Survival and Fecundity Parameters of Two Drosophila suzukii (Diptera: Drosophilidae) Morphs on Variable Diet Under Suboptimal Temperatures

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Abstract

Life history parameters are used to estimate population dynamics, mortality, and reproduction in insects relative to their surrounding environment. For Drosophila suzukii Matsumura (Diptera: Drosophilidae), an invasive agricultural pest, previous studies have estimated net reproductive rate (Ro), generation time (T), and intrinsic rate of population increase (rm). A main limitation is that these estimates were measured under relatively favorable settings, and do not reflect environmental conditions and physiological states encountered during dormancy periods. Therefore, this study investigated the impacts of 1) low temperatures and 2) dietary protein: carbohydrate ratios (P:C) on both survival and fecundity parameters of D. suzukii summer morphs (SM) and postoverwintering winter morphs (WM) over physiological age (degree-days, DD). In both morphs, reproductive rates were higher and lifespan was longer when flies were exposed to low protein (P:C 1:4) or carbohydrate-only diets (P:C 0:1) compared with high protein diets (P:C 1:1). WM had higher reproductive rates and longer generation times than SM on optimal 1:4 diet in all trialed temperatures, but at the lowest temperatures, SM had higher reproductive rates than WM in carbohydrate-only and high protein diets. This likely reflected delayed oogenesis and hindered reproduction after an overwintering period in WM receiving suboptimal diets. Oviposition for SM and WM receiving 1:4 diet commenced from 0 to 100 DD, and peaked between 400 and 500 DD, earlier than flies receiving 0:1 diet. These results suggest that dietary protein has a crucial role in early oogenesis, particularly for postoverwintering WM. The parameters developed here reflect the population dynamics of D. suzukii before and after the crop growing season, an essential time for population buildup, survival, and early and late host infestation.

Key words: Carbohydrate, life history, overwintering, protein

The spotted-wing drosophila, Drosophila suzukii Matsumura (Diptera: Drosophilidae) is an invasive agricultural pest in America and Europe (Lee et al. 2011, Walsh et al. 2011, Dos Santos et al. 2017). Female flies lay their eggs in ripening berries and cherries, and resulting larvae lead to crop loss (Lee et al. 2016). As D. suzukii colonizes new regions, it encounters challenging environmental conditions and variable hosts (Gutierrez et al. 2016). To better understand the population biology of D. suzukii in newly invaded areas, a growing number of studies have explored various mortality and reproductive parameters of D. suzukii (Emiljanowicz et al. 2014, Tochen et al. 2014, Asplen et al. 2015, Wiman et al. 2016). Comprehensive knowledge of life history parameters of D. suzukii under both summer and winter conditions can assist in the development of improved management practices.

Temperature-related life history parameters provide important information on the survival and reproductive potential of an insect under different environmental conditions and diets. Survival and fecundity data obtained in laboratory conditions can yield information about population dynamics and structure in the field. Detailed knowledge of life history parameters for invasive and economically damaging insects is particularly important as they can provide valuable information on the adaptability of such insects to variable and suboptimal environmental and nutrient conditions. Many laboratory-based studies are limited in that conditions are controlled within narrow ranges to reduce confounding factors, and consequently it is difficult to account for the great variability of environmental conditions found in the wild.

A study by Emiljanowicz et al. (2014) determined several D. suzukii life history and reproductive parameters, including age-specific survivorship and gross maternity. These life table parameters were determined at favorable temperatures (22°C), using an optimal cornmeal diet. These life parameters provided useful information on the survival and reproductive potential of an insect under different environmental conditions and diets. Survival and fecundity data obtained in laboratory conditions can yield information about population dynamics and structure in the field. Detailed knowledge of life history parameters for invasive and economically damaging insects is particularly important as they can provide valuable information on the adaptability of such insects to variable and suboptimal environmental and nutrient conditions. Many laboratory-based studies are limited in that conditions are controlled within narrow ranges to reduce confounding factors, and consequently it is difficult to account for the great variability of environmental conditions found in the wild.

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baseline values to estimate reproduction and lifespan periods of D. suzukii populations during ideal temperatures and when food resources are abundant.

