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ORIGINAL ARTICLE

Winter fruit contribution to the performance of the invasive fruit fly *Drosophila suzukii* under different thermal regimes

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Abstract Polyphagous insect species develop using multiple host plants. Often considered beneficial, polyphagy can also be costly as host nutritional quality may vary. *Drosophila suzukii* (Matsumura) is an invasive species that can develop on numerous fruit species over the annual cycle. Here, we assessed the contribution of winter-available fruit to the development of seasonal populations of *D. suzukii*, under fluctuating late winter/early spring temperature regimes. We infested an artificial diet and three suitable fruit species available in winter/early spring (*Aucuba japonica*, *Elaeagnus × submacrophylla*, *Viscum album*) with *D. suzukii* larvae under three temperature regimes: constant 20 °C, fluctuating controlled regime of 8–15 °C (12 h of light at 8 °C and 12 h of dark at 15 °C), and uncontrolled outdoor regime during spring. As expected, fly performance was impaired by early spring-like environmental conditions, whatever the development diet, and the winter fruit were suboptimal diets compared to the artificial diet, whatever the thermal regime. However, under cold fluctuating temperature regimes, the ranking of fruit supporting the best performance changed, highlighting the occurrence of physiological trade-offs. Winter-acclimated females preferentially oviposited in *A. japonica* and/or *E. × submacrophylla*, whatever the thermal regime, which does not support the preference–performance hypothesis. This finding is also discussed in the context of *D. suzukii* management strategies.

Key words life history traits; overwintering; polyphagy; preference–performance hypothesis; thermal fluctuations; trade-off

Introduction

In temperate regions, winter poses significant food scarcity challenges for most organisms (Danks, 1978; Moore & Lee, 1991; Folwarczny *et al.*, 2022). During this time, the diversity of native fruit-bearing plants is limited (Thompson & Willson, 1979; Herrera, 1982),

though some invasive species may provide additional resources (Greenberg & Walter, 2010). Most frugivorous insects enter dormancy to overwinter, relying on predormancy energy reserves (Bale & Hayward, 2010; Storey & Storey, 2012; Sinclair, 2015; Gill *et al.*, 2017; Lehmann *et al.*, 2017). However, insects that remain active during winter rely on seasonal fruit and most are polyphagous allowing them to switch resources (Kennedy & Storer, 2000; Butterworth *et al.*, 2023). For instance, *Drosophila melanogaster* switches its feeding preference from yeast to plants at low winter temperature (Brankatschk *et al.*, 2018). While polyphagy is often considered advantageous, it can also reduce offspring

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performance (e.g., developmental rate, survival) depending on host plant quality (Janz, 2003; Poyet *et al.*, 2015). The “bet-hedging” strategy (Simons, 2011) mitigates this risk by spreading oviposition across multiple host plants (Jaenike, 1990; Singer, 2010). This may result in a trade-off if the most abundant host is not optimal for offspring performance (Singer, 2010). Many successful pest insects are polyphagous (Singer, 2010; Wilson *et al.*, 2012), including the invasive fruit fly *Drosophila suzukii*, that remains active during winter if conditions permit (Ulmer *et al.*, 2024).

Originating from Asia, *D. suzukii* Matsumura (Diptera: Drosophilidae) has spread across different continents since 2008 (Ørsted & Ørsted, 2019; Aouari *et al.*, 2022), infesting a variety of crops and wild fruit (Poyet *et al.*, 2015; Kenis *et al.*, 2016). Its invasive success is attributed to its polyphagy (Poyet *et al.*, 2015), temperature-induced phenotypic plasticity (Framout *et al.*, 2018), high fertility (Rota-Stabelli *et al.*, 2013) and low biotic pressures in invaded regions (Poyet *et al.*, 2013; Miller *et al.*, 2015). Unlike other drosophilids, it can oviposit in unripe or ripening fruit due to its serrated ovipositor (Clemente *et al.*, 2018) and is active all year-round, with population densities fluctuating based on environmental factors, such as temperature, humidity and the availability of food resources (Lee *et al.*, 2015; Arnó *et al.*, 2016; Shearer *et al.*, 2016; Tochen *et al.*, 2016; Wang *et al.*, 2016; Ulmer *et al.*, 2022).

Low temperatures slow the growth of ectotherms, generally leading to larger adult size and greater longevity (Angilletta *et al.*, 2004; Denlinger & Lee, 2010). The effects of low temperature on *D. suzukii* performance have been extensively explored both under laboratory (Tochen *et al.*, 2014; Shearer *et al.*, 2016; Wallingford *et al.*, 2016; Rendon *et al.*, 2019; Panel *et al.*, 2020; Schlesener *et al.*, 2020; Colinet & Kustre, 2024; Raynaud-Berton *et al.*, 2024) and field conditions (Shearer *et al.*, 2016; Wallingford *et al.*, 2016; Grassi *et al.*, 2018). Development of *D. suzukii* at low temperatures (< 10 °C) induces the production of winter-acclimated individuals with increased melanization (Toxopeus *et al.*, 2016; Framout *et al.*, 2018; Colinet & Klustre, 2024), potentially aiding thermoregulation and pathogen resistance (Clusella Trullas *et al.*, 2007; Colinet & Kustre, 2024).

Winter-acclimated *D. suzukii* flies enter reproductive dormancy, and females resume egg maturation as temperatures rise in spring (Grassi *et al.*, 2018), while searching for suitable winter/early spring host plants to oviposit. However, available fruit for oviposition are scarce and vary in nutritional content (Poyet *et al.*, 2015; Shu *et al.*, 2022; Deconninck *et al.*, 2024a; Deconninck *et al.*, 2024b), with limited choice at the end of win-

ter (Grassi *et al.*, 2018; Deconninck *et al.*, 2024c). Examples of suitable hosts include a variety of ornamental fruit species found in gardens and parks as well as wild species bearing fruit during winter, such as *Aucuba japonica*, *Elaeagnus × submacrophylla*, *Hedera helix*, *Lonicera nitida*, *Mahonia* spp., *Rosa canina*, *Skimmia japonica*, *Symphoricarpos* spp., and *Viscum album* (Poyet *et al.*, 2015; Kenis *et al.*, 2016; Grassi *et al.*, 2018; Panel *et al.*, 2018). Among these, *A. japonica*, *E. × submacrophylla*, *Mahonia* spp. and *V. album* fruit have been shown to support development of *D. suzukii* in lab settings, but have primarily been studied at a constant 20 °C, which may not reflect natural conditions (Poyet *et al.*, 2015; Panel *et al.*, 2018). Furthermore, nutritional factors such as protein:carbohydrate (P:C) ratio likely influence larval development and adult performance (Jaramillo *et al.*, 2015; Silva-Soares *et al.*, 2017; Young *et al.*, 2018). While the “preference–performance” (also known as “mother knows best”) hypothesis suggests that females choose hosts optimizing offspring fitness (Jaenike, 1990; Gripenberg *et al.*, 2010; García-Robledo & Horvitz, 2012), evidence of its application to *D. suzukii* is mixed (Burrack *et al.*, 2013; Poyet *et al.*, 2015; Olazcuaga *et al.*, 2019). Other biotic and abiotic parameters in the natural environment might influence the host preference of females (e.g., the female microbiota; Henry *et al.*, 2020).

Our study investigated the performance of *D. suzukii* on winter fruit under realistic temperature regimes reflecting the late winter/beginning of spring conditions. We compared optimal, constant lab conditions with more ecologically relevant, natural trophic and thermal conditions. Specifically we assessed the performance of flies under contrasting conditions: (1) an optimal control environment combining constant 20 °C and artificial diet, and (2) more ecologically relevant conditions using fluctuating temperatures (either a controlled regime of 8–15 °C or uncontrolled outdoor conditions in early spring) and winter fruit as food (*A. japonica*, *E. × submacrophylla* or *V. album*). We addressed four hypotheses: (1) Under cold fluctuating temperature regimes, *D. suzukii* performance would be impaired compared to a constant 20 °C, regardless of diet and (2) performance would also be impaired in winter fruit compared to an optimal artificial diet, regardless of temperature regime; (3) trade-offs may occur between development and reproductive traits based on the fruit in which the larvae developed (Chakraborty *et al.*, 2023); and (4) females would oviposit on the most suitable fruit, as per the preference–performance hypothesis, but preference may change with temperature, because of the nutritional requirements of winter and summer individuals may differ (Rendon *et al.*, 2019).

