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Effects of Delayed Mating and Access to Water on Oviposition and Longevity in Female *Amyelois transitella*

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ABSTRACT: The navel orangeworm, *Amyelois transitella* (Walker) (Lepidoptera: Pyralidae), is a key pest of high-value irrigated nut crops in the arid Central Valley of California. Mating disruption is an established pest management technique for this pest, with reduced non-target impacts. This study compared laboratory survivorship and fertility data with field measurements to improve understanding of factors determining abundance of this species in the presence and absence of mating disruption. While the relative humidity is generally higher in almond orchards compared to readings from meteorological stations, the data indicate little free water in the absence of irrigation. Access to free water has a minor effect on the fertility of females if they mate soon after emergence, but a major effect if mating is delayed for 7 days. Leslie matrix projections indicate that changes in adult survivorship have much less impact than changes in larval survivorship. These findings indicate that control tactics limiting reproduction and survival of immature stages are more important for this species than those targeting adults.

KEYWORDS: *Amyelois transitella*, delayed mating, oviposition

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Introduction

The navel orangeworm, *Amyelois transitella* (Walker) (Lepidoptera: Pyralidae), is a key pest of almonds, pistachios, and walnuts in California.[1–3] These crops are collectively worth over $7 billion a year in unprocessed form.[4] Most of these crops in California are produced in the Central Valley, which extends east to west between the Coastal and Sierra Nevada mountain ranges and north to south from approximately 40 to 35° north latitude. This Central Valley is further divided by an estuary into the San Joaquin River Valley in the south, and the Sacramento River Valley in the north. The navel orangeworm is more abundant and causes greater damage in the hotter, drier San Joaquin Valley. Nut crops are irrigated in the Central Valley and require 60 to 110 cm of water per year to produce a commercially viable crop.[5–7] Because of the variety of irrigation technology and soil types encountered, the frequency and amount of water available in the orchard is variable within these nut crops.

The navel orangeworm is a polyphagous generalist feeder, which attacks taxonomically diverse tree fruits and nuts.[8] It is typically most attracted to host material as dried and blackened "mummies" after much fruit has been harvested or fallen.[9,10] Studies of larval development indicate that survival and development speed are highly dependent on host quality, which itself varies with phenological and other factors.[11–13] The navel orangeworm is considered a neotropical species, and native hosts from which potential biological control agents were taken have been from arid habitats.[14] It is also a strong flier[15] with a moderately high capacity for dispersal.[16,17]

Mating disruption is a pest management tactic involving release of synthetic sex pheromones to prevent mating and reduce the presence of damaging immature stages of target pests, usually Lepidoptera. Currently, mating disruption is used on 770,000 hectares of agricultural crops.[18] Mating disruption is particularly advantageous for pests that are hidden inside the host for much of their development and therefore not exposed to insecticides, such as the navel orangeworm. Efficacy of mating disruption has been demonstrated for the navel orangeworm,[19] and currently more than 12,000 hectares of almonds (primarily) and pistachios are under mating disruption treatment. Early studies of other Lepidoptera found mated females in mating disruption blocks despite evidence of efficacy such as reduced male response to pheromone lures, reduced mating of sentinel females, reduced abundance of immature stages, and/or reduced crop damage.[20–23] Demographic analyses demonstrated that reduced lifetime fertility and reduced rate of population growth can result from delayed first mating,[24,25] but the impact of delayed first mating varies between species.[26] Such studies are affected by assumptions about survivorship of females in the field.[26]

The impact of delayed first mating on population growth could potentially be affected by other aspects of the life history of the target pest, including developmental regulation of oogenesis[27] and phenology of the pest with respect to its host. Studies over the last century have demonstrated that the Phycitinae (the subfamily that includes the navel orangeworm) can take water and nutrition as adults, but vary in the extent to which they benefit from imbibed fluids.[28,29] The impact of availability of water could potentially be an important variable for a pest infesting an irrigated crop grown in an arid environment.

In this study, extremes of time of first mating and access to water were used to examine the impact of these factors. Meteorological data, obtained from individual orchards and from publicly available records from meteorological stations, were used to obtain a more refined perspective of field-relevant conditions. These data establish field relevance of the laboratory data reported here. Life table analysis and demographic projections were used to examine the implications of the experimental treatments. These data and analyses were used to address three questions about the navel orangeworm. First, how important is water intake for reproduction? Second, what is the relative importance of reduced or delayed mating vs prevention of mating for control by mating disruption? And third, what is the relative importance of adult and larval survivorship for population growth? The results indicate that, for this species, control tactics limiting reproduction and survival of immature stages are more important than those targeting adults.