A study by Tochen et al. (2014) estimated net reproductive rate, rate of population increase, mean generation time, and lower, optimal, and upper developmental thresholds of D. suzukii developing in blueberry and cherry at temperatures ranging from 10 to 30°C. Instead of using an optimal diet, this study included food sources that D. suzukii would realistically encounter in commercial production fields. Tochen et al. (2014) found that D. suzukii fecundity was higher on cherries than on blueberries. While it is possible that soluble sugar content may have been higher in one fruit than the other, there might also be different associated yeasts which provide essential sources of protein for D. suzukii (Hamby and Becher 2016) that may have impacted the parameters from this study. It is plausible that differences in the nutritional values of the studied fruit could have contributed to differences in these parameters, but that was not determined in that study. While D. suzukii larvae have limited opportunity to behaviorally adapt to dietary medium, adults can select from a diverse landscape to meet their optimal nutritional needs. Dietary protein: carbohydrate (P:C) ratios affect fecundity and survival in the closely related Drosophila melanogaster (Bruce et al. 2013, Lee 2015), but currently there is no detailed information on the impact of dietary protein and carbohydrates on life table parameters of D. suzukii adults at various temperatures.

Asplen et al. (2015) estimated D. suzukii developmental rate and mortality under favorable temperatures, and this study also provided valuable contributions to the understanding of population dynamics. The authors, however, acknowledged that the life table parameters used in their model were not obtained from a wide range of field conditions. Three key pieces of information are lacking: 1) fecundity and mortality at low temperatures; 2) data on D. suzukii that have gone through reproductive diapause; and 3) host plant (diet) effects. In addition to these constraints, the study by Asplen et al. (2015) estimates life history parameters by using fly age (calendar days) as opposed to physiological age at constant temperatures.

Physiological age, as opposed to calendar-based age, is a more appropriate estimation of insect age as these parameters can be used to estimate D. suzukii mortality and fecundity regardless of temperature and accounts for accumulation of degree days (DD; Wiman et al. 2016). DD-based population models can be used to estimate pest abundance and the timing of reproduction events (Nyamukondwa et al. 2013, Haridas et al. 2016). These models also have the advantage that they can be uniformly applied every year, by using daily temperature fluctuations in order to estimate biologically relevant events.

Drosophila suzukii most likely overwinters as adults (Dalton et al. 2011), and females mature eggs during early spring (Grassi et al. 2018) when the DD start to accumulate. The use of DD models for management practices is limited during summer, when generations overlap and the models can no longer estimate discrete life history events. DD models can, however, be useful right after the overwintering period, when adult WM females reach increased reproductive maturity during the period of early crop ripening. Overwintering females can take refuge in unnanaged areas adjacent to crops, and oviposit in early ripening crops. DD models can provide estimates for when overwintering D. suzukii females have reached reproductive maturity, and, therefore, infest fruit. To simulate more accurately the early-season reproductive maturation in the field, it is important to use life history parameters that are realistically found under these environmental conditions (ranging from approximately 5 to 18°C). A limitation with current physiological-age models (Wiman et al. 2016) is that they do not take into account the overwintering period of female D. suzukii. Because a reproductive diapause can alter the timing of expected egg lay and peak fecundity assumed by current DD models, it is important to understand how reproduction parameters can be modified after an overwintering period.

Another factor that has not been considered in prior life tables is the impact of the phenotypical change in D. suzukii, i.e., ‘winter morphs’ (WM) and ‘summer morphs’ (SM). WM develop at lower temperatures, and have higher cold tolerance than SM (Shearer et al. 2016). Currently all the life history parameters have been developed on SM, and do not account for phenotype population shifts in response to decreasing temperatures. In temperate regions, the WM phenotype is typically encountered in the field when DD start accumulating during spring (Shearer et al. 2016). For this reason, it is essential to understand the mortality and fecundity parameters of WM during this period.

It is difficult to account for the great variability of environmental conditions found in the wild. The parameters defined in previous studies may not represent what happens when flies are exposed to lower temperatures and suboptimal diets. Considering the limitations of the existing studies on life history parameters in D. suzukii, this study has the goal to explore some key unknown variables that can influence D. suzukii mortality and fecundity. These variables include the role of dietary protein: carbohydrate (P:C) ratios, lower-range temperatures (suboptimal for D. suzukii reproduction), simulated overwintering period, and differences between summer and WM phenotypes.