Materials and methods

Insect rearing

The *D. suzukii* wild strain used, supplied by ECO-BIO laboratory (Rennes, France), was initiated in 2019 from adults collected on raspberries in Rennes, France (48°7'2.158"N, 1°40'40.053"W). This common *Wolbachia*-free strain is standard for experiments within the DroThermal project (<https://www.drothermal.cnrs.fr>). The population was maintained on a banana-based medium (water 50 mL, fresh banana 200 g, yeast 15 g, ethanol 15 mL, sugar 10 g, agar 10 g, NipaginTM 2 g) at 20 °C under a 12 h : 12 h light-dark cycle.

Fruit collection

Branches of *V. album*, *A. japonica* and *E. ×submacrophylla* with fruit were collected weekly between January 20, and April 20, 2023 in the region of Amiens, northern France (49°54'0.01"N, 2°18'0"W) (Table S1). They were kept hydrated with moistened cotton wool and stored outdoors in insect-proof nylon mesh cages (30 cm × 30 cm × 30 cm) inside plastic greenhouses (150 cm × 90 cm × 60 cm) for use within the week. Only ripe, intact fruit, assessed visually for color and firmness, were selected. For each infestation session, a random batch of 10 fruit was stored at −80 °C for nutritional analyses (proteins, carbohydrates; see Supporting Information).

Developmental diets and temperature regimes

To examine the effects of fruit and temperature on *D. suzukii* development and performance, we used four diets: *A. japonica*, *E. ×submacrophylla* and *V. album* fruit (referred to as *Aucuba*, *Elaeagnus*, and *Viscum*, respectively), and a control carrot-based artificial diet (water 250 mL, sucrose 12.5 g, agar 3.75 g, brewer's yeast 7.5 g, cornmeal 5 g, carrot powder 12.5 g, NipaginTM 0.4 g), which optimally supports *D. suzukii* development (Enriquez *et al.*, 2018). Flies were naïve to all four diets, as they differed from the rearing diet.

Each diet was manually infested with five first instar larvae (L1) of *D. suzukii* that were obtained by allowing 1- to 6-d-old females to oviposit for 8 h on cherry medium (agar 1.5 g, water 50 mL, cherry juice 50 mL), then incubating eggs for 48 h at 20 °C until L1 emerged. Fruit were incised (incision length ~4 mm) for deposition of larvae, weighed (± 0.01 g; Traveler TA152, Ohaus Corporation, USA), and placed in 30 mm × 55 mm plastic vials with water-saturated cotton. Larvae on the control

diet were placed directly onto 1 mL of carrot diet in 2 mL Eppendorf tubes sealed with cotton.

Samples were then assigned to one of three temperature regimes: CR for constant regime (constant 20 °C, L:D = 12 h : 12 h, 75% RH, Snijders ECP01E phytotron), FCR for fluctuating controlled regime (fluctuating 8–15 °C, L:D = 12 h : 12 h, 75% RH, Memmert HPP200 phytotron, with 12 h of light at 8 °C and 12 h of dark at 15 °C, transitioning over 15 min to warm and 45 min to cool), and UNR for uncontrolled outdoor regime (March 24, to June 30, 2023, with vials placed in insect-proof nylon mesh cages within open greenhouses). Greenhouse temperatures were recorded with HOBO dataloggers every 15 min.

Life history trait measurements

To evaluate the combined effects of thermal regime and larval diet on *D. suzukii* fitness, we measured several life history traits. Emergence was monitored daily, and newly emerged individuals were sexed and randomly assigned to one of four assays: (1) starvation resistance, (2) survival with food, (3) ovarian load (females only), and (4) energy content (females only). Development time (*i.e.*, time from L1 deposition to emergence), emergence success and sex ratio were recorded for all individuals.

Starvation resistance and survival with food for 15 d Upon emergence, adults were individually introduced into 5 mL tubes (12 mm × 75 mm) with either distilled water-saturated cotton (starvation) or filter paper (7.5 mm × 15 mm) soaked in a nutrient solution (water + 2% sugar + 5% yeast, refreshed every 2 d; Plantamp *et al.*, 2017), and kept at 20 °C, L:D = 12 h: 12 h, 75% RH (Snijders ECP01E phytotron). Mortality was checked daily and the cotton was rehydrated as needed. Deceased individuals were stored in 70% ethanol for further morphometric measurements.

Ovarian load Since *D. suzukii* is a synovigenic species, with females requiring feeding to mature their eggs, females were maintained under conditions similar to those of the “Survival with food for 15 d” assay. After 3 d, they were frozen at −20 °C (Reyes-Ramirez *et al.*, 2023) and subsequently dissected in 1% PBS to count mature eggs (stage 14, with visible respiratory filaments; Fig. S1) in both ovaries using a stereomicroscope (Plantamp *et al.*, 2017). Remains of dissected individuals were stored in 70% ethanol for further morphometric measurements.

Energy content Upon emergence, females were frozen at −20 °C, weighed with a precision balance (± 0.01 mg; QUINTIX125D-1S; Sartorius, Germany),

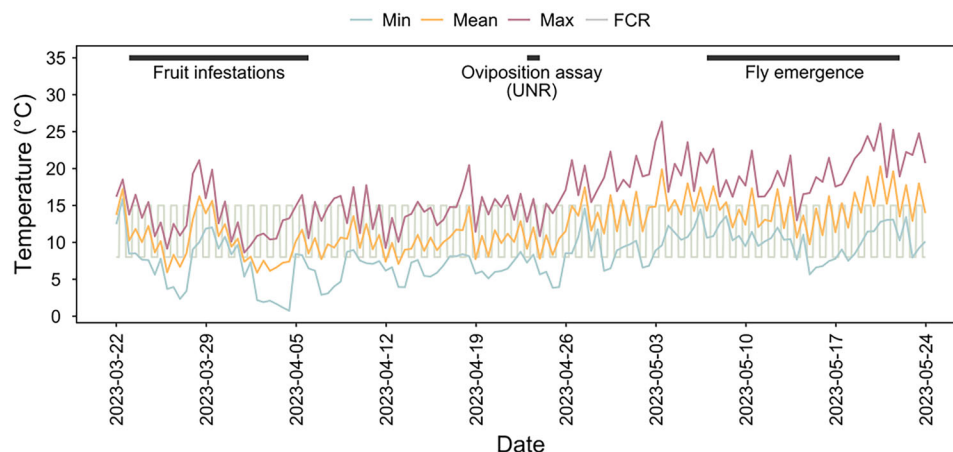


Fig. 1 Field temperature records during the experiment, between March 22 and May 24, 2023. Colored lines represent minimum, mean and maximum temperatures every 12 h in the uncontrolled outdoor regime (UNR). The gray line corresponds to the temperature under the fluctuating controlled regime (8–15 °C, FCR). Fruit infestation under UNR took place between March 24 and April 7, 2023. The oviposition assay under UNR took place between April 24 and 25, 2023. Fly emergence started 8 and ended 23 May, 2023.

and analyzed for whole-body energy. Proteins, free sugars, lipids and glycogen were quantified per Foray *et al.* (2012), with modifications (Supporting Information). Total energy content was calculated in Joules using conversion factors (proteins 16.0 J/mg, carbohydrates 16.0 J/mg, lipids 37.65 J/g; Giron & Casas, 2003; Clavé *et al.*, 2022). Twenty flies were analyzed per treatment, except for those from *Elaeagnus* under UNR ($n = 16$).

Morphometric analyses Wing length and width, and tibia length were measured for flies from “Starvation resistance,” “Survival with food for 15 d,” and “Ovarian load” assays, following Gilchrist *et al.* (2001) with a Leica M205C stereomicroscope equipped with a Leica MC170 HD camera and the software Leica Application Suite (Fig. S2A, B). Wing area index was calculated as $(\text{wing length } 1 + \text{wing length } 2) \times \text{wing width}$ (Ulmer *et al.*, 2024). The number of fully melanized abdominal tergites was recorded for flies in the “Starvation resistance” and “Survival with food for 15 d” assays (Fig. S2B).

