Spotted Wing Drosophila Winter Biology

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Spotted wing drosophila (SWD) is a serious pest of small fruits. This invasive fruit fly lays her eggs under the skin of growing and ripening fruits of cultivated and wild host plants. The species was first confirmed in the northeastern US in 2011 and has caused serious crop losses in New York State every year since its arrival. Populations tend to stay very low through the spring, which makes June-bearing strawberry and earlier ripening varieties of blueberry and summer raspberry crops less vulnerable to infestation than berry crops that ripen later in the summer and fall. Fall-bearing raspberries begin to ripen at a point in the growing season when SWD populations are so high, frequent insecticide applications are necessary to control this pest for the life of the crop. Good chemical control often requires weekly foliar applications and good resistance management calls for alternating use of several modes of action. Aside from being very costly, many growers are suffering under "spray fatigue" when attempting schedules that provide good SWD control in fall-bearing raspberry.

> **"Entomologists and cold climate biologists are currently working to determine if there is a northern limit for SWD winter survival and whether or not summer infestations are from local overwintering populations or if they are migrating from milder, southern climates. This information could help with predicting the arrival or severity of yearly infestations."**

Reproductive diapause in SWD could provide some respite to spray fatigue, as the shortening day lengths and cooler temperatures experienced by flies in the fall will trigger a pause in normal reproductive development until environmental conditions improve. Diapausing flies experience changes to their metabolism that improve overwintering survival, like a halt in egg maturation in exchange for improvements to starvation and cold tolerance.

Immature SWD that are growing into adults during the fall also experience cooler temperatures. Development is slowed when larvae experience cooler temperatures, and long periods of near freezing temperatures can kill immature stages. This emphasizes the importance of post-harvest refrigeration of fruit headed to market (Zaman 2014). However, temperatures that do not kill larvae act to make them more tolerant to winter stress, as the slowed development at moderately cool temperatures (50–60°F) results in larger, darker adults (Figure 1). These winter forms, or "winter morphs," are better at tolerating cold, starvation, and desiccation, which contributes to their chance of overwintering survival.

In this study, we looked for evidence of reproductive diapause in local populations in the Finger Lakes region of New York. We also explored the role of day length and temperature in preparing SWD for winter stress by screening lab-reared and field-captured winter morphs for their acute cold tolerance.

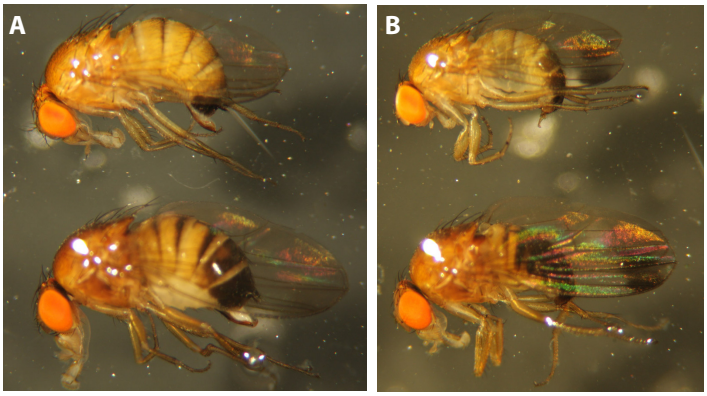

Figure 1. Size and color comparison between summer morph (above) and winter morph flies (below) in (A) female and (B) male SWD.

Materials and Methods

Reproductive status of field-captured SWD females. Flies were trapped weekly at two sites in Ontario Co., NY, using whole wheat bread dough-baited cup traps with apple cider vinegar as a drowning solution. Female SWD were preserved in ethanol through the fall of 2014 and were later dissected in saline solution to determine their reproductive status. Females found to carry mature eggs were considered reproductively mature (Figure 1A), while females with completely undeveloped ovaries were potentially diapausing (Figure 1B). The number of females assessed for reproductive status varied each month, and sample sizes for July–December were 25, 128, 138, 100, 80, and 40 females, respectively. Temperature data were retrieved from nearby weather stations (http://newa.cornell.edu/).

