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EFFECT OF SUGAR TYPE ON FOOD INTAKE AND LIPID DYNAMICS IN ADULT *AGRAULIS VANILLAE* L. (NYMPHALIDAE)

PETER G. MAY

Department of Biology, Stetson University, DeLand, Florida 32720

ABSTRACT. Newly emerged, laboratory-reared adults of *Agraulis vanillae* L. were tested for feeding response to artificial nectars containing either glucose, fructose, or sucrose. Daily meal size and mass change (particularly lipids) over a five-day period (three of which were feeding days) were compared among individuals feeding on different sugars. Butterflies fed sucrose or fructose ingested significantly larger meals in the first two days of feeding than did individuals fed glucose. Total intake over the three-day experimental period was also significantly greater in sucrose- and fructose-fed individuals. Fructose- and sucrose-fed individuals did not differ from each other in total intake. Sucrose- and fructose-fed individuals differed in mass change and lipid change from individuals fed glucose or not fed at all. Individuals on sucrose and fructose diets increased in mass, and accumulated or lost little lipid, while those on glucose or no adult food lost significant amounts of total mass, lipid mass, and lean mass. Individuals on glucose diets appeared more efficient in maintaining lipid reserves per unit energy ingested than did those in the sucrose and fructose groups. Results are discussed with respect to sugar composition of butterfly-pollinated flowers, foraging energetics, and carbohydrate metabolism.

Additional key words: nectar, sugars, meal size, adult feeding.

There are consistent relations between presence and concentrations of a variety of nectar constituents, including sugars and amino acids, and the type of animal the nectar is intended to attract (Watt et al. 1974, Baker & Baker 1975, 1979, 1982, 1983, Lanza 1988). Flowers pollinated by hummingbirds and hawkmoths produce nectars high in oligosaccharides; this is thought to be related to the high energy demands of these animals (Hainsworth & Wolf 1976, Stiles 1976). However, butterfly flowers are also generally rich in sucrose (but not always; see Watt et al. 1974), though butterflies as a group are thought to have relatively low energy demands (Heinrich 1975). Further, given a choice between nectars containing sucrose, fructose, or glucose, some butterflies show a clear preference for sucrose nectars over glucose nectars (Ehrhardt 1991, 1992).

Although there is great diversity in the importance of food intake among adult lepidopterans relative to reserves from larval feeding (Boggs 1986, May 1992), studies of food intake among nectar-feeding lepidopterans generally have shown that carbohydrates in the diet significantly increase female fecundity (e.g., Stern & Smith 1960, Murphy et al. 1983, Leather 1984, Carroll & Quiring 1992). Lepidopterans that require nectar as adults therefore should evolve preferences for those carbohydrates that are most effective at increasing fecundity or other fitness components (Pyke 1984).

In this study, I examine effects of sugar type (sucrose, fructose, or glucose) on adult food intake and accumulation of lipid reserves in *Agraulis vanillae* L., which is an avid flower visitor. I asked three main questions:

a) Do these butterflies respond differently to artificial nectars of the three sugar types equal in concentration and therefore in total energy content?

b) Do diets composed of different sugar types influence the rate at which metabolic reserves, particularly lipids, are stored or exhausted?

c) Do adults compensate for low emergence weights by greater adult food intake to supplement lower metabolic reserves from larval feeding, as suggested by Boggs (1981) and May (1992)?

METHODS AND MATERIALS

The gulf fritillary, *Agraulis vanillae* L. (Nymphalidae), is a heliconiine butterfly that frequents a variety of open and disturbed habitats in Florida, from about mid-May until November. It typically is found near its larval food plant, *Passiflora incarnata* L. (Passifloraceae). Oviposition occurs throughout the flight season, eggs are laid singly on host plants or on nearby vegetation, and there are multiple, overlapping generations per year. Most females are reproductively mature and capable of ovipositing within 12–18 hours after emergence (Arbogast 1965). Large-scale southerly migrations take place from late August through November (Walker 1978), although little is known of the destination and overwintering biology of the migrants. Adult longevity is from 2–3 weeks (Arbogast 1965, May, unpubl. data). Food habits of adults in the field and their effects on lipid reserves have been studied extensively (May 1992).