Behavioral assays

To simulate *D. suzukii*'s fruit choice during early-spring conditions, we produced winter-acclimated individuals by rearing them on a banana-based substrate at 14 °C, 12 h : 12 h, 75% RH (Panasonic MLR-352H phytotron). An oviposition choice experiment was conducted to assess fruit preference according to temperature regimes (CR, FCR, UNR). Each test involved placing one fruit from each of the three plant species in a 10 cm × 10 cm

× 7.5 cm plastic box, with fruit randomly positioned in the three corners and a water-soaked cotton in the fourth. Fruit stems were held in place to prevent any movement. A 5 cm × 5 cm hole covered with nylon mesh was drilled into the box lid for ventilation. Three females and two males (3–8 d-old) were added and allowed to oviposit for 24 h, after which eggs on each fruit were counted. We performed 20 replicates per thermal regime condition. The UNR experiment occurred on April 24–25, 2023, while CR and FCR experiments were conducted on May 13–17, 2023 (Fig. 1).

Data analyses

All data were analyzed in R version 4.2.2 (R Core Team, 2021). An ANOVA was performed to compare the nutritional composition of the different fruit species (square-root-transformed protein content and P:C ratio, and log-transformed glucose), with Tukey's HSD *post hoc* tests when significant. Generalized linear models with a binomial distribution and logit link were used to assess the effects of temperature regime, diet and their interaction on emergence rate and sex ratio, followed by *post hoc* tests using the “emmeans” package (Lenth *et al.*, 2024) when significant. ANOVA was also used to evaluate the effects of diet, temperature regime and their interaction on morphometric traits, mass, development time and energy content (log-transformed), followed by Tukey's HSD tests when significant. General linear models with quasi-Poisson error distributions examined female ovarian load and female egg laying preference, followed by *post hoc* comparisons using the

Table 1 Number of *D. suzukii* females used in statistical analyses (see Table S2 for total number of individuals that emerged and were available for experiment).

Temperature regime	Diet	Longevity	Starvation resistance	Ovarian load	Energy content	Morphometric measurement	Development time
CR	Artificial	40	58	30	20	94	191
	<i>Aucuba</i>	42	35	30	20	90	151
	<i>Elaeagnus</i>	38	28	33	20	80	139
	<i>Viscum</i>	60	106	32	20	92	258
FCR	Artificial	48	35	30	18	88	160
	<i>Aucuba</i>	26	23	20	17	66	95
	<i>Elaeagnus</i>	15	16	14	20	39	71
	<i>Viscum</i>	61	46	30	20	90	242
UNR	Artificial	35	34	33	19	89	147
	<i>Aucuba</i>	60	31	31	19	91	208
	<i>Elaeagnus</i>	30	0	0	16	23	47
	<i>Viscum</i>	56	36	32	19	80	266

CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h : 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023.

“emmeans” package (Lenth *et al.*, 2024) when significant. General linear models with Poisson error distributions were also used to assess the differences in numbers of melanized tergites between temperature regimes. Kaplan–Meier curves and log-rank tests assessed survival rates with and without food. To decipher the influence of temperature regime and diet on the performance of *D. suzukii*, a Principal Component Analysis (PCA) was performed using the mean of each studied life history traits of females under each condition (12 combinations × 11 traits), excluding starvation resistance for *Elaeagnus* under UNR due to missing data. We did so because some life history traits were measured in different batches of fly, limiting the use of a formula to obtain an individual performance index such as the one used in Dettler *et al.* (2024). Chi-square tests evaluated oviposition preference based on mean egg-laying proportions in each fruit in each box, and general linear models with quasi-Poisson errors tested the effects of temperature, diet and their interaction on mean egg-laying, followed by *post hoc* comparisons using the “emmeans” package (Lenth *et al.*, 2024) when significant. Sample sizes for analyses are in Table 1 and total flies used in Table S2.

Results

UNR temperature regime

Between March 24, and June 30, 2023, the temperature under the UNR regime ranged between 0.7 °C (min) and

33.8 °C (max) with a mean of 15.2 ± 6.1 °C (mean ± SD) (Fig. 1). Between the first day of infestation and the first day of fly emergence (May 8), the temperature under the UNR regime ranged between 0.7 and 26.4 °C with a mean of 11.2 ± 3.9 °C.

Fruit composition

The fruit differed in their nutritional composition ($P < 0.0001$; Table S3). *Aucuba* fruit had the highest protein content (2.30 ± 1.03 mg/g fresh fruit) and an intermediate glucose content (3.43 ± 1.51 mg/g), as well as an intermediate P:C ratio (0.74 ± 0.35) (Table 2). *Viscum* fruit had an intermediate protein content (1.82 ± 0.79 mg/g) and the highest glucose content (4.16 ± 1.35 mg/g), leading to the lowest P:C ratio (0.44 ± 0.19). With only 0.63 ± 0.34 mg/g protein and 0.48 ± 0.19 mg/g glucose, *Elaeagnus* was the nutritionally poorest fruit although it had the highest P:C ratio (1.40 ± 0.68).

Emergence rate and sex ratio

The emergence rate of *D. suzukii* was impacted by temperature ($P < 0.0001$), diet ($P < 0.0001$) and their interaction ($P < 0.0001$; Table S4). Under CR, the emergence rate was maximized when developing in artificial diet and *Viscum* fruit (mean ± SD: 0.83 ± 0.30 and 0.88 ± 0.18 , respectively), while it was significantly lower in *Aucuba* and *Elaeagnus* fruit (0.39 ± 0.29 and 0.36 ± 0.38 , respectively; Fig. 2A). Under fluctuating regimes,

Table 2 Nutritional composition of the three fruit species used in the study.

	Fruit	N	Min	Mean ± SD	Max	Differences ($P < 0.01$)
Protein (mg/g fresh fruit)	<i>Aucuba</i>	70	0.80	2.30 ± 1.03	5.52	a
	<i>Elaeagnus</i>	50	0.04	0.63 ± 0.34	1.90	b
	<i>Viscum</i>	70	0.25	1.82 ± 0.79	3.30	c
Glucose (mg/g fresh fruit)	<i>Aucuba</i>	70	1.60	3.43 ± 1.51	8.40	a
	<i>Elaeagnus</i>	50	0.20	0.48 ± 0.19	1.30	b
	<i>Viscum</i>	70	1.70	4.16 ± 1.35	7.30	c
P:C ratio	<i>Aucuba</i>	70	0.20	0.74 ± 0.35	1.73	a
	<i>Elaeagnus</i>	50	0.08	1.40 ± 0.68	3.60	b
	<i>Viscum</i>	70	0.07	0.44 ± 0.19	1.10	c

Note: Differences between the three fruit species were analyzed using ANOVA. Different letters indicate significant differences at $P < 0.05$ (Tukey's HSD).

emergence rates were significantly reduced in all fruit diets compared to the artificial control diet. The artificial diet produced the highest emergence rate both in FCR and UNR (0.82 ± 0.23 and 0.76 ± 0.27 , respectively). *Viscum* fruit had the second highest emergence rate (0.70 ± 0.30 under FCR and 0.64 ± 0.33 under UNR). *Aucuba* and *Elaeagnus* fruit emergence rates were similarly low under FCR (0.15 ± 0.21 and 0.16 ± 0.29 , respectively). The emergence rate from *Aucuba* fruit was significantly higher under UNR (0.21 ± 0.27) than under FCR (0.15 ± 0.21), but the one from *Elaeagnus* fruit was significantly lower (0.07 ± 0.21).

The mean sex ratio of emerged individuals was 0.48 ± 0.33 (M:F). Diet had no effect on the sex ratio ($P = 0.1679$; Table S5). Temperature regime had a significant influence ($P = 0.0008$) with a lower proportion of males emerging under FCR than under CR (mean sex ratio ± SD: 0.45 ± 0.34 and 0.50 ± 0.30 , respectively; $P = 0.0125$), while the proportion of males emerging under UNR was intermediate (0.48 ± 0.34 , $P = 0.0844$ and $P = 0.8542$ for CR and FCR, respectively). Details are provided in Table S6.