Developmental Acclimation and Acute Cold Tolerance Screening. Developmentally acclimated flies, or winter morphs, were lab-reared in climate-controlled chambers (Percival Scientific Inc., Perry, IA). Colony flies (~ 7 d old), maintained on standard cornmeal diet, were allowed to oviposit in rearing bottles for 24 h in summer conditions (77 ± 2°F, 16: 8 h L:D, 50% RH). Adult flies were removed and bottles containing eggs were moved to chambers set to acclimation treatments. Three developmental acclimation treatments were evaluated: summer morphs (SM; 77 ± 2°F, 16: 8 h L:D), long day winter morphs (longWM; 59 ± 2°F, 16: 8 h L:D), and short day winter morphs (shortWM; 59 ± 2°F, 12:12 h L:D). Development time for SM flies is roughly 10 d, while WM flies begin emerging from pupae after roughly 1 month. Emerging WMs were transferred to new rearing bottles and held at their corresponding day lengths but a cooler 50 ± 2°F for 7 d prior to assays.

Live flies were captured in the field using a similar whole

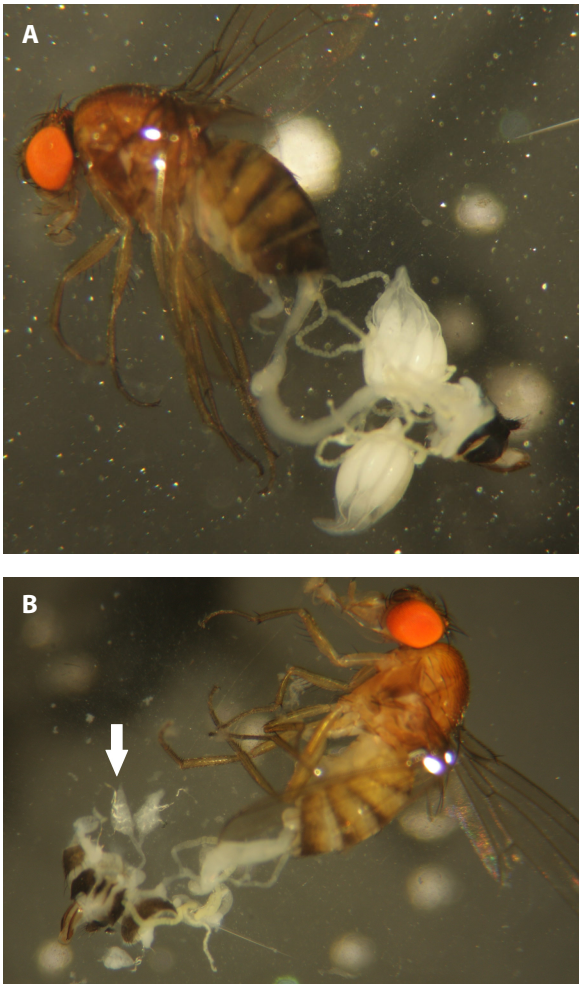

Figure 2. Dissected ovaries containing several mature eggs (A) and completely undeveloped ovaries (B).

