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Abstract. The effects of single meals of different sucrose concentrations on feeding responses and survival of 8–24-h-old, 1–2-, 10–12- and 31–36-day-old female and male western cherry fruit flies, *Rhagoletis indifferens* Curran, were determined. Feeding time and food consumption response patterns in both sexes within age groups were curvilinear. Feeding times increased as sucrose concentrations increased, and were longest when the sucrose concentration was 100% (dry). Consumption of dilute wet sucrose was low, whereas consumption of concentrated wet sucrose was high. However, consumption of dry, 100% sucrose was also low. One to 2-day-old flies of both sexes that had not previously fed consumed more sucrose foods than unfed 8–24-h-old flies and 10–12- and 31–36-day-old flies that had been starved for 16–24 h. Females consumed more than males, but they consumed the same amount as males per mg bodyweight. When fed single 20% and 60% sucrose meals, 1–2-day-old flies survived longer compared to flies in all other age groups, with 31–36-day-old flies surviving shortest. Despite age-related differences in survival, in general, no sex differences in survival were seen in flies fed sucrose within any age groups, or in flies fed sucrose-yeast, cherry juice and honeydew foods. The results suggest that sugar-feeding behaviours and the energy invested in sugar 'seeking' by both sexes of *R. indifferens* should be the same throughout life.

Key words. Cherry fruit fly, feeding responses, *Rhagoletis indifferens*, sucrose concentrations, survival, tephritid.

Introduction

Both sexes of the western cherry fruit fly, *Rhagoletis indifferens* Curran, as is typical of tephritid fruit flies, require a continuous source of sugar for survival (Fluke & Allen, 1931; Hagen, 1953). In nature, sugar sources vary in concentration and form (i.e. wet or dry) and may affect feeding responses, feeding frequency, the amounts of energy obtained and, consequently, short- and long-term survival. Natural sugar sources for flies include juices from cherries, *Prunus avium* (Frick *et al.*, 1954), either as part of the fruit or splattered on leaves, possibly insect honeydew, as for the apple maggot, *R. pomonella* (Neilson & Wood, 1966), and leachates, which consist of nutrients such as sugars and amino acids on the surfaces of leaves (Tukey, 1971), and which may play a role in the nutrition of *R. pomonella* (Hendrichs *et al.*, 1993a). Sugar concentration is well known to affect feeding responses in the blowfly *Phormia regina* (Dethier *et al.*, 1956) and in *R. pomonella* (Duan & Prokopy, 1993; Hendrichs *et al.*, 1993b): in general, as sugar concentration increases, so does the feeding time. Although this may be true in all higher Diptera, the feeding responses of most tephritid flies, including *R. indifferens*, over an entire range of sucrose concentrations or to wet vs. dry sugar foods have not been quantified. Such responses could influence the effectiveness of sugar as feeding stimulants in bait sprays for fly management.

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Female *R. indifferens* are larger than males and presumably consume more sugar, but the effects of sugar feeding and age on short-term survival differences between sexes have not been determined. If females consume sugar more than males, but survive for shorter periods, it would be expected that the metabolic rates of females are much higher than those of males, possibly because of greater activity levels or energy consumption related to reproductive costs. *Phormia regina* females exhibited cyclic respiration rates that were correlated with gonadotrophic cycles. Females also utilized more oxygen than males both on a μL per specimen and μL per mg basis (Calabrese & Stoffolano, 1974). If female *R. indifferens* consume more sugar and survive longer than the males, it could mean females either have the same or different metabolic rates, but if there is no difference in survival, it probably would mean that females have the same metabolic rate as males, and consume more simply because they have to maintain more body mass. Indeed, consistent with this last hypothesis, when the weights of female and male *R. pomonella* are taken into account, only small differences in long-term sucrose intake between the sexes are observed (Webster *et al.*, 1979). To address the question of sugar metabolism and requirements by the sexes, survival needs to be determined because tephritid flies with free access to sucrose under caged conditions probably feed more than they need to in order to survive and reproduce. The tropical tephritid *Anastrepha serpentina* consumes more sucrose than it needs when it has unlimited access to it, resulting in reduced egg production (Jácome *et al.*, 1999). Age differences in sugar feeding by *R. pomonella* have been demonstrated (Webster *et al.*, 1979), but age has not been related to sugar requirements for survival. Determining the relationships between food consumption, age and survival is important to explain feeding responses of *R. indifferens* and the fundamental question of how much female and male flies need to eat in order to survive, and ultimately to explain any differences in foraging behaviours between the sexes.

In this study, the main objectives were to determine the effects of sex and sucrose concentrations on the feeding responses of *R. indifferens* of different ages and how these are related to short-term survival. Feeding responses to and survival on sucrose-yeast solutions and natural substances were also determined. Implications of sugar consumption-survival results on foraging behaviours by the sexes are discussed.

Materials and methods

All flies were obtained as larvae from field-infested sweet and sour cherry fruit in central Washington in June and July 2000 and 2001. Pupae were stored for 6–10 months at 3 °C, after which they were moved to a 27–28 °C room with 16 h of light (12–42 W m^{-2}) and 50–70% relative humidity (RH). Adults emerged over 8–24-h periods after 3–4 weeks. After emergence, flies were maintained in plastic test cages 8.5 cm high × 8.5 cm wide with nylon organdy tops. Flies had continuous access to deionized water saturated in cotton wicks. Flies in all experiments were fed in a 22 °C room with 45% RH. After feedings, flies were placed back into cages and returned to the previous room.