Methods

Orchard environment and regional climate. The orchard environment was characterized by comparing data collected in summer 2011 in two Fresno County almond orchards and a California Irrigation Management Information System (CIMIS) data recorder site.[30] A broader comparison was also made by accessing CIMIS data for five summers from 18 CIMIS sites located over approximately 200 km of the southern end of the San Joaquin Valley (from Madera to Bakersfield).[30]

The two orchards monitored were a surface-irrigated organic orchard near Kerman CA (6°40′54.77″N 120° 5′57.86″W) and a micro-sprinkler irrigated conventional orchard near Coalinga CA (36°25′43.67″N 120°23′0.35″W). Sensors from a temperature/relative humidity data logger (Hobo Pro V2, Onset Computer Corp.) were placed near a main scaffold limb, approximately 2 m from the ground, in the interior of the canopy of a tree in the interior of the orchard. Data were collected hourly from 9 June to 23 August, 2011. Readings from these orchards were compared to hourly data over the same time period from CIMIS station 105, located near Tranquility CA (36°38′3N 120°22′55W). Daily maximum and minimum relative humidity levels were selected from each of the three locations. Important seasonal trends were not evident in plots of the data, so the mean maximum and mean minimum relative humidity were compared between the three locations.

For the wider comparison, hourly readings of precipitation, temperature, relative humidity, and dew point were obtained from CIMIS stations 39, 80, 86, 138, 142, 169, 182, 188, and 203 in the eastern San Joaquin Valley, and 7, 15, 21, 54, 105, 124, 146, 190, and 205 in the western San Joaquin Valley (Fig. 1). The stations were designated as “east” or “west” based on whether they were closer to Highway 99, along the east side of the Valley, or Interstate 5, along the west side of the Valley. (The Coalinga orchard was very close to Interstate 5. The Kerman orchard was between Highway 99 and Interstate 5, but closer to Highway 99). Based on initial examination, data were not used from stations 2 and 5 because of missing or questionable precipitation data. Data were examined from 1 May to 30 September of 2010 to 2013, and 1 May to 15 September of 2014. SAS software[31] was used to record precipitation as positive (if there were measurable precipitation) or negative. Dew point events were recorded as positive if the temperature was at or below the dew point, or negative otherwise. Maximum and minimum relative humidity levels were selected for each day examined from each station, and precipitation and dew point were considered positive for the day if there had been a positive event during the day, or negative otherwise.

Female longevity, fecundity, fertility, and ovipositional period. Insects used in this study were from a laboratory colony founded in 2005 from infested pistachios, and maintained for approximately 40 generations at the start of the study. The colony was maintained at 26°C, 60% relative humidity, 16:8 L:D, and on wheat bran diet.[32] Degree-day accumulation under this regime is similar to that under normal June conditions in Central California. A 4-watt 120-volt incandescent bulb came on 1 hour before the main chamber lights to increase the proportion of adults that mated.[33] Unmated males and females were obtained by isolating the