Methods and Materials

Drosophila suzukii fly colonies were maintained at the Horticultural Crops Research Unit (HCRU), United States Department of Agriculture - Agricultural Research Service (USDA - ARS) in Corvallis, OR. Trialed flies were the first-third generation of lab-reared flies, from wild, field collected flies. Parental flies were kept in a walk-in controlled environment chamber (22°C; 16:8 (L:D) h; 60% RH), and provided with a cornmeal agar diet for food and oviposition (for detailed diet, refer Woltz et al. 2015). For these experiments, we did not track life history of immatures (eggs, larvae, and pupae), so all data collected are for the adult stage.

Rearing of WM Flies

WM flies were reared from August 2016 to August 2017, following the methods of Wallingford and Loeb (2016). Parental flies were allowed to oviposit in petri dishes containing cornmeal agar diet, and after 24 h diet dishes with eggs were transferred to a ‘WM rearing chamber’ (12:12 (L:D) h; 14 ± 1°C; 70% RH Percival E-30B, Percival Scientific Inc., Boone, IA), where larvae developed in the media. Adult WM flies emerged after ~1 mo, and groups of 50 0-d old flies (mixed males and females) were transferred to 8 oz polypropylene rearing bottles (Genesee Scientific, San Diego, CA), and provided with ~2 ml of cornmeal agar diet on a 35 mm petri dish (Corning Falcon, Fisher Scientific, Hampton, NH) at the base of the bottle. After 8–10 d in the WM rearing chamber, female flies were separated into groups of 20–25, placed in new bottles with cornmeal diet, and transferred to a ‘cold-hardening’ climate-controlled chamber (12:12 (L:D) h; 7.7 ± 0.1°C; 74.5 ± 1.0 RH) for 1 wk. To absorb condensation, one 11 mm filter paper was inserted in the bottle.

After 1 wk in the ‘cold-hardening’ chamber, females were transferred to a simulated ‘overwintering’ controlled-temperature room for 5 wk (1.83 ± 0.53°C; 93.1 ± 5.3 RH, 8:16 (L:D) h), daytime light intensity 204.4 lux). To simulate food resource depletion,
females had access to cornmeal agar diet during Week 1 of overwintering, and the cornmeal agar diet was removed and replaced with a minimal agar diet (32 g LB agar Thermo Fisher, 1 l dH2O) during Weeks 2–5 of overwintering. There is some evidence of a true reproductive diapause in D. suzukii (Rossi-Stacconi et al. 2016), and we, therefore, assumed that females in our simulated overwintering conditions entered reproductive diapause. After 5 wk in simulated overwintering, any surviving females were individually paired with a 3–4-wk-old WM mature male, and randomly assigned to different diet and temperature treatments (see section on Effects of Diet and Temperature on Lifespan and Fecundity).

Rearing of SM Flies
SM flies used in this experiment were reared from April to August 2017 by allowing parental flies to oviposit in petri dishes containing cornmeal agar diet, and incubating the eggs at 22°C, 18:6 (L:D), where larvae developed. Newly emerged flies (Day 0 individuals) were offered a sugar agar diet (130 g sucrose, 32 g LB agar, Thermoﬁsher, 1 l dH2O) for 24 h. After 24 h (when males develop their characteristic wing spots), one male and one female were randomly assigned to different diet and temperature treatments (see section on Effects of Diet and Temperature on Lifespan and Fecundity).

Effects of Diet and Temperature on Lifespan and Fecundity
Overwintered WM females (paired with WM male) and newly emerged SM females (paired with SM male) were individually placed in one 8 oz rearing bottle with an 11 mm filter paper, and randomly assigned to diet/temperature treatments. At the time when flies were placed into treatments, WM were 78 calendar days old since adult emergence, after cold hardening and overwintering; SM were 1-d-old since adult emergence. Rather than exposing WM and SM to the exact same pretreatment conditions, our intention was to simulate settings that would be encountered during shifting environmental conditions. Flies were randomly assigned to one of five agar diets varying in protein (P) to carbohydrate (C) ratios (P:C 0:0, 0:1, 1:4, 1:2, 1:1), and one of five temperature regimes (discussed in what follows). These diets were selected based on macronutrient ratios that enhance Drosophila lifespan and fecundity (Lee 2015). Agar diets were prepared with sucrose and yeast hydrolysate (MP Biomedicals #103304, Santa Ana, CA), using yeast hydrolysate (Y) to sucrose (S) ratios of 0:0, 0:1, 1:1.6, 1:0.7, and 1:0.2, respectively (Lee 2015, Ponton et al. 2015). Each diet contained a total of 180 g Y + S, and 32 g LB agar (#822700025, ThermoFisher Scientiﬁc) in 11 dH2O, and 3.7 ml 1M propionic acid, 0.69 g methyl-paraben, and 6.9 ml 95% ethanol as anti-mold agents. Approximately 2 ml of agar diet were poured in a 35 mm petri dish placed at the base of the rearing bottle, where flies could freely feed and oviposit.