To determine food consumption, female and male flies were placed inside 1–2 g capacity gelatin capsules (Eli Lilly, Indianapolis, IN) and weighed before and immediately after single meals with a microbalance (Sartorius, Goettingen, Germany). Meals were sucrose (C & H Sugar Co, Crockett, CA, USA) and sucrose-yeast (yeast: Sigma Chem., St Louis, MO, USA) solutions, dry sucrose and cherry juice and aphid honeydew. A single fly was placed inside a 5.0 cm × 1.4 cm glass vial, after which food was inserted into the opening of the vial. The fly walked until it encountered the food, whereupon it started to feed (proboscis contact with food surface). Feeding was observed and timed until the fly left the food. If the fly returned to feed within 1 min, the feeding bouts were considered continuous and were pooled as a single meal. Observations suggested that if a fly did not return within this time, it was satiated (for a least several more minutes): it lifted its proboscis from the food, abruptly walked off or away from it, and climbed up the side of the vial. However, within 1 min, a fly that lifted its proboscis from the food often stayed on or near it, displaying regurgitation or bubbling behaviour (Hendrichs *et al.*, 1992, 1993b), and then resumed feeding. Flies were considered nonfeeders if there was no response after they had tarsal contact with the food for ≥30 s. After feeding, the fly was returned to its cage.

In experiment 1, fly responses to various sucrose concentrations were determined. Four age groups of each sex were tested: (i) 8–24-h-old (newly emerged); (ii) 1–2-day-old; (iii) 10–12-day-old; and (iv) 31–36-day-old. The oldest age group could be tested for both sexes because the longevity of female and male *R. indifferens* is similar, with 50% and 100% mortality occurring at 84 days and 110 days, respectively, under 26.7 °C and 45–55% RH laboratory conditions (Frick *et al.*, 1954). Eight to 24-h-old flies that had not previously fed were offered 20% and 60% sucrose solutions (wt : wt) saturated in cotton. One to 2-day-old flies, also unfed, were offered 0, 2, 10, 20, 40, 60 and 80% sucrose solutions saturated in cotton or dry, 100% sucrose. Forty-five grams of sucrose were dissolved in 20 g of water, mixed with 1 g of cotton, and air-dried to make the 100% sucrose. Ten to 12-day-old and 31–36-day-old flies were exposed continuously to an 80% sucrose–20% yeast diet and were starved 16–24 h (approximately the same period as 1–2-day-old flies) before feeding. Females and males in these two age groups had continuous access to mates before feedings. Ten to 12-day-old flies were offered 20% and 60% sucrose and 31–36-day-old flies were offered 0, 20, 40, 60 and 80% sucrose solutions or dry, 100% sucrose. Flies were not offered oviposition sites. Each treatment consisted of 9–43 flies (replicates) of each sex, except in the 10–12-day-old class, which consisted of five flies in a few treatments because of reduced fly availability. Higher numbers were included in the 1–2-day-old controls because this group was included each time the other seven concentration treatments were tested.

To determine if responses to sucrose of 31–36-day-old females that had laid eggs differed from those that were deprived of oviposition sites, females that had been continuously exposed to the 80% sucrose−20% yeast diet were given cherries for oviposition at 22–26 days. Cherries were replaced with new ones every 3 days, and oviposition confirmed. Flies were starved for 16 h and then offered 20% and 60% sucrose. There were nine replicates for each concentration.

In experiment 2, fly responses to sucrose-yeast foods and natural substances were determined. One to 2-day-old flies that had never fed were offered 20%−12%, 47%−6% and 60%−12% sucrose–yeast solutions and a dry 88% sucrose−12% yeast food saturated in cotton (5.6 g of food mixed in 0.5 g of cotton). The precise percentages chosen were based on their effectiveness in maintaining fly colonies and use in related solute evaporative experiments not reported here. Sweet cherry ('Bing') juice in the flesh of opened ripe fruit or saturated in cotton were also offered. Cherries were fresh, ≤3 weeks old (from harvest), or were 2–3 months old, having been stored at 3 °C in 100% nitrogen during this time. Sugar concentrations of 20 fresh and 20 stored cherries were 18–23% (the rest was water and solutes), based on refractometer (Atago N1, Japan) readings. Flies were also offered dry aphid (*Myzus cerasi*) honeydew on cherry leaves that was obtained 6 months before the study from fly infested trees. There were 10–19 replicates per treatment.

After feeding, survival of all flies in experiments 1 and 2 was checked every 24 h. For 8–24-hour- and 1–2-day-old flies, survival was determined from emergence. For the latter, 0.5 day was subtracted from days survived to adjust for emergence occurring over 24 h. For the 10–12- and 31–36-day-old flies, survival was determined from the time the sucrose-yeast diet was removed, not from the time flies were fed the treatment meals. Observations indicated that females and males did not fly against cages or display strong escape responses that could result in injury.

