Comparison of Delayed Female Mating on Reproductive Biology of Codling Moth and Obliquebanded Leafroller

VINCENT P. JONES,[1] NIK G. WIMAN, AND JAY F. BRUNNER

Department of Entomology, Tree Fruit Research and Extension Center, Washington State University,
1100 N. Western Ave., Wenatchee, WA 98801

ABSTRACT   Delay of mating was examined as a possible mechanism for population decreases associated with mating disruption for codling moth, *Cydia pomonella* L., and obliquebanded leafroller, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae). We examined the effect of delaying female mating 0, 2, 4, or 6 d while holding male age constant on life table parameters of both species. We found that increasing delays in mating were accompanied by two responses: (1) an increase in the percentage of sterile pairs and (2) a reduction in net reproductive rate and population growth unrelated to sterility. On a percentage basis, obliquebanded leafroller population growth was more strongly affected than codling moth. However, the net fertility rate of obliquebanded leafroller was nearly eight-fold higher than that of codling moth, so that obliquebanded leafroller females that experienced a 4-d delay in mating had nearly the same reproductive rate as codling moth females that experienced no delay. Leslie matrix simulations using life tables with field-based adult longevity estimates showed that codling moth females experiencing >2-d delay in mating resulted in decreases in population density or extinction within two generations. In contrast, obliquebanded leafroller females delayed <6 d showed rapid population growth that decreased as female age at mating increased; only the 6-d delay treatment resulted in decreased population levels. Our results indicate that obliquebanded leafroller females must on average experience a much longer delay in mating to significantly reduce population growth compared with codling moth females, suggesting that delay of mating likely plays a greater role in codling moth mating disruption than for obliquebanded leafroller.

KEY WORDS   *Cydia pomonella*, *Choristoneura rosaceana*, mating disruption, delayed mating, population dynamics

Management programs for insects attacking apple in Washington State have been in a state of flux for the past decade (Brunner et al. 2005). A major driving factor has been the Federal Food Quality Protection Act of 1996 (FQPA), which has made huge changes in the availability of organophosphate (OP) insecticides for not only codling moth, but also secondary pests (Brunner et al. 2001). Although FQPA legislated changes have resulted in cancellation of several insecticides, it has also sped the adoption of mating disruption for codling moth and stimulated registration of a number of OP alternatives. Mating disruption is currently being used on nearly 75% of the Washington apple and pear acreage (J.F.B., unpublished data), and its success with codling moth fueled the hopes that tortricid leafrollers [obliquebanded leafroller, *Choristoneura rosaceana* (Harris) and *Pandemis* leafroller, *Pandemis pyrusana* Kearfott] attacking apple could be managed in the same fashion. However, attempts to implement mating disruption for both obliquebanded leafroller and *Pandemis* leafroller have

not met with consistent success (Gut and Brunner 1992, Agnello et al. 1996, Knight et al. 1996, 1998, Lawson et al. 1996), and currently, mating disruption is not considered a commercially acceptable alternative to some of the newer insecticides (Smith et al. 2007).

Although codling moth mating disruption has generally had a high rate of success, occasional inconsistencies have lead to the realization by both researchers and growers that understanding the mechanisms by which mating disruption acts on a population is critical to its long-term sustainability as a management tool (Barclay and Judd 1995, Jones and Aihara-Sasaki 2001). In addition, knowing the mechanisms that operate at the population level may help explain why mating disruption works well for codling moth but not for obliquebanded leafroller.

A logical starting point for understanding how mating disruption operates is to examine a population under mating disruption and to determine exactly how mating disruption can reduce the population growth rate. Initially, it was assumed that mating disruption prevented mate finding, but studies have shown that

[1] Corresponding author, e-mail: vpjones@wsu.edu.

the percentage of mated females in a mating disruption area may still be relatively high compared with nonmating disruption control areas (although it may be depressed) (Agnello et al. 1996, Knight et al. 1996, Lawson et al. 1996). A basic tenant of population biology is that the age at which first reproduction occurs is one of the most important factors governing population growth rates (Lewontin 1965, Carey 1993). This principle has led to a number of studies of varying complexity that have been performed on a wide range of pest species to better understand the implications of this premise mostly for colony production. This principle is also one of a number of possible explanations for how mating disruption reduces population growth rates. Unfortunately, many studies either use a small sample size or report simple statistics (such as the mean number of eggs produced per female over her entire life span) that cannot be used as a basis for understanding population dynamics.

