



North American invasion of Spotted-Wing *Drosophila* (*Drosophila suzukii*): A mechanistic model of population dynamics



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ABSTRACT

Drosophila suzukii is a relatively new threat to the soft-skinned fruit industry in North America. The presence of this pest in North America is a concern and assessing the risk of potential infestation and damage can help guide regional management strategies. We have developed a continuous time stage structured population model parameterized with empirical data based on laboratory observations. The principle environmental driver of vital rates (mortality, fecundity and development) for the model is temperature though our results suggest that reproductive diapause and quality of fruit available to the population may also have significant effect on population size. The model was run with several generalized temperature profiles and various observed temperature data sets for locations known to be important for berry production. While southern regions appear to be most suitable for supporting high population densities due to warm temperatures throughout the year, northern regions with moderate temperatures may also be susceptible due to a lack of extreme cold or heat, both of which limit development and increase mortality.

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1. Introduction

Reports of *Drosophila suzukii*, commonly known as Spotted Wing *Drosophila*, originating from the mainland of Japan have been present since the 1930s (Kanzawa, 1939). However, its rise as a pest of global significance has taken place largely over the past 35 years and in continental North America since circa 2009 (Hauser, 2011). *D. suzukii* has been confirmed or suspected present in countries across all continents except Australia and Antarctica (Asplen et al., 2015) and has a wide range of reported hosts including strawberries, raspberries, blueberries, blackberries, peaches, nectarines, pears, sweet and sour cherries, plums, apricots and both table and wine varieties of grape (Walsh et al., 2011).

D. suzukii is one of only two known species of *Drosophila* that prefer fresh, soft-skinned fruit at or near the stage of optimal harvest ripeness (Lee et al., 2011; Walsh et al., 2011). Females of this species possess a serrated ovipositor that allows them to attack pre-harvest fruit. Early detection of infestation is difficult as the oviposition incision is small and the visible consequences of larval

feeding do not immediately appear. Empirical data for North America are not yet readily available but Bolda et al. (2010) provides a benchmark estimate of potential yield losses due to *D. suzukii* infestation at 20%. Based on 2008 harvest yields, this would result in a >\$500 million loss in the US states of Washington, Oregon and California alone (accounting for strawberries, blueberries, raspberries, blackberries and cherries only). While the western United States and Canada are important regions for the soft-skinned fruit industry in North America there are other regions that are likely to be concerned about the spread and impact of *D. suzukii*.

Due to its potential to cause significant economic losses in many areas of North America and the need to establish effective pest management strategies, we developed a mechanistic, continuous time mathematical model with overlapping generations. Wherever possible, the model has been parameterized using experimental and observational data on *D. suzukii* life history (see Emiljanowicz et al., 2014; Ryan et al., 2016, for further information).

We have two principle objectives in constructing this model: (i) to gain a better understanding of the temporal and spatial patterns of *D. suzukii* population growth, and hence risk, that result from particular assumptions about crucial mechanisms; and (ii) to create a useful tool for answering interesting “what if” questions regarding *D. suzukii* invasion, climate and climatic change.

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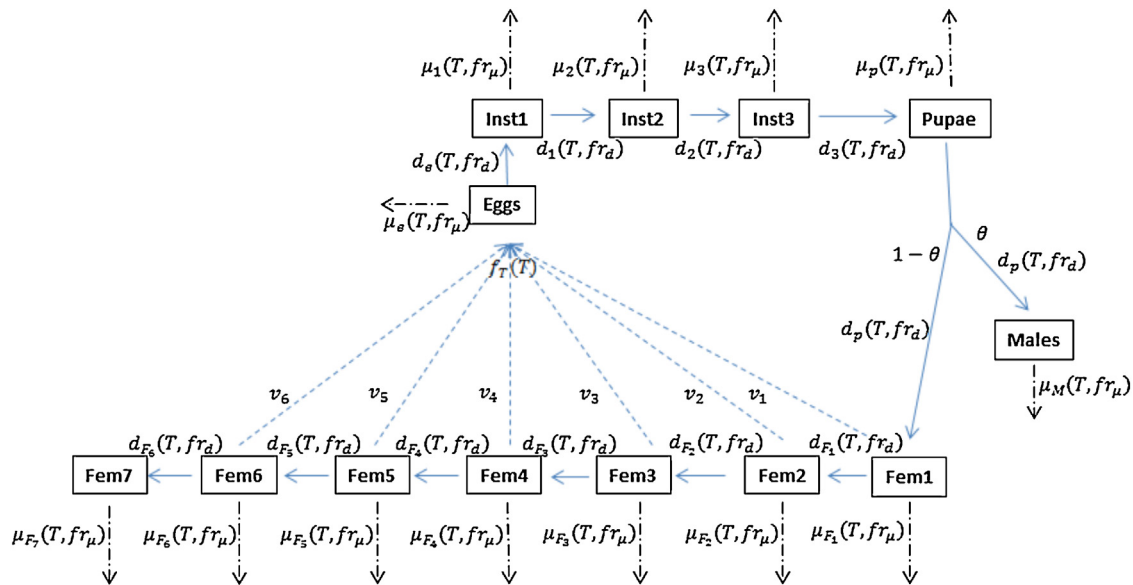


Fig. 1. Schematic of the modelled population stage structure and relationships between state variable equations including principal input and output parameters. Most development and mortality processes are temperature (T) dependent and rely on the fruit submodel (fr) when included. Here mortality is represented as the sum of intrinsic and extrinsic factors (see main text).

