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ORIGINAL RESEARCH PAPER

Effects of temperature on the reproduction and development of *Drosophila suzukii* (Diptera: Drosophilidae)

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Abstract The objective of this study was to elucidate how temperature affects the reproduction and development of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), an emerging major pest of blueberry in Japan. Although extensive studies of the biology of this pest have been carried out, the effects of temperature on its reproduction and development remain unknown. We found that when adults mated at 31 °C for 4 days, none of the eggs hatched. Female oviposition and egg hatching rate were also reduced as temperature increased during the oviposition period. When *D. suzukii* larvae developed above 31 °C, pupation and adult eclosion were abolished. According to field observations, adult *D. suzukii* ceased to appear from the end of July 2010, when the average temperature exceeded 28 °C or when the temperature within a day exceeded 33 °C for 8 h or more. Experiments in which the mating temperature fluctuated within a day revealed that both the number of eggs oviposited and their hatch rate were significantly suppressed when the daily temperature regime during mating was either 31 °C for 12 h/25 °C for 12 h or 33 °C for 8 h/25 °C for 16 h, relative to the values at 25 °C for 24 h.

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Introduction

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), also known by the common name spotted-wing drosophila, is one of the most serious pests of thin-skinned fruits including blueberry, cherry, raspberry, grape and strawberry (Kanzawa 1939; Lee et al. 2011a, b; Sasaki and Sato 1995; Walsh et al. 2011). Whereas most *Drosophila* species oviposit on rotted fruits, *D. suzukii* females possess a serrated ovipositor, which allows them to lay eggs into fresh fruits before harvesting (Kanzawa 1939; Sasaki and Abe 1993; Walsh et al. 2011). Blueberry was initially introduced into Japan in the 1950s and has spread widely since the 1990s. No severe pests had been observed prior to this rapid increase in cultivation area, but in 2002 *D. suzukii* caused serious economic damage to fresh blueberry fruits in Chiba Prefecture, and this was the first report of *D. suzukii* as a blueberry pest in Japan (Kawase et al. 2007; Shimizu 2006). Although one of the two major species, Highbush blueberry, *Vaccinium corymbosum* L. (HB), harvested in July, receives serious damage from *D. suzukii*, the other species, Rabbiteye blueberry, *V. virgatum* Aiton (RE), harvested in August, suffers little damage in Tokyo (Drs. J. Shimada, T. Shimizu and T. Motobayashi, personal communication). The temperature in Tokyo is higher in August than in July, suggesting that higher temperature reduces either or both the reproductive activity and development of *D. suzukii*, although the effects of temperature on reproduction and development of this species have not been studied to date.

The objective of this study was thus to elucidate whether temperature affected the reproduction and development of

D. suzukii on blueberry. We examined the relationships among (1) temperature during oviposition and reproduction; (2) temperature during mating and reproduction; and (3) temperature during larval and pupal stages and percentage of pupation and adult eclosion. Finally, we examined (4) the occurrence of adult flies in a blueberry field and (5) the reproduction of *D. suzukii* females under fluctuating temperatures within each day, reflecting the fluctuating temperatures during July in Tokyo. The effect of temperature on reproduction and development of *D. suzukii* is discussed.

Materials and methods

Insects

Drosophila suzukii was obtained from Tokyo Metropolitan University and originated in Yamagata Prefecture. The flies were reared in glass tubes (diameter 25 × 90 mm) with general cornmeal/yeast medium, as used for rearing *D. melanogaster*. The medium contains the following: glucose 100 g, cornmeal 90 g, yeast 40 g, agar 7 g, propionic acid 3 ml (minimum concentration 98 %), Bokinin solution 10 ml and water to 1000 ml. Bokinin solution is 10 % butyl 4-hydroxybenzoate in 70 % ethanol. All insect rearing and experimentation was conducted under a photoperiod of 16L:8D and 60 % relative humidity in an incubator.

