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Running Head: Knight. Adjusting the phenology model of codling moth

Adjusting the Phenology Model of Codling Moth (Lepidoptera: Tortricidae) in Washington State Apple Orchards

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ABSTRACT Field studies were conducted with codling moth, *Cydia pomonella* (L.), to fit cumulative curves for the occurrence of injured fruits and male moth catches in sex pheromone-baited traps as a function of accumulated degree days following the start of moth flight. Twelve data sets were collected from seven apple, *Malus domestica* Bordhausen, orchards in Washington State from 2003 to 2006. No clear temporal separation occurred between the end and the start of the first and second generation in either moth flight or the occurrence of new fruit injury. Cumulative data were grouped across years for orchards either treated with sex pheromone dispensers or untreated and fit to logistic equations for both the first and second generation. A cumulative model for egg hatch was generated by backtracking cumulative fruit injury one day (subtracting the mean daily degree day accumulation during the previous sampling interval). No significant differences were found for the cumulative curves of moth flight or egg hatch between pheromone-treated and untreated orchards, thus these data were combined. These new models for moth flight and egg hatch were then compared (ANCOVA) with widely-used tabular, predictive models (old model) also fit to logistic equations for each generation. The cumulative flight curves for the new and old models were statistically different (slopes) for the first but not the second generation. Cumulative egg hatch in the new model was significantly different from the old model (intercepts and slopes) for both generations. Most strikingly, the timing of 50% egg hatch during the first generation was delayed 100 degree days in the new versus the old model. The potential impact of this change in the characterization of codling moth's phenology on the effectiveness of insecticide programs targeting eggs and newly eclosed larvae was examined. Possible explanations for this significant difference between the models are discussed.

Keywords*:* *Cydia pomonella*, apple, phenology, pest management

GLENN (1922) first proposed using summations of physiological time (degree days) from January 1 to predict the seasonal occurrence of various life stages of codling moth, Cy*dia pomonella* (L.). Adoption of this approach, however, was slow for 50 years as the method was deemed cumbersome prior to the onset of the computer-age and tailored spray timings were not considered to be necessary, while apple growers used preventative cover sprays of lead arsenate, DDT, or other long-lasting materials (Batiste et al. 1973). Concurrent with a shift towards integrated orchard pest management this approach was re-evaluated in the 1970's to substitute the use of unnecessary insecticides with greater knowledge of pest and natural enemies densities and their phenology (Croft and Hoyt 1983).

Prediction of key events of codling moth's phenology (first and peak egg hatch of each generation) from easily measured biological reference points (Biofix), such as male catches in sex pheromone-baited traps was developed and validated (Riedl et al. 1976). Today, the prediction of first egg hatch of the overwintering generation of codling moth at 139 degree days summed from the first sustained male catch in sex pheromone-baited traps (Biofix 1) has become a widely adopted tool used to time the first insecticide spray (Barnett et al. 1991, Barnes et al. 1993, Beers et al.1993). Unfortunately, the reliability of predicting other key events in codling moth's phenology, such as peak egg hatch or egg hatch during the second generation or using other reference points, such as peak moth catches (Biofix 2, 3), proved to be low (Riedl et al. 1976), and have not been widely adopted . Instead, the second and subsequent seasonal sprays are usually timed based on a calendar dates, i.e. 2 – 3 wk intervals depending on an estimate of pest pressure and the expected residual effectiveness of the insecticide (Brunner et al. 1982, Beers et al. 1993).

Compared with the effectiveness of the current calendar-based spray program further improvements in the management of codling moth may be possible if growers can better target the peak periods of pest densities. The periods of oviposition and egg hatch for each generation of codling moth last approximately 6 wks, and 2-3 sprays would be required depending on the insecticide's residual effectiveness to achieve complete coverage of both time periods (Riedl et al. 1976). However, apple growers in Washington State on average apply fewer sprays (NASS 2005), and because weather and operational factors can both impact the deposit and retention of effective residues, the relative effectiveness of codling moth control programs may be highly variable during the season. Thus spray timing decisions are critical to achieve control of codling moth. Knowledge of the timing of peak oviposition and egg hatch during each generation remains an important piece of information needed to allocate resources and design an optimal management program.

Predicting the first egg hatch from first male moth catch has proved to be rather straightforward and consistent (Riedl et al. 1976, Beers and Brunner 1992). The length of this interval for codling moth is due to the occurrence of a male protandry (Howell 1991), a pre-ovipositional period for the mated female (Hagley 1973), and the degree days required for completion of egg development (Richardson et al. 1982). The shape of the cumulative curve of egg hatch for each generation, however, is more variable and is likely influenced by several factors impacting the occurrence and rate of several important activities of adult codling moth: sex pheromone release, mating, and egg laying. First, the lower temperature threshold for full expression of mating or oviposition, 15.6 ºC (Eyer 1934) is substantially higher than for physiological development of immature stages, 10 ºC (Glenn 1922). Thus degree days can accumulate that drive egg development in a predictive model even though few to no females were mated or a limited number of eggs were deposited under poor field conditions. Second, codling moth's sexual behaviors can be strongly affected by climatic conditions in addition to temperatures below physiological thresholds, such as wind, rain, and relative humidity that can occur during the restricted time periods of codling moth activity, i.e. dusk (Howell 1991). Thus, the intercept and slopes of the observed cumulative curves for oviposition and subsequent egg hatch plotted on a degree-day scale could vary significantly from predictive models based only on physiological development (Knight and Weiss 1996).