In experiment 3, the objective was to determine daily feeding patterns and consumption of wet and dry sucrose-yeast foods by female and male flies over a longer term. Foods were the wet 60% sucrose−12% yeast solution and the dry 88% sucrose−12% yeast food. Flies were fed and weighed once each day for 10 consecutive days beginning at 1–2 days. There were five or six replicates of each sex per treatment.

Feeding response data for 1–2- and 31–36-day-old flies were subjected to regression analysis. Within 20% and 60% sucrose concentrations, two-way analysis of variance (ANOVA) (sex × age effects) was performed, followed by the Duncan New Multiple Range Test (Winer *et al.*, 1991). Between sex (within food type) and among food type (within sexes) data were analysed with one-way ANOVA. Data were analysed using the SAS statistical software package (version 8, SAS Inc., Cary, NC).

Results

In experiment 1, 1–2-day-old and 31–36-day-old females and males showed the same curvilinear response patterns to sucrose concentrations (Figs 1 and 2). However, females weighed 5.66 ± 0.04 mg ($n = 236$) and consumed significantly more sucrose ($P < 0.05$) than males (Figs 1 and 2), which weighed 4.13 ± 0.04 mg ($n = 203$). Results from ANOVA indicated there were no differences in feeding times between sexes within any age group ($P > 0.05$).

There were significant sex and age effects on amounts of sucrose consumed. One to 2-day-old flies consumed more of 20% and 60% concentrations than flies of other ages (Table 1). Sucrose concentration-dependent feeding times were less predictable and weaker (lower r^2) in 31–36 (Fig. 2) than 1–2-day-old flies (Fig. 1). Responses of the older flies were lower as well: 18% and 36% ($n = 11$) of females and males, respectively, did not respond to 100% sucrose, whereas all 1–2-day-old flies ($n = 15$ females and 17 males) responded immediately. Females, aged 31–36 days, fed for the same times and consumed the same amount of food as same-aged females deprived of oviposition sites ($P > 0.05$).

Despite greater sucrose consumption by females, females and males within age groups usually consumed the same amount of sucrose per mg bodyweight (Table 2). Survival in both sexes increased as wet sucrose concentrations increased but, at 100% dry sucrose, it decreased (Table 2). Although 1–2-day-old females survived longer than males on four of the seven sucrose concentrations, females and males in other ages survived equally long (Table 2).

There were significant effects of age on survival in flies that consumed 20% and 60% sucrose concentrations, with 1–2-day-old flies surviving longest (Table 3). Thirty-one to 36-day-old females that had oviposited and were fed 20% and 60% sucrose died slightly earlier than same-aged females that had been deprived of oviposition sites (Table 2) ($F = 8.12$, $P = 0.0102$; $F = 6.16$, $P = 0.0225$, respectively, d.f. = 1, 19).

In experiment 2, 1–2-day-old females and males fed for the same times in six of seven cases, but females (bodyweight of 5.57 ± 0.08 mg, $n = 80$) consumed larger amounts of sucrose-yeast foods and natural substances than males (bodyweight of 4.32 ± 0.05 mg, $n = 73$) in five of seven cases (Table 4). Survival did not differ between the sexes except for 20% sucrose−12% yeast and 88% sucrose−12% yeast solutions (Table 5). For both sexes, the effects of a single cherry juice meal on survival were similar to those of a single 20% sucrose meal, and those of a single aphid honeydew meal were closest to those of a 100% sucrose meal (Tables 2 and 5). Within sexes, more concentrated wet food types generally resulted in longer feeding times and longer survival (Tables 4 and 5). However, when food was dry, feeding time was long, but consumption and survival were reduced (Tables 4 and 5).

In experiment 3 (Fig. 3), both female and male flies consumed more 60% sucrose−12% yeast food at 1–2 days than the following 3–11 days ($P < 0.05$). Females consumed 0.852 mg and males 0.602 mg of wet food/day (dry weights