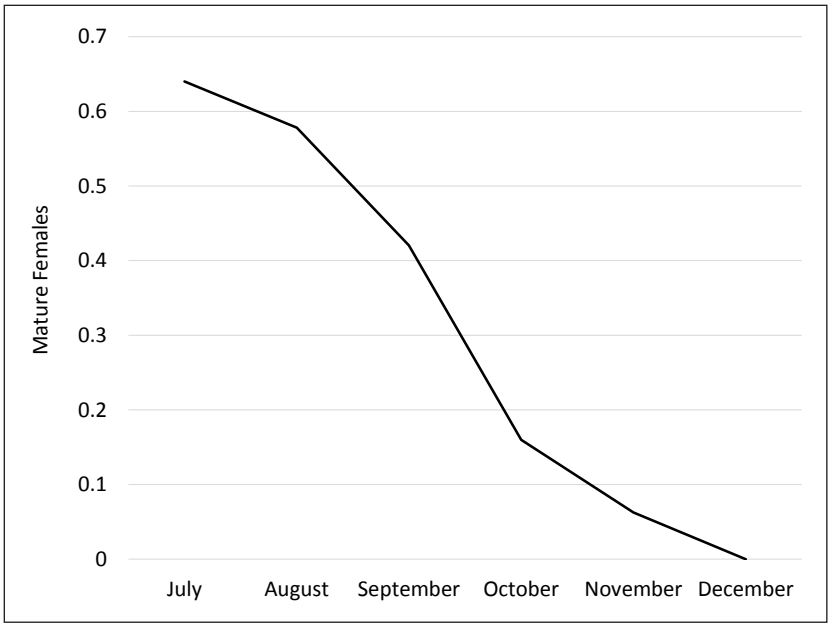

Figure 3. Proportion of field-captured females carrying mature eggs through the fall of 2014.

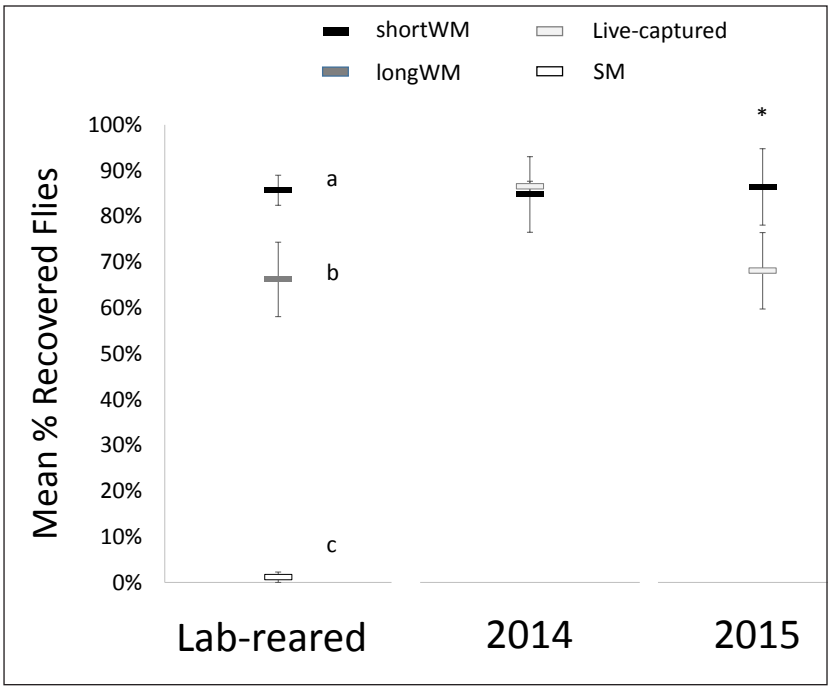

Figure 4. Chill coma recovery (% mean ± SEM) of lab-reared winter morph (WM), summer morph (SM) and live captured flies. Cohorts of ~30 flies were exposed to 16 h of 26.6 ± 0.4°F and recovery was observed after 60 min at room temperature. Values with the same letter are not significantly different according to Tukey's HSD and an asterisk indicates significant difference according to a Student's t-test (α = 0.05).

wheat bait as described previously, except the bait was placed into an empty container rather than over a drowning solution. Thirty traps were hung within the canopy of several cultivated and wild host plants at research farms belonging to NYSAES. Flies were collected on various dates falling between October 20 and November 10 in 2014 and 2015. Weather data were acquired from nearby weather stations (http://newa.cornell.edu/). Cohorts were brought to the lab where they were cold-anesthetized on ice and identified as SWD.