The occurrence of first egg hatch of codling moth in the spring relative to the start of male moth catches in sex pheromone-baited traps has been widely validated (Riedl et al. 1976, Jorgensen et al. 1979), including in Washington State (Beers and Brunner 1992); but data for the timing of peak oviposition and egg hatch during each generation are more limited: one orchard for two years in Michigan (Riedl et al. 1976) and five orchards for one year in Utah (Jorgensen et al. 1979). Data on the cumulative moth flight and egg hatch curves as a function of degree days developed in Michigan were transferred and used in Washington State orchards without further validation (Brunner et al. 1982). The potential error associated with extending phenology data from one region to another without validation is reflected by the significant difference in the mean generation time (cumulative degree days) of codling moth found in California versus Michigan orchards (Pitcairn et al. 1992).

Since 1991, the pest management program for codling moth in Washington State has evolved away from an exclusive use of organophosphate insecticides to a dynamic and variable mix of sex pheromone for mating disruption, granulosis virus, and a suite of synthetic insecticides (synthetic pyrethroids, organophosphates, neonicotinyls, and insect growth regulators) targeting both eggs and larvae (Brunner et al. 2005a). Recommendations for codling moth management advises growers to consider product efficacy, compatibility with various other orchard operations (worker re-entry restrictions), the need to manage other pests, such as leafrollers; and the principles of resistance management (rotation of materials with different modes of action) (Brunner et al. 2005b). Several 6-spray programs have been proposed that target the entire period of egg laying or hatch with various combinations of insecticides (Brunner et al. 2005a), but growers are hesitant about using these intensive spray programs to supplement their use of mating disruption due to cost and the various externalities associated with insecticide use, i.e. disruption of biological control, scheduling of other management practices, worker safety, and environmental issues. Sex pheromone-baited traps are widely used to establish effective action thresholds to either time sprays following peak catches or to avoid the use of unnecessary sprays during the season (Gut and Brunner 1996). Unfortunately, this approach is hampered by the lack in standardization of the various factors affecting trap performance (Knight and Christianson 1999) and is particularly difficult in orchards treated with sex pheromone (Knight and Light 2005). The failure of traps to detect local infestations of codling moth (‘false negatives’) is a key factor impacting grower’s effective management of codling moth (Riedl et al. 1986).

Data on the timing of male moth flights and occurrence of fruit injury in a variable mix of seven Washington State apple orchards were collected during seasonal investigations of the effectiveness of new insecticide-based programs for codling moth from 2003 to 2006. Interestingly, the data for first generation egg hatch fit a cumulative curve that was shifted significantly later in the season than the predicted values in the old model. The impact of this temporal shift in the timing of egg hatch on the effectiveness of codling moth management programs in Washington State is explored. Several potential factors that may contribute to this difference are discussed.

Materials and Methods

Field studies. Studies were conducted in seven apple orchards in Washington State during the four year study (Table 1). The Orondo site in Douglas County (47.71 N,120.10 W) was a conventional, 10-ha 'Delicious' and 'Golden Delicious' orchard that had been abandoned for 1 yr prior to the study. Three orchards situated near Parker in Yakima County were included in the study. The Parker 1 orchard (46.60 N,120.46 W) in 2003 was a certified 2.0-ha organic block of 'Golden Delicious'. The Parker 2 orchard (46.61 N,120.47 W) monitored in 2004 was a 0.5-ha mixed-cultivar, certified organic orchard. The Parker 3 orchard (46.61 N,120.48 W) monitored in both 2005 and 2006 was a 2.0-ha mixed block of 'Red Delicious' and 'Golden Delicious'. This site was originally a conventional orchard but has been used as an experimental research block since 2001. One or two interplanted 'Delicious' and 'Golden Delicious' orchards (0.5 and 4.0-ha) near Moxee in Yakima County (46.56 N,120.39 W) were included in the study each year. These orchards were certified organic through 2003 but have been used as experimental research sites since 2004. An unsprayed 0.5-ha 'Red Delicious' block at a private experimental farm near Zillah in Yakima, County (46.40 N,120.26 W) was monitored in 2005 and 2006. Mean tree heights in all orchards ranged from 4.0 – 5.2 m and trees were planted at densities of 400 – 500 per ha. All but the Zillah orchard were watered with under-tree irrigation systems. No insecticide sprays were applied to any of the areas monitored in these orchards during the study. The Parker

1, Parker 2, and Moxee 1 orchards were all treated with 1,000 sex pheromone dispensers per ha (Isomate-C PLUS™, Pacific Biocontrol, Vancouver, WA).

Two to five trees with a full fruit load were randomly selected in each orchard at the beginning of the season to provide an estimated sample of 2- to 3,000 fruits. During the 2003-2005 seasons, trees in each orchard were sampled twice per week. Fruit injury in orchards in 2003 was sampled only for the first generation. Fruit injury in orchards in 2006 was sampled once per week. One or two scouts examined all fruit on each designated tree using ladders on each sample date. Sampling time on each date ranged from one to two hrs per orchard depending on the number of fruits checked, the number of fruits removed, and tree size. The mean (SE) number of degree days that accumulated between sample dates were 36.6 (4.6) and 83.3 (8.4) when trees were sampled semiweekly or weekly, respectively. In general, degree day intervals were shorter early in the season and longer during the second codling moth generation. A small sample of injured-fruits collected from orchards in 2003-2004 was dissected and all larvae were categorized as first to third instars based on head capsule widths (Weitzner and Whalon 1987). A variable proportion of fruits in all orchards had multiple injuries. Data on the total number of injuries not the number of injured fruits were recorded. The cumulative proportion of fruits removed from the designated trees with codling moth injuries by the end of the season were < 0.60 in all sites except for Moxee 2 in 2004. Due to the low numbers of uninjured fruits present in this orchard later in the season, data for the second generation were not included in the analyses.