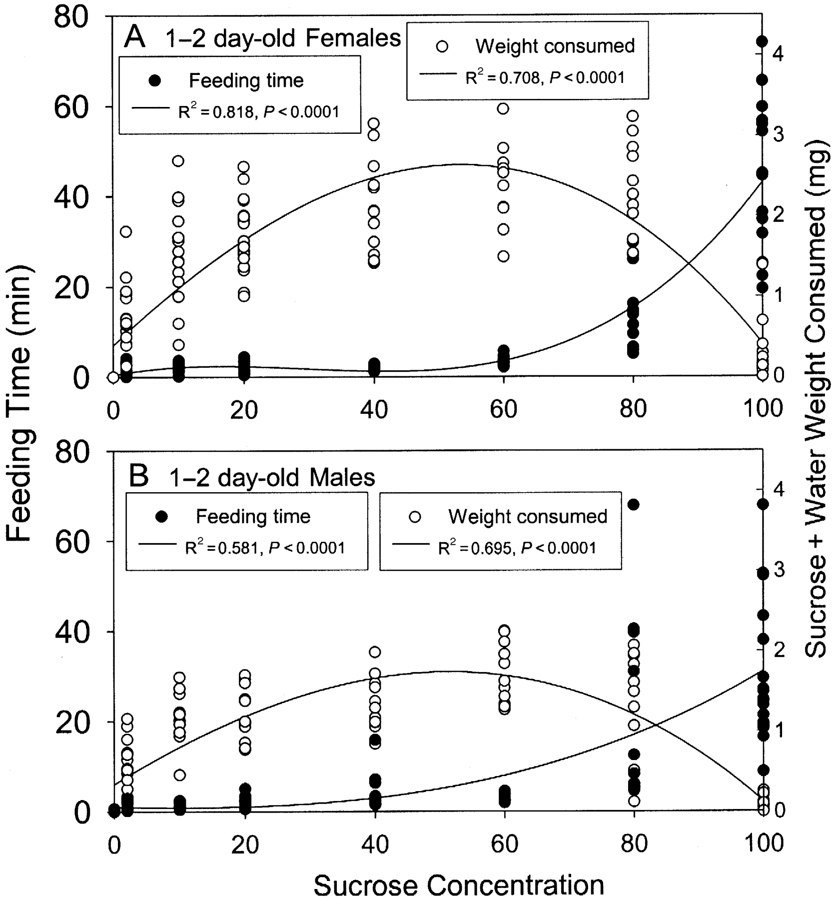

Fig. 1. Effects of sucrose concentrations on feeding time and sucrose and water (except 100% sucrose) consumed in (A) female and (B) male *Rhagoletis indifferens* fed single meals at 1–2 days post emergence.

of 0.613 and 0.433 mg day^{-1}). Flies consumed the same amount of 88% sucrose–12% yeast food at 1–2 days as they did from 3–11 days ($P > 0.05$). Consumption of dry food/day averaged 0.254 mg for females and 0.228 mg for males.

Discussion

Females and males of *R. indifferens* respond in essentially the same manner to increasingly higher sucrose concentrations. Sucrose concentration and food form have a highly significant effect on feeding times and consumption responses in both sexes, resulting in curvilinear patterns. These patterns are probably caused by the greater difficulty in processing and ingesting increasingly more concentrated wet sucrose foods. Dry 100% sucrose is most difficult to ingest, possibly because flies are limited by the amount of liquid that they can regurgitate and reingest in a single feeding. Such clear curvilinear response patterns to wet and dry foods are consistent with the knowledge that more concentrated sucrose causes prolonged feeding in higher Diptera (Dethier *et al.*, 1956), including *R. pomonella* (Duan & Prokopy, 1993; Hendrichs *et al.*, 1993b). Although both sexes of *R. indifferens* feed for the same lengths of time on respective sucrose concentrations, females are larger, consume significantly more food than males and thus extract food more efficiently per unit time. Female *R. pomonella* also consume more dry sucrose than males (Webster *et al.*, 1979), but male Mediterranean fruit flies, *Ceratitis capitata*, ingested larger quantities of 4% and 16% sucrose solutions than females when offered free access to them using the J-pipette technique (Galun *et al.*, 1985), indicating greater sucrose consumption by females is not always the rule within tephritid flies.

Effects of age on feeding responses are pronounced in both sexes. Eight to 24-h-old *R. indifferens* consume less food than unfed 1–2-day-old flies, probably because they are less ‘hungry’ than the latter group. The additional starvation period of 1–2-day-old flies probably increases the flies’ sensitivity to sucrose or allows increased crop and abdomen space to accommodate larger meals. Flies aged 31–36-days-old and starved for 16–24 h are unable to consume meals as large as those of flies aged 1–2-days-old, even if the older flies are also energy deprived. Perhaps the abdominal space of older females is more limited than in 1–2-day-old females because of high egg loads, but reduced

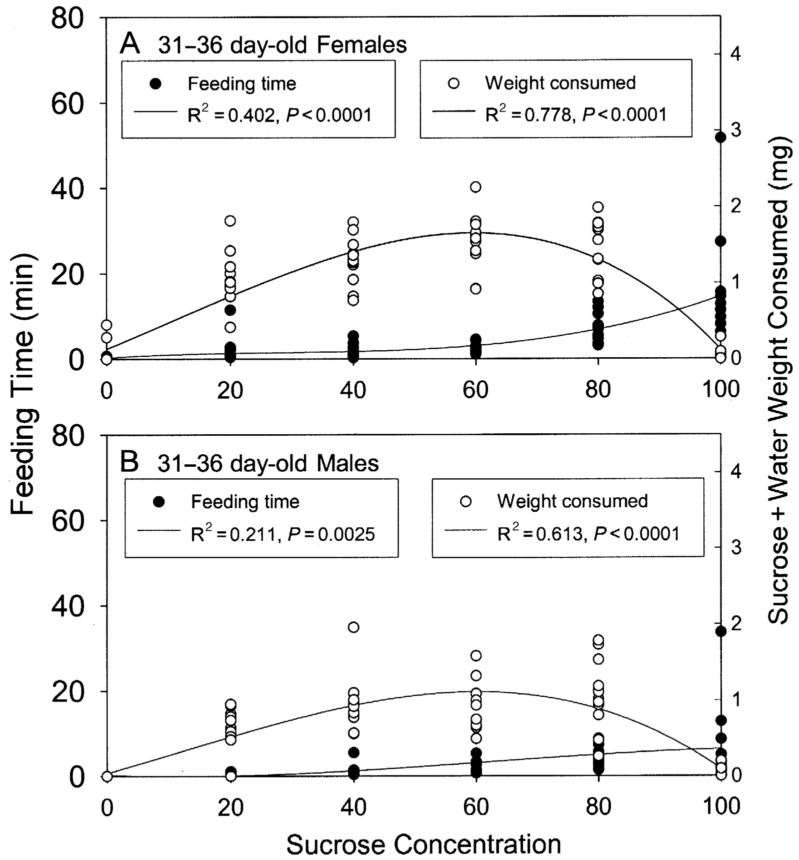

Fig. 2. Effects of sucrose concentrations on feeding time and sucrose and water (except 100% sucrose) consumed in (A) female and (B) male *Rhagoletis indifferens* fed single meals at 31–36 days post emergence.