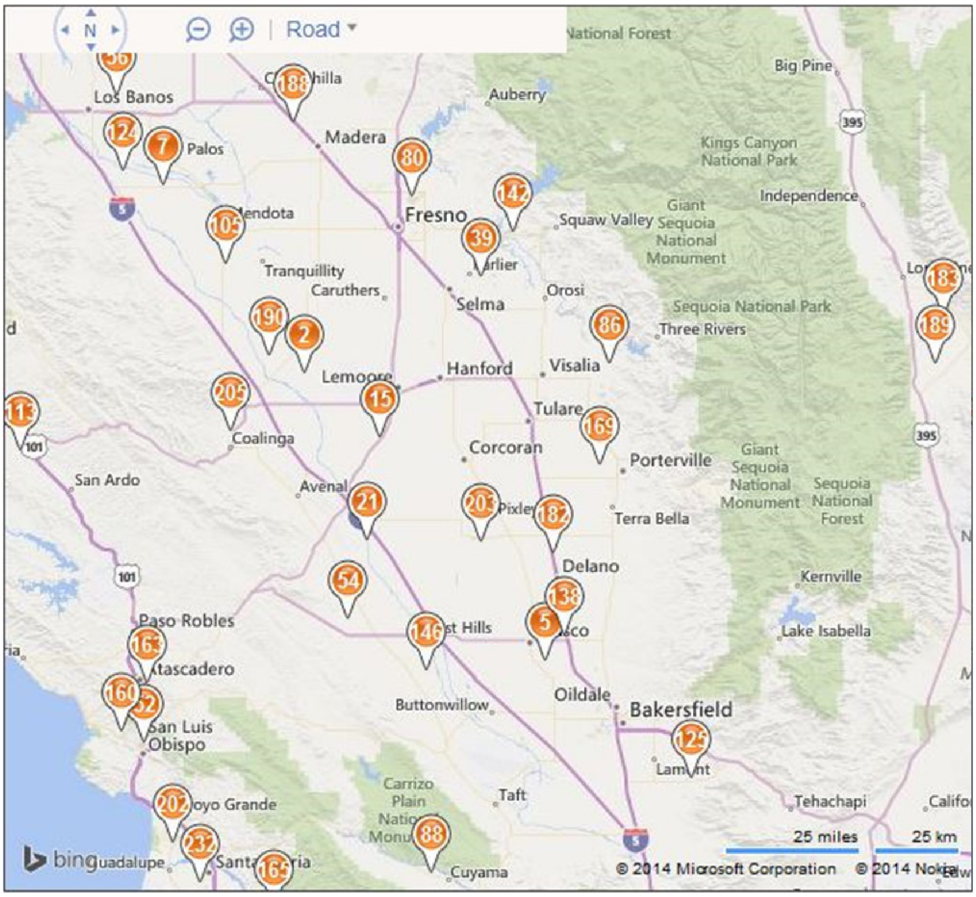

Figure 1. Location of CIMIS meteorological stations used for comparison of humidity in the east and west side of the southern San Joaquin Valley. Stations categorized as east side included (from north to south) 188, 80, 142, 39, 86, 169, 203, 182, and 138. Stations categorized as west side included (from north to south) 124, 105, 190, 2, 205, 15, 21, 54, and 146. Generally, the east side of the Valley, adjacent to the higher Sierra Nevada Mountains, receives greater annual rainfall than the west side, in the rain shadow of the lower Coastal Range (U.S. National Climatic Data Center, http://www.ncdc.noaa.gov/).

sexes as mature last instar larvae, based on the presence or absence of testes (visible through the dorsal integument).

An experiment was conducted with three replicates (cohorts) of 9–10 mated females each. There were two levels each for the two effects—age of first mating and access to water—providing four treatments: (1) females mated the first night following eclosion and with no access to water as adults; (2) females mated the first night following eclosion and with continuous access to water; (3) females mated the seventh night following eclosion and with no access to water as adults; and (4) females mated the seventh night and with continuous access to water. The study was performed under the rearing conditions described above. The relative humidity in the rearing environment was considered field-relevant based on observations from the data loggers and meteorological stations. Males and females were the same age at the time of mating, and there was no mortality in either sex prior to mating.

Mated females were obtained by isolating males and females at the beginning of photophase following the night of eclosion. We have previously found no correlation between size and total fecundity of females isolated in this manner; perhaps because the process of isolating larvae within a narrow window of time results in relatively homogeneous pupal size. Individuals were randomly assigned to one of the four previously mentioned treatments. Five males and five females for the same treatment were then placed at the appropriate time in a 946-mL glass jar with a wire mesh lid and containing round 15-cm filter paper (Whatman one Qualitative, GE Healthcare) folded into pleats (Burks et al 2011a), thereby providing a perch for copulation. At the beginning of the next photophase, mated adults were isolated in copula, allowed to separate, and the mated females were then placed individually in 470-mL glass jars covered with a wire mesh lid and containing 9-cm filter paper.[34]

The filter paper in the 470-mL female isolation jars was changed every 2 days until death and held under colony conditions to count and assess fertility. Fertile eggs turn red before hatching,[9] generally after 4 days under colony conditions; thus egg paper was counted several times after 4 days to be certain of discerning fertile and non-fertile eggs.

Constant access to water was provided for treatments 2 and 4 by placing saturated cotton balls under a 30-mL plastic cup, which was inverted on top of the wire mesh covering the 946-mL mating jars and the 470-mL isolation jars. Water and mortality were checked daily, and following death, the spermatophore was dissected from the bursa copulatrix to confirm mating status.

Data analysis. The data were analyzed using the SAS System.[31] A mixed-model repeated ANOVA was used to compare the daily high and low relative humidity between the two orchard canopies and a meteorological station. The locations were fixed effects, and the days were a repeated random effect. Comparisons of maximum and minimum relative humidity among the 18 CIMIS stations were based on averages of each location over the four summers. This averaging was based on initial examinations of plots showing no consistent trends in the May–September period. Student's t test was used to compare daily high and low relative humidity between the east- and west-side locations. Pearson's χ^2 was used with contingency tables to compare frequency of rain, and of dew on non-rainy days, between the east and west sides.

The effect of age of first mating and access to water on total fecundity (total eggs laid), percent fertility, longevity, and the ovipositional period (defined as the time between oviposition of the first and the last fertile egg) was examined using a mixed-model two-way factorial ANOVA.[35] The main (fixed) effects were age of first mating, access to water, and their interaction. Cohort was a random effect. Total fertility and total fecundity were transformed as $\sqrt{\text{count}} + 0.5$ for variance stabilization; and percent fertile eggs was transformed as arcsine of the square root of the proportion.[35] When the interaction was significant, differences between the means were examined using the Tukey test for multiple comparisons.[35] For this analysis, daily longevity data were used. Untransformed means and standard errors are presented in the tables, and because the covariance estimate for cohort was small compared to the residual, the mean was presented for all cohorts. For the ovipositional period, females that laid no fertile eggs were not considered so the respective total sample size was 23, 27, 8, and 21 for treatments 1–4 above.