Male codling moths were monitored in each orchard with two delta-shaped plastic traps (Pherocon® VI, Trécé Inc., Adair, OK) baited with sex pheromone. Traps were attached to plastic poles and placed in the upper third of the tree canopy. Traps were spaced 50 – 100 m apart and > 10 m from the edge of the orchard. Orchards treated with sex pheromone dispensers were monitored with Biolure™ 10x lures (Suterra LLC, Bend, OR). The remaining orchards were monitored with Pherocon® CM-L2™ lures (Trécé Inc.). Both lure types were replaced every 8 wks. Traps were checked once or twice per wk and sticky liners were replaced frequently (every week in most orchards).

Air temperatures within orchards were monitored every 5 min with digital recorders (Avatel, Fort Bragg, CA) housed in screened shelters and daily maximum and minimum temperatures were recorded. Data were entered into an Excel spreadsheet and daily degree days with a lower and horizontal upper threshold of 10 ºC and 31.1 ºC, respectively, were calculated with a modified sine wave function (Baskerville and Emin 1969).

Model development. Several adjustments of both moth catch and fruit injury data were made prior to analyses. First, the occurrence of each fruit injury was assumed to have occurred on average 1 d after egg hatch. The mean daily degree day total during the previous 3 – 7 d sampling interval (range in values for first and second generation were 5 – 13 and 8 - 16 degree days, respectively) was subtracted from the cumulative degree days summed from Biofix 1 for each sample date. This adjustment assumed that it would take on average one day for newly eclosed codling moth larvae to find and penetrate fruit and for the injury to be visible to a scout. This seemed to be a reasonable approximation as Hall (1934) found that codling moth neonates required a mean time of 150 min to locate and penetrate fruit, and because larval frass can be detected on the surface of attacked fruits within 24 h (unpublished data). Second, the moth catch that occurred on the Biofix date was assigned the degree day total that accumulated on the day the trap was checked. Third, the ends of moth flight and egg hatch were assumed to occur at 444 and 567 and 1044 and 1189 degree days after Biofix for the first and second generations, respectively, to match the values used in the old model (Beers et al. 1993). Fourth, to assign moth catches and egg hatch to either of the two generations, data were interpolated back from the first sample date that corresponded to the second (> 444 and > 567 degree days) or third generation (> 1044 and > 1189 degree days) for moth catches and egg hatch, respectively (Beers et al. 1993). Fifth, the final cumulative value for each generation was adjusted from 1.0 to 0.995 to allow these data to be used in the statistical fit of the logistic models.

The data for cumulative proportions of moth catch and egg hatch for each generation were fit to logistic response functions where Y is the proportion of the event completed and X is the cumulative degree day total from Biofix (Neter and Wasserman 1974).

$$E(Y) = e^{(\ _0+\ _1{}^{*}X)} / (1 + e^{(\ _0+\ _1{}^{*}X)})$$

The two parameters of the logistic equation ($_0$ and $_1$) were estimated with linear regression by first transforming the proportions (*p*) into logits (*p'*).

$$p' = \log_e (p/(1-p))$$

The tabular data from Brunner et al. (1982) (old model) for cumulative moth flight and egg hatch as a function of degree days summed from Biofix were transformed and also fit to logistic equations.

Estimating the efficacy of insecticide timing. The significance of the change in the prediction of cumulative egg hatch between the old and new model was evaluated by considering the potential impact of spray timing for a generic insecticide timed for either eggs or neonate larvae. The expected proportions of first generation eggs killed by an ovicide applied at three timings were evaluated: 28, 56, or 258 degree days after Biofix. The ovicide was assumed to kill 95 and 90% of the eggs laid during the first and second week after the spray application. The number of eggs expected to be laid during each of these weekly intervals with both models was estimated using mean weekly accumulation of degree days at that point of the season. These estimates were calculated with field temperatures taken from 12 field data sets. For example, the mean weekly degree day total for these sites increased from 47 to 82 from the interval of 28 to 389 degree days after Biofix 1. The portion of the total complement of eggs laid during each of these intervals was determined by using the equations for egg hatch and subtracting 86 degree days for the estimated mean egg developmental time (Richardson et al. 1982).

A similar approach was used to evaluate the relative effectiveness of insecticide spray timings targeting neonate larvae based on the different cumulative curves of first generation egg hatch in the two models. The first larval spray was applied at 139 degree days after Biofix 1 and two additional sprays were applied at two wk intervals. The proportion of neonates killed was assumed to be 99 and 95% during the first and second week after each spray application. The effectiveness of the three spray timings in removing a portion of the total neonate population during the first generation was determined with each model.

Data analysis. All data were entered into a statistical computer package and data were transformed to fit the logistic equations (Analytical Software 2002). ANCOVA was used to detect significant differences ($P < 0.05$) in either the slope or intercept of the logistic regressions of the new and old model for cumulative moth flight and egg hatch of each generation (Neter and Wasserman 1974). Data collected from orchards treated with and without sex pheromone dispensers were compared with ANCOVA. No significant differences were found between these data sets and all the data were combined in the subsequent analyses with the old model.

Results

Field data. Population densities of codling moth were high in all orchards (Table 1). Both mean moth catch and numbers of injuries increased between generations. Seasonal patterns of moth flight were fairly consistent in all four years though counts were much lower during 2004 (Fig. 1a). Flights peaked during mid-May. Moth captures were lowest in late-June, but still averaged 10 – 35 moths per trap. Moth flight in the second generation peaked in late-July.

Fruit injury was first found in orchards beginning in late-May or about 4 wks after the start of moth flight (Fig. 1b). Levels of new fruit injury peaked in mid-June in 2003 and 2005, and a week later in the other two years. Relatively high levels of new fruit injuries were detected in late-June in all four years. The lowest levels of new fruit injury occurred during a 2 - 3 wk period in July, New fruit injuries increased sharply in early-August and gradually declined over the remainder of the season (Fig. 1b).