The use of life tables is perhaps the best way to evaluate how different potential mechanisms might impact the efficacy of mating disruption because they provide a logical framework to assess changes in population growth rate. In particular, this approach allows the use of Leslie matrix models to evaluate the interaction of different factors on population growth using simulation.

The purpose of this study was to determine the effects of delayed female mating on population growth of codling moth and obliquebanded leafroller. The two species have different life histories with regards to reproduction; the codling moth deposits its eggs singly and has a relatively low population growth rate, whereas the obliquebanded leafroller deposits eggs in a large mass and has a relatively high population growth rate (Beers et al. 1993). Thus, a comparison of the two species may help explain the disparity observed in mating disruption success.

Materials and Methods

Codling moths used in the experiments were reared on an artificial diet and were obtained from the USDA–ARS Yakima Agricultural Research Laboratory (YARL) in Wapato, WA; the insects were of the nondiapausing strain. Moths were shipped to Washington State University's Tree Fruit Research and Extension Center (WSU–TFREC) in Wenatchee, WA, as last-instar larvae and pupae in cardboard bands. In the laboratory, the pupae were removed from the bands, sorted by sex, and placed in cages (3 liters) for emergence in a temperature cabinet (22°C, RH $\approx$ 75%), with a 16:8 (L:D) photoperiod and honey water solution. Cages were examined daily for emergence, and newly emerged females were divided into treatments in which they were paired with 0- to 1-d-old males on the day of emergence (=day 0), or at 2, 4, or 6 d after female emergence. Moth pairs were placed into individual 355-ml screened cages and examined daily for male and female mortality, egg production, and egg hatch. Each pair was provided with a honey water solution for the duration of life.

Obliquebanded leafroller moths were obtained from the WSU-TFREC colony and were reared on an artificial pinto bean diet (Shorey and Hale 1965). Last-instar caterpillars were placed in plastic cups (96 cm^3) and allowed to pupate. After pupation, the same handling and processing methods described for codling moth were applied. Females were caged individually in 500-ml screened cages with 0- to 1-d-old males on the day of emergence or at 2, 4, or 6 d later. The cages used for obliquebanded leafroller rearing were lined with wax paper, and egg masses deposited on the wax paper were removed from cups daily or circled with different colored markers to distinguish the date when oviposition occurred. The wax paper was cut so that all the egg masses laid by a mating pair on a given day were placed in a single rearing container to evaluate egg hatch by counting emerging larvae. Individual eggs were not counted because obliquebanded leafroller females lay eggs in a mass with overlapping eggs, making it very difficult to count single eggs or to determine hatch rates.

All life table statistics were calculated using the methods of Carey (1993). We developed fertility/fecundity tables from our laboratory data. Because we only followed each egg to the point of hatching (to get egg hatch rates) and not to adulthood, we did not have estimates of larval survival to develop a complete life table nor did we have the true sex ratio. For development of the life table, we set the sex ratio to 50:50 and used estimates of 70% of hatching eggs surviving to the adult stage for obliquebanded leafroller (M. D. Doerr and J.F.B, unpublished data) and 36% of the hatched codling moth eggs surviving to the adult stage in our laboratory studies (N.G.W. and V.P.J., unpublished data). The estimates of survival were developed at the same temperature and humidity as used in our experiments. The mortality in the larval stage was uniformly applied across the entire immature period so that the entire mortality in the immature stages equaled either the 70 or 36% survival figure. Although these values may not be representative of field mortality, the effect of their inaccuracies are minor because the same values are used across all the four delay treatments, and we are comparing the relative growth rate among the four treatments and not the absolute values. The life table parameters calculated included l_x (age-specific survivorship), h_x (age-specific hatch rate—codling moth only), $\sum L_x M_x h_x$ (mortality corrected production of progeny = net fertility rates), mean age of net fertility, r (intrinsic rate of population growth), and population doubling time (ln2/r). For codling moth only, we also calculated the net reproductive rate ($R_o = \sum L_x m_x$). R_o was not calculated for obliquebanded leafroller because we were not able to calculate h_x (age-specific hatch rate) because of the difficulty in distinguishing individual eggs in a given mass. The adult codling moth fertility table was calculated by pooling the replicates to give cohort sizes of 75, 110, 122, and 161 mating pairs for the 0-, 2-, 4-, and 6-d delays, respectively. The obliquebanded leafroller cohort sizes were 102, 130, 160, and 220 mating pairs for the 0-, 2-, 4-, and 6-d delays, respectively.