Third through fifth instar larvae were collected during summer 1990 from several populations in the DeLand, Florida area (29°06′ latitude, 81°22′ longitude) and taken to the laboratory for rearing. Larvae were fed in the laboratory with field-collected foliage of *Passiflora incarnata,* and were maintained at ambient photoperiod and heated for 12 hours a day to 28–30°C. Nighttime temperatures were approximately 26°C. Pupae were maintained under similar conditions, and upon adult emergence, I allowed each individual to expel meconial wastes before determining sex, wet mass, and forewing length. Wet mass was determined by weighing freshly emerged individuals in tared glassine envelopes. Butterflies were assigned to feeding treatment on the basis of emergence order in a repeating sequence of fructose, glucose, and sucrose (the first adult was fed fructose, the second glucose, the third sucrose, the fourth fructose, and so on). In addition, several adults with split or otherwise

nonfunctional probosces were maintained without food under the same conditions as the feeding butterflies for comparison. However, as these individuals were not randomly assigned to treatment, they were excluded from statistical analyses.

After postemergence data were collected, each butterfly was marked and placed in a 60 × 60 × 70 cm screened flight cage exposed to the same environmental conditions as the larvae and pupae. Beginning on the day after emergence, individuals were fed to satiation once a day on a 31% (weight/weight) aqueous solution of either sucrose, fructose, or glucose. Flowers visited by *Agraulis* range from 18–40% sucrose equivalents (May 1992); 31% was chosen somewhat arbitrarily within this range. Sugar solutions were heated to approximately 28°C before feeding trials began. The insects were fed from microcapillary tubes containing the appropriate sugar solution using the procedure described by May (1985). An individual was considered satiated after withdrawing its proboscis from the microcapillary tube three times. Volume of nectar consumed was recorded for three consecutive days, and on the fifth day after emergence each individual was weighed and frozen for lipid extraction.

Before lipid extraction, individual butterflies were dried to constant mass in a drying oven at approximately 50–60°C and weighed within 30 minutes after removal from the drying oven. Lipid extraction followed the technique of Brower (1985). Each butterfly was homogenized in a centrifuge tube with 10 ml of petroleum ether, then vortexed and placed in a shaking water bath at 35°C for 30 minutes, with vortexing every 10 minutes. Solids were allowed to settle for 30 minutes, and the supernatant was withdrawn with a Pasteur pipet and transferred to a preweighed aluminum pan on a 30°C hot plate. The remaining solids were extracted again with an additional 15 ml of petroleum ether, vortexed and the procedure was repeated. Weighing pans with supernatant were allowed to evaporate overnight in a fume hood, and the remaining lipids were weighed. Lean mass was calculated as dry mass minus lipid mass.

To estimate changes in lipid stores over the course of the experiment, I estimated emergence lipid reserves using the regression of final wet mass vs. lipid mass of all individuals at the end of the experiment, assuming that the same relationship held for individuals at emergence. Regressions for males and females gave identical equations ($y = 0.07x - 0.003$, where y is lipid mass and x is final wet mass; $F = 30.66$, $P = 0.0001$ for females, $F = 12.35$, $P = 0.003$ for males). Emergence lipid mass was estimated by substituting emergence wet mass for final wet mass in this regression. For example, a butterfly weighing 250 mg at emergence would be estimated to have an emergence lipid mass of

TABLE 1. Meal sizes of *Agraulis vanillae* adults fed different sugars. Figures indicate mean ± SE; sample size in parentheses.

Meal volume (μL)	Treatment		
	Sucrose	Fructose	Glucose
Day 1	88.7 ± 7.2 (14)	83.2 ± 6.5 (15)	25.6 ± 3.7 (16)
Day 2	56.7 ± 6.5 (14)	58.0 ± 5.5 (15)	29.6 ± 3.3 (15)
Day 3	44.4 ± 7.5 (13)	36.1 ± 5.4 (15)	28.6 ± 4.8 (15)
Total	189.8 ± 18.7 (13)	177.3 ± 9.8 (15)	83.8 ± 9.6 (15)

0.07 × 250 − 0.003 mg of lipid (17.5 mg). Change in lipid mass was calculated as estimated emergence lipid mass − final lipid mass.

I calculated two values, one intended to indicate the relations between energy ingested and the amount of lipid stored, and the other an estimate of total energy expenditure. The first, labeled Energy Use Ratio (stored energy/ingested energy), is the ratio between energy remaining as stored lipid at the end of the experiment (calculated as lipid mass (μg) × 0.039J/μg [from Schmidt-Nielsen 1975]) and energy ingested in the adult diet (calculated as total volume consumed (μL) × 5.78J/μL [see Bolten et al. 1979 for details of calculation]). This figure should indicate how efficiently the butterflies use ingested energy and convert it to lipid reserves. The second estimate, Total Energy Expenditure, is calculated as energy intake by the adult plus energy released from lipid metabolism (estimated as change in lipid mass multiplied by the energy content of lipid, as explained above). This latter estimate is a rough approximation at best, due to estimation errors introduced by using the regression described above to estimate emergence lipid reserves.