Model development. Data for both cumulative moth flight and egg hatch fit logistic equations fairly well (Tables 2 and 3, Fig. 2a, b, r^2's ≥ 0.85. The tabular data from Brunner et al. (1982) fit the logistic equations more closely, r^2's > 0.97. Cumulative data for moth flight and egg hatch were similar in both generations for codling moth in orchards treated with or without sex pheromone dispensers (Table 2). The slope of the regression equation for cumulative moth flight during the first generation differed significantly between the new and old model (Table 3, Fig. 3a). In contrast, no statistical difference (ANCOVA) was found for the new and old model's predictions of the second generation cumulative flight. The new model's curves for cumulative egg hatch were significantly different (intercepts and slopes) from the old model for both generations (Table 3, Fig. 3b). In particular, the midpoint of the new curve (proportion = 0.50) was approximately 100 degree days later than the curve generated from the old model during the first generation (Fig. 3b). The new model predicted a slightly faster and then slower accumulation of egg hatch early and then late in the cumulative curve than the old model during the second generation.

Estimating the efficacy of insecticide timing. The effectiveness of the timing of either a generic ovicide or larvicide spray application varied depending on which model was used to predict the phenology of codling moth (Table 4). With the old model, the highest proportion of eggs were killed with a spray timed at 100 degree days after Biofix 1, while the new model showed a strong improvement in control if the ovicide was delayed until 258 degree days after Biofix 1. This late timing of the ovicides corresponded closely to the second larvicide timing (Biofix + 139 degree days + 2 wks).

The significant differences in the two models' predictions of first generation egg hatch created relative differences in the effectiveness of the three larvicide applications. With the old model either the first or second spray would be the most important spray timings to reduce codling moth injury, while the third spray contributed a much lower amount of control (Table 4). In contrast, the new model suggests that the first spray is the least effective timing as it targets the eclosion of only 10% of the larval population. Instead, the second and then the third spray would be more important to the overall level of larval control that was achieved in this exercise.

Discussion

Knowledge of the start date and the temporal shape of the cumulative curve of egg hatch are both key factors in constructing an effective intra-generational management program for codling moth. In commercial orchards, codling moth is a low-density pest and sampling the relatively large orchard canopies for its widely-scattered eggs is problematic (Batiste et al. 1973). Instead, the start of codling moth egg hatch in the spring can be predicted with either the accumulation of degree days from January 1st (Headlee 1931, Glenn and Brain 1982) or from the start of sustained male moth flight (Riedl et al. 1976, Jorgensen et al. 1979, Brunner et al. 1982). By linking the start of their seasonal spray program for codling moth to the presence of the first individuals of the most susceptible life stages, growers' can time subsequent sprays based on the residual toxicity of each insecticide (Gratwick et al. 1965, Hameed and Allen 1976). Unfortunately, a variety of factors can interplay to create time periods when residues are lower than the minimum effective dosage, i.e. precipitation, overhead irrigation, poor spray coverage, and elevated tolerances to insecticides (Howell and Maitlen 1987, Brunner et al. 2005a). In addition, growers may further increase the number and / or length of these time periods by stretching spray intervals due to economics, regulations, conservation of natural enemies, low moth catches in monitoring traps or a failure to detect eggs or injured fruits in the orchard. Insecticide usage surveys in Washington State suggest that on average, apple growers apply less than the 4 – 6 sprays needed for complete seasonal protection from codling moth (NASS 2005). Thus, growers' relative success in allocating a scarce resource (insecticide residues) to cover the key periods of pest abundance will likely correlate closely with their crop losses at harvest.

Several studies monitoring codling moth with sex pheromone-baited sticky traps during the 1970's found that a distinct time period, defined by low weekly moth catches, occurred between generations beginning in late June and lasting 3 to 4 wks (Batiste et al. 1970, Madsen and Vakenti 1973, Riedl and Croft 1974, Westigard and Graves 1976). Pitcairn et al. (1992), however, in their modeling of the generation time of codling moth in California discarded approximately 40% of the 250 intra-generation data sets of male moth catches collected from 1978 to 1988 because they could not detect a clear separation between generations. Similarly, data collected from unsprayed Washington State apple orchards from 2002 - 2006 failed to detect a time interval between generations where moth catches were low, i.e. < 20% of the peak and < 5 moths / wk (Fig 1a). Factors, such as differences in trap and lure maintenance (Riedl et al. 1986), impact of seasonal sprays (Riedl and Croft 1974), or a quantitative shift in the phenology of codling moth (Boivin et al. 2003) could account for this apparent change in the flight patterns of male codling moth to sex pheromone-baited traps. Significant changes in the structure of orchard training systems over the last 40 yrs could also have had some impact on the variability of codling moth's phenology (Kührt et al. 2006).

Studies conducted in the 1970's found that a gap occurred in the timing of oviposition by female moths between the first and second generation (Riedl et al. 1976, Jorgensen et al. 1979). In contrast, new fruit injury by codling moth was found every week in orchards sampled from 2002 to 2006, and was particularly high in late June and the first week of July (Fig. 1b). This period coincides with the timing of the third cover spray (Biofix 1 + 139 degree days + 4 wks). Obviously, growers failing to apply a third cover spray for the first generation or experiencing one or more factors previously listed that would shorten this spray's effectiveness could experience significant levels of codling moth injury at this point in the season (Table 3). In addition, stretching the spray interval between generations during July would further jeopardize codling moth management.