Age-specific fertility and mortality were evaluated using life table analysis. Two-day intervals were used, and for longevity, the average number of females surviving at the interval midpoint was used. The net reproductive rate (R_o), the intrinsic rate of increase (r_m), the finite rate of increase (λ), and the doubling time (DT) were determined using the methods described by Portilla et al.[36] Survival plots, superimposed over histograms of bi-daily oviposition, were used as a visual comparison of the effects on survivorship and fertility. Leslie matrix models[37] were used to project population growth for each of the four treatments involving age of first mating and access to water. Matrix projections, for females only, started with 20 newly emerged females and were run over 125 days. Life parameter statistics were calculated and Leslie matrix projections were made for larval survival of 35% and 10%, based on the range of survivorship observed in a previous study of *A. transitella* on bran diet and almonds.[11] Mortality was applied evenly over immature development.

Results

Orchard environment and regional climate. Data from the CIMIS meteorological station at Tranquility revealed a wide range between daily high and low relative humidity levels (Fig. 2A). They also revealed much day-to-day variability, particularly in high relative humidity. No temporal trends are apparent in plots of the CIMIS or orchard data, so comparison of means over the season is appropriate.

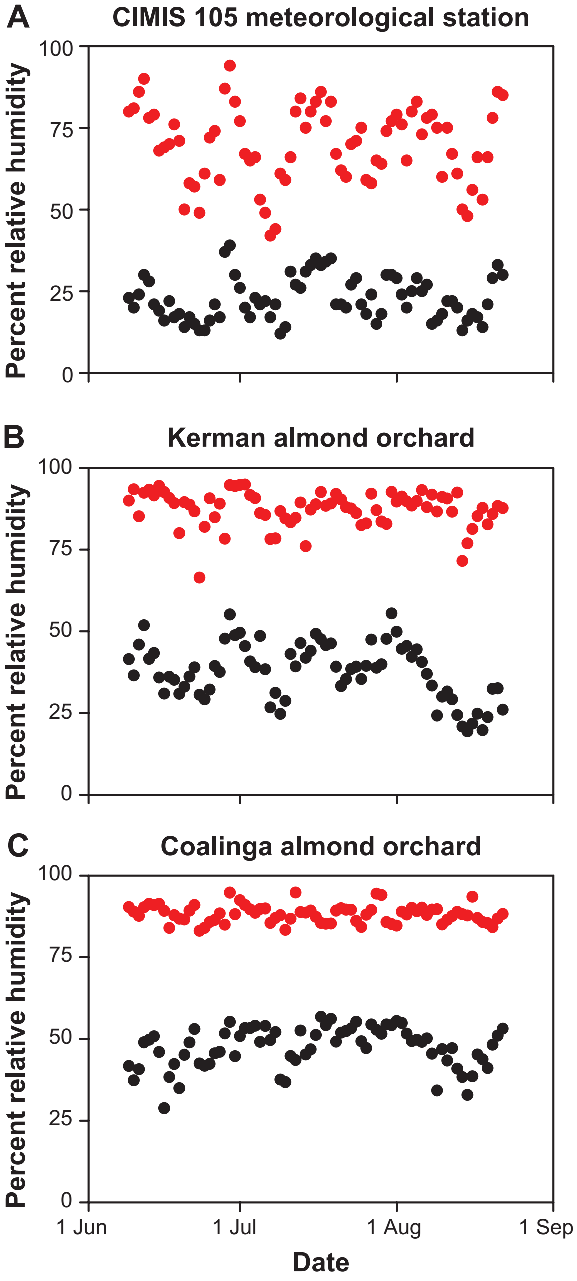

Figure 2. Daily high and low relative humidity from 9 June to 23 August, 2011 at (**A**) a CIMIS meteorological station near Tranquility, CA; (**B**) a surface-irrigated organic almond orchard near Kerman, CA; and (**C**) a micro-sprinkler irrigated almond orchard near Coalinga, CA. Red dots indicate daily high, and black dots indicate daily low. Sensors at the meteorological station were over open ground, whereas sensors in the orchards were within the canopy.

Table 1. Daily maximum and minimum relative humidity (R.H., mean ± S.D.) in two almond orchards and at a meteorological data collection site from 9 June to 23 August, 2011.

SITE	LOW R.H.	HIGH R.H.
Kerman orchard	38 ± 8.7b	87 ± 5.4a
Coalinga orchard	47 ± 6.3a	88 ± 2.7a
CIMIS 105	23 ± 6.6c	70 ± 11.8b
$F_{2,222}$	217.77***	138.22***

Notes: Means followed by different letters are significantly different ($P < 0.05$, mixed-model ANOVA). ***$P < 0.0001$.

The CIMIS meteorological stations are generally over grass or open ground. In contrast, the measurements taken inside the canopy of the almond orchards revealed higher relative humidity both during the daytime low and the nighttime high (Fig. 2, Table 1). The micro-sprinkler irrigated orchard (Coalinga) had less day-to-day variability in relative humidity compared to the surface-irrigated orchard (Kerman) (Fig. 2). The Coalinga orchard had greater minimum relative humidity within the canopy during the day, but maximum relative humidity levels were similar between the two sites at night (Table 1).