Temperature regimes for WM were selected to simulate increasing temperatures in early spring after winter. WM pairs were placed in rearing bottles with one randomly assigned diet treatment (P:C 0:1, 1:4, 1:2, 1:1) inside a controlled-environment chamber (Percival LED 30HL1, Percival Scientiﬁc Inc., Perry, IA) with a 12:12 (L:D) h cycle and 200 Lux. The conditions in the chambers were 7.19 ± 0.04°C, 77.23 ± 2.21 RH; 8.79 ± 0.23°C, 74.59 ± 1.0 RH; 11.52 ± 0.38°C, 84.41 ± 5.95 RH; 14.38 ± 0.41°C, 75.55 ± 1.30 RH, and 16.98 ± 0.18°C, 90.35 ± 0.53 RH. For clarity, these temperature treatments will be referred to henceforth as ‘7°C’, ‘9°C’, ‘12°C’, ‘14°C’, and ‘17°C’, respectively. Sample sizes for WM in each treatment ranged between n = 18 and 27.

Temperature regimes for SM were selected to simulate decreasing temperatures in autumn, before overwintering. SM were exposed to four diet treatments (P:C 0:1, 1:4, 1:2, 1:1), and three temperature regimes (9°C, 14°C, and 17°C). SM were placed simultaneously in the same controlled-environment chambers as WM. Preliminary observations showed that SM did not survive more than 2 d in P:0,0 diet; therefore, this diet was not tested in these trials. The lowest temperature was selected on the basis that D. suzukii SM females did not lay eggs below 10°C (Tochen et al. 2014); hence, we excluded 7°C for SM. Sample sizes for SM in each treatment ranged between n = 11 and 18.

Diet dishes were changed weekly, and the total number of eggs present in the agar diet was counted. Because of the difficulty of finding burrowing larvae in the diet, only eggs were counted. Dead males were replaced with a 3–4-wk-old WM, or a 1–3-d-old SM, such that females were always paired with males through the experiment. Experiments were terminated when the female died.

Temperature and Diet-Related Life Table Parameters
This study used ‘Lotka’ life tables of D. suzukii adults to calculate reproductive parameters (Carey 2001). For WM and SM in each diet/temperature treatment, we calculated three life history parameters. The net fecundity rate (R) was defined as the average lifetime production of eggs for a newborn female, and was calculated using the equation $R_x = \Sigma I_x M_x$, where $I_x$ is the proportion of females surviving on Day x (age-specific survival; Carey 2001), and $M_x$ is the average number of eggs laid per female (age-specific fecundity). The mean generation time (T) was defined as the time required for a population to increase by a factor equal to the net reproductive rate, and was calculated using the equation $T = \Sigma e^{-\lambda x} M_x$/(γR_x), where γ is age in days, and $R_x$ is the net fecundity rate. The intrinsic rate of population increase ($r_\infty$) was defined as the rate of natural increase in a closed population that has been subject to constant age-specific schedules of fertility and mortality, and was calculated using the equation $r_\infty = \ln R_x/T$ (Emiljanowicz et al. 2014, Tochen et al. 2014).

Physiological Age-Specific Mortality and Fecundity
For calculating age-specific mortality and fecundity models, data from all temperature treatments was transformed into DD (physiological age) and pooled for each diet. DD were calculated using a lower threshold of 7.2°C (Tochen et al. 2014). For SM, we used accumulated DD starting since adult emergence (when flies were placed into diet and temperature treatments). For WM, we used accumulated DD starting from the day when female flies were removed from simulated overwintering and placed into diet/temperature treatments. This was done to enable direct comparisons with field phenology studies, where DD are accumulated from 0 after winter.