Recommendations for spray timing in Washington State have typically considered each generation separately (Brunner et al. 1982, Beers et al. 1993). For example, after the first spray application at 139 degree days following Biofix 1, additional sprays for first generation are calendar-based, 2 – 3 wk intervals and based on cumulative catch of moths. Insecticide sprays for the second generation are independently timed based on the accumulation of 694 degree days summed from Biofix 1 (Beers et al. 1993). Unfortunately, this effectively expands the spray interval at mid-season (late June to late July) to 3 – 4 wks. Management of codling moth within infested orchards could likely be improved if spray timing was based on maintaining an effective minimum deposit among the currently registered insecticides for codling moth throughout the season.

The codling moth phenology data collected in Michigan in 1973-74 were fit into a generalized phenology model format (PETE) that was subsequently incorporated into various state-wide computer-based agricultural networks (Welch et al. 1978, Croft and Knight 1983). This generic model format uses a kth-ordered distributive delay process to advance insects through substages, the rate of which is determined by each stage's degree day requirements and daily temperatures (Manetsch 1976). PETE is a deterministic model that generates a fixed output when plotted on a degree day scale. The influence of stochastic events such as temperature or rainfall that can significantly impact daily fecundity are not included (Howell 1991). Further improvement in phenological modeling of codling moth has been achieved with the inclusion of climatic factors' impacts on both mating success and fecundity, particularly early in the season (Knight 2004a). Cool springtime temperatures were found to retard the oviposition rate of codling moth when plotted on a degree day scale. This could explain the proportionally greater shift that occurred in the timing of egg hatch versus moth flight in the new versus the old model

(Figs. 3a, b).

The codling moth PETE model was adopted in Washington State (Brunner et al. 1982) and validated by comparing its prediction with observed first egg hatch in the field (Beers and Brunner 1992). Data on the cumulative curves of codling moth oviposition, egg hatch, or fruit injury has not been reported previously from Washington State orchards or compared with populations in Michigan. Significant differences in the phenology of codling moth are known to exist between different geographical areas, such as California versus Michigan (Pitcairn et al. 1992). The PETE model developed in Michigan where codling moth has 1 to 2 generations did not fit the phenology of codling moth in North Carolina; where similar to populations in California, it has 2 to 4 generations (Rock and Shaeffer 1983). Data used to develop this new model were largely collected from orchards in Yakima County. Further validation of these equations is needed for orchards in other regions in Washington State and for orchards in other geographical areas.

The pleiotropic costs associated with insecticide resistance alleles have been found to affect the timing of spring emergence, the rate of larval development, and the seasonal timing of diapause in codling moth in strains exhibiting high levels of resistance to either diflubenzuron (10,000-fold) or deltamethrin (80-fold) (Boivin et al. 2001, 2004). Boivin et al. (2003) suggest that the maintenance of a polymorphic codling moth population in the field is achieved by the trade-offs between the negative pleiotropic costs of resistance on female fecundity and longevity and egg fertility and the selective advantages for resistant individuals escaping current spray timings designed for the phenology of susceptible populations. The phenology of a mixed genotypic population of codling moth would likely be similar to the data found for populations in

Washington State in this study – no change in the initiation of moth flight or egg hatch, but broader periods of overlapping moth flight and oviposition among generations. Interestingly, a significant positive correlation was found for a delay in the median date of spring emergence and levels of tolerance to azinphosmethyl among field-collected populations in Washington State (Knight 2004b). These data support the hypothesis that codling moth, in response to strong selection pressure imposed by insecticide usage, may have evolved a phenology different than that previously described by Riedl et al. (1976). Successful future management of codling moth will require careful consideration of these changes.

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Table 1. Summary of codling moth counts of male moths caught in sex pheromone-baited traps and injured fruits sampled on selected trees in apple orchards monitored during one or both generations from 2003 to 2006

			1st generation		2nd generation	
		Biofix	cumulative counts [b]		cumulative counts [c]	
Orchard	Year	date [a]	No. moths	No. injuries	No. moths	No. injuries
Orondo	2003	4/22	452	1679	57	-
Moxee1	2003	4/28	320	562	393	-
Parker1	2003	4/28	189	600	324	-
Moxee1	2004	4/29	67	398	183	1187
Moxee2	2004	4/29	77	2035	373	-
Parker2	2004	4/19	126	423	248	847
Moxee1	2005	4/25	228	72	260	228
Zillah	2005	4/22	314	77	415	240
Parker3	2005	4/20	444	184	280	385
Moxee2	2006	5/04	-	185	-	1668
Zillah	2006	5/01	152	126	356	833
Parker3	2006	4/27	436	609	326	1131
Mean (SE):			255.0 (44.1)	579.2 (182.9)	292.3 (31.4)	814.9 (180.6)

[a] The start of sustained male moth catches in a sex pheromone-baited trap (Biofix 1).

[b] Cumulative counts from the timing of first moth catch to 444 and 567 degree days for male moth catches and injured fruits, respectively.

[c] Cumulative counts from the timing of first moth catch to 1044 and 1189 degree days for moth catches and injured fruits, respectively.

Table 2. Model parameters of logistic equations fit to cumulative emergence and egg hatch for both the first and second codling moth generations from apple orchards treated with or without sex pheromone dispensers, 2003-2006

Orchard treatment [a] / generation	Intercept	Slope	Adjusted R^2	ANCOVA *P*-values Intercepts	ANCOVA *P*-values Slopes
Cumulative moth flight					
Sex pheromone / 1st	-3.4417	0.0098	0.88	0.22	0.34
No pheromone / 1st	-3.0576	0.0105	0.85		
Sex pheromone / 2nd	-11.1586	0.0108	0.90	0.34	0.19
No pheromone / 2nd	-11.3795	0.0083	0.91		
Cumulative egg hatch					
Sex pheromone / 1st	-8.2650	0.0123	0.92	0.65	0.83
No pheromone / 1st	-8.0692	0.0124	0.91		
Sex pheromone / 2nd	-11.3368	0.0070	0.85	0.77	0.76
No pheromone / 2nd	-11.6536	0.0072	0.85		

Orchards treated with sex pheromone (5 data sets) received 1,000 Isomate-C PLUS™ sex pheromone dispensers per ha, and the other orchards (7 data sets) were left untreated.