Reproduction bioassay conditions

A preliminary experiment showed that antifungal agents consisting of 0.1 ml Bokinin solution and 0.03 ml propionic acid in 100 ml grape juice agar prevented fungal development at 25 °C for 72 h and affected neither oviposition nor the egg hatching rate of *D. suzukii* (data not shown). Modified grape juice agar [2 % agar containing 0.1 % Bokinin solution and 0.03 % propionic acid with 100 % grape juice (Welch's)] was heated and poured into 9-cm-diameter petri dishes (approximately 10 ml/dish) under sterile conditions. Grape juice agar is commonly used for studies of *D. melanogaster* (Salvaterra et al. 2006) and was modified in this study by adding the above antifungal agents to preserve the agar for longer, until egg hatching. This agar rendered the oviposited fly eggs easily visible and countable.

The number of eggs laid during 24 h by females of different ages after adult emergence and the percentage of eggs that hatched within 48 h after the females were removed were determined using these grape juice agar plates. While the hatch rate did not fluctuate, the number of eggs laid was significantly lower for females younger than 4 days old, but did not change significantly after 4 days old (supplementary materials, Fig. 1S). Thus, the following experiments were done using 4-day-old females.

Relationship between reproduction and temperature during oviposition

The relationship between reproduction of *D. suzukii* and temperature during oviposition was examined as follows. Newly emerged flies (within 24 h; Day 0 adults) were reared in groups (30–50 female and male flies) in the glass tubes on general medium for 4 days at 25 °C, and females were then transferred individually onto grape juice agar plates and kept for 24 h at 25, 28, 31 or 33 °C. The flies were removed, and the number of eggs laid was counted under a dissecting microscope (×10). The eggs were kept at 25, 28, 31 or 33 °C for 48 h, and the number of larvae that hatched was counted under the microscope. The total number of female flies used in the experiment was 43, 29, 32 and 32 for 25, 28, 31 and 33 °C, respectively. The number of eggs oviposited was analyzed by the Kruskal-Wallis test. Statistical significance of differences among the four temperatures was calculated using the Steel-Dwass test. The percentage of eggs hatched was analyzed by one-way ANOVA after arcsine transformation. Post hoc analyses were performed with the Tukey-Kramer multiple range test when the ANOVA F ratio was significant at $p < 0.05$.

Relationship between reproduction and temperature during mating

Day 0 adults (female and male, 30–50 in total) were reared on general medium in the glass tubes for 4 days at 25, 28, 31 or 33 °C to allow them to mate, and Day 4 female flies were transferred individually to grape juice agar plates and kept for 24 h at 25 °C. The resulting eggs were kept at 25 °C for 48 h, and the numbers of laid eggs and percentage of hatched larvae were counted and analyzed as described above.

Relationship between pre-adult development and temperature

Drosophila suzukii larvae were transferred individually, within 24 h of hatching, to general medium in half-ounce cups and reared at 25, 28, 31 or 33 °C. The insects were observed daily, and larval development, pupation, adult eclosion and death were recorded. The percentage pupation (number of larvae that pupated divided by number of larvae examined, multiplied by 100) and percentage adult eclosion (number of pupae that eclosed to adults divided by number of larvae examined, multiplied by 100) were analyzed by one-way ANOVA after arcsine transformation.

Larval period (time from egg hatching to pupation) and pupal period (time from pupation to adult eclosion) were analyzed by Kruskal–Wallis and Steel–Dwass multiple comparison. In each replication 35 larvae were examined, with five replications at 25 °C, 7 at 28 °C, 6 at 31 °C and 3 at 33 °C.

Field monitoring

Occurrence of *D. suzukii* was monitored at a blueberry orchard in Tokyo University of Agriculture and Technology (Fuchu, Tokyo; 35°41′N, 139°29′E), which was located within a larger orchard (0.78 ha) additionally planted with persimmon (*Diospyros kaki* Thunb.) (0.3 ha), kiwi fruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa*) (0.08 ha) and pear (*Pyrus pyrifolia* var. *culta*) (0.2 ha). “Sake-honey traps,” modified from 500-ml PET bottles and containing 50-ml liquid food (1:5 honey:sake) (Sasaki and Abe 1993), were placed in the orchard. Traps were placed 30 cm above the ground, shaded by the blueberry trees to which they were attached. Twelve traps were placed in the orchard from 10 May to 4 July 2010 and 13 from 5 July 2010 to 13 January 2011. Among 82 HB plants planted in an area of 0.04 ha, 7 traps were attached; 6 traps were attached among 54 RE plants in an area of 0.04 ha. No chemical pesticide was used in the blueberry orchard during the time of observation. The traps were checked every 14–21 days, and captured insects were transferred into 80 % ethanol. *Drosophila suzukii* adults were identified by the spot on the male’s wing and the male’s foreleg hair morphology, and by the ovipositor of the female (Dr. K. Tamura, personal communication). Air temperature in the orchard was monitored using a digital thermometer (Ondotori RTR-51A, T&D Corp., Nagano, Japan) placed at a height of 120 cm above the ground and shaded by a thermal insulation sheet (DuPont Tyvek, DuPont-Asahi Flash Spun Products Co., Ltd., Tokyo, Japan).