Examination of 18 CIMIS stations reveals that the daily variation in relative humidity seen in 2011 at the CIMIS station near Tranquility is consistent with a general long-term trend in the region. There was no significant difference in the number of days with precipitation between the east-side and west-side stations (Supplementary Table 1). While the daytime minimum relative humidity levels were similar between the east-side and west-side stations, the nighttime maximum relative humidity was significantly greater for the east-side stations (Supplementary Table 2). It was rare for the temperature to drop to the dew point (<2% of days in all cases), but this happened more frequently on the east side than in the west side (Supplementary Table 3).

Female longevity, fecundity, fertility, and ovipositional period. Age of first mating and access to water both had a statistically significant effect on total fecundity and percent fertility (Table 2). The interaction term was also significant for total fecundity, but not for percent fertility ($P > 0.05$). For total (lifetime) fertility, there were significant effects caused by age of first mating and access to water, while the interaction term was not quite significant. In contrast to longevity, ovipositional period (defined as the time between oviposition of the first and the last fertile egg) was affected by age of first mating but not by access to water (Table 2). Females mated on the first day post-eclosion laid fertile eggs over a period of 8–9 days whereas, for females mated 7 days post-eclosion, this period was 4–5 days.

The plot of age-specific fertility and mortality shows that most oviposition occurred before mortality was observed (Fig. 3). No female, and none of the males held as mated for females mated 7 days post-eclosion, died before then. The earliest mortality among females was a female that died the first day after mating. In all cases—even when first mating was delayed for 7 days—over 95% of fertile eggs were laid before median mortality (Fig. 3).

The life table parameters show a population increase under each of the four treatments when a 35% larval survival rate was assumed. However, assuming a 10% larval survival rate, a declining population is predicted if mating is delayed until day 7 and there is no access to water (Table 3); as indicated by a negative intrinsic rate of increase (r_m) and a finite rate of increase (λ) of <1. The net reproductive rate, R_o, represents the mean number of females born to each female in the current cohort. Since the denominator for this proportion includes larvae that do not survive to sexual maturity, R_o was smaller than the average fecundity in Table 2 after adjusting for fertility (only fertile eggs were used in the life table) and sex ratio.

The Leslie matrix projections showed that the access to water, or lack thereof, made relatively little difference to females mated on the first day after eclosion (Fig. 4). Populations in which females mated on day 1 increased five to six orders of magnitude when 35% larval survival was assumed. In contrast, populations in which mating was delayed until 7 days post-eclosion increased by three orders of magnitude with access to water, and only a single order of magnitude without access to water. Similar trends were seen when 10%

Table 2. Total fecundity, percent fertility, longevity, and ovipositional period (mean ± SE) of *Amyelois transitella* with or without access to water and mated to same-aged males 1 or 7 days post-eclosion.

ACCESS TO WATER	AGE MATED (d)	NO. FEMALES	TOTAL EGGS LAID	% FERTILE EGGS	LONGEVITY (d POST-ECLOSION)	OVIPOSITIONAL PERIOD (d)
Constant	1	29	203 ± 22a	85 ± 5	17 ± 0.6	9 ± 0.8
	7	29	120 ± 18b	52 ± 7	17 ± 0.5	5 ± 0.6
None	1	29	175 ± 17ab	68 ± 8	14 ± 0.7	8 ± 0.6
	7	29	41 ± 10c	13 ± 5	16 ± 0.6	4 ± 0.5
F value for		Age	44.19***	49.11***	3.41	31.99***
		Water	12.46***	20.43***	13.64***	2.44
		Interaction	4.72*	3.28	1.72	0.2

Notes: Mixed-model ANOVA with 1 numerator and 110 denominator df; 1 numerator and 73 denominator df for ovipositional period. *$P < 0.05$, ***$P < 0.001$.