Table 3. Model parameters of logistic equations fit to cumulative emergence and egg hatch from first moth catch from apple orchards monitored from 2003-2006 and compared with similar equations fit to tabular values of an older model for both the first and second codling moth generations

Model [a] / generation	Intercept	Slope	Adjusted R^2	ANCOVA P-values Intercepts	ANCOVA P-values Slopes
		Cumulative moth flight			
Old model / 1st	-3.1204	0.0196	0.97	0.52	0.02
New model / 1st	-3.1568	0.0103	0.85		
Old model / 2nd	-11.158	0.0148	0.99	0.34	0.62
New model / 2nd	-10.743	0.0083	0.91		
		Cumulative egg hatch			
Old model / 1st	-5.9834	0.0204	0.97	< 0.0001	< 0.0001
New model / 1st	-8.1947	0.0124	0.91		
Old model / 2nd	-13.494	0.0151	0.98	< 0.0001	< 0.0001
New model / 2nd	-11.478	0.0071	0.85		

[a] Data used to fit the logistic equation to the old model were taken from Beers et al. (1993).

Table 4. Comparison of the expected effectiveness of spray timing for an ovicide applied at one of three timings and the individual effect of each application in a three-spray larvicide program based on the old and new model predictions

		Proportion of life stage killed [b]	
		Old model	New Model
Insecticide	Timing (degree days) [a]		
Ovicide	28	0.25	0.04
Ovicide	56	0.34	0.06
Ovicide	258	0.21	0.51
Larvicide	139	0.42	0.10
Larvicide	258 [c]	0.41	0.51
Larvicide	394 [c]	0.12	0.33

[a] Degree days were accumulated from the first sustained male moth catch (Biofix) in sex pheromone-baited traps.

[b] The ovicide was assumed to kill 95 and 90% of all eggs deposited during the first and second week after application. The larvicide was assumed to kill 99 and 95% of all neonate larvae during the first and second week after application. Mean weekly degree day totals used to estimate the proportion of each life stage exposed to the insecticides were based on field data and ranged from 50 to 86.

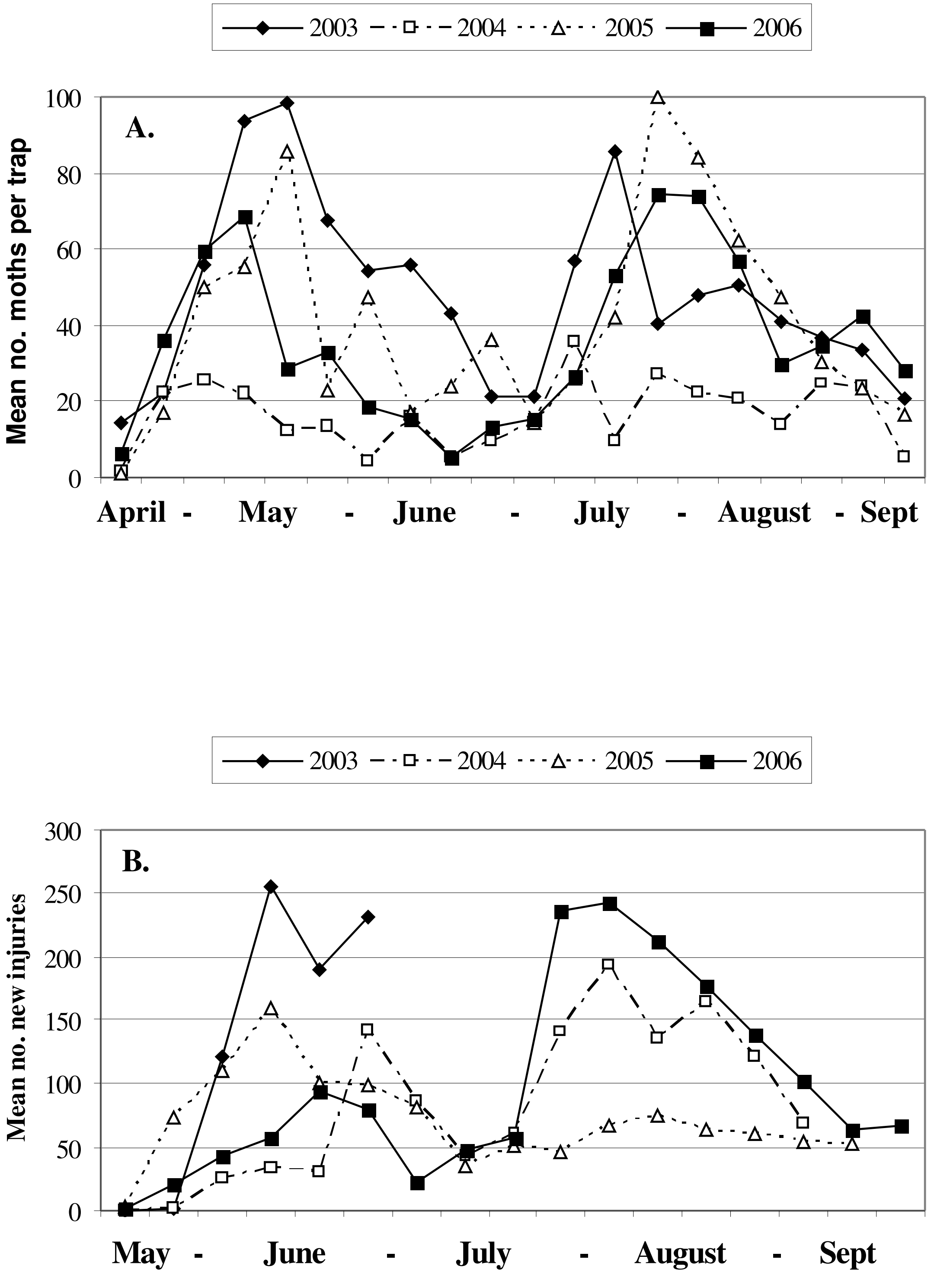
[c] The second and third larvicide sprays were applied at two-wk intervals.