Effect of fluctuating temperature on reproduction of *D. suzukii*

Based on actual temperature fluctuations in Fuchu, Tokyo, in 2010 (Fig. 4b), two sets of fluctuating temperature regimes were organized in a programmable incubator (MIR554, Sanyo Electric Co./Panasonic, Osaka, Japan) as follows. The photoperiod schedule was lights on at 08:00 and lights off at 00:00. Set1 involved 31 °C from 08:00 to 20:00 and 25 °C from 20:00 to 08:00 (i.e., 31 °C × 12 h + 25 °C × 12 h). Set2 involved 33 °C from 08:00 to 16:00 and 25 °C from 16:00 to 08:00 (i.e., 33 °C × 8 h + 25 °C × 16 h). The average temperature of set1 and set2 was 28 °C and 27.6 °C, respectively, similar to that recorded on 21 July (27.3 °C), after which *D. suzukii* occurrence declined dramatically (Fig. 4a). Newly emerged adults (at 25 °C within 24 h; female and male) were reared in each temperature set until Day 4 for mating. Female flies were then transferred individually to grape juice agar plates and allowed to oviposit for 24 h at 25 °C. Ten female flies were used per treatment. As described above, they were removed, and the number of eggs oviposited during 24 h was counted under a microscope. After a further 48 h, the egg hatching rate was determined. The number of eggs oviposited and the percentage of eggs hatched were analyzed as described above.

Results

Relationship between reproduction and temperature during oviposition

The 4-day-old mated females were allowed to oviposit on grape juice agar plates at 25, 28, 31 or 33 °C for 24 h. The number of eggs laid and the percentage of eggs hatched under different temperatures are shown in Fig. 1. At increasing temperatures, the number of eggs laid per female decreased significantly ($H = 49.6$, $df = 3$, $p < 0.01$). Each increment in temperature resulted in a significant decrease in the number of eggs oviposited, except between 28 and 31 °C. As the oviposition temperature increased, the percentage of eggs that hatched also decreased significantly ($F = 16.9$, $df = 3$, $p < 0.01$). A statistically significant difference was only observed at 33 °C relative to the lower temperatures from 25 to 31 °C. Thus, an oviposition temperature of 33 °C severely affected oviposition and the hatching rate.

Relationship between reproduction and temperature during mating

Adult flies within 24 h of emergence were mated at 25, 28, 31 and 33 °C for 4 days, and individual females were allowed to oviposit on grape juice agar plates at 25 °C for 24 h. Since neither male nor female flies survived for 4 days during mating at 33 °C, no data are shown for this temperature. The number of eggs laid per female was 25.7 ± 1.3, 12.0 ± 2.7 and 3.35 ± 1.3 (average ± SE) at 25, 28 and 31 °C, respectively (Fig. 2a). The number of eggs oviposited decreased significantly as the mating temperature increased ($H = 42.1$, $df = 2$, $p < 0.01$). The percentage of eggs that hatched also decreased significantly as the mating temperature increased (Fig. 2b): 83.0 ± 3.6, 43.7 ± 10.4 and 0 ± 0 % (average ± SE) hatched at 25, 28 and 31 °C, respectively ($F = 31.4$, $df = 2$, $p < 0.01$). Thus, reproductive success was abolished at 31 °C.