The survival and reproduction data over physiological time was fit to Gompertz and Cauchy functions as done by Wiman et al. (2016).

Physiological age-specific mortality ($l_x$) of adults was fitted using a two-parameter probability density Gompertz function; $y = 1/(1+e^{b(x-a)})$, where $a$ is the shape, $b$ is the rate, $x$ is DD, and $y$ is proportion surviving. The Gompertz model assumes that mortality increases exponentially as a function of age, and it contains two parameters, the initial mortality rate, and the exponential rate or increase in mortality (Carey 2001).

The age-specific fecundity ($M_x$) was plotted by averaging egg lay data over 100 DD intervals and subsequently fitted using the Cauchy distribution function, $y = 1/(\pi a (1 + ((x-b)/a)^2)^c)$, where $x$ is DD, $y$ is age-specific fecundity ($M_x$), and $a$, $b$, and $c$ are constants. Data were fitted using the open-source statistical environment R version
3.4.3 (R Development Core Team 2008). Survival data were fitted using R packages ‘survival’ (Therneau 2015) and ‘flexsurv’ (Jackson 2016). Pearson’s chi-square was used as a goodness-of-fit test for survival and maternity models (Agresti 2007).

Results

Temperature and Diet-related Life Table Parameters

The generation time (T, in days) was generally longer in WM than in SM, and it ranged from 87 to 220 d in WM, and 23 to 81 d in SM (Table 1). The net fecundity rate (Ro) ranged from 0.37 eggs to 91 eggs in WM, and 1.06 eggs to 51 eggs in SM (Table 1). The intrinsic rate of population increase ($r_m$) ranged from 0 to 0.035 in WM, and 0.003 to 0.078 in SM (Table 1). For $r_m$ values, a zero value suggests null population growth under these conditions.

Physiological Age-Specific Mortality and Fecundity

The Gompertz function ($y = \frac{1}{1 + e^{-(x-a)^b}}$) used to fit survival data, provided a good fit for all diet treatments. The statistical parameters for these fits are summarized in Table 2. As expected, the lowest survival rates were observed when D. suzukii were exposed to P:C 0:0 diets, where WM flies survived up to 78 DD. Aside from flies in 0:0, the lowest survival estimates for WM were recorded in P:C 1:1, where flies survived up to 423 DD. The highest survival estimates for WM were in P:C 0:1 diet, where flies survived up to 1790 DD, followed by P:C 1:4 with survival up to 1644 DD (Fig. 1a). The lowest survival rates for SM were observed when flies were exposed to P:C 1:4 diet, with an estimate of 38 eggs per DD interval at its peak (400 DD after adult emergence, Fig. 2b). Like WM, SM fecundity in P:C 0:1 diets also peaked later than all the other diet treatments, with an estimate of 17 eggs per DD interval at its peak (700 DD after adult emergence; Fig. 2b).

Table 1. Drosophila suzukii life table parameters for winter morphs (WM) and summer morphs (SM) at different temperatures and diets

| Temperature (°C) | Diet (P:C) | Winter morphs | Summer morphs | Winter morphs | Summer morphs | Winter morphs | Summer morphs |
|-----------------|-----------|---------------|---------------|---------------|---------------|---------------|---------------|
| 7               | 0:1       | 4.220         | 19.631        | 0.011         | 0.011         | 133.100       | 156.045       |
|                 | 1:4       | 5.070         | 34.891        | 0.029         | 0.068         | 137.309       | 52.228        |
|                 | 1:2       | 0.000         | 9.000         | 0.013         | 0.038         | 164.389       | 58.453        |
|                 | 1:1       | 0.000         | 6.063         | 0.000         | 0.053         | 112.000       | 34.062        |
| 9               | 0:1       | 4.423         | 37.601        | 0.017         | 0.025         | 198.650       | 145.051       |
|                 | 1:4       | 51.965        | 26.163        | 0.023         | 0.025         | 140.374       | 113.638       |
|                 | 1:2       | 8.261         | 3.481         | 0.011         | 0.011         | 112.000       | 34.062        |
|                 | 1:1       | 0.375         | 20.845        | 0.024         | 0.037         | 148.680       | 81.354        |
| 12              | 0:1       | 30.095        | 20.845        | 0.029         | 0.058         | 138.724       | 58.749        |
|                 | 1:4       | 37.601        | 20.845        | 0.025         | 0.062         | 122.341       | 46.630        |
|                 | 1:2       | 26.163        | 20.845        | 0.010         | 0.041         | 104.880       | 39.182        |
|                 | 1:1       | 3.481         | 20.845        | 0.017         | 0.003         | 87.655        | 23.625        |

Bold values indicate the highest and lowest values for each parameter.