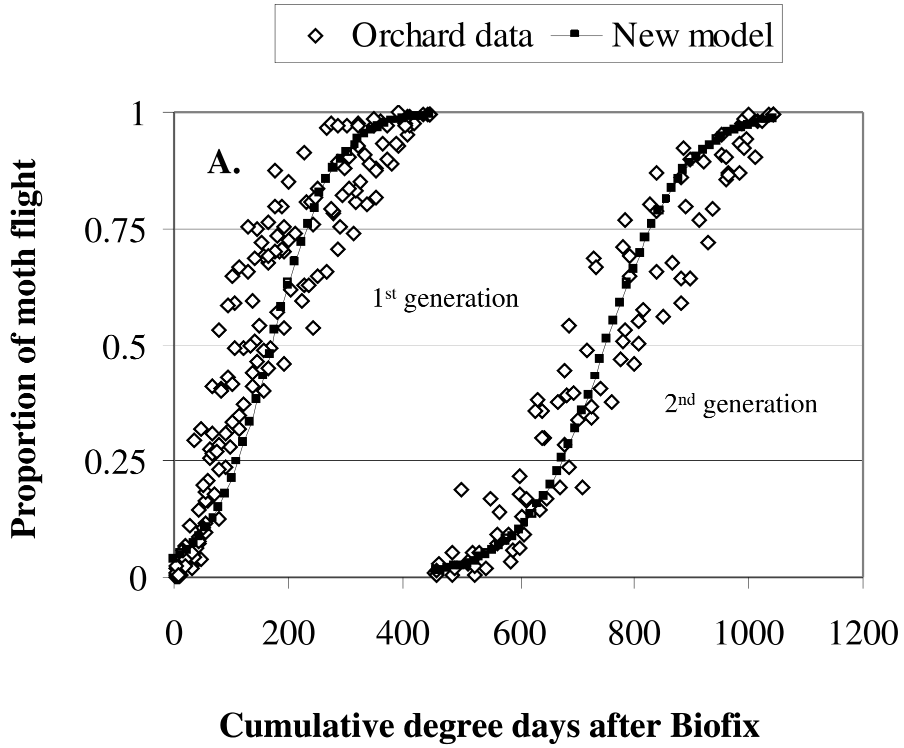
Figure Captions

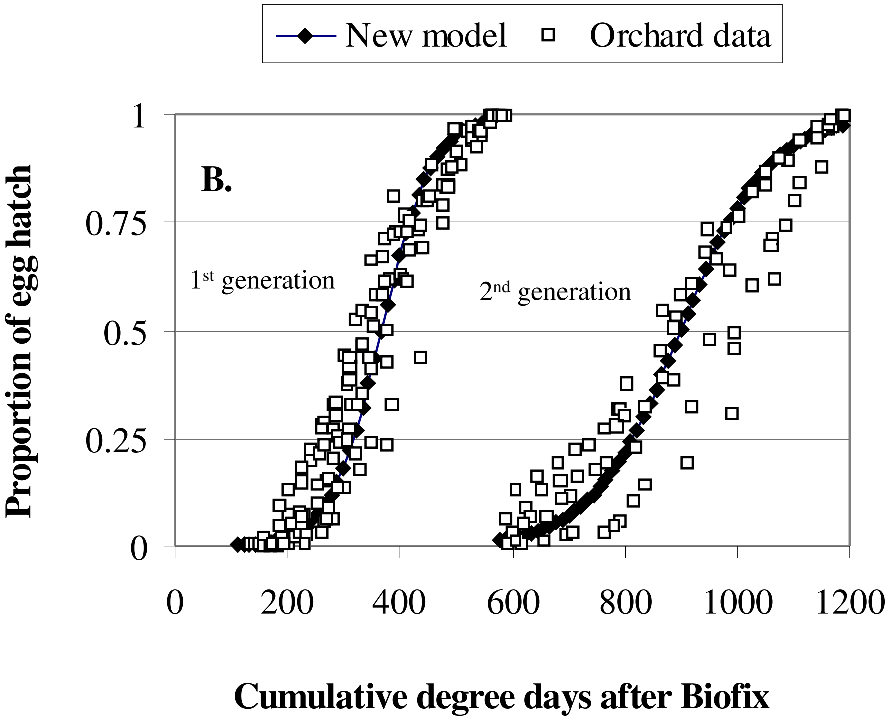
Figure 1. Seasonal mean catches of male moths in sex pheromone-baited traps (A.) and new fruit injuries (B) in Washington State apple orchards monitored from 2003 to 2006.