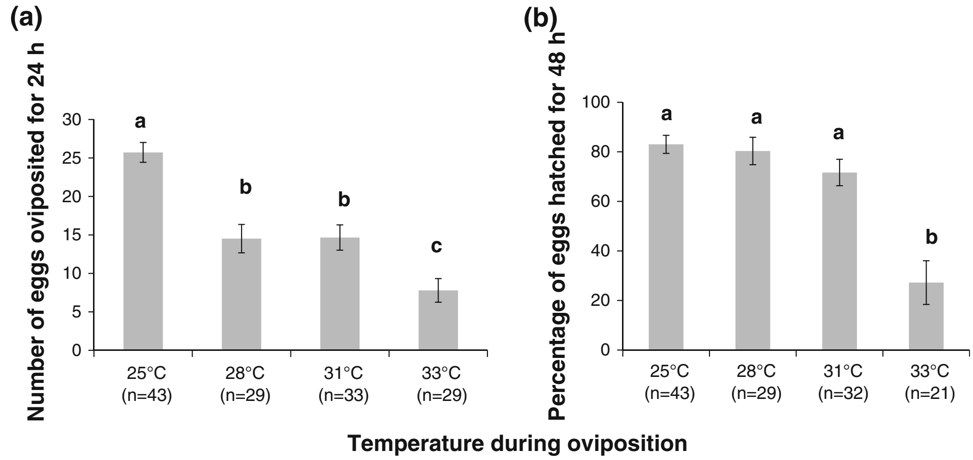

Fig. 1 Relationship between reproduction of *Drosophila suzukii* and temperature during oviposition. **a** Number of eggs laid during 24 h. **b** Percentage of eggs that hatched during 48 h. Mating was done for 4 days at 25 °C in all treatments. Death of female flies occurred at 31 °C and 33 °C. *Bars* indicate standard errors. *Different letters* denote a significant difference

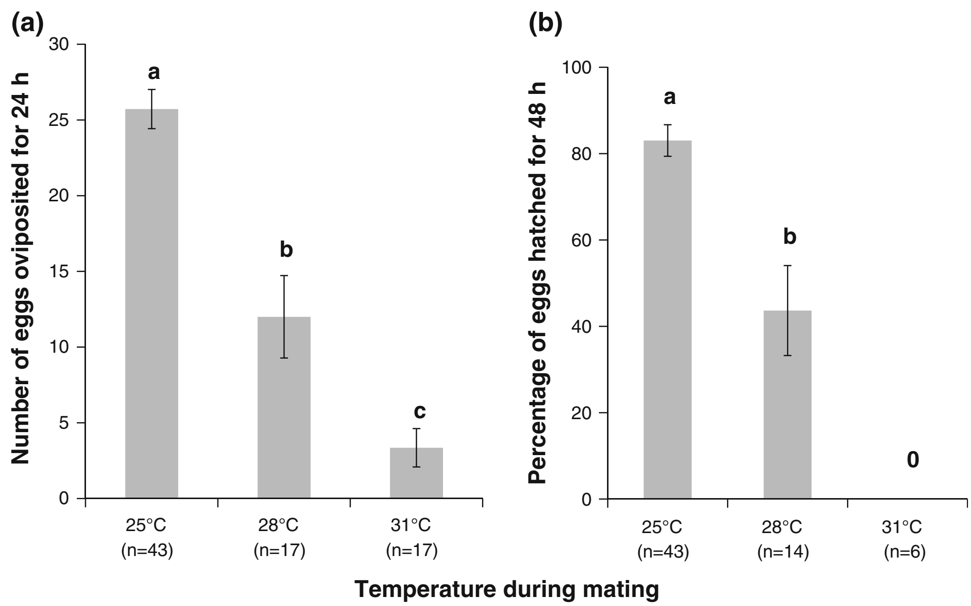

Fig. 2 Relationship between reproduction of *Drosophila suzukii* and temperature during mating. **a** Number of eggs laid during 24 h. **b** Percentage of eggs that hatched during 48 h. Death of female flies occurred at 31 °C, and all flies died during the 4-day mating period at 33 °C. *Bars* indicate standard errors. *Different letters* denote a significant difference