abdominal space cannot be the explanation for lower consumption in males. Compared with 1–2-day-old flies, 31–36-day-old flies are less responsive to 100% sucrose, suggesting that reduced sensitivity of sugar receptors related to age may also be responsible for the smaller meals. In at least *R. pomonella*, sugar feeding is also highest early in life: free intake of dry sucrose and protein foods by females and males is highest 3 days after emergence and lower thereafter (Webster *et al.*, 1979). In the Caribbean fruit fly, *Anastrepha suspensa*, patterns differ, as free consumption of sucrose solution is low when flies are 1 day old, but increases daily afterward for 1 week (Landolt & Davis-Hernandez, 1993).

Table 1. Summary of two-way ANOVA: effects of sex (d.f. = 1), age (d.f. = 3) and sex × age interaction (d.f. = 3) on feeding responses of *Rhagoletis indifferens* to sucrose. Error d.f. = 84 (20% sucrose) and 74 (60% sucrose).

	20% Sucrose		60% Sucrose	
Effect	*F*	*P*	*F*	*P*
Feeding time				
Sex	0.40	0.531	0.06	0.815
Age[a]	3.18	0.028	6.14	0.001
Sex × age	1.87	0.137	0.84	0.475
Age comparisons[b]	1 = 2 = 4; 3 = 4; 1, 2 > 3		1 = 2 > 3 = 4	
Amount consumed				
Sex	21.58	< 0.0001	24.68	< 0.0001
Age[a]	26.32	< 0.0001	35.81	< 0.0001
Sex × age	0.76	0.518	2.61	0.058
Sex and age comparisons[b]	Female > male; 2 > 1 > 4 > 3		Female > male; 2 > 1 = 4 > 3	

[a]Age groups: 1 = 8–24 h; 2 = 1–2 days; 3 = 10–12 days; 4 = 31–36 days.
[b]Duncan New Multiple Range Test.

Table 2. Mean mg sucrose foods per mg bodyweight consumed and days survived ± SE by female and male *Rhagoletis indifferens* of four age groups offered single meals of sucrose.

	Sucrose food consumed/bodyweight (mg)		Survival (days)	
% Sucrose	Females	Males	Females	Males
8–24 h ($n = 11$–13)				
20	0.213 ± 0.024^a	0.223 ± 0.019^a	3.1 ± 0.2^a	3.4 ± 0.2^a
60	0.269 ± 0.081^a	0.279 ± 0.020^a	4.8 ± 1.3^a	4.6 ± 0.2^a
1–2 days ($n = 14$–43)				
0	0 ± 0^a	0.026 ± 0.018^a	3.5 ± 0.1^a	3.7 ± 0.1^a
2	0.140 ± 0.018^a	0.153 ± 0.022^a	3.4 ± 0.2^a	3.1 ± 0.2^a
10	0.277 ± 0.030^a	0.265 ± 0.029^a	4.2 ± 0.1^a	3.3 ± 0.1^b
20	0.303 ± 0.017^a	0.296 ± 0.024^a	4.1 ± 0.1^a	3.9 ± 0.2^a
40	0.367 ± 0.029^a	0.341 ± 0.023^a	5.4 ± 0.1^a	4.9 ± 0.2^b
60	0.422 ± 0.036^a	0.410 ± 0.028^a	6.1 ± 0.2^a	6.1 ± 0.1^a
80	0.436 ± 0.031^a	0.329 ± 0.050^a	6.8 ± 0.2^a	5.9 ± 0.2^b
100	0.051 ± 0.014^a	0.019 ± 0.005^b	4.4 ± 0.2^a	3.9 ± 0.1^b
10–12 days ($n = 5$–11)				
0	0 ± 0^a	0 ± 0^a	3.5 ± 0.6^a	3.2 ± 0.3^a
20	0.112 ± 0.012^a	0.103 ± 0.044^a	3.1 ± 0.2^a	3.4 ± 0.2^a
60	0.149 ± 0.017^a	0.235 ± 0.036^b	4.3 ± 0.1^a	4.2 ± 0.2^a
31–36 days ($n = 9$–13)				
0	0.013 ± 0.009^a	0 ± 0^a	2.0 ± 0.2^a	2.2 ± 0.2^a
20	0.173 ± 0.016^a	0.154 ± 0.027^a	2.9 ± 0.2^a	2.6 ± 0.2^a
20[a]	0.147 ± 0.023		2.1 ± 0.1	
40	0.227 ± 0.015^a	0.247 ± 0.030^a	3.4 ± 0.1^a	3.0 ± 0.2^a
60	0.259 ± 0.022^a	0.236 ± 0.022^a	4.1 ± 0.2^a	3.9 ± 0.3^a
60[a]	0.211 ± 0.017		3.3 ± 0.2	
80	0.259 ± 0.018^a	0.252 ± 0.034^a	4.2 ± 0.2^a	4.4 ± 0.2^a
100	0.008 ± 0.005^a	0.009 ± 0.005^a	2.6 ± 0.2^a	2.6 ± 0.2^a

Means of females and males within each concentration followed by different superscript letters are significantly different ($P < 0.05$).
[a]Provided oviposition sites beginning at 22–26 days old.
n, Number of flies per concentration.