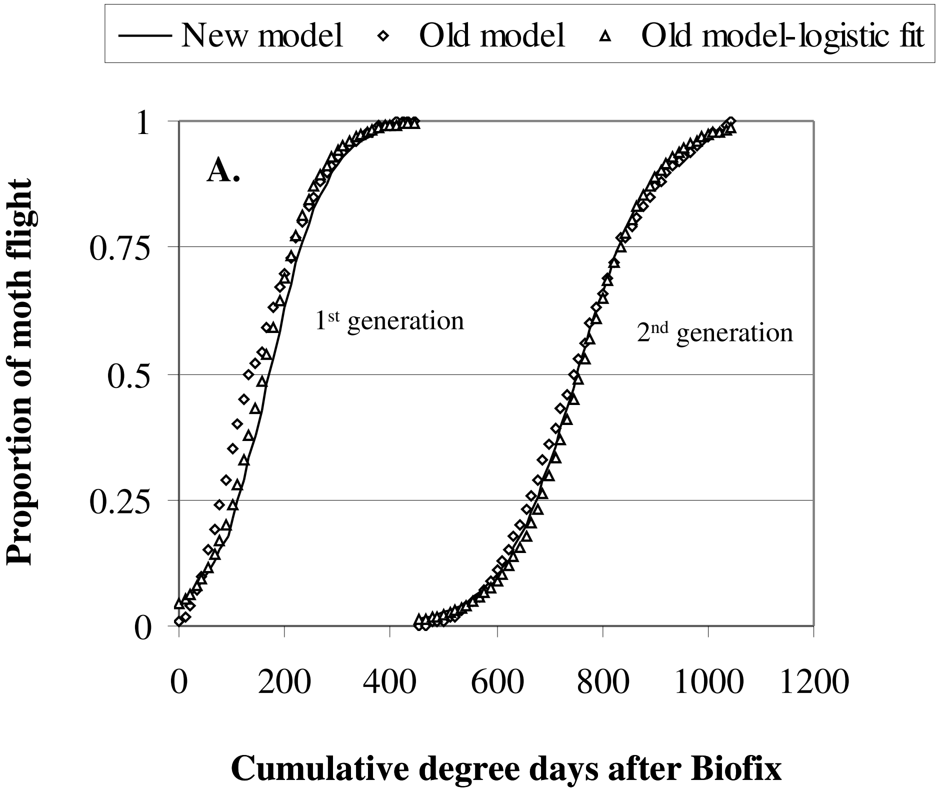
Figure 2. The proportion of moth flight (A.) and egg hatch (B.) during each generation from orchard field data (open squares) and predicted by the new logistic model as a function of degree days cumulated from Biofix.

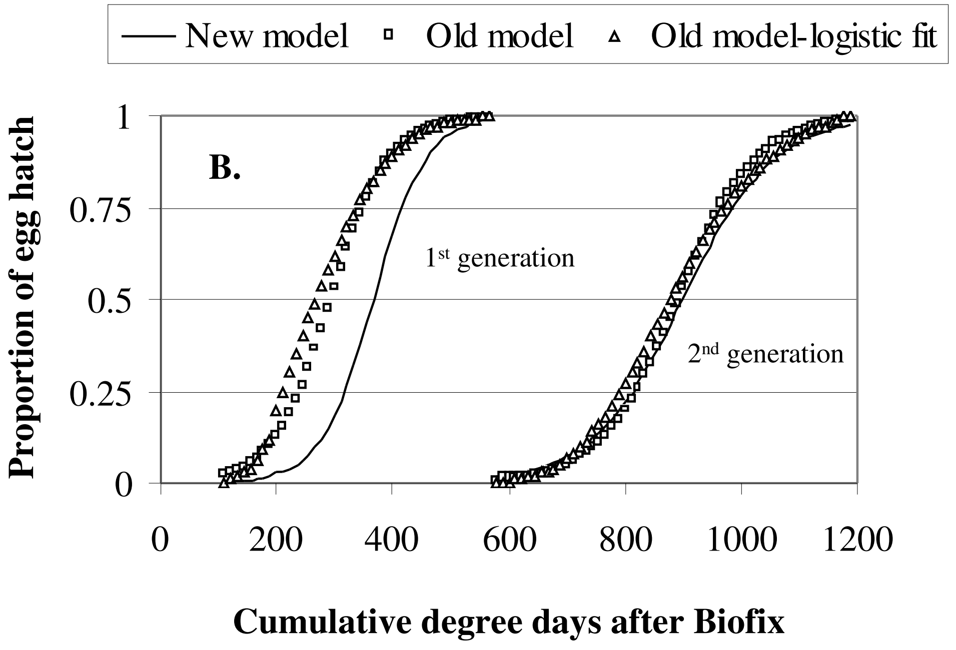
Figure 3. Predictions of the proportion of moth flight (A.) and egg hatch (B.) as a function of degree days cumulated from Biofix in the new logistic model, tabular values for the old model (Beers et al. 1993), and the fit of these data to a logistic equation.


2003
2004
2005
2006
A.
Mean no. moths per trap
0
20
40
60
80
100
April - May - June - July - August - Sept
2003
2004
2005
2006
B.
Mean no. new injuries
0
50
100
150
200
250
300
May - June - July - August - Sept


◇ Orchard data
■ New model
A.
Proportion of moth flight
1
0.75
0.5
0.25
0
1st generation
2nd generation
0
200
400
600
800
1000
1200
Cumulative degree days after Biofix


◆ New model
□ Orchard data
B.
Proportion of egg hatch
1
0.75
0.5
0.25
0
1st generation
2nd generation
0
200
400
600
800
1000
1200
Cumulative degree days after Biofix


New model
Old model
Old model-logistic fit
A.
Proportion of moth flight
1
0.75
0.5
0.25
0
1st generation
2nd generation
0
200
400
600
800
1000
1200
Cumulative degree days after Biofix


New model
Old model
Old model-logistic fit
B.
Proportion of egg hatch
1
0.75
0.5
0.25
0
1st generation
2nd generation
0
200
400
600
800
1000
1200
Cumulative degree days after Biofix