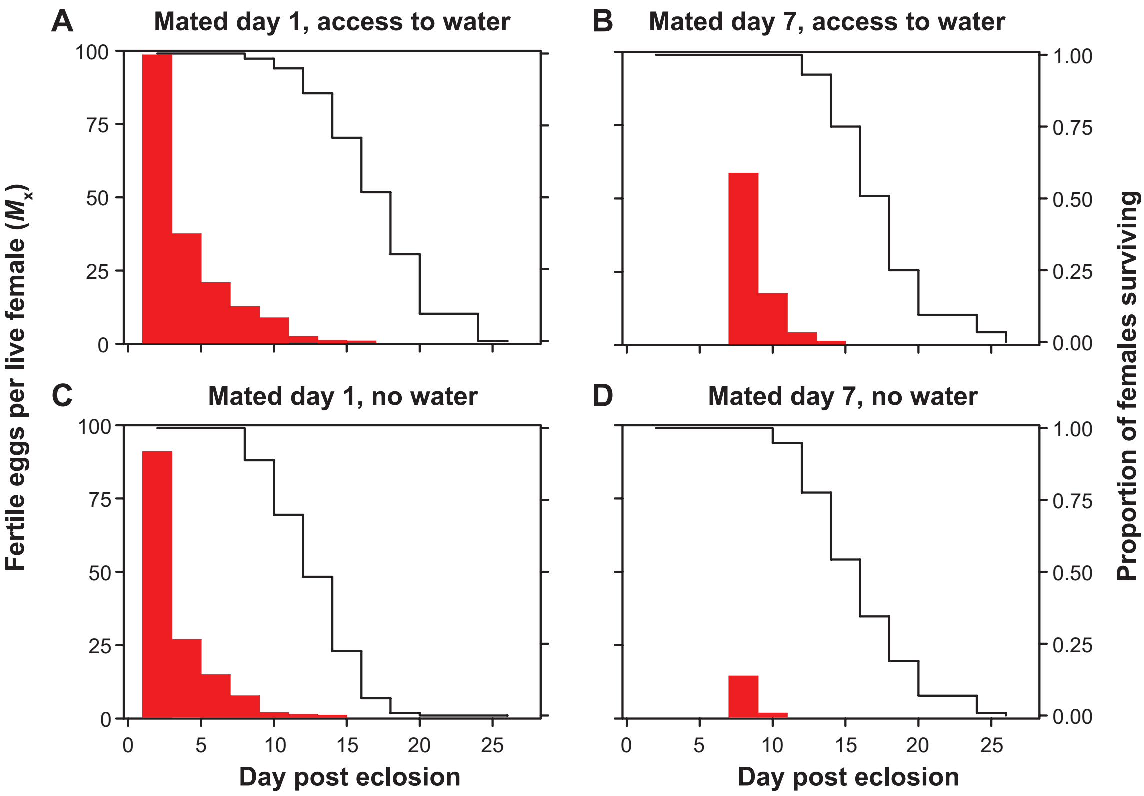

Figure 3. Age-specific fertility and mortality for *Amyelois transitella* adults at two-day intervals following mating either (**A**, **C**) 1 day or (**B**, **D**) 7 days after eclosion with either (**A**, **B**) ad libitum access to water or (**C**, **D**) no access to water as an adult.

larval survival was assumed, but in that case, the increase in population over the simulation period was only four orders of magnitude under the most favorable circumstances.

Discussion

Orchard meteorological data were used to establish the field relevance of this laboratory study. The San Joaquin Valley is known for long summers with high daytime temperatures and low relative humidity. It is therefore easy to forget that this region is also characterized by daily temperature swings averaging >17°C,[38] and concurrent changes in relative humidity as documented in the CIMIS data set. The comparison of relative humidity in the orchards to that recorded by the meteorological stations illustrates that the orchard canopy further moderates relative humidity. The 60% relative humidity in the environmental chambers where the laboratory study was

Table 3. Life table parameters for *Amyelois transitella*, assuming either 35% or 10% survival from neonate to adult.

	MATED DAY 1		MATED DAY 7	
	WATER	NO WATER	WATER	NO WATER
35% Survival to adult				
Parameter				
Net reproductive rate R_o	31.9	25.1	14.3	2.89
Intrinsic rate of increase r_m	0.095	0.089	0.064	0.026
Finite rate of increase λ	1.099	1.093	1.066	1.026
Doubling time *DT* (days)	7.33	7.77	10.86	27
10% Survival to adult				
Net reproductive rate R_o	9.1	7.2	4.1	0.824
Intrinsic rate of increase r_m	0.06	0.054	0.0337	−0.0047
Finite rate of increase λ	1.062	1.056	1.034	0.995
Doubling time *DT* (days)	11.52	12.73	20.54	N/A