Some 1–2-day-old females survive longer than males but, across all age groups, there are no differences. This supports the hypothesis that females require more sugar simply because of a larger body mass and not because of a higher metabolism or greater need for sugar. One to 2-day-old females that survive longer than males also consume slightly more sucrose per bodyweight than males, but because differences in consumption are variable, this is not statistically different (Table 2). This suggests that the few cases of an inconsistent sugar consumption–survival relationship between the sexes may be an experimental artifact.

Not surprisingly, because age affected sucrose consumption, it also affected survival in both sexes. Eight to 24-hour and 31–36-day-old flies did not survive as long as 1–2-day-old flies, possibly because the former two groups are unable to consume meals as large as the latter group. When solutions are dilute, solutes are concentrated by regurgitation and bubbling behaviour (Hendrichs *et al.*, 1992, 1993b), but

Table 3. Summary of two-way ANOVA: effects of sex (d.f. = 1), age (d.f. = 3) and sex × age interaction (d.f. = 3) on short-term survival of *Rhagoletis indifferens* after consumption of single sucrose meals. Error d.f. = 84 (20% sucrose) and 74 (60% sucrose).

	Days survived			
	20% Sucrose		60% Sucrose	
Effect	*F*	*P*	*F*	*P*
Sex	0.11	0.738	0.28	0.596
Age[a]	18.43	< 0.0001	25.95	< 0.0001
Sex × age	1.25	0.298	0.11	0.953
Age Comparisons[b]	2 > 3 = 1 > 4		2 > 1, 3, 4; 1 = 3; 3 = 4; 1 > 4	

[a]Age groups: 1 = 8–24 h; 2 = 1–2 days; 3 = 10–12 days; 4 = 31–36 days.
[b]Duncan New Multiple Range Test.

Table 4. Effects of single meals of sucrose-yeast foods and natural substances on feeding time and mg food consumed ± SE of previously unfed female and male *Rhagoletis indifferens*. $n = 10–19$ flies/treatment. Flies were fed 1–2 days after emergence.

	Feeding time (min)		Food consumed (mg)[a]	
Food	Females	Males	Females	Males
% Sucrose–yeast solutions				
20–12	1.80 ± 0.19$^{a(c)}$	1.62 ± 0.19$^{a(c)}$	1.82 ± 0.13$^{a(b)}$	1.54 ± 0.10$^{a(ab)}$
47–6	4.87 ± 1.11$^{a(bc)}$	3.36 ± 0.50$^{a(c)}$	2.39 ± 0.15$^{a(a)}$	1.74 ± 0.08$^{b(a)}$
60–12	14.42 ± 2.63$^{a(b)}$	20.60 ± 1.07$^{b(b)}$	2.34 ± 0.16$^{a(a)}$	1.79 ± 0.08$^{b(a)}$
88–12 (dry)	61.53 ± 5.78$^{a(a)}$	63.34 ± 6.06$^{a(a)}$	0.36 ± 0.03$^{a(e)}$	0.24 ± 0.05$^{b(d)}$
Natural substances				
Cherry juice (flesh)	10.38 + 2.83$^{a(bc)}$	4.42 + 0.61$^{a(c)}$	1.33 + 0.20$^{a(c)}$	1.31 + 0.10$^{a(b)}$
Cherry juice[b]	3.99 ± 0.65$^{a(bc)}$	4.22 ± 1.22$^{a(c)}$	1.91 ± 0.16$^{a(b)}$	1.45 ± 0.31$^{b(b)}$
Aphid honeydew[c]	59.58 ± 10.27$^{a(a)}$	60.05 ± 7.19$^{a(a)}$	0.88 ± 0.13$^{a(d)}$	0.53 ± 0.05$^{b(c)}$

[a]Wet foods include water weight.
[b]Saturated in cotton.
[c]On cherry leaves. Means of females and males within food types followed by different letters outside parentheses indicate significant differences (Duncan New Multiple Range Test, $P < 0.05$). Means within female or male columns and among all food types followed by different superscript letters inside parentheses indicate significant differences (Duncan New Multiple Range Test, $P < 0.05$).

the one meal prevented this, resulting in reduced survival. A 1–2-day food deprivation period after emergence apparently increases the amount of food that can be consumed, the interval before the next feeding, and survival. However, differential survival between 1- and 2- and 31–36-day-old flies is not totally related to food consumption because 31–36-day-old unfed flies died earlier than 1–2-day-old unfed flies. It is likely that a combination of food intake and age-related processes, such as increased cellular breakdown, affects differential short-term survival in young and old flies. Similarly, flies that had oviposited consume smaller single meals, which, together with stress resulting from repeated ovipositions (*R. indifferens* can lay 10–15 eggs/day), may cause reduced survival. Females of *C. capitata* that are deprived of a host for oviposition also survive longer than those that have oviposited (Carey *et al.*, 1986).