Development time

Development time was influenced by temperature ($P < 0.0001$), diet ($P < 0.0001$) and their interaction ($P < 0.0001$; Table S7). It was shorter under CR (mean 16.4 ± 3.1 d), than under FCR and UNR (44.3 ± 5.0 and 43.3 ± 5.3 d, respectively; Fig. 2B). Under CR, the artificial diet allowed the shortest development time (13.6 ± 0.8 d), followed by *Elaeagnus* (14.7 ± 1.2 d), *Viscum* (16.7 ± 1.4 d) and *Aucuba* (21.0 ± 3.3 d). Under FCR, although considerably longer, the development time remained the short-

est on the artificial diet (39.6 ± 1.2 d) and the longest on *Aucuba* (51.8 ± 5.2 d), while it was intermediate on *Elaeagnus* and *Viscum* (44.4 ± 3.0 d and 44.1 ± 2.8 d, respectively). The relationship changed under UNR with *Elaeagnus* fruit allowing the shortest development time (39.7 ± 3.9 d), while the artificial diet and *Viscum* fruit induced an intermediate development time (41.5 ± 3.8 d and 41.3 ± 3.6 d, respectively), and development in *Aucuba* remained the longest (48.0 ± 5.3 d).

Morphometric measurements

The wing area index and the tibia size of female *D. sukukii* were impacted by temperature ($P < 0.0001$), diet ($P < 0.0001$) and their interaction ($P < 0.0001$; Table S7). The wing area index was the smallest under CR (2.75 ± 0.51 mm²), intermediate under UNR (3.14 ± 0.48 mm²) and largest under FCR (3.35 ± 0.44 mm²). The tibia size was also the smallest under CR (0.77 ± 0.09 mm), but was the longest under UNR (0.82 ± 0.08 mm) and intermediate under FCR (0.80 ± 0.08). Under all temperature regimes, *D. sukukii* females had the largest wings and the longest tibiae when developing on the artificial diet (3.44 ± 0.33 mm² and 0.86 ± 0.05 mm, respectively), the smallest when developing on *Aucuba* fruit (2.61 ± 0.56 mm² and 0.72 ± 0.08 mm, respectively), and intermediate when developing on *Elaeagnus* (2.97 ± 0.49 mm² and 0.79 ± 0.08 mm, respectively) or *Viscum* (3.12 ± 0.39 mm² and 0.81 ± 0.06 mm, respectively) fruit (wing area index results in Fig. 2C; morphometric measurement details in Table S8).

Cold temperatures significantly increased the number of melanized tergites ($P < 0.0001$; Table S9). Under

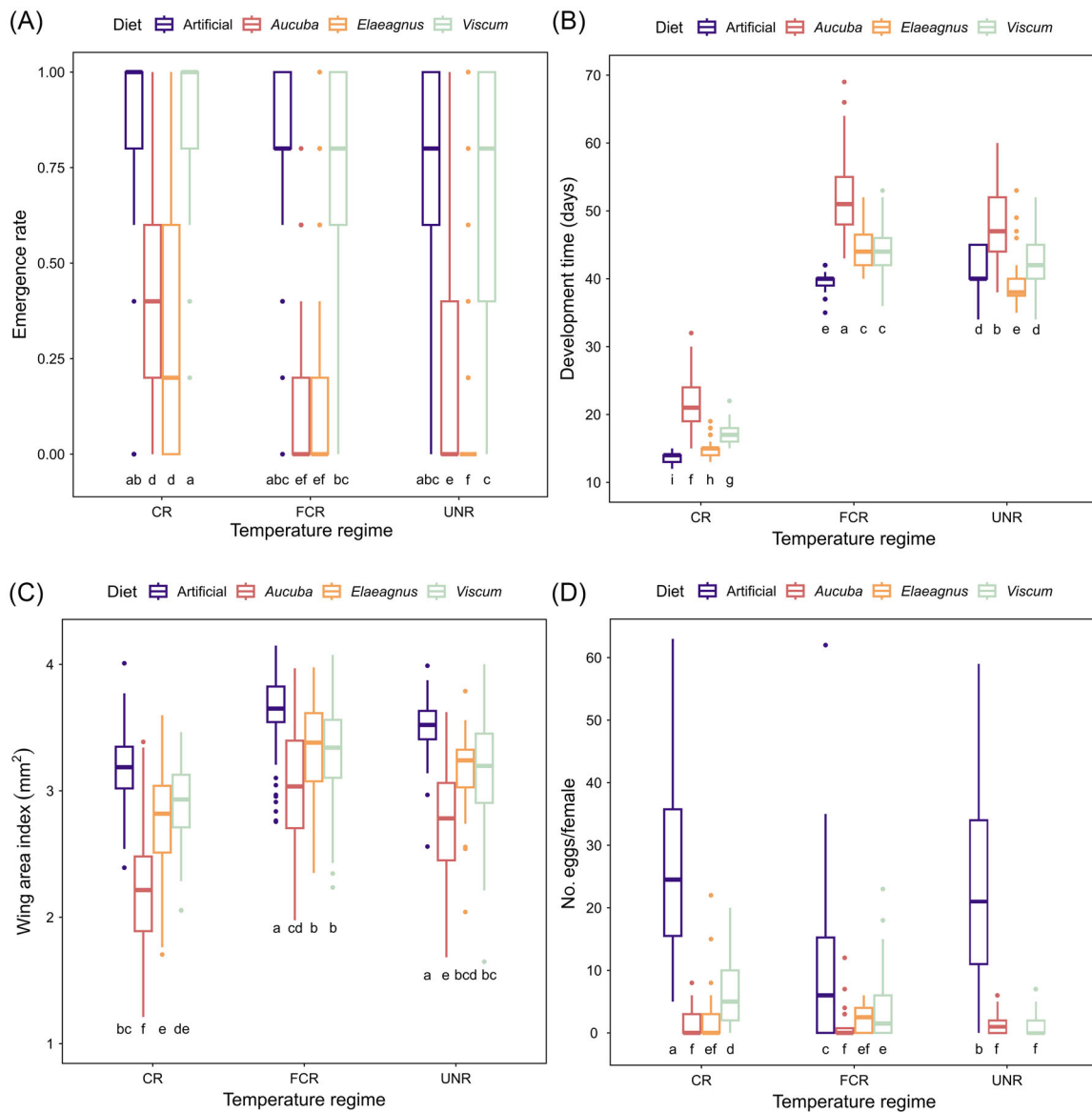


Fig. 2 Emergence rate (A), female development time (B), female wing area index (C), and ovarian load (D) of *Drosophila suzukii* that developed in artificial diet (control), *Aucuba japonica*, *Elaeagnus* × *submacrophylla* or *Viscum album* fruit under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h; 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023). Different letters indicate significant differences at $P < 0.05$ (A: GLM using a binomial distribution with logit link function; B and C: ANOVA followed by Tukey’s HSD; D: GLM with quasi-Poisson error distributions).

FCR and UNR, emerging flies were darker than under CR (Fig. S3).

Mass and energy content

The mass of emerged females was influenced by temperature ($P = 0.0332$), diet ($P < 0.0001$) and their

interaction ($P = 0.0003$; Table S7). Under all temperature regimes, females were the heaviest when developing on the artificial diet (1.92 ± 0.22 mg). Under CR, females that developed on *Aucuba* fruit were the lightest (0.73 ± 0.21 mg), and those developing on *Elaeagnus* and *Viscum* fruit were of intermediate mass (1.22 ± 0.32 and 1.32 ± 0.28 mg, respectively). Under FCR and UNR, there was no significant difference in the mass of females

that developed on the three fruit species, but all were lighter than those developing on the artificial diet (details in Table S8).

The total energy content of emerged females was influenced by temperature ($P < 0.0001$), diet ($P = 0.0001$), and their interaction ($P = 0.0014$; Table S7). Under CR, total energy content did not differ significantly between diets, with an overall mean of 4.31 ± 1.28 J/mg (Fig. 3; details in Table S10). However, under FCR and UNR, total energy content varied between diets, being maximized in flies developing on the artificial diet and *Aucuba* fruit (UNR: 5.82 ± 0.94 and 6.03 ± 1.96 J/mg, respectively), intermediate in those on *Elaeagnus* (UNR: 4.85 ± 1.34 mg/J) and least in those on *Viscum* (4.39 ± 1.57 J/mg).

