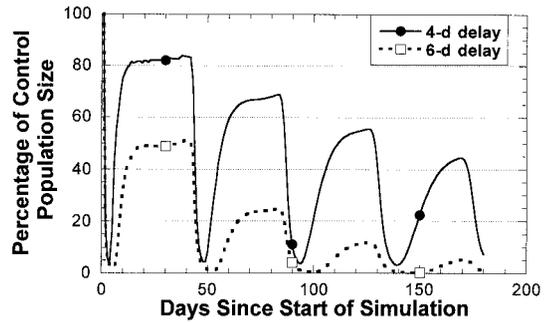
<sup>a</sup> Gross schedules assume no mortality occurs (i.e., the female lives to the last possible day of the cohort).

<sup>b</sup> Net schedules assume mortality occurs at the average rate (i.e., the female dies as the average point for the cohort).

starts increasing before the other two treatments (Fig. 4 A-C). By the start of the fourth generation, the control population begins increasing 10 and 14 d before the 4- and 6-d delay treatments. If the data for the 4- and 6-d delays are graphed as the percentage of the control treatment, the asynchrony is visible as a change in the shape of the curves; they start out as



**Fig. 4.** Population growth of koa seedworm predicted by Leslie matrices when mating was delayed 4 and 6 d past the normal 1-d preoviposition period. (A) Total population level (all stages combined). (B) Population level of the larval stage only. (C) Population level of the adult female stage only.



**Fig. 5.** Total population sizes of koa seedworm subjected to a 4- and 6-d delay in mating expressed as a percentage of the total population size of the no delay (control) treatment.

fairly flat-topped curves and gradually become more peaked (Fig. 5).

The increased mortality simulations showed that population levels were reduced as mortality increased during the first week of adult life regardless of the delay treatment. However, within a delay treatment there was no asynchrony between the different mortality levels (Fig. 6 A-C).

The comparison of the additional mortality simulations to the no additional mortality simulations showed that the relative population sizes decreased as the length of delay increased (Fig. 7). For example, adding 35% mortality in the 1-d delay simulation resulted in the population size decreasing 65.1% at 70 d, but resulted in the populations where mating was delayed 4- and 6-d decreasing 76.8 and 86.5% compared with their respective no additional mortality simulations.

Comparison of the 4-d delay population simulation with no additional mortality to the 1-d delay simulation showed that between 10 and 20% additional mortality was required for the relative population sizes in the 1-d simulation to be roughly equivalent to the 4-d delay population. The 1-d delay treatment required >35%, but <50% additional mortality for the populations to be roughly equivalent to the 6-d delay.

**Discussion**

Our results are similar to previous studies in that with increasing delays in mating the egg production and egg fertility decline. However, the drop in egg fertility in our study appears to be primarily because the early period of peak egg fertility is eliminated in the longer delay treatments. The daily fertility rate is very similar between those with 1 d and those delayed either 4 or 6 d once mating begins for all treatments. Our experiments do not allow us to determine if reduced daily viability is related to sperm storage, decreased mating, or smaller sperm packets being transferred. We also found no significant differences in longevity or in preoviposition periods between the different delays, whereas several studies have shown one or both to occur (Barrer 1976, Ellis and Steele 1982, Proshold et al. 1982, Leather et al. 1985, Lingren

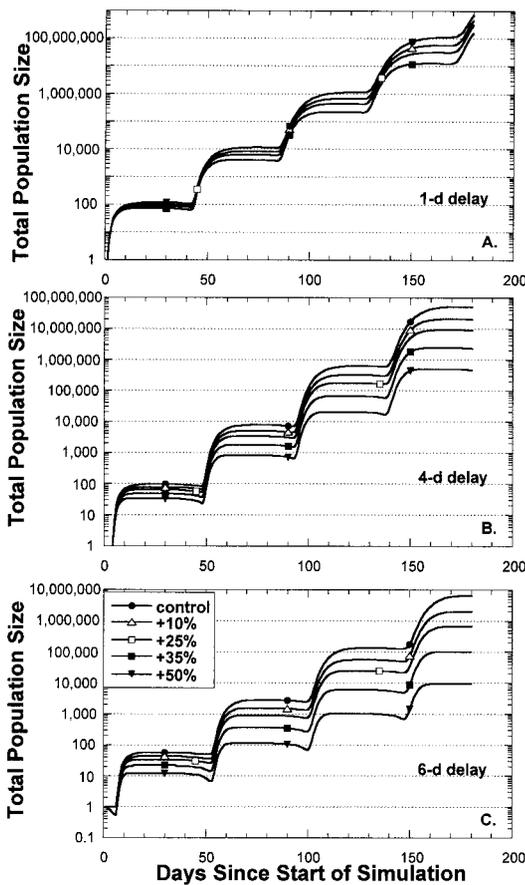


Fig. 6. Total predicted population sizes of koa seedworm subjected to five levels of additional mortality during the first 7 d after emergence as adults. (A) No delay in mating. (B) Mating delayed 4 d. (C) Mating delayed 6 d.

et al. 1988, van der Krann and van der Straten 1988, Unnithan and Paye 1991, Rojas and Cibrian-Tovar 1994, Proshold 1996). The differences in our study and the previous studies may be related to biological differences between species and how they react to delayed mating. However, it is also possible that for some of the studies, the small sample sizes allow a few individuals functioning as outliers (in terms of longevity or preoviposition period) to affect the resulting statistics.