Discussion

This study demonstrates the impact of various dietary protein to carbohydrate ratios on important life table parameters of D. suzukii: net reproductive rate, rate of population increase, and generation time. Overall, a low protein to carbohydrate (P:C 1:4) diet composition resulted in D. suzukii higher reproductive values coupled with longer survival periods, while diets containing high protein (P:C 1:1) levels resulted in lower reproductive values and shorter survival periods. Drosophila suzukii had the shortest survival periods when exposed to agar + water only diet (P:C 0:0), and the longest survival periods when exposed to carbohydrate-only diets (P:C 0:1), indicating the importance of carbohydrates as an essential resource for survival. Tochen et al. (2014) evaluated measured net fecundity rate ($r_m$), intrinsic rate of population increase ($r_m$), and mean generation time (T, in days) in SM in blueberries and cherries at 14 and 18°C. Given that fresh fruit is high in soluble sugars, we expected that the life parameters reported for D. suzukii development in cherries and blueberries would be similar to the ones we reported for P:C 0:1.
As expected, low temperatures also influenced life table parameters in SM. Specifically, reproductive rates were lower, and generation times were longer compared with the parameters reported in previous studies at higher temperatures. For instance, the reported net reproductive rate (R*) in this study at 17°C on a beneficial 1:4 diet (51) was lower than the R* reported by Tochen et al. (2014) at 22°C in cherries (195), and by Emilianowicz et al. (2014) at 22°C on cornmeal diet (240). Likewise, the mean generation time (T) in this study at 17°C on 1:4 diet (50) was longer than the T reported by Tochen et al. (2014) at 22°C in cherries (24), and by Emilianowicz et al. (2014) at 22°C on cornmeal diet (30). While comparisons between these studies are confounded by different diets, decreasing temperatures in flies exposed to optimal diet (P:C 1:4) also resulted in longer generation times and lower reproductive rates. At low temperatures, egg maturation is decreased (Toxopeus et al. 2016), and insect metabolism is slower (Storey and Storey 2012), which explains the differences observed at our experimental colder temperatures.

This study demonstrated that both WM and SM flies could live longer than 1,000 DD when exposed to P:C 0:1 diets as opposed to the 410 DD previously reported on flies reared on fruit (Wiman et al. 2016). Drosophila suzukii females exposed to P:C 0:0 and 1:1 diet in this study, however, displayed 100% mortality by 410 DD. While carbohydrates are an essential nutrient for long lifespans, D. suzukii trades off a slightly lower lifespan for a higher reproductive rate when ingesting low protein diets (1:4), and increased protein consumption (P:C 1:1) resulted in a shorter lifespan. It is possible that different macronutrient intake ratios can cause large variability in lifespan, and such ratios should be taken into account for life table parameter estimates.

Drosophila suzukii SM and WM females exposed to low protein diets (P:C 1:4) reached peak fecundity at a later physiological age (400–500 DD) compared with flies exposed to high protein diets (P:C 1:1; ~200 DD). Peak fecundity reported by Wiman et al. (2016) was 200 DD, similar to flies exposed to high protein diets in our study. These earlier fecundity peaks usually correspond with longer lifespans. It is possible that high protein diets accelerate metabolic processes for egg production and cell aging (Souloukis and Partridge 2016). Earlier egg production in turn resulted in earlier mortality, possibly due to the reproductive cost. Peak fecundity levels of ~15 eggs per 80 DD interval reported by Wiman et al. (2016) were similar to SM and WM fed P:C 0:1 diet (16–18 eggs per 100 DD interval) in this study. Higher peak fecundity levels were, however, found for both morphs of D. suzukii exposed to low protein diets (P:C 1:4; 30–40 eggs per 100 DD interval) in this study. It is likely that the fruit used to rear adult flies in previous studies (Tochen et al. 2014, Wiman et al. 2016) caused differences in age-specific survival and fecundity parameters.