Because we reared each mating pair separately, we could determine the percentage of pairs that laid no fertile eggs. This allowed us to examine the effect that a delay in mating had on sterility of mating pairs. We also were able to recalculate the life tables to eliminate the sterile pairs to determine whether changes in fertility were independent of sterility.

We analyzed and present the laboratory-derived l_x curves for adult females, but for Leslie matrix projections, we only used estimates of field l_x curves (Jones and Wiman 2008) to correct for bias in survival rates caused by the more benign environment typically found in laboratory studies. The field-based l_x curves provided by Jones and Wiman (2008) were developed using the same colonies used in this study but were presented on a degree-day scale. We converted them back to a calendar date basis by dividing by the degree-days accumulated per day in the laboratory studies (12 DD per day for both species). We also decided to restrict the simulations to only those based on the life tables that excluded sterile pairs. This eliminates the concern that the high sterility was an artifact of rearing or that the experimental cages were suboptimal for mating.

The resulting life tables were used to generate Leslie matrix models for each delay interval. A Leslie matrix model 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 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 [=12 DD] 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 our studies was initiated by 16 newly emerged adult females in all four treatments. The birth elements in the top row of the matrices were modified to incorporate the daily fertility function and were thus calculated using $h_x m_x$ (age-specific fertile female progeny production) rather than just m_x (age-specific female progeny production). We used the daily fertility function because this allowed rough comparisons between the species. All matrix multiplication was performed using Stata 9.2 (Statacorp 2005). We used the matrices to project the population levels for each stage on a daily basis for a period roughly equal to two generations for both species ($\approx$120 d).
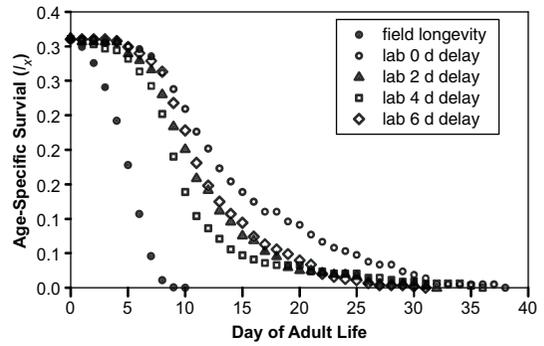

Fig. 1. Comparison of age-specific survival of adult female codling moth in the laboratory and field (field data from Jones and Wiman 2008).

Results

Codling Moth Life Table Statistics. Examination of the l_x curves for the codling moth showed no apparent trend related to increasing delay of mating (Fig. 1). The 0-d delay treatment had the longest survival, the 2- and 6-d delays were intermediate and nearly identical, and the 4-d delay had the shortest longevity. Longevity in the field was considerably shorter than observed in the laboratory assays, with maximum longevity of 10 d compared with 25+ d in any of the laboratory treatments (Fig. 1).

The percentage of mating pairs that were sterile showed a steady increase as female age at time of mating increased (Table 1). The majority of the effect was completed by day 4, with only a slight increase in sterility between days 4 and 6. In addition to the sterility associated with pairs not mating, there was a decrease in egg hatch as female age at mating increased; this occurred even when the sterile pairs were eliminated from the analysis (Table 1).

The net fertility rates were all heavily influenced by the number of days that mating was delayed, regardless of which mortality schedule was used and whether sterile pairs were included with the data set or not (Table 1). When using the laboratory-derived l_x curves, there appeared to be a plateau in net fertility that occurred by 4 d after mating; there were only minor differences between the 4- and 6-d delay treatments. The reduction in egg production resulted in increases in the time required for the population to double by 10, 14, and 22% between the 0-d delay treatments (with sterile pairs included) and the 2-, 4-, and 6-d delay treatments, respectively.