Ovarian load

Female ovarian load was influenced by temperature ($P < 0.0001$), diet ($P < 0.0001$), and their interaction ($P = 0.0008$; Table S11). Overall, the number of mature eggs was reduced under UNR and FCR compared to CR (Fig. 2D). Under all temperature regimes, the ovarian load was greatest in females developing on the artificial diet (20.4 ± 16.7), even though the number of eggs was significantly lower under FCR (10.8 ± 13.7). Under CR, females developing on *Viscum* fruit had more eggs (6.9 ± 6.0) than those on *Aucuba* (1.7 ± 2.4) or *Elaeagnus* (2.4 ± 4.8). Under FCR and UNR, there were no significant differences between the ovarian loads of females developing on the different fruit. Insufficient females emerged to measure the ovarian load of those developing on *Elaeagnus* fruit under UNR (Table S2).

Starvation resistance and 15 d survival

Starvation resistance was influenced by temperature ($P < 0.0001$), diet ($P < 0.0001$), sex ($P < 0.0001$), and their interaction ($P < 0.0001$). Females had higher starvation resistance than males ($P < 0.0001$) and we only considered females for further analyses. Under all temperature regimes, starvation resistance was greatest in females developing on the artificial diet (median: 4 d with 95% CI = [4, 4]) compared to all fruit (median: 3 d [3, 3]; $P < 0.0001$). Starvation resistance was also slightly greater under UNR (median: 3 d [3, 4]) compared to CR (median: 3 d [3, 3]; $P = 0.0062$) and FCR (median: 3 d [3, 3]; $P = 0.0083$). Starvation resistance was differentially influenced by the diet depending on the temperature regime (Fig. 4A; Table S12): under CR, it was greatest in females that emerged from the artificial diet (median: 4 d [4, 4]) and shortest in females emerging from all other

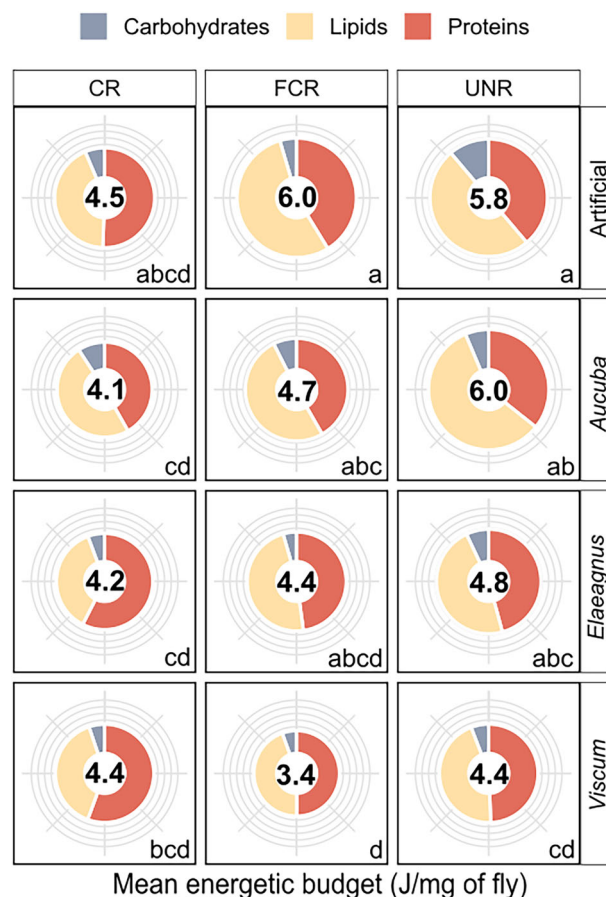


Fig. 3 Energy content of *D. sukuzii* flies emerging from artificial diet (Artificial), *Aucuba japonica*, *Elaeagnus* × *submacrophylla*, or *Viscum album* fruits under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023). The size of the circle is proportional to the mean total energy content of the fly in each treatment combination (also indicated in the circle center). $n = 20$, except for Artificial and *Aucuba* in FCR ($n = 18$ and $n = 17$, respectively), Artificial, *Aucuba* and *Viscum* in UNR ($n = 19$), and *Elaeagnus* in UNR ($n = 16$). The lower sample size is due to removal of aberrant values. Differences in total energy content between fruit species and temperature treatment were analyzed by ANOVA followed by Tukey's HSD tests. When significant, differences are indicated with different letters.

fruit (median: 3 d [3, 3] for *Aucuba* and *Viscum*, 3 d [2, 3] for *Elaeagnus*; $P < 0.0001$); under FCR, it was greatest in artificial diet (median: 4 d [4, 4]), intermediate in *Aucuba* and *Elaeagnus* (both median: 3 d [3, 3]), and shortest in *Viscum* (median: 2 d [2, 2]; $P < 0.0001$); finally under UNR, it was again greatest for females that developed on the artificial diet (median: 4 d [4, 4]) and shortest in those

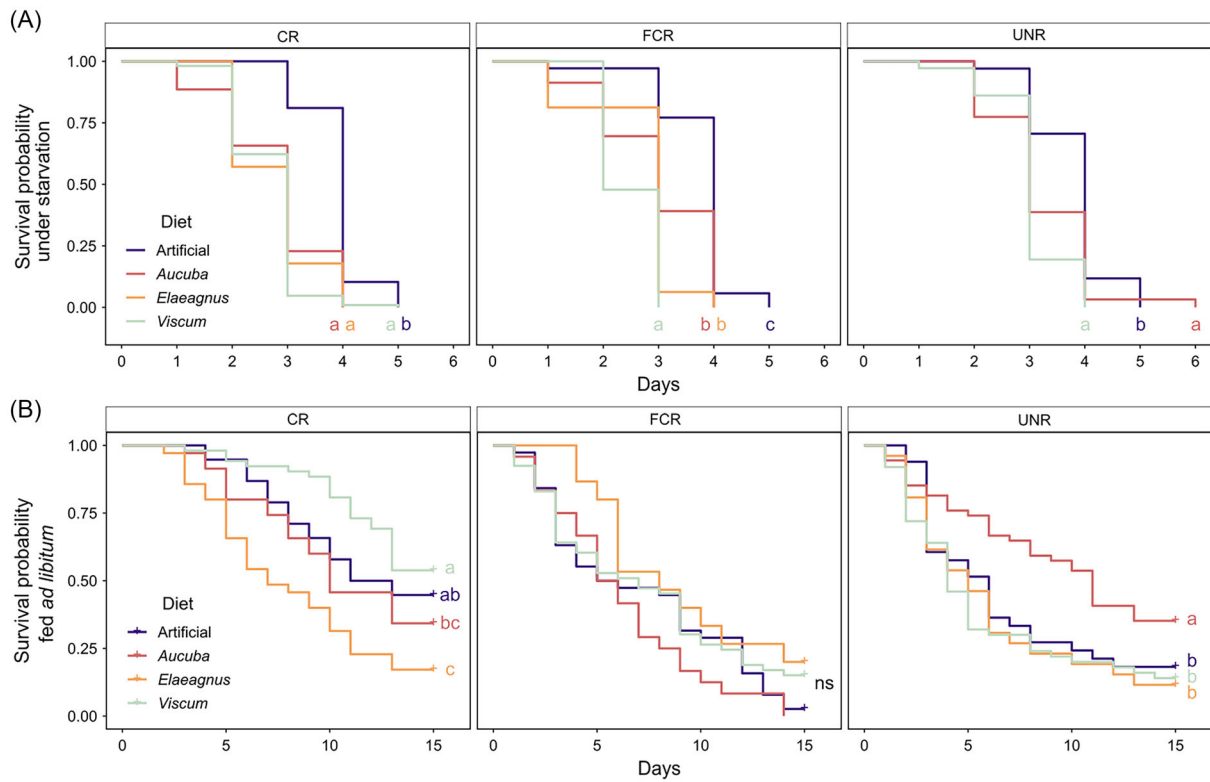


Fig. 4 Survival probability of *D. suzukii* females that developed and emerged from artificial diet (control), *Aucuba japonica*, *Elaeagnus* × *submacrophylla* or *Viscum album* fruit under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023): (A) Survival of individuals that were under starvation and only had access to water (“Starvation resistance”); (B) 15 d survival of individuals that were hydrated and fed *ad libitum* with a nutrient solution. Different letters indicate significant differences at $P < 0.05$ (log-rank test).

developing in *Aucuba* and *Viscum* (median: 3 d [3, 4] and 3 d [3, 3], respectively; $P = 0.0002$), with no data for *Elaeagnus*.