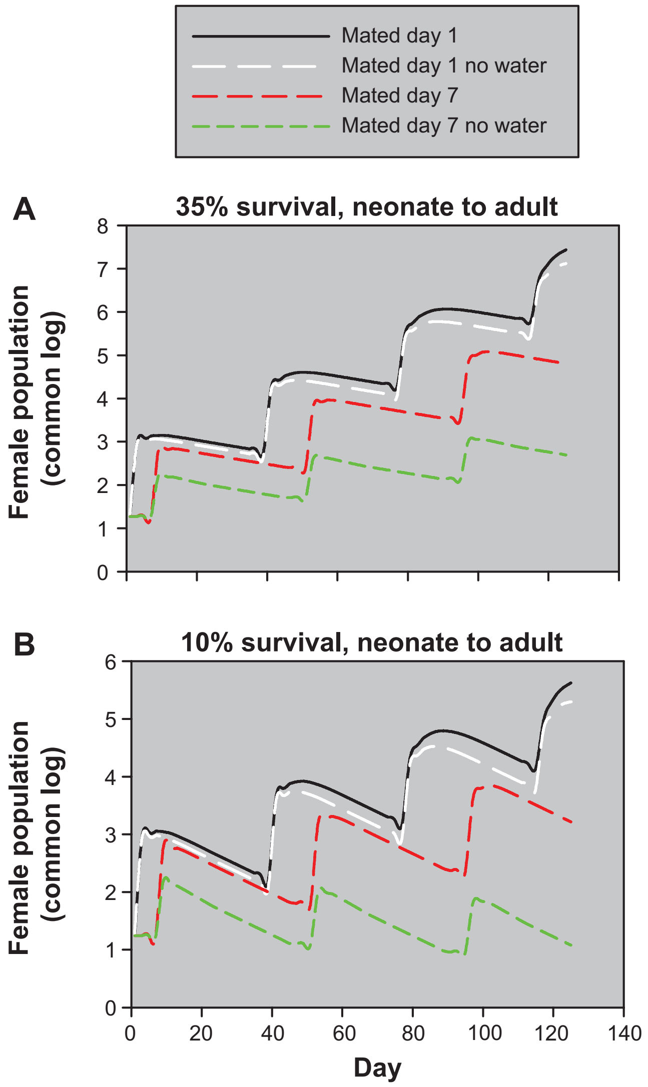

Figure 4. Leslie matrix projections of the population of *Amyelois transitella* over 125 days, assuming either (**A**) 35% survival from neonate to adult or (**B**) 10% survival from neonate to adult.

conducted is therefore reasonably representative of orchard conditions. The CIMIS data indicated that, under conditions where the sensors were located, the dew point was rarely reached under summer conditions. It is possible that the dew point was reached more often closer to the ground than at the 1.5 m height of the temperature and relative humidity sensors. Many conventional growers use herbicides to maintain a bare orchard floor through much of the growing season. Weed control in organic orchards is more dependent on periodic tillage. Thus the author occasionally found dew on weedy ground cover at the Kerman site, but not at the Coalinga site where the orchard floor was bare.

Access to water and time of first mating had affected the response variables differently, as revealed by the factorial ANOVA (Table 2). For both total fecundity (total eggs laid) and percent fertility, there was a significant reduction because of both delay in mating from day 1 to day 7 and restriction of water. In the case of total fecundity, the interaction term was also significant, indicating that the effect of delayed mating was greater when water was withheld. In the case of fertility, this interaction term was not quite significant. For longevity, access to water had a significant effect, whereas age of first mating did not. Longevity can increase with delayed mating in insects because of delaying costs of reproductions, but this is observed in some studies while not in others.[39] In the present study, water-deprived females mated on day 1 lived less time than those mated on day 7. While this difference in longevity caused by age of first mating in water-deprived females is nominal and not statistically significant, it suggests that the energetic costs of mating were exacerbated when there was no access to water. In contrast to longevity, the ovipositional period (the time between oviposition of the first and the last fertile egg) was affected by age of first mating, but not by access to water. This reduction in the ovipositional period by delayed mating was apparently not because of restriction by longevity, as indicated by the lack of a significant effect of age of first mating on longevity and as illustrated by Figure 3.

The laboratory data suggest that the navel orangeworm imbibed and benefited from water provided from cotton pads. Moths were occasionally seen, during the scotophase, perched inverted with the proboscis extended to the cotton pads. These observations are consistent with previous studies of other moths of the subfamily Phycitinae.[28,29] One study of the almond moth, *Cadra cautella* (Walker), found that deprivation of water resulted in a 45% decrease in total fecundity.[29] An earlier comparative study comparing effects of access to water in the almond moth, the Mediterranean flour moth, *Ephestia kuehniella* (Zeller), and the tobacco moth, *E. elutella* (Hübner), found that water deprivation decreased fecundity in the almond moth and the tobacco moth, but not in the Mediterranean flour moth.[28] Thus there is evidence that moths from this group can imbibe fluid, and benefit from it to various degrees. Compared to the almond moth, the data from this study show little benefit of water to the navel orangeworm, particularly if mated the first night following eclosion.

The longevity data in this study indicated that females lived long after fertility ceased. However, senescence was evident by 7 days post-eclosion. Older moths were more docile. This is consistent with flight mill data from this species showing declining flight capacity 7 days post-eclosion, but not earlier.[15] A previous study examined longevity of the codling moth, *Cydia pomonella* (L.), and the obliquebanded leafroller, *Choristoneura rosaceana* (Harris), by placing in vials inside delta traps within apple canopies in an attempt to expose moths to abiotic stress without the confounding influence of variable biotic risks; eg, predation.[40] As described previously, the environmental chambers used in this study seem to represent orchard abiotic stress well. It is quite plausible that the navel orangeworm becomes more vulnerable to predation after 7 days. It should, however, be noted that the median survivorship for females of this species could be shortened considerably with little effect on lifetime fertility (Fig. 3). For example, for the group mated 1 day post-eclosion and with free access to water, shortening the survival of all females by 6 days results in a 0.4% reduction in net reproductive rate (R_o).