Overall, our results indicate that even if the percentage of females mated in control and treated areas is not different, a mating delay of 4–6 d is enough to significantly reduce the population growth rate. By itself, the lower growth rate will result in decreased damage, and mating disruption may be a reasonable management tool despite no apparent differences in mating ratios. In situations where multiple mating of the pest insect can increase the reproductive output (Fadamiro and Baker 1999), the effect delaying both the initial and any subsequent mating may have even greater consequences to population dynamics than we observed in our experimental manipulations where

the males remained in the same cage as the females for the entire experiment.

Our study demonstrated that population growth of the 4-d delay population was more similar to the control population growth than to the 6-d delay population. These data suggest that there may be a threshold of delay required to obtain successful population suppression in the field. For example, if the mating disruption technology used (e.g., dispensers, MSTR, puffers) cannot delay mating  $>2$ –3 d in koa seedworm, then the likely effect on population dynamics would be relatively small. However, our simulation studies indicate that the delay in mating should have a synergistic effect with natural enemy mortality that occurs early in the adults' lifespan. Thus, natural enemies previously considered unimportant may be critical factors in helping to determine the variability in results between mating disruption treatments in different areas. In sites where natural enemy-induced mortality is greater than a certain threshold, the additional mortality may result in acceptable control. This is especially likely in cropping systems where broad-spectrum pesticide use is being replaced by mating disruption.

The studies performed herein used a constant delay in mating, but in reality, from a population perspective, the delay will vary according to some sort of frequency distribution. The mean delay and the shape and symmetry of the distribution will determine the effect of delayed mating on population growth and hence control. The shape of this curve is also likely to be a function of the population density (e.g., density-dependent mating) and any effects of the pheromone on male searching behavior (such as increased movement). As such, a reasonable approach would be to get estimates of these effects within the range of densities of economic concern and use sensitivity analysis to determine their importance in population dynamics.

The changes in generation time and the asynchrony of the populations seen in the Leslie matrix simulations are important when comparing control and

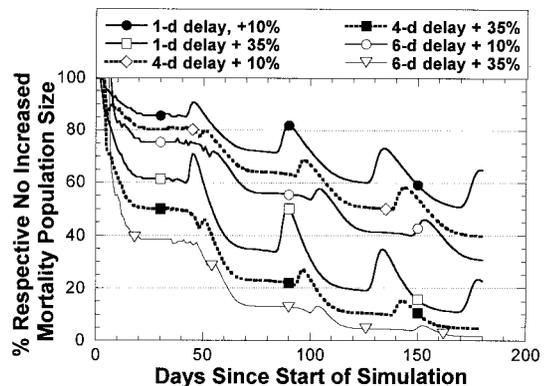


Fig. 7. Relative size of the 4-d delay population when no additional mortality is imposed in the first week of adult life and the no delay (control) populations when an additional 10, 20, or 35% mortality are imposed in the first week of adult life.

treated areas. First, the asynchrony may result in different damages at harvest (or any other arbitrarily chosen time) because of the greater number of generations occurring in the control and treated areas (see Fig. 5, compare the differences in relative population size between 30 and 55 d). This effect is likely to be extremely important in situations where multiple generations of the pest occur and where a single feeding bout, oviposition puncture, or individual present can result in rejection of the commodity (e.g., a caterpillar feeding on a fruit). By being able to harvest before the next generation begins to emerge, the crop is exposed to much less potential damage.

For *C. illepidata* in particular, the time of reproduction was strictly limited. Even though egg production continued until 39 d after adult emergence in the 1-d delay treatment, no eggs were fertile in any treatment by 26 d after emergence. The infertility declined in all three treatments at about the same time and approximately the same rate. The low rate of fertility at times greater than  $\approx 18$  d is interesting because females are still producing eggs, but a large portion of them do not hatch. This is probably an artifact of the longer lifespan of females in the laboratory, but may also occur in certain circumstances in the field. If it does, it would help explain why presence of *C. illepidata* eggs on macadamia and litchi are such poor predictors of larval damage for integrated pest management (IPM) purposes (Jones 1995).

Overall, the demographic effects of delayed mating are the result of the different behavioral-physiological mechanisms proposed for mating disruption (Bartell 1982, Cardé and Minks 1995). Unfortunately, understanding the behavioral-physiological mechanisms alone do not provide insights into the population biology that underlies the success or failure of mating disruption. The demographic approach adds a strong theoretical framework to integrate the effects of natural enemies, delayed mating, multiple mating, and other potential factors that may influence population dynamics occurring in mating disruption areas.

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