Cold tolerance of lab-reared and live-captured flies was determined by assessing their recovery from exposure to freezing temperatures. Cohorts of SWD (~30 flies/cohort, 50:50 male:female) were isolated in vials containing cotton plugs soaked in distilled water and held on ice for ~1 h prior to assay, to maintain chill coma. Each cohort of cold-anesthetized flies was transferred to a ceramic Peltier plate so that temperatures at the plate surface could be recorded over the duration of each experiment, and plates were held in a programmable freezer (Thermal Product Solutions, Williamsport, PA). Recovery from chill coma was compared after 16 h of exposure to 26.6 ± 0.4°F followed by 1 hr of recovery time at room temperature. Recovered flies were standing and able to walk. Screening was replicated using 8–12 cohorts, depending on the availability of flies during capture periods.

Results

Reproductive status of field-captured SWD females. A steep decline was seen in the proportion of females carrying mature eggs through the fall of 2014, particularly through September and October (Fig 3). There was no effect of collection site on number of reproductively mature fe-

males, but there was an effect of month ($F = 26.58$, $p < 0.0001$). A post-hoc Tukey's mean separation test found that the number of reproductively mature females captured in July, August, and September was significantly different from the number captured in October, November, and December. Day lengths through September and October ranged from 11.8–13.3 h and 10.3–11.8 h, respectively. The average temperatures in September and October were 60°F and 53°F, respectively, and weekly accumulated growing degree days (base 50°F) were 345 and 196, respectively.

Developmental Acclimation

More shortWMs recovered from chill coma than longWM and SM flies ($F_{2,33} = 50.8$, $p < 0.0001$; Fig 4). While there was no difference between lab reared shortWM and live-captured flies in 2014, fewer live captured flies recovered from chill coma than shortWMs in 2015 ($t_{1,19} = 2.0$, $p = 0.0337$).

The average temperatures during the collection periods in 2014 and 2015 were 47°F and 51°F, respectively, and weekly accumulated growing degree days (base 50°F) were 40 and 93, respectively.

Discussion

A suspension in egg production was observed in female SWD captured in the Finger Lakes region of New York in 2014. A strong decline in egg-carrying females was seen from September to October and no eggs were found in dissected females by December (Figure 3). This is similar to a pattern observed in Oregon, Italy, and Japan, associated with shortening day lengths (< 14 h) and sustained cool temperatures (<55°F) normally experienced in the fall. While this suspension in egg production may come too late in the season for many fall crops, those growers who extend their season in high tunnel systems should take note.

Whether or not SWD successfully overwinters in the northeastern U.S. remains a point of speculation. Even with acclimation, SWD is very susceptible to low temperatures and can be killed by short exposures to temperatures below 23°F. Winter temperatures in New York regularly drop below this lethal threshold, and acclimated flies selecting a protected overwintering location may rarely experience acutely lethal temperatures. Here we found that 80% and 60% of field-captured SWD survived exposure to 26.6°F in 2014 and 2015, respectively (Figure 4), and this temperature represents the extreme end of what might be experienced at the soil surface. Although overwintering site selection behavior is still unclear, searches in Oregon have found individual flies under tree bark, inside tree collars, under leaf litter, in dropped apple fruit, and one fly under a board in a greenhouse (Dreves 2014). Flies that find themselves under tree bark are likely to experience ambient temperatures and therefore lethal temperatures during New York winters.

On the other hand, those flies that spend the winter at the soil surface under snow cover or even in man-made structures will stand a better chance of surviving the cold. Chronic cold tolerance studies in Oregon found that WM flies could survive several months of 33.8°F (Shearer et al. 2016). These flies need only tolerate starvation and avoid desiccation. By shifting energy use from egg production to fat storage in the fall, a diapausing winter morph fly is more capable of surviving for months at a time. Because the melanin responsible for coloration also increases the thickness of the flies' exoskeleton, a darker appearance indicates an increase in desiccation resistance.

In conclusion, fall conditions trigger winter acclimation in SWD, including a halt in reproduction, potentially reducing infestations in extended-season fruit crops. Additionally, this acclimation combined with proper site selection could make overwintering a possibility for SWD in northern climates. Entomologists and cold climate biologists are currently working to determine if there is a northern limit for SWD winter survival and whether or not summer infestations are from local overwintering populations or if they are migrating from milder, southern climates. This information could help with predicting the arrival or severity of yearly infestations.

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