With free access to water, there was a 55% reduction in R_o of the navel orangeworm when age of first mating was delayed from 1 to 7 days post-eclosion. In comparison, previous studies on the codling moth found decreases of 52–58% in R_o when the age of first mating was 4 days post-eclosion rather than the day of eclosion.[24,26] The obliquebanded leafroller had a greater proportional decrease in net fertility with a 4-day delay, but also much greater net fertility than the codling moth.[26] Thus on an absolute basis, the latter species was less impacted by delayed mating compared to the former. The net fertility observed for the navel orangeworm in this study is intermediate between that of the codling moth and the obliquebanded leafroller. In the previous study, laboratory fertility and survival curves were from the codling moth and the obliquebanded leafroller provided with honey water.[26] Previous experiments on the navel orangeworm found that sugar solutions did not increase female longevity or fecundity, and the total fecundity reported here for navel orangeworm females with access to water is similar to that in a previous study in which moths were provided 10% sucrose.[41] The codling moth and the obliquebanded leafroller are both of the family Tortricidae, whereas the navel orangeworm is of the family Pyralidae. Pyralid females generally emerge with most of their eggs.[27] In contrast, tortricid females eclose with few or no mature eggs.[42] Some tortricid species, including the codling moth, increase egg maturation by 50% following mating.[42] Logically, species that complete egg maturation prior to mating might be expected to be less affected by delay in first mating compared to those that require mating for maturation of the full complement of eggs.[39]

While navel orangeworm females benefited from free access to water in the laboratory, three lines of reasoning suggest that access to water is not an important factor in its distribution and abundance in the field. First, in the absence of mating disruption (ie, the majority of tree nut plantings in California), it is likely that females are mated soon after eclosion. The laboratory data indicate that the access to water is of minor importance under that circumstance. Second, there is greater navel orangeworm abundance on the west side of the San Joaquin Valley, which is drier than the east side. Third, water deficit can result in earlier splitting of almond hulls,[43] making more host material available to females and neonates. Leslie matrix projections based on mating on the first day after eclosion indicate that a population without access to free water but with 13% egg-to-adult survival will increase more rapidly than a population with access to water but with a 10% egg-to-adult survival.

This scenario concerning larval survival highlights another important difference between the navel orangeworm and the codling moth. The latter is well adapted for development on apple and a few other hosts,[44] and in the absence of effective insecticide programs, suitable hosts generally are not a limiting factor for the codling moth females in such host crops.[45] In contrast, in almonds the navel orangeworm must develop principally on mummies from the previous season prior to hullsplit, so suitable host material is often more limiting.[11] The values of 35% and 10% egg-to-adult survival used with the Leslie matrix models in this study represent the range of survival found in a previous study using laboratory diet and almonds under laboratory and semi-controlled field conditions.[11] The projections reported here suggest that field survivorship might often be even lower.

The predictions from scenarios reported here indicate that small changes in larval survivorship have greater impact compared to larger changes in adult survivorship. This finding suggests that, for the navel orangeworm, control measures targeting larvae have greater effect on population growth compared to those targeting adults. This finding of greater importance of larval mortality is also consistent with a study that found greater control of navel orangeworm control applications of methoxyfenozide, a reduced risk compound with very good ovicidal and larvicidal activity, compared to a mixture of phosmet and permethrin (the latter of which is more toxic to adults).[46] It also suggests that the effects of mating disruption and compounds such as methoxyfenozide may be additive or synergistic. Research is needed to test this hypothesis.

Conclusion

In the laboratory, access to water improved fertility slightly for navel orangeworm females first mated 1 day after eclosion, but greatly improved fertility for females first mated 7 days post-eclosion. However, observations from this laboratory study and from the field suggest that access to free water generally is not a determining factor for navel orangeworm distribution and abundance. Observations from this study, and consideration of the physiology of this species, suggest that the efficacy previously demonstrated for mating disruption for the navel orangeworm is more because of prevention of mating than because of delayed or reduced mating. Predictions from Leslie matrix models following modifications of adult and larval survivorship suggest that the latter is more important than the former for population growth of this species. These findings indicate that, for navel orangeworm, control tactics limiting reproduction and survival of immature stages are more important than those targeting adults.

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Author Contributions

Conceived and designed the experiments: CSB. Analyzed the data: CSB. Wrote the first draft of the manuscript: CSB. Agree with manuscript results and conclusions: CSB. Made critical revisions: CSB. The author reviewed and approved of the final manuscript.

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Supplementary Data

Supplementary Table 1. Percent of days with measurable precipitation, May through September of 2010 through 2014, in east and west San Joaquin Valley CIMIS stations.

REGION	DAYS OBSERVED	% DAYS WITH RAIN
East	6390	3.6%
West	6733	3.6%

Note: $\chi^2 = 0.88$, $P > 0.05$.

Supplementary Table 2. Daily high and low relative humidity (R.H., mean ± SE), May through September of 2010 through 2014, in east and west San Joaquin Valley CIMIS stations.

REGION	STATIONS	LOW R.H.	HIGH R.H.
East	9	23 ± 0.8	76 ± 1.9a
West	9	22 ± 1.3	63 ± 3.6b

Notes: Low R.H., $t = 0.88$, df = 16; $P = 0.39$. High R.H., $t = 3.36$, df = 16; $P = 0.0039$.

Supplementary Table 3. Proportion of days with no precipitation in which the temperature was equal to the dew point.

REGION	DAYS OBSERVED	% DAYS WITH TEMPERATURE EQUAL TO DEW POINT
East	6079	1.66%
West	6460	0.84%

Note: $\chi^2 = 16.074$, $P < 0.0001$.