Survival with food for 15 d was influenced by temperature ($P < 0.0001$), diet ($P < 0.0001$), and their interaction ($P < 0.0001$). Sex also had an effect, with males surviving longer ($P = 0.039$). We only considered females for further analyses. Female survival was influenced by temperature ($P < 0.0001$) and the interaction between temperature and diet, while diet alone had no significant effect ($P = 0.14$). Females survived longer under CR (median: 12 d) compared to FCR and UNR (median: 6 d both; $P < 0.0001$). The influence of diet on female survival differed between temperature regimes (Fig. 4B; Table S12): under CR, survival was greatest in females that developed in *Viscum* fruit (median: 15 d), intermediate in those that developed in artificial diet (median: 12 d) and *Aucuba* fruit (median: 10 d), and shortest in those developing in *Elaeagnus* fruit (median: 7 d); however, under FCR, diet had no influence on female survival ($P = 0.17$) and, under

UNR, females developing in *Aucuba* had highest survival (median: 11 d) compared to all other diets (median: 4–6 d; $P = 0.025$).

Effect of temperature regime and diet on D. suzukii performance

In the PCA, the first two principal components (PC) explained 66.6% of variation and grouped the diet and temperature regimes according to the life history traits of *D. suzukii* (Fig. 5). PC1 (39.5% of variation) represented a trophic resource quality gradient, with the artificial diet on its positive part and the three fruit species on its negative part. Along PC1, flies developed on the artificial diet were positively correlated with the energy content (glucose, protein, and lipid content), morphometric measurements (mass, tibia size, and wing length), emergence rate, and ovarian load. Conversely, flies developing on *Aucuba* fruit under CR were

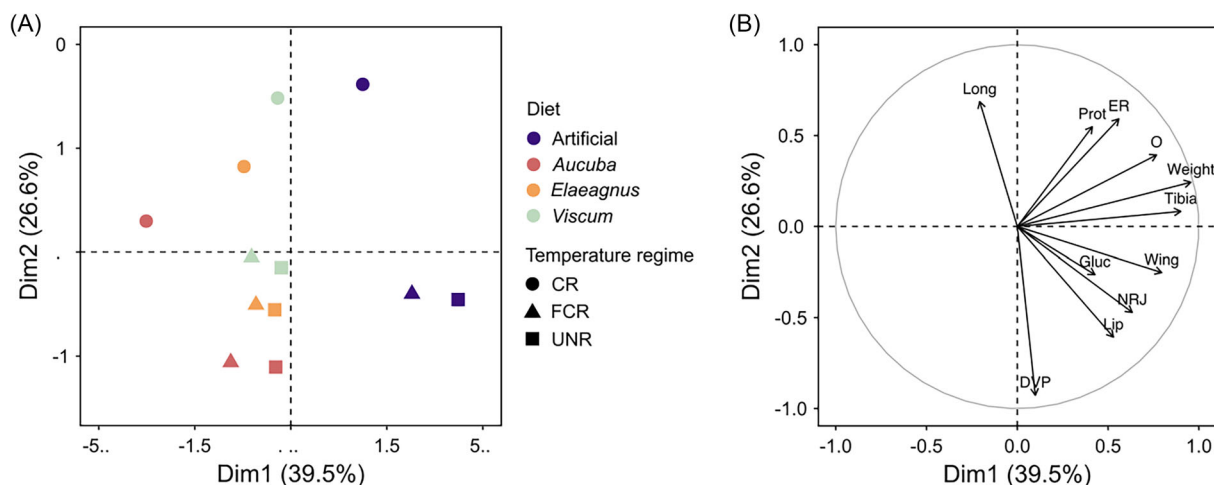


Fig. 5 (A) Diagram of the experimental modalities from principal component analysis (PCA) performed on the mean values of life history traits in *D. suzukii* flies that developed and emerged in each combination of experimental treatment, i.e., from artificial diet (control), *Aucuba japonica*, *Elaeagnus* \times *submacrophylla* or *Viscum album* fruit under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023). The percentages of explained variance for each axis are in parentheses. (B) Correlation circle of the 11 life history traits of *D. suzukii* flies (DVP: development time; ER: emergence rate; Gluc: glucose concentration; Lipid: lipid concentration; Long: longevity; NRJ: energy content; O: ovarian load; Prot: Protein concentration; Tibia: tibia size; Weight: mass; Wing: wing area index).

negatively correlated with those factors. Flies developing on *Aucuba* (under FCR and UNR), *Elaeagnus* and *Viscum* fruit overlapped considerably, with intermediate values for most of these factors and along PC1. PC2 (26.6% of variation) represented a gradient of thermal regime suitability from fluctuating and colder to constant and warmer regimes. On PC2, flies that developed under CR showed rapid development but low longevity while those that developed under the fluctuating regimes (FCR and UNR) had long development and extended longevity. For each type of fruit substrate, plots of FCR and UNR were closely overlaid in the PCA diagram.

Behavioral assays

Behavioral assays under UNR took place between 24 and April 25, 2023, during which time the mean temperature was 9.8 ± 2.2 °C (min: 6.0 °C; max: 15.9 °C; Fig. 1), conditions broadly similar to those of FCR (mean: 11.5 °C; min: 8 °C; max: 15 °C). Winter-acclimated *D. suzukii* females laid significantly more eggs under CR than under FCR and UNR, with a mean \pm SD of 12.7 ± 13.2 eggs under CR against 0.4 ± 1.1 eggs under FCR ($P < 0.0001$) and 0.7 ± 2.4 eggs under UNR ($P < 0.0001$) (Fig. 6). The mean number of eggs laid under FCR and UNR did not differ significantly ($P = 0.1726$). Oviposition preference also differed between the experimental temperature regimes (Fig. 6; Table S13). Under CR and UNR, *Aucuba*

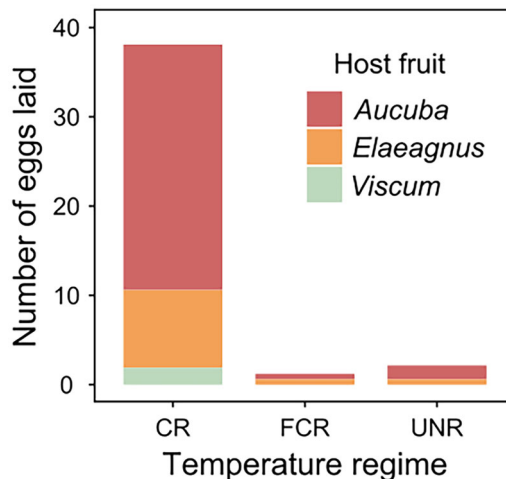


Fig. 6 Oviposition preference of winter-acclimated *D. suzukii* females in the presence of fruit of *Aucuba japonica*, *Elaeagnus* \times *submacrophylla* and *Viscum album* (one of each) for 24 h under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023). Each bar plot corresponds to the mean number of eggs laid per box ($n = 20$) in each fruit.

fruit were preferred over *Elaeagnus* and *Viscum* fruit ($P < 0.0001$). On average, 72.2% and 72.1% of eggs were laid in *Aucuba* under CR and UNR, respectively. However, under FCR, *Elaeagnus* and *Aucuba* were preferred

over *Viscum* ($P < 0.0001$) but had the same proportion of 50% of the eggs laid on them. Under all temperature regimes, *Viscum* fruit were the least preferred, with 5% (CR) or zero (FCR and UNR) eggs laid on them ($P < 0.0001$).

Discussion

Our aim was to assess the contribution of winter-available fruit to the development of spring populations of *D. suzukii*, under fluctuating late winter/early spring temperature regimes. Here, we consider (1) how *D. suzukii* development was influenced by early spring-like conditions; (2) the suitability of the three fruit species compared to an optimal artificial diet at 20 °C; (3) how this suitability changed under early spring-like conditions and how physiological trade-offs contribute (or not) to adaptation of spring fly populations; (4) the importance of combining field and laboratory studies to better understand the causes and ecological consequences of an invasive species.