Relationship between pre-adult development and temperature

Newly hatched larvae were transferred to general medium within 24 h and reared individually at 25, 28, 31 and 33 °C. All larvae died during the larval stage at 33 °C. The durations of the larval stage at 25, 28 and 31 °C were 6.4 ± 0.1, 6.4 ± 0.1 and 8.2 ± 0.1 days, respectively; the larval period was significantly longer at 31 °C than at 25 and 28 °C ($H = 186.7$, $df = 2$, $p < 0.01$). The percentage of pupation was 97.1 ± 1.6, 88.1 ± 4.1, 57.6 ± 6.9 % and 0 % at 25, 28, 31 and 33 °C, respectively (Fig. 3a). The pupation rate decreased significantly as temperature increased ($F = 68.2$, $df = 3$, $p < 0.01$) and was significantly lower at 31 °C than at 25 and 28 °C. The pupal periods for insects reared at 25, 28 and 31 °C were 4.9 ± 0.05, 4.3 ± 0.04 and 4.0 ± 0.00 days, respectively; the pupal period was significantly longer at 25 °C than at 28 and 31 °C ($H = 73.3$, $df = 2$, $p < 0.01$). Adult eclosion was also significantly affected by increasing temperature ($F = 127.2$, $df = 2$, $p < 0.01$) and was 82.2 ± 4.0, 65.3 ± 3.4 and 2.83 ± 2.8 % at 25, 28 and 31 °C, respectively (Fig. 3b). Pupae maintained at 31 °C showed a significant decrease in adult eclosion, and only three pupae in one replication among six (n = 35/replication) emerged successfully to adults.

Occurrence of *D. suzukii* in the blueberry orchard

Air temperatures and adult captures of *D. suzukii* by the sake-honey traps are shown in Fig. 4a. In Japan, female *D. subpulchrella* Takamori adults, like those of *D. suzukii*, have a serrated ovipositor and lay eggs in intact fruits (Sasaki and Abe 1993; Takamori et al. 2006). Adult male *D. suzukii* and

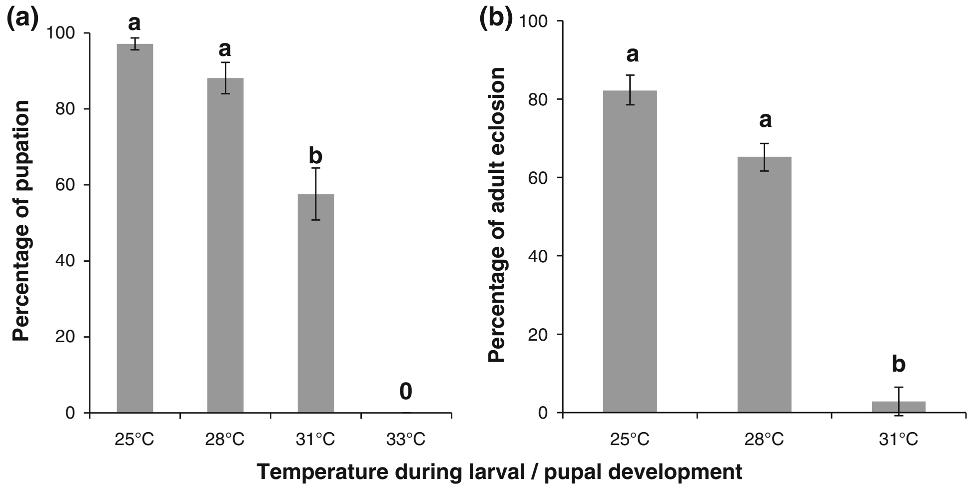

Fig. 3 Relationship between development of *Drosophila suzukii* and temperature during pre-adult stages. **a** Percentage of pupation. **b** Percentage of adult eclosion. Newly hatched neonate larvae were reared under various temperatures until adult eclosion. A total of 35 larvae were examined for each temperature, with five replications at 25 °C, seven at 28 °C, six at 31 °C and three at 33 °C. Since no pupae were obtained at 33 °C (**a**), adult eclosion at this temperature is not displayed in **b**. *Bars* indicate standard errors. *Different letters* denote a significant difference

D. subpulchrella have spotted wings but can be distinguished by the sex comb on their forelegs (Dr. K. Tamura, personal communication). Based on this morphological distinction, only *D. suzukii* males were counted in these traps. *Drosophila melanogaster* and other *Drosophila* species was occurred in the rotten fruit on the ground.