When the field-derived l_x function was used to calculate the life table parameters, the reductions in net female fertility rates were more severe, and they did not level off after the 4-d delay in female mating (Table 1). The increased mortality used in the field-derived mortality curve results in two major effects on the population growth curve. First, fewer females survive to mating, thus eliminating both themselves and their progeny. Second, even if they survive long enough to mate, their longevity after mating is considerably shorter, making it less likely they will pro-

Table 1. Life table parameters for codling moth developed using laboratory or field l_x curves

Life table parameter	Laboratory l_x curves				Field l_x curves			
	0 d	2 d	4 d	6 d	0 d	2 d	4 d	6 d
All pairs included (*N*)	75	110	122	161				
Percent sterile pairs	34.7	43.6	52.5	54.7				
Mean percent hatch	50.0	52.9	38.6	29.1	57.4	59.5	49.5	7.8
Net fertility rate ($\Sigma L_x M_x h_x$)	13.1	9.6	4.2	3.6	6.7	2.8	1.0	0.1
Mean age net fertility	57.9	60.0	60.9	62.8	55.7	57.2	58.3	60.1
Net reproductive rate ($R_o = \Sigma L_x m_x$)	13.1	9.0	5.5	6.3	5.9	2.4	1.0	0.6
Doubling time (d)	13.7	15.0	15.5	16.6	30.0	39.7	71.7	87.2
r	0.051	0.046	0.045	0.042	0.023	0.017	0.010	0.008
Sterile pairs eliminated (*N*)	49	62	58	73				
Mean percent hatch	55.0	57.8	44.8	40.5	60.7	63.0	57.4	16.6
Net fertility rate ($\Sigma L_x M_x h_x$)	20.0	16.6	8.8	8.0	8.5	3.8	1.6	0.6
Mean age net fertility	57.9	59.9	60.9	62.8	55.7	57.2	58.3	60.0
Net reproductive rate ($R_o = \Sigma L_x m_x$)	18.2	14.4	9.9	9.9	8.5	3.8	1.5	0.6
Doubling time (d)	12.8	13.3	13.8	14.9	23.5	27.7	42.2	49.6
r	0.054	0.052	0.050	0.046	0.030	0.025	0.016	0.014

duce as many progeny. These factors result in dramatically lower estimates of the population growth rate compared with those obtained using the laboratory-derived l_x curves (Table 1).

Obliquebanded Leafroller Life Table Statistics. Unlike the l_x curves generated for codling moth, the laboratory l_x curves for obliquebanded leafroller were nearly identical for all of the different delay treatments (Fig. 2). As with the field data for the codling moth, the obliquebanded leafroller field l_x curves dropped considerably faster than the laboratory curves (Fig. 2).

The percentage of mating pairs that were sterile started at about the same level as codling moth ($\approx$34%) but increased much more dramatically to 47, 67, and 83% for females mated 2, 4, and 6 d after emergence (Table 2).

The obliquebanded leafroller was much more sensitive to the delay in mating than codling moth regardless of whether laboratory or field l_x curves were used and whether sterile pairs were included or not (Table 2). Using the laboratory l_x curve and fecundity/fertility data from all pairs (i.e., sterile pairs included) showed that even a 2-d delay resulted in 41% reduction in the net fertility rate compared with the 0-d treatment, and the 4- and 6-d delays caused 74 and 93%

Fig. 2. Comparison of age-specific survival of adult female obliquebanded leafroller in the laboratory and field (field data from Jones and Wiman 2008).

reductions, respectively. When sterile pairs were excluded, we still found that the reductions in net fertility rate compared with the 0-d treatment were 29, 50, and 76% for the 2-, 4-, and 6-d delay, respectively. Despite the larger percentage reductions found with obliquebanded leafroller, the higher initial reproductive rate resulted in a higher net fertility rate than for codling moth for all delay treatments except the 6-d delay with sterile pairs included.

As was observed with codling moth, the field-derived l_x curve dramatically increased the effect of delayed mating compared with the laboratory-derived curve. In the situation where sterile pairs were included, the net fertility rate dropped $\approx$62, 93, and 99.5% compared with the 0-d delay treatment for the moths delayed 2, 4, or 6 d, respectively (Table 2). When the sterile pairs were eliminated, we still saw $\approx$54, 88, and 98.7% reduction in the net fertility rate compared with the 0-d delay treatment. The population double times showed the same trends as with codling moth, but the impacts were considerably greater on a percentage basis (Table 2).