Although free sucrose foods are not found in nature, the similar responses of flies to cherry juice and honeydew indicate that the food consumption patterns and levels seen in the laboratory may occur in nature. The natural foods and their form affect feeding responses and survival in much the same way as artificial sucrose foods, as the wet cherry juice is easier for flies to process than the dried honeydew. These results indicate that solute concentrations of foods in nature can be deduced from feeding duration in both sexes.

As with sucrose only, in general, 1–2-day-old females and males fed on sucrose-yeast and natural foods survive equally long. Yeast plays no role in survival because protein cannot be used by tephritids for energy (Tsiropoulos, 1981; Cangussu & Zucoloto, 1992). Thus, the short survival of flies fed 20% sucrose−12% yeast, dry 88% sucrose−12%

Table 5. Effects of single meals of sucrose-yeast foods and natural substances on mg food consumed per bodyweight and survival ± SE of previously unfed female and male *Rhagoletis indifferens*. $n = 10–19$ flies/treatment. Flies were fed 1–2 days after emergence.

	Food consumed/bodyweight[a] (mg^{-1})		Survival (days)	
Food	Females	Males	Females	Males
% Sucrose–yeast solutions				
20–12	0.338 ± 0.025$^{a(b)}$	0.352 ± 0.018$^{a(bc)}$	3.8 ± 0.1$^{a(c)}$	4.3 ± 0.1$^{b(cd)}$
47–6	0.408 ± 0.022$^{a(ab)}$	0.407 ± 0.026$^{a(ab)}$	5.7 ± 0.1$^{a(a)}$	5.5 ± 0.1$^{a(b)}$
60–12	0.443 ± 0.032$^{a(a)}$	0.422 ± 0.019$^{a(a)}$	5.9 ± 0.3$^{a(a)}$	6.0 ± 0.2$^{a(a)}$
88–12 (dry)	0.064 ± 0.003$^{a(d)}$	0.055 ± 0.009$^{a(e)}$	4.6 ± 0.2$^{a(b)}$	4.1 ± 0.2$^{b(cd)}$
Natural substances				
Cherry juice (flesh)	0.238 + 0.038$^{a(c)}$	0.297 + 0.023$^{a(c)}$	3.7 + 0.2$^{a(c)}$	3.9 + 0.1$^{a(de)}$
Cherry juice[b]	0.330 ± 0.017$^{a(b)}$	0.332 ± 0.031$^{a(c)}$	3.9 ± 0.1$^{a(c)}$	3.6 ± 0.1$^{a(e)}$
Aphid honeydew[c]	0.170 ± 0.033$^{a(c)}$	0.125 ± 0.013$^{a(d)}$	4.7 ± 0.2$^{a(b)}$	4.5 ± 0.2$^{a(c)}$

[a]Wet foods include water weight.
[b]Saturated in cotton.
[c]On cherry leaves. Means of females and males within food types followed by different superscript letters outside parentheses indicate significant differences (Duncan New Multiple Range Test, $P < 0.05$). Means within female or male columns and among all food types followed by different superscript letters inside parentheses indicate significant differences (Duncan New Multiple Range Test, $P < 0.05$).