Drosophila suzukii numbers peaked twice during the year, with an interval in summer during August and September between the two peaks. *D. suzukii* adults first occurred on 20 June (average temperature 25 °C); notably, however, none were captured from 3 August (average temperature 30.3 °C) to 28 September (21.0 °C). The peaks of adult capture in the blueberry orchard were 4 July and 27 October. Adults persisted in the orchard until 23 December. HB blueberry fruits were seen from May until July, but not in August, whereas RE fruits appeared from May until August, but not in September (data not shown).

More precise temperature fluctuations within a day are shown in Fig. 4b from 4 July to 3 August. Those 31 days included 4 consecutive days when the temperature exceeded 33 °C for more than 8 h (19–22 July; Fig. 4b). Adults appeared again from 13 October in the blueberry orchard. From October, no blueberry fruits were available, but American pokeweed (*Phytolacca americana* L.), persimmon and kiwi fruit were ripening near the blueberry orchard.

Relationship between reproduction of *D. suzukii* and fluctuating temperature

The above experiments were done at constant temperature, but daily temperatures fluctuate under natural conditions. According to the field monitoring in 2010, capture of *D. suzukii* declined dramatically over the 14 days from 21 July to 3 August (Fig. 4a). During those days, the estimated average temperature was 29.3 °C (Fig. 4a), but the temperature exceeded 33 °C for more than 8 h within a day on 4 consecutive days, as noted above (19–22 July; Fig. 4b). Two sets of fluctuating temperature were therefore applied during the 4-day mating period, set1 consisting of 31 °C for 12 h and 25 °C for 12 h (average temperature was 28 °C) and set2 consisting of 33 °C for 8 h and 25 °C for 16 h (average temperature was 27.6 °C). The mean numbers of eggs laid under set1 and set2 conditions were 7.0 ± 3.1 and 10.3 ± 4.5, respectively (Fig. 5a), and were significantly lower than 25.7 ± 1.29, the number laid by females that mated and oviposited at 25 °C ($H = 20.7$, $df = 2$, $p < 0.01$). The percentages of eggs that hatched for set1 and set2 were 15.6 ± 6.1 and 21.3 ± 8.8 %, respectively (Fig. 5b), although, among ten females examined, six from set1 and five from set2 did not lay any eggs. The percentages of eggs that hatched for set1 and set2 were also significantly lower than those (82.3 ± 3.9 %) for females that mated and oviposited at 25 °C ($F = 29.0$, $df = 2$, $p < 0.01$).

Discussion

The number of eggs laid and percentage of eggs hatched were both affected by temperature during mating and oviposition, and higher temperature during the larval and pupal period also affected the survival of *D. suzukii* (Figs. 1, 2, 3). Thus, reproduction and survival were suppressed by higher temperature at all stages of the *D. suzukii* life cycle. This finding is consistent with the previously