Codling Moth Simulations. The simulations showed that when the mating was delayed 2 d or less, the populations increased rapidly (Fig. 3). However, females 4 or 6 d old at the time of mating caused a relatively rapid decline in the population trajectory toward extinction. If viewed as the percentage of the control population size, the 2-d delay resulted in 63 and 87% reductions after one and two generations, respectively. However, the 2-d delay still resulted in 4.7- and 7.8-fold growth over the initial population size of 16 females after one and two generations, respectively.

Obliquebanded Leafroller Simulations. In marked contrast to the codling moth simulations, a mating delay of at least 6 d was required to cause reductions in population size of the obliquebanded leafroller (Fig. 4). Females that were delayed 4 d showed 6.3- and 29-fold increases over the initial population size of 16 females after one and two generations, respectively. Perhaps the greatest difference between the obliquebanded leafroller and codling moth simulations is the
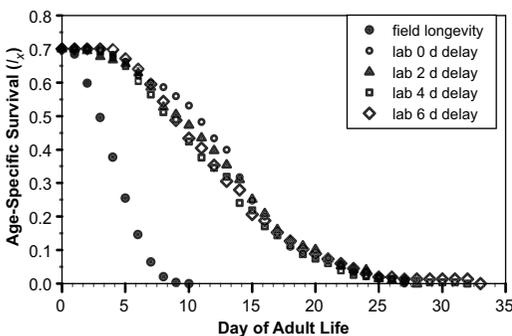
Table 2. Life table parameters for the obliquebanded leafroller developed using laboratory or field l_x curves

Life table parameter	Laboratory l_x curves				Field l_x curves			
	0 d	2 d	4 d	6 d	0 d	2 d	4 d	6 d
All pairs included (N)	102	130	160	220				
Percent sterile pairs	34.3	46.9	66.9	83.2				
Net fertility rate ($\Sigma L_x M_x h_x$)	158.5	93.8	40.9	10.9	88.9	34.0	6.3	0.4
Mean age net fertility	42.7	44.2	46.2	48.1	56.3	57.8	59.3	61.2
Doubling time (d)	9.3	10.6	13.3	21.0	13.6	16.8	25.6	54.7
r	0.075	0.066	0.052	0.033	0.051	0.041	0.027	0.013
Sterile pairs eliminated (N)	67	69	53	37				
Net fertility rate ($\Sigma L_x M_x h_x$)	240.2	171.3	119.0	57.1	133.8	61.5	16.1	1.7
Mean age net fertility	42.7	44.1	46.2	47.6	56.3	57.7	59.3	61.0
Doubling time (d)	8.4	9.2	10.2	12.2	12.0	13.7	16.6	22.6
r	0.082	0.076	0.068	0.057	0.058	0.051	0.042	0.031

sheer magnitude of the population growth rates; the 0-d females for codling moth would result in roughly 1,500 individuals after two generations versus 62,700 individuals for the obliquebanded leafroller.

Discussion

In reviewing 13 studies on delayed mating, Jones and Aihara-Sasaki (2001) found four effects were commonly reported to occur as the delay in mating increased: (1) increases in the longevity of the female, (2) eggs produced per female decreases, (3) gross percentage of eggs oviposited decreases, and (4) the period after mating but before egg deposition (pre-oviposition period) increases. For both the codling moth and obliquebanded leafroller, we found no evidence to support either (1) or (4) and confirmed that the major factors were (2) and (3). In this respect, our codling moth data and those of Vickers (1997) agree. However, our codling moth data showed a much lower R_o than reported by Vickers (1997). Some of the differences might be ascribed to the differences in colonies of codling moth used, but some are also likely a result of the method Vickers used to calculate R_o; i.e., Vickers (1997) used an approximation from a partial life table that was set to start after mating, whereas ours started after adult emergence. Regardless, on a percentage basis, our reduction in R_o is greater at 2-d but similar at the 4-d delays: Vickers (1997) reported 12 and 52% reductions compared with the control,

whereas we found 31 and 58% reductions in R_o with sterile pairs included or 20 and 46% when the sterile pairs were excluded.