Impaired and extended development under colder and fluctuating temperature regimes

The FCR regime, designed to mimic natural conditions, closely resembled the UNR regime. Both fluctuating temperature regimes applied here reduced fly emergence and extended development time compared to CR, consistent with previous studies. For instance, Schlesener *et al.* (2020) reported a 40% reduction in *D. suzukii* egg-to-adult survival and a ~20 d increase in development time when temperatures dropped from 18 to 13 °C. In our study, emergence decreased by 20%, and development extended by ~25 d under cold fluctuating regimes. Similarly, Sánchez-Ramos *et al.* (2019) found that constant and fluctuating cold regimes slowed *D. suzukii* development, with a longer development time at constant 10 °C (65.6 ± 0.5 d) than at 4–16 °C (55.19 ± 0.25 d).

Temperature slightly, but significantly, affected sex ratios, with fewer males emerging under FCR compared to CR, unlike findings from Schlesener *et al.* (2020) and Raynaud-Berton *et al.* (2024) who did not find any effect of temperature on sex ratios. Emerged flies from FCR and UNR were darker than in CR, as a result of cold-acclimation as reported in winter-acclimated phenotypes (Colinet & Klustre, 2024). Under all diets, cold temperature regimes did not impact final fly mass, though they produced larger wings. Wing area index values in FCR and UNR resembled those of field-captured flies from late winter/early spring (Ulmer *et al.*, 2024). Wing mor-

phology is critical for flight (David *et al.*, 1997; Ray *et al.*, 2016) and mating (Ewing, 1964; Yeh & True, 2014). Studies in *D. melanogaster* have indicated that flies reared and acclimated in cold conditions have improved flying abilities due to increased wing area (Frazier *et al.*, 2008; Huisamen *et al.*, 2022; Colinet & Kustre, 2024). Larger wings in *D. suzukii* at the end of winter could potentially boost flight speed (Framout *et al.*, 2018) and aid in food foraging during scarce early spring periods (Poyet *et al.*, 2015; Panel *et al.*, 2018). Larger wings may also increase male mating success (Menezes *et al.*, 2013).

While winter-acclimated individuals generally show greater longevity in cold (Tochen *et al.*, 2014; Schlesener *et al.*, 2020), flies in our study that had developed under cold regimes displayed reduced longevity when placed at 20 °C post-emergence. This could result from acclimation to cold, with flies developing under cold regimes not being adapted to constant 20 °C temperature (Kristensen *et al.*, 2008), in line with the thermal compensation hypothesis (TCH; Le Lann *et al.*, 2011). According to the TCH, under common temperature conditions, cold-acclimated ectotherm individuals present a higher metabolic rate than those that developed at higher temperature, resulting in a reduced longevity (Le Lann *et al.*, 2011). There could also be costs associated with larger wings and melanin production (Talloen *et al.*, 2004; Roff & Fairban, 2013). However, flies from UNR exhibited greater starvation resistance than those from CR or even FCR, potentially due to slightly higher energy reserves under UNR (Ballard *et al.*, 2008). Such trade-offs between development time and survival are common in frugivorous *Drosophila* species (Sevenster & Van Alphen, 1993; Tu & Tatar, 2003).

Low temperatures notably reduced ovarian load, especially in females developing on the artificial diet. Development under cold resulted in fewer mature eggs in 3-d-old females, consistent with Wallingford *et al.* (2016), who reported a decline from eight to less than two mature eggs in the ovaries of 7-d-old *D. suzukii* females reared at 20 °C and 15 °C, respectively. In our study, the reduction in mature eggs was more pronounced under FCR than UNR, possibly linked to differences in female energy reserves. Energy content was higher under UNR and may have supported egg maturation (cf. Berger *et al.*, 2008).

Ranking of D. suzukii performance in different winter-available fruit

Performance of *D. suzukii* was maximized when developing on the artificial diet compared to the three

winter-available fruit, supporting our second hypothesis. Consistent with previous studies (Poyet *et al.*, 2015; Panel *et al.*, 2018), *D. suzukii* exhibited intermediate performance on *Viscum* and *Elaeagnus*, while *Aucuba* ranked lowest under controlled conditions (CR), where temperature was not a developmental constraint. The emergence rate between flies developing in *Viscum* and those in the artificial diet (0.83 and 0.88, respectively) was not different. In contrast, emergence rates on *Aucuba* and *Elaeagnus* were reduced by around half (0.39 and 0.38, respectively). While low emergence from *Aucuba* aligns with previous studies (Lee *et al.*, 2015; Poyet *et al.*, 2015; Panel *et al.*, 2018), the result for *Elaeagnus* was unexpected given its usual status as a suitable host for *D. suzukii* (Poyet *et al.*, 2015; Panel *et al.*, 2018; Deconninck *et al.*, 2024c). The high P:C ratio in the collected *Elaeagnus* fruit (1.40) could explain the lower emergence, as *D. suzukii* typically thrives on diets with lower protein levels (Silva-Soares *et al.*, 2017; Rendon *et al.*, 2018). *Viscum* had the lowest P:C ratio (0.44) with high emergence rate, while *Aucuba*, with an intermediate P:C ratio (0.74), showed intermediate emergence rate.

Elaeagnus fruit promoted faster development without reducing body mass or wing area, suggesting a high larval quality resource (Edgar, 2006; Jaramillo *et al.*, 2015). Previous studies reported similar patterns, although our findings diverge slightly regarding development time in *Viscum* (Poyet *et al.*, 2015; Panel *et al.*, 2018). Under a constant 20 °C regime, ovarian load was highest when developing on *Viscum* fruit, again likely due to the intermediate P:C ratio that maximizes the number of ovarioles (Silva-Soares *et al.*, 2017). No difference in starvation resistance were found among fruit, which is consistent with an overall similar energy content of flies under CR across diets. Longevity was longest when developing on *Viscum*, intermediate on *Aucuba* and shortest on *Elaeagnus*, likely influenced by dietary sugar concentration (Shu *et al.*, 2022). In our PCA analysis, most life history traits, except development time and longevity, supported our initial hypothesis, with *Elaeagnus* and *Viscum* of intermediate quality and *Aucuba* being the least favorable.

Other fruit properties likely contributed to the variability in *D. suzukii* performance. For instance, despite having a suitable P:C ratio, *Aucuba* fruit were the least suitable as observed in most life history traits. Fruit of this species are fibrous, making crawling and access to nutrients difficult for feeding larvae (House, 1969). They also contain secondary metabolites such as aucubin, an iridoid glycoside which has been shown to exhibit deterrent (Biere *et al.*, 2004) and toxic (Vivekanandhan *et al.*, 2022) properties against insects, in addition to its antimi-

crobial activity (Rombouts & Links, 1954), which could also be detrimental to *D. suzukii* larval development.

Fruit suitability differs under colder and fluctuating temperature regimes

Under colder fluctuating temperature regimes, the ranking of fruit supporting the best performance changed as illustrated by the PCA results. *Aucuba* fruit became comparable to *Elaeagnus* and *Viscum* in most life history traits, even supporting greater longevity than the latter. This could be attributed to the high energy content of flies developing on *Aucuba* under FCR and UNR, which matches that of the artificial diet. However, these flies exhibited the lowest ovarian load, suggesting a trade-off between survival and reproduction, a phenomenon recognized in the literature (e.g., Zera & Harshman, 2001; Hunt *et al.*, 2004; Lee *et al.*, 2008; De Loof, 2011; Attisano *et al.*, 2012; Blacher *et al.*, 2017). Under low-quality diets, survival often takes precedence over reproduction (Holliday, 1989; Boggs & Ross, 1993; Zera & Harshman, 2001; Attisano *et al.*, 2012), and specific nutrients can influence this trade-off. For instance, adding methionine to a restricted diet in *D. melanogaster* maximized fecundity without compromising lifespan (Grandison *et al.*, 2009). Temperature also plays a role in balancing fecundity and longevity (Marshall & Sinclair, 2010). For *D. suzukii*, selecting fruit that enhance longevity over reproduction could boost the fitness of the first generation of females emerging in late winter/early spring, when resources are limited. Given that *D. suzukii* is a synovigenic species, prolonged survival and larger wings may significantly enhance foraging success (Poyet *et al.*, 2015; Panel *et al.*, 2018). Therefore, although *Aucuba* may provide a suboptimal diet under a constant mild temperature of 20 °C, it could still be a valuable diet for pioneer *D. suzukii* females early in the season.

Maladaptive fruit choice?