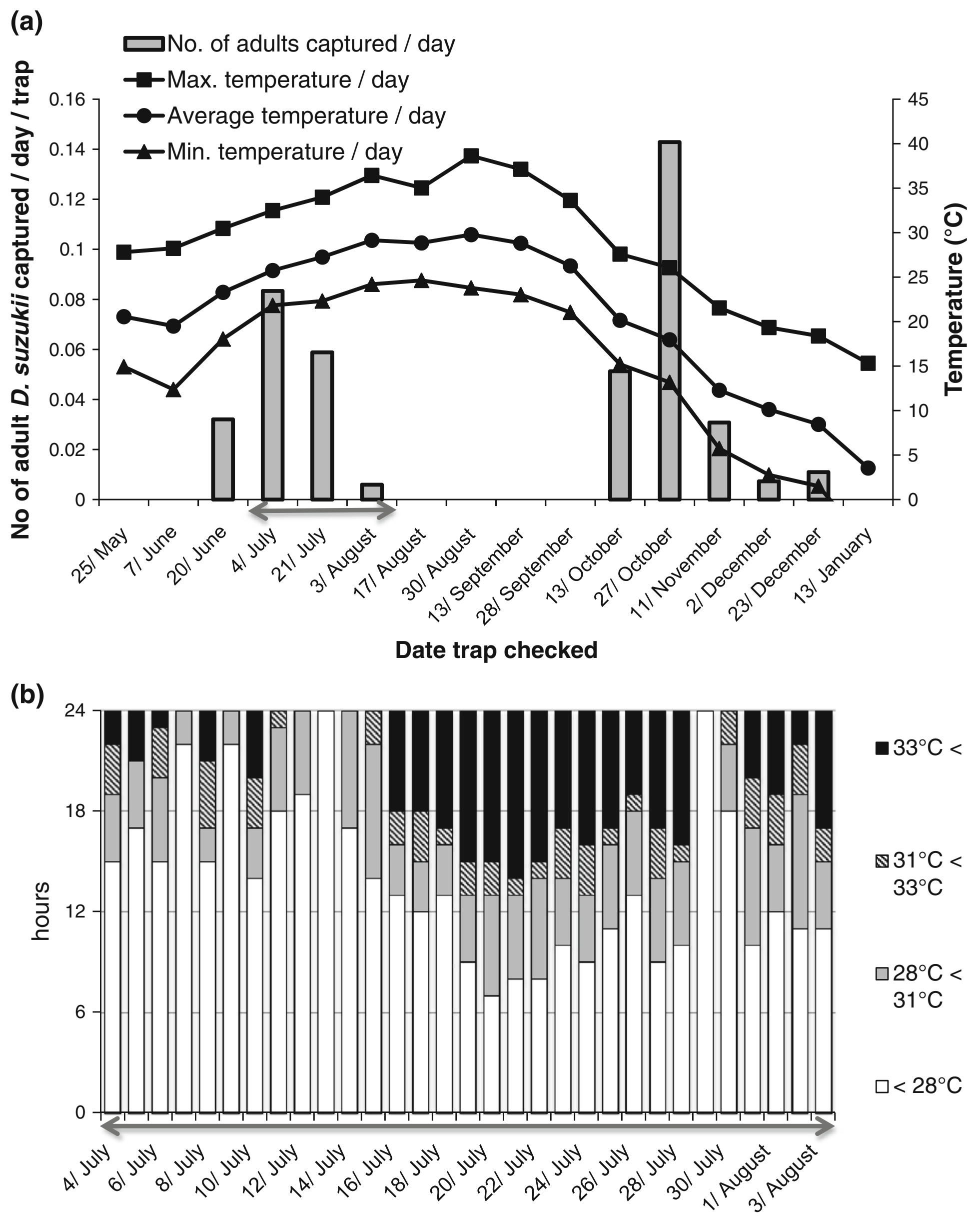

Fig. 4 Number of adult *Drosophila suzukii* captured in the blueberry orchard (**a**) and detailed temperatures during the summer period when the occurrence of *D. suzukii* declined in Tokyo (**b**). **a** Maximum (Max.), minimum (Min.) and average air temperatures were monitored in the same orchard. Sake-honey traps were used to capture adult flies, and the average number of adults captured per day per trap is shown. The *double-headed arrow* in **a** indicates the period of detailed temperatures that is shown in **b**. **b** Temperature was recorded every hour with an automated temperature-monitoring device

reported temperature response of *D. suzukii* (Kanzawa 1934; Kimura 2004). Kimura (2004) studied the geographical differences between populations of Drosophila species obtained from different parts of Japan and revealed that the 50 % lethal temperature for adult *D. suzukii* was 32.2–32.7 °C in strains from both Sapporo (43.1°N) and Tokyo (35.5°N).