On strictly a percentage basis, the obliquebanded leafroller had the greatest reductions in net fertility rate and corresponding increase in population doubling time as mating was delayed 2, 4, or 6 d. However, the net fertility rate of the population for the obliquebanded leafroller was 12- to 13-fold higher than the codling moth for females that experienced no delay in mating (Tables 1 and 2). Obliquebanded leafroller females that experienced a 4-d delay in mating had a higher net female reproductive rate than codling moth females that experienced no delay in mating, regardless of whether longevity was laboratory or field derived.

The use of the field longevity curves provides a much better picture than laboratory data of the effect of delayed mating that may occur in the field. The rearing of insects under optimal environmental conditions and using diet supplements that either may be rare or nonexistent in nature (e.g., honey water) greatly distorts our understanding of population dynamics (Jones and Wiman 2008) and underestimates the importance of delayed mating as a mechanism restricting population growth. Specifically, an unrealistic longevity estimate dilutes the importance of mortality that would occur before mating (=killing not only the individuals but preventing their production of progeny) and the reduced longevity after mating (reducing the oviposition period). Thus, any factor
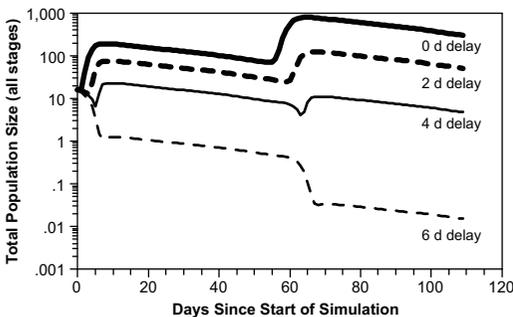

Fig. 3. Leslie matrix projections of the population level of all female stages of codling moth over a 120-d period. All simulations started with 16 adult females.
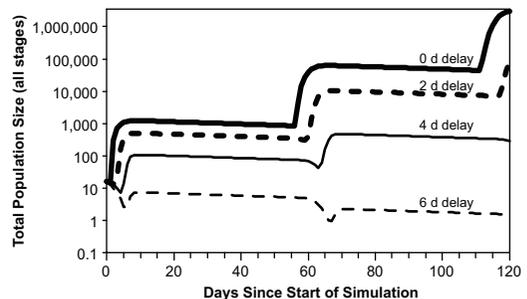

Fig. 4. Leslie matrix projections of the population level of all female stages of obliquebanded leafroller over a 120-d period. All simulations started with 16 adult females.

that changes the survivorship curve either before or after mating reduces population growth. In the case of mating disruption, factors such as biological control or supplemental pesticide applications can dramatically stabilize population growth, even if the magnitude of the added mortality factor is relatively small (Jones and Aihara-Sasaki 2001).

In terms of how the delay in mating can translate into efficacy of mating disruption, it is clear that obliquebanded leafroller females must experience, on average, a much greater delay in mating than codling moth females to result in significant population reductions. However, to understand the importance of delayed mating in population reduction, we still require population level estimates of what proportion of the population mates at different ages after adult emergence in mating disruption versus nonmating disruption situations. It is also important to point out that, from the standpoint of mating disruption efficacy, if a significant proportion of the females are unmated as a result of the treatment, that effect will have a much stronger influence on growth rates than that of delayed mating, unless the whole population experiences a delay of extraordinary length.

Although this study does shed light on the effects of the delay in female mating on population growth, several other factors still need to be considered. First, the age of the males used in mating may have strong effects on egg production even if mating is successful, and this effect needs to be examined. For example, an old male may not transfer enough sperm for maximum egg production but may transfer enough that pheromone production is curtailed after mating (Delisle et al. 2000). Second, although it is seldom noted with moths, there may be age-related mate discrimination by either sex. Our data provide at least some support for age-based discrimination at least by males, because females of both species showed an increase in sterility with increased age when male age was held constant at 1–2 d old. Further work on age-based discrimination by females should be conducted.

Although delayed mating has been suggested as a partial explanation of how mating disruption affects population growth, it should be clear that delayed mating affects population growth even in the absence of mating disruption. For example, delayed mating can easily occur because of abiotic factors such as wind, high or low temperatures, or rainfall. Thus, the role of delayed mating thus provides us with another tool to help understand of the effect of abiotic factors on population dynamics.