A mechanistic model can help us to meet both of these objectives. Mechanisms are a critical part of biological understanding. “What if” questions usually involve changes in the environment, autecology, or synecology of the organism. These questions require changes to the model system that are not readily accommodated in non-mechanistic approaches.

By mechanistic we mean that the model is based upon what we think are the most important mechanistic processes that determine population dynamics. Such models are particularly useful because they allow any model prediction to be traced back to the process(es) that most influences it. Since mechanistic models often have many parameters, all of which are tunable, our goal is only to achieve satisfactory quantitative behavior. Our goal is not forecasting, for which statistical models are often better suited (see e.g., Thornley and France, 2007; for further discussion).

1.1. *D. suzukii* life history

D. suzukii develop through the following stages (with average duration reported in days based on laboratory diet and at a constant temperature of 22 °C): egg (1.4 d), three larval instars (6 d total), pupae (5.8 d), and adult (72 d) (see Emiljanowicz et al., 2014; for details).

Various *Drosophila* species are subject to a reproductive diapause regulated primarily by photoperiod and temperature (Ohtsu et al., 1993). As the number of hours of daylight decreases, reproduction ceases for several species (Saunders et al., 1989; Kimura, 1990). According to Saunders et al. (1989) diapause may be terminated by either an increase in the number of daylight hours, or more importantly for temperate regions, an increase in temperatures (approximately 18 °C for *Drosophila melanogaster*). It has been suggested that *D. suzukii* also experiences a reproductive diapause. Mitsui et al. (2010) found that populations of *D. suzukii* in central Japan had reproductively mature ovaries during summer months, while ovaries were underdeveloped for females trapped in colder months. However, to the best of our knowledge, the specific details of diapause induction and termination have not been elucidated for this species.

D. suzukii experiences both intrinsic and extrinsic mortality. Intrinsic mortality rate is the per capita rate of mortality assumed

to be the result of biological aging. It can be contrasted with extrinsic mortality which is assumed to be the result of environmental hazards such as natural enemies (predators, parasites and pathogens). Intrinsic mortality rates have been estimated in the lab (Emiljanowicz et al., 2014) under optimal conditions. These rates are not likely to be density dependent, at least in the field; but field-based rates are difficult to estimate. Similarly, extrinsic mortality rates are exceedingly difficult to estimate, at least in the field, which are arguably the only meaningful estimates of these rates.

D. suzukii vital rates are known to be temperature dependent, and development rates may also depend upon host fruit quality (Burrack et al., 2013; Lee et al., 2015). In the laboratory, optimal development rates occur at 28.2 °C (Ryan et al., 2016; Tochen et al., 2014). Optimal fecundity rates occur at 22.9 °C (Ryan et al., 2016; Tochen et al., 2014). The lower and upper developmental thresholds occur at 8 °C and 31 °C (Ryan et al., 2016) and 7.2 °C and 42.1 °C (Tochen et al., 2014). While the results are similar for most observations, we used the estimates provided by Ryan et al. because they were based on experiments that used a finer temperature scale, which, in particular, captured the upper developmental threshold rather than extrapolating it from the fitted curve as Tochen et al. did.

In terms of winter survival, Dalton et al. (2011) conducted laboratory experiments and found that acclimated adult *D. suzukii* can survive for up to 88 days in 10 °C temperatures including a seven day freeze period (from day 18 to day 25) but that adult longevity decreases as temperature decreases. Pupae can survive for 103 days at 10 °C including the seven day freeze period. Their results also suggest that *D. suzukii* is rendered sterile at these low temperatures. They conclude that few individuals are likely to survive the relatively moderate winters of the Pacific Northwest. More recently, Jakobs et al. (2015) found that 80% of control specimens died after 1 h of exposure to cold temperatures (−7 °C) and similar mortality rates were observed after a few days at 0 °C (70–90 h). Survivorship improved with cold acclimation and under fluctuating temperatures but, similar to the work of Dalton et al. (2011) they conclude that *D. suzukii* is not well-adapted to survive temperate winters based on phenotypic characteristics alone. These results suggest that the presence of *D. suzukii* in climates with longer, colder winters is likely due to a combination of overwintering in man-made

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