In this study, 4-day-old adult females were used in all experiments, and the number of eggs laid per day by one female fly of that age on grape juice agar plates at 25 °C was 23.4 ± 4.0 (Fig. 1S). Egg oviposition by single *D. suzukii* females has been studied previously on fruits including cherry, blueberry and wine grape (Kanzawa 1939; Kinjo et al. 2013; Lee et al. 2011a). Kanzawa (1939) reported that the average numbers of eggs laid by *D. suzukii* on cherry fruits ranged from 7 to 16, while Lee et al. (2011a) found that the average numbers of eggs laid daily by a single female on blueberry fruits of California cultivars were from 9.7 (Emerald) to 13.3 (Misty). Thus, our values for the number of eggs oviposited using the grape juice agar plate method are higher than those obtained for real fruits. Kinjo et al. (2013) revealed that more eggs were laid in blueberries of cultivars possessing softer fruits than in those having firmer fruits. Moreover, *D. suzukii* tends to oviposit at the softer parts of fruits, which implies that the fly spends time searching for parts of fruits to lay eggs (unpublished observation). Adult female flies may thus lay more eggs on grape juice agar, which has uniform firmness

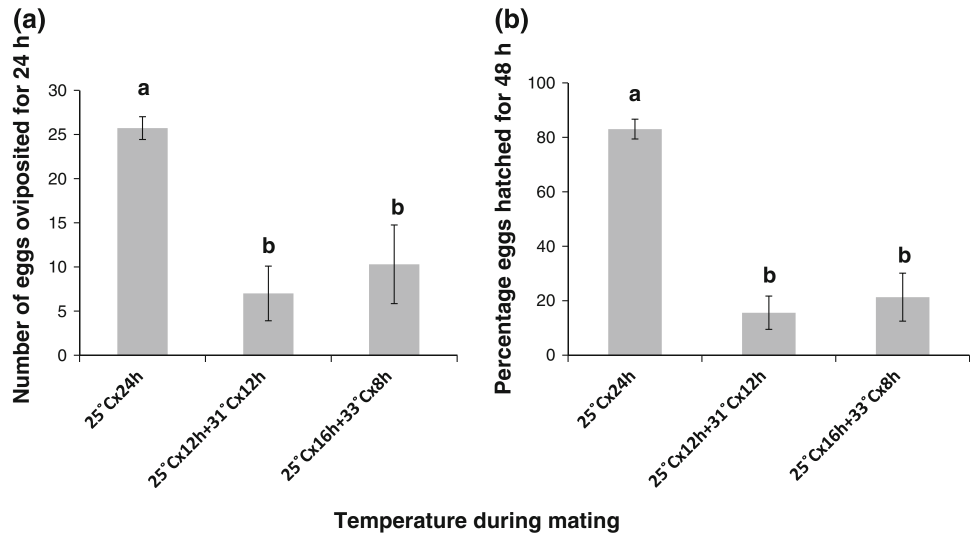

Fig. 5 Relationship between reproductivity and temperature during mating of *Drosophila suzukii*. **a** Number of eggs laid. **b** Percentage of eggs hatched. Mating was done for 4 days at fluctuating temperatures within a day, and oviposition was done at 25 °C for 24 h in all treatments. Total number of female flies examined was ten in each treatment. *Bars* indicate standard errors. *Different letters* denote a significant difference

and is likely to be softer than real fruits, because their searching and handling time is reduced.

Field trapping revealed that *D. suzukii* adults occurred twice in a year, with essentially none captured in August or September (Fig. 4a). Similar results were obtained previously from cherry fields in Yamanashi and Fukushima Prefectures and at lower-altitude areas in Nagano Prefecture (Kanzawa 1939; Mitsui et al. 2010; Sasaki and Abe 1993). The second peak occurrence may have been delayed to 27 October rather than during September as recorded in the previous studies, because the temperature was unusually high in 2010.

Therefore, two sets of fluctuating temperatures were examined. Both sets (set1: 31 °C × 12 h + 25 °C × 12 h; set2: 33 °C × 8 h + 25 °C × 16 h) affected the number of eggs laid and their hatchability (Fig. 5). Thus, the disappearance of *D. suzukii* adults in August in 2010 can be explained by suppressed reproduction of adult flies at the higher temperature.

To optimize the cultural control of *D. suzukii*, fruit cultivars that can be harvested during higher temperature periods should be adopted. Plant factories are also attracting increasing attention for blueberry production in Japan. If *D. suzukii* were to invade such facilities, physical control using cultivation temperatures above 31 °C for 4 days should successfully eliminate the reproduction of *D. suzukii*.

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