References Cited

Agnello, A. M., W. H. Reissig, S. M. Spangler, R. E. Charlton, and D. P. Kain. 1996. Trap response and fruit damage by obliquebanded leafroller (Lepidoptera: Tortricidae) in pheromone-treated apple orchards in New York. Environ. Entomol. 25: 268–282.

Barclay, H. J., and G.J.R. Judd. 1995. Models for mating disruption by means of pheromone for insect pest control. Res. Popul. Ecol. 37: 239–247.

Beers, E. H., J. F. Brunner, M. J. Willett, and G. M. Warner. 1993. Orchard pest management: a resource book for the Pacific Northwest. Good Fruit Grower, Yakima, WA.

Brunner, J. F., S. C. Welter, C. O. Calkins, R. Hilton, E. H. Beers, J. E. Dunley, T. R. Unruh, A. L. Knight, R. A. van Steenwyk, and P. Van Buskirk. 2001. Mating disruption of codling moth: a perspective from the western United States. IOBC Wprs. Bull. 5: 207–225.

Brunner, J. F., J. D. Dunley, E. H. Beers, and V. P. Jones. 2005. Building a multi-tactic biologically intensive pest management system for Washington orchards, pp. 131–143. *In* A. Felsot and K. Racke (eds.), Certified organic and biologically derived pesticides: environmental, health and efficacy assessment. American Chemical Society, New Orleans, LA.

Carey, J. R. 1993. Applied demography for biologists with special emphasis on insects. Oxford University Press, New York.

Delisle, J., J. Picimbon, and J. Simard. 2000. Regulation of pheromone inhibition in mated females of *Choristoneura fumiferana* and *C. rosaceana.* J. Ins. Physiol. 46: 913–921.

Gut, L. J., and J. F. Brunner. 1992. Mating disruption of codling moth and leafrollers. Proc. Wash. St. Hort. Assoc. 88: 281–284.

Jones, V. P., and M. Aihara-Sasaki. 2001. Demographic analysis of delayed mating in mating disruption: a case study with *Cryptophlebia illepida* (Lepidoptera: Tortricidae). J. Econ. Entomol. 94: 785–792.

Jones, V. P., and N. G. Wiman. 2008. Longevity of adult codling moth and obliquebanded leafroller in Washington apple orchards. J. Ins. Sci. 8: 10.

Knight, A. L., S. Cockfield, D. Thomson, and D. Neff. 1996. Developing mating disruption for leafrollers. Proc. Wash. St. Hort. Assoc. 92: 211–212.

Knight, A. L., D. R. Thomson, and S. D. Cockfield. 1998. Developing mating disruption of obliquebanded leafroller (Lepidoptera: Tortricidae) in Washington State. Environ. Entomol. 27: 1080–1088.

Lawson, D. S., W. H. Reissig, A. M. Agnello, J. P. Nyrop, and W. L. Roelofs. 1996. Interference with the mate-finding communication system of the obliquebanded leafroller (Lepidoptera: Tortricidae) using synthetic sex pheromones. Environ. Entomol. 25: 895–905.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33: 183–212.

Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35: 213–245.

Lewontin, R. C. 1965. Selection for colonizing ability, pp. 77–94. *In* A. G. Baker and G. L. Stebbins (eds.), The genetics of colonizing species. Academic Press, New York.

Pielou, E. C. 1977. Mathematical ecology. Wiley, New York.

Shorey, H. H., and R. L. Hale. 1965. Mass-rearing of the larvae of nine noctuid species on a simple artificial medium. J. Econ. Entomol. 58: 522–524.

Smith, T. J., J. D. Dunley, E. H. Beers, J. F. Brunner, G. G. Grove, C. Xiao, D. Elfving, F. Peryea, R. Parker, M. Bush, C. Daniel, T. Maxwell, and S. Foss. 2007. Crop protection guide for tree fruits in Washington. College of Ag-

riculture and Home Economics, Washington State University, Pullman, WA.

Southwood, T.R.E., and P. A. Henderson. 2000. Ecological methods, 3rd ed. Blackwell, Malden, MA.

Statacorp. 2005. Stata statistical software computer program, version 9.2. Statacorp, College Station, TX.

Vickers, R. A. 1997. Effect of delayed mating on oviposition pattern, fecundity and fertility in codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). Aust. J. Entomol. 36: 179–182.