Our study examined the egg-laying behavior of winter-acclimated *D. suzukii* individuals given a choice among three common and suitable winter fruit. We hypothesized that food preference would shift based on temperature regimes, as the nutritional needs of winter and summer individuals might differ (Rendon *et al.*, 2019). Contrary to our expectations, regardless of the thermal regime, most eggs were laid on *Aucuba* and *Elaeagnus* fruit. Females only oviposited in *Viscum* fruit under the constant 20 °C regime, and even then, it was the least preferred option. This behavior seems maladaptive, given that

Viscum optimized fly performance, while *Aucuba* produced the poorest results in emergence rate, development time, morphometric characteristics, ovarian load and survival. However, under FCR, *Aucuba* maximized fly energy content, leading to longer survival compared to other diets. Conversely, *Viscum* fruit, while resulting in the lowest energy content, allowed for an increased emergence rate. This indicates a potential trade-off where adult survival may be prioritized over the risk of non-emergence, aligning with a K strategy (Taylor & Condra, 1980). Thus, *D. suzukii* selecting *Aucuba* might produce fewer offspring, but these may survive longer. Alternatively, the preference for *Aucuba* could also reflect a coevolutionary history between *D. suzukii* and the plant in their native ranges (Mitsui *et al.*, 2010). Overall, our findings do not support the preference–performance hypothesis.

Various parameters influence insect fruit choice, and *D. suzukii* is known to be sensitive to color (Bühlmann & Gossner, 2022), shape and size (Bühlmann & Gossner, 2022), firmness (Sato *et al.*, 2021), skin texture (Bühlmann & Gossner, 2022) and odor (Cha *et al.*, 2012). While we did not test for odor differences, the fruit used in this study differed across several other traits: *Aucuba* fruit are oblong (~1 cm), red, with smooth skin (Abe, 2001); *Elaeagnus* fruit are oblong (~1.5 cm), soft, orange-deep-red silvery with rough skin (Edwards, 2017; Abdalla, 2019); *Viscum* fruit are ovoid (~0.9 cm), white and become translucent as they ripen, with smooth skin (Thomas *et al.*, 2023). *Viscum* fruit combine small size with low contrast color, while *D. suzukii* favors contrasting colors (Little *et al.*, 2019), particularly red, orange or black, and larger fruit (Bühlmann & Gossner, 2022). Future studies should also consider these traits in behavioral assays. Lastly, although the preference for *Aucuba* and *Elaeagnus* for oviposition appears maladaptive, it may be leveraged in trap strategies to protect fruit crops during spring (Ulmer *et al.*, 2020; Fragnière *et al.*, 2024). However, as these fruit allow some development, they would be less effective than dead-end trap plants to control pest populations (Ulmer *et al.*, 2020; Fragnière *et al.*, 2024). Their use could even be counterproductive as *Elaeagnus* can be a major host plant for the fly in early spring under certain environmental conditions in the field (Deconninck *et al.*, 2024c) and because host plants susceptibility to *D. suzukii* infestation highly varies with site location and latitude-associated climatic factors (Ulmer *et al.*, 2022).

Ecological consequences

D. suzukii demonstrates a remarkable ability to overwinter and resume reproduction as temperatures increase

in early spring. Overwintering individuals contribute to the initial population growth of the new year. In this study, we showed that low temperature regimes impaired the overall performance of the flies compared to a standard rearing regime, while the three fruit trialed yielded equivalent performance under natural field fluctuating temperature conditions. Utilizing any of these three fruit after *D. suzukii* females reinitiated oogenesis (which can occur as early as January; Grassi *et al.*, 2018) might result in the production of viable adults capable of generating the next fly generation and infesting early-season commercial crops (Deconninck *et al.*, 2024c). However, our assessment was limited to dissection of the ovaries and we have not directly tested fertility and oviposition of females developed on winter fruits. To confirm that winter females are capable of laying fertilized, viable eggs, further studies are required.

In natural field conditions, *Viscum* fruit can be heavily infested (Deconninck *et al.*, 2024a), sometimes more so than those of *Aucuba* or *Elaeagnus* (Deconninck *et al.*, 2024c). The phenology of fruit ripeness may restrict flies to the most readily available suitable fruit, even if that does not maximize performance. *Viscum* fruit are available for several months during winter and spring (Thomas *et al.*, 2023; Deconninck *et al.*, 2024a), which can lead to heavy infestations when they are among the few available fruit-bearing plants (Deconninck *et al.*, 2024c). The abundance and management of a specific fruit-bearing plant species in an area also influences the fly infestation rate (Begon, 1975). For instance, trees infested by *Viscum* typically host about 20 individuals, and can rise to nearly 300 individuals per tree in *Pinus nigra* plantations, providing a substantial reservoir of fruit (Thomas *et al.*, 2023). In contrast, *Aucuba* and *Elaeagnus* bushes are often planted in urban areas with a patchy distribution and are regularly pruned (Prior, 1881; Abe, 2001; Edwards, 2017; Abdalla, 2019).

The fruit selection by *D. suzukii* under fluctuating cold regimes aligns with infestation rates observed in the Netherlands in April and May 2017, where *Aucuba* fruit were more infested than those of *Elaeagnus*, with no eggs found in *Viscum* (Panel *et al.*, 2018). This contrasts with field data obtained in France in April and May 2022, which reported the highest infestations in *Elaeagnus* fruit, followed by *Viscum* and *Aucuba* (Deconninck *et al.*, 2024c). Field infestation rates are rather indicative of population choices and can be influenced by the overall abundance of fruit in an area, making direct comparisons between these studies and our experimental data challenging. Nonetheless, all these studies suggest that fruit choice by *D. suzukii* females can vary not only according to fruit availability and characteristics, but also according

to experienced temperature regimes. Field and laboratory experiments serve as complementary approaches to understanding the drivers of fruit infestation in natural environments and the trade-offs between life history traits influenced by environmental conditions (e.g., temperature or trophic resources). Our study illustrates that laboratory experiments using controlled fluctuating regimes resemble experiments conducted under natural conditions, while the behavioral assay suggests the complementarity of both field and laboratory studies.

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Data availability statement

All data supporting the results and the code used to generate the figures is freely available on Zenodo.org (10.5281/zenodo.14008325). The DOI represents all versions, and will always resolve to the latest one.

Disclosure

The authors have nothing to disclose.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Ovarian load of female *D. suzukii*.

Fig. S2 Morphometric measurement (wing and tibia size) and count of the melanized abdominal tergites in *D. suzukii*.

Fig. S3 Number of melanized tergites (mean \pm SD) of *D. suzukii* flies that emerged under the different temperature regimes.

Table S1 Period of fruit collection.

Table S2 Total number of individuals available for each experiment (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023).

Table S3 Differences in nutritional composition (proteins, glucose, P:C ratio) between fruits.

Table S4 Influence of diet, temperature and their interaction on *D. suzukii* emergence rate.

Table S5 Influence of diet, temperature and their interaction on *D. suzukii* sex ratio (M:F).

Table S6 Sex ratio (M:F) of emerging *D. suzukii* under different combinations of temperature regime (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023) and diet.

Table S7 Influence of diet, temperature and their interaction on *D. suzukii* morphometric measurements (wing area index and tibia size), mass, energy content (J/mg of fly biomass) and development time.

Table S8 Morphometric measurement (mean ± SD) of flies emerging from artificial diet, *Aucuba japonica*, *Elaeagnus × submacrophylla* or *Viscum album* fruits under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR:

uncontrolled outdoor regime between March 24, and June 31, 2023).

Table S9 Influence of temperature regime on the number of melanized tergites of *D. suzukii*.

Table S10 Energy content (mean ± SD) of flies emerging from artificial diet, *Aucuba japonica*, *Elaeagnus × submacrophylla* or *Viscum album* fruits under different temperature regimes (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023).

Table S11 Influence of diet, temperature, and their interaction on *D. suzukii* female ovarian load.

Table S12 Influence of different diets under each temperature regime (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023) on *D. suzukii* starvation resistance and longevity (Survival with food for 15 d).

Table S13 Differences in oviposition choice between fruit types under each temperature regime (CR: 20 °C; FCR: fluctuating controlled regime of 8–15 °C 12 h: 12 h; UNR: uncontrolled outdoor regime between March 24, and June 31, 2023).