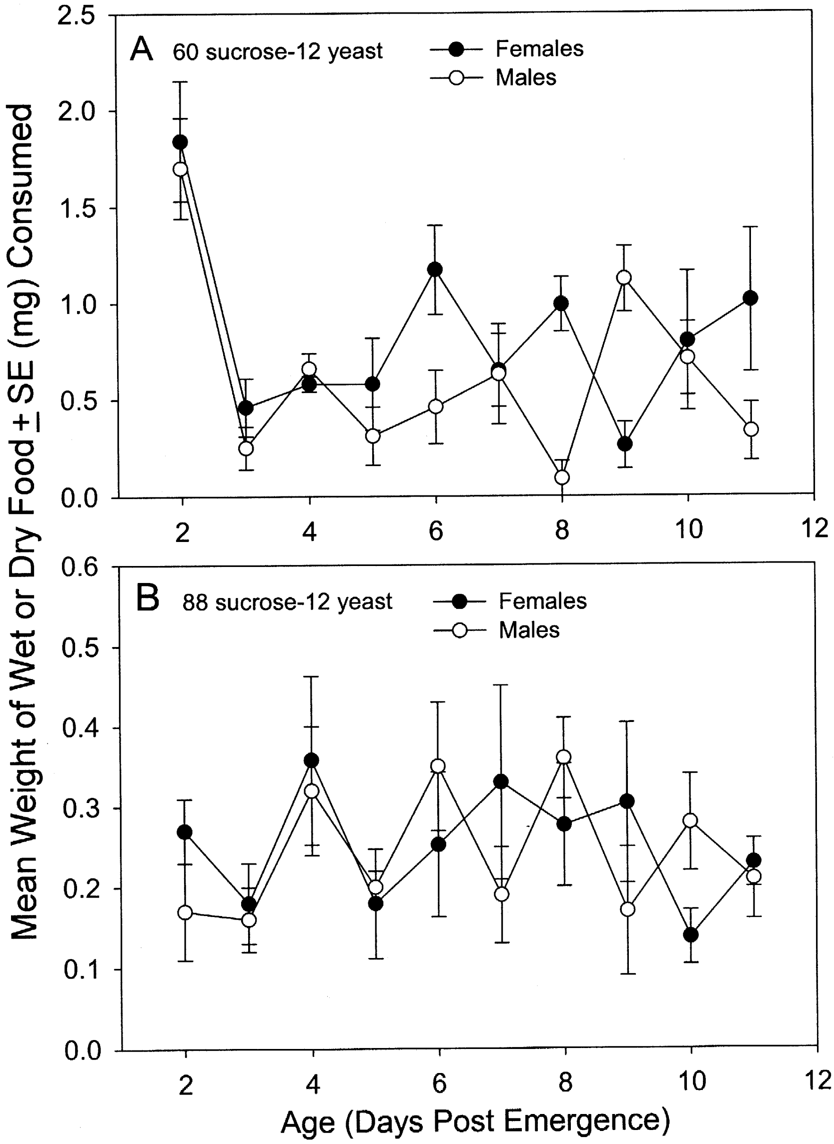

Fig. 3. Daily consumption by female and male *Rhagoletis indifferens* of single (A) wet 60% sucrose–12% yeast (including water) and (B) dry 88% sucrose–12% yeast (no water) meals. The first meal was offered on day 2.

yeast or cherry juice is not surprising because the amount of sugar consumed is the same or probably similar to that in a single 20% sucrose meal. Sweet cherry juice is high in glucose and fructose (Girard & Kopp, 1998) (18–23% in the current study) and, because these sugars are the monosaccharide components of sucrose, they are as nutritive as 20% sucrose for fly survival. Aphid honeydew consists mostly of glucose, fructose and saccharose, as well as smaller amounts of melezitose and raffinose (Nemec & Starý, 1990). All, or some combination of these, may provide energy for fly survival, but those most useful for *R. indifferens* need to be determined. In *P. regina*, melezitose and sucrose are of equal nutritive value (Hassett *et al.*, 1950). Flies consumed less honeydew than cherry juice, but flies survived longer on honeydew than on the juice. This suggests honeydew has a higher sugar concentration than cherry juice or that sugars in it are more nutritive. In nature, feeding on honeydew and its positive effect on survival should reduce the time spent foraging for other sugar sources. Whether *R. indifferens* feeds on honeydew in nature needs to be investigated.

Female and male flies respond to the 60% sucrose–12% yeast food readily each day, suggesting the sexes are equally dependent on substantial amounts of sugar. Whether the food is wet or dry greatly affects consumption levels and patterns over the longer term in both sexes. Flies aged 1–11-days-old engorged themselves on the 60% sucrose–12% yeast solution daily, but it is not known if flies feed on sugar this way in nature. In nature, flies may engorge themselves on dilute cherry juice from ripe fruit newly-damaged by birds. The regurgitation and bubbling behaviour (Hendrichs *et al*., 1992, 1993b) may concentrate the sugars in the juice, making repeated meals of juice highly valuable for survival. However, when birds are not abundant and damaged fruit are scarce, sugar sources are likely to be scattered or occur in nonconcentrated form. It has been proposed for *R. pomonella* that leachates play an important role in nutrition (Hendrichs *et al*., 1993a). If this is true for *R. indifferens*, the feeding responses to dry 100% sucrose, honeydew and daily responses to the dry 88% sucrose–12% yeast food in the laboratory may most resemble those in nature because leachates are not heavily concentrated wet sources of sugars (Tukey, 1971). This may explain the 'grazing' behaviours of flies on leaf surfaces (Hendrichs & Prokopy, 1993).

If it is assumed that cherry trees generally have low amounts of concentrated sugar sources, a large amount of the day should be spent by both sexes foraging for sugars. However, feeding by *R. indifferens* is difficult to observe in nature. Females engage in more searching behaviours than males, which spend most of the daylight hours clinging to the undersides of fruit (Yee, 2002). Compared to males, females may feed more frequently, which may explain their greater activity. Aside from sugars on leaves and damaged fruit, females can also feed on juice from punctures that they make on intact fruit with their ovipositors (Frick *et al*., 1954). Males must leave intact fruit periodically to obtain the high amounts of sugar needed, perhaps at frequent intervals. This may also occur earlier or later in the day, times when fewer males are seen on fruit and female presence on them is reduced. Because the relative abundance of females and males on fruit vs. leaves does not change over the season (Yee, 2002), any sugar-feeding differences related to prevalence on one vs. the other substrate should be seen in both young and old flies.

In summary, the results of the present study show that female and male *R. indifferens* respond similarly to sucrose, and that the sexes have the same sugar requirements on a per bodyweight basis at all ages. Sucrose concentrations and fly age, at first and later feedings, affect how much sucrose is consumed and how long flies can survive until the next feed. The results suggest that sugar-feeding behaviours and the energy invested in sugar 'seeking' by both sexes of *R. indifferens* should be the same throughout life. Given that female and male behaviours differ greatly, the ways in which the sexes obtain the substantial amounts of sugars needed for survival may also differ and need to be investigated.

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