### Table 2. Drosophila suzukii winter morph (WM) and summer morph (SM) physiological-age (DD) survival parameters using a Gompertz function (y = 1/(1+e(b*x+a))) for data generated under five diet conditions

| Morph | Diet (P:C) | R²  | df  | F     | P       | Parameter a  | Parameter b  |
|-------|------------|-----|-----|-------|---------|-------------|-------------|
| Winter | 0:1        | 0.98 | 417 | 36,759| <0.001  | -2.146      | 0.0048      |
| Winter | 1:4        | 0.96 | 376 | 28,720| <0.001  | -1.879      | 0.0048      |
| Winter | 1:2        | 0.97 | 251 | 20,091| <0.001  | -2.548      | 0.01         |
| Winter | 1:1        | 0.96 | 105 | 8164  | <0.001  | -2.638      | 0.0275      |
| Winter | 0:0        | 0.97 | 39  | 1854  | <0.001  | -2.417      | 0.0905      |
| Winter | 0:1        | 0.98 | 996 | 207,833| <0.001  | -2.351      | 0.0032      |
| Winter | 1:4        | 0.98 | 715 | 161,711| <0.001  | -2.514      | 0.0046      |
| Winter | 1:2        | 0.99 | 530 | 195,671| <0.001  | -2.346      | 0.00707     |
| Winter | 1:1        | 0.95 | 282 | 8211  | <0.001  | -1.772      | 0.0173      |

As expected, low temperatures also influenced life table parameters in cherries and blueberries were, however, not similar compared with our parameters for SM in P:C 0:1 diet at 14 and 17°C. In fact, blueberries and cherries have a P:C ratio of 1:13 and 1:12, respectively (USDA 2018), and these small quantities of protein can influence survival and fecundity. Yeast and bacteria associated with wounded fruit and D. suzukii guts (Hamby et al. 2016) may additionally provide some dietary protein; therefore, it is possible that D. suzukii adults feeding on fruit are exposed to dietary characteristics more closely related to those of a low or medium protein diet, as opposed to a carbohydrate-only diet. The study by Tochen et al. (2014) also included immature stage data developing in cherries and blueberries, whereas we did not manipulate larval diet, and this may also be a possible cause for discrepancies between life table parameters.
There were some key differences in survival and fecundity between WM and SM. First, WM females had longer generation times (T) than SM in all diets and temperatures. Second, WM had a higher net reproductive rate (R₀) than SM on low protein diets (P:C 0:1:4) in all trialed temperatures. Unexpectedly, SM had higher reproductive rates than WM at the lowest temperatures when exposed to carbohydrate-only or high protein diets. While we assumed that WM would be better suited for reproduction at low temperatures, it is possible that the overwintering period hindered fecundity for females, and SM in suboptimal diets may have a reproductive advantage in the absence of a diapause period. While we do not have WM and SM comparisons at higher temperatures (optimal for reproduction), it is evident that WM perform better than SM at the trialed temperatures in optimal diets. In the field, both WM and SM can be found simultaneously during autumn (Shearer et al. 2016), when temperatures are similar to the ones we tested. In all diets, SM fecundity peaked sooner compared with WM, but this also reflects a shorter lifespan. Although WM exhibit expression of genes that are associated with reproductive diapause (Shearer et al. 2016), this study shows that at suboptimal temperatures, WM have a greater reproductive potential over a longer generation time compared with SM when exposed to favorable low protein diets.

The present study provides new information on several life history parameters of D. suzukii adults. The variable temperatures and diets replicated a range of suboptimal environmental and dietary conditions that may typically be encountered by both SM and WM D. suzukii adults in the field. Although the different temperatures used in this study were static and did not reflect the temporal variability present in field conditions, the physiological-age data from this and previous studies allowed us to compare information gathered in multiple field locations and environmental conditions and allowed a comparison of the impact of diet. We also restrained female flies to no-choice enclosures; future studies should explore the macronutrient geometric
framework of *D. suzukii* by including diet choice and quantifying food consumption. The range of life parameters provided can ultimately be used in refined population models to better describe different scenarios for early-season population buildup, and bottle-neck survival. From a pest management perspective, this information can be further used to develop nutrient-based baits effective to attract (Cai et al. 2018, Wong et al. 2018) and reduce eggload in postoverwintering females, as it has been done with other pest tephritle flies (Yee 2010).

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