RESULTS

The type of sugar present in artificial nectars significantly affected meal size, and subsequently affected the size of lipid reserves. Butterflies fed longer on sucrose and fructose nectars than glucose nectar (Table 1). Two-way analyses of variance (ANOVAs) using sugar type and sex of the butterfly as classifying variables showed no significant effects of sex or interactions between sex and diet among variables, so male and female data were combined and analyzed with one-way ANOVAs. These analyses showed significant effects of sugar type on day 1, day 2, and total volumes (respectively, $F = 36.3$, $P = 0.0001$; $F = 9.5$, $P = 0.0004$; $F = 20.2$, $P = 0.0001$). Meal volume on day 3 did not differ significantly among groups ($F = 1.8$, $P = 0.186$). For the three variables that showed significant differences, multiple comparison tests (Scheffe's F-test) showed that sucrose and fructose meal volumes did not differ significantly (at the 0.05 level), but both were significantly greater than glucose meal volumes.

TABLE 2. Body size and composition characteristics of *Agraulis vanillae* adults fed different sugars. Figures indicate mean ± SE; sample size in parentheses.

	Treatment			
	Sucrose	Fructose	Glucose	No food
Final wet mass (mg)				
Male	245 ± 34 (3)	274 ± 8 (7)	187 ± 10 (5)	119 (1)
Female	330 ± 24 (9)	322 ± 29 (7)	252 ± 13 (11)	215 ± 34 (4)
Final dry mass				
Male	92 ± 14 (3)	105 ± 3 (7)	77 ± 6 (5)	47 (1)
Female	124 ± 9 (10)	108 ± 6 (7)	95 ± 4 (11)	84 ± 11 (4)
Lipid mass				
Male	13 ± 5 (3)	15 ± 2 (7)	11 ± 2 (5)	6 (1)
Female	24 ± 3 (10)	16 ± 2 (7)	14 ± 2 (11)	11 ± 3 (4)
Lean mass				
Male	79 ± 10 (3)	90 ± 3 (8)	66 ± 5 (5)	41 (1)
Female	101 ± 6 (10)	92 ± 4 (7)	81 ± 3 (11)	73 ± 8 (4)
Mass change				
Male	12 ± 15 (3)	23 ± 10 (7)	−73 ± 22 (5)	−142 (1)
Female	7 ± 20 (9)	8 ± 35 (7)	−66 ± 16 (11)	−97 ± 8 (4)
% Lipid (of dry mass)	17.3 ± 1.1 (13)	14.6 ± 0.9 (15)	14.1 ± 1.0 (16)	12.7 ± 2.0 (5)

Differences in meal sizes due to sugar type significantly affected changes in weight and lipid storage among the treatment groups (Table 2). Although females are capable of oviposition within one day after emergence (Arbogast 1965), no oviposition occurred among caged females during the experiment, so any resources allocated to egg development are reflected in the body masses determined for females. Two-way ANOVAs of emergence weight and forewing lengths, using sex and treatment as classifying variables, showed significant sexual differences in body size (females are larger in linear dimensions and mass at emergence), but no significant differences in starting conditions among treatments (Table 3). Thus, changes in body size and composition measured on the fifth day (after three days of feeding) can be attributed to the effects of the different sugars on feeding and mass accumulation or depletion. Two-way ANOVAs using sex and treatment as the classifying variables showed that wet mass, dry mass, and lean mass at the end of the experiment varied significantly among treatments and between sexes (Table 3). Mass change varied significantly among treatments, but not between sexes. Lipid mass varied significantly between sexes, but differences among treatments were slightly above the level of significance ($P = 0.08$). Percent lipid (of dry mass) did not vary significantly among treatments or sexes; the data in Table 3 are for

TABLE 3. Results of 2-way ANOVA's of body composition characteristics. Statistical significance indicated by bold type.

Variable	Effect of		
	Treatment	Sex	Interaction
Emergence mass	F = 0.176	**F = 8.817**	F = 0.009
	P = 0.839	**P = 0.005**	P = 0.991
Forewing length	F = 0.407	F = 3.487	F = 1.101
	P = 0.668	P = 0.068	P = 0.341
Final wet mass	**F = 7.989**	**F = 12.72**	F = 0.311
	P = 0.001	**P = 0.001**	P = 0.734
Dry mass	**F = 5.698**	**F = 8.229**	F = 1.876
	P = 0.007	**P = 0.007**	P = 0.167
Lipid mass	F = 2.636	**F = 5.454**	F = 1.826
	P = 0.085	**P = 0.025**	P = 0.175
Lean mass	**F = 6.973**	**F = 8.466**	F = 1.811
	P = 0.003	**P = 0.006**	P = 0.177
Mass change	**F = 8.608**	F = 0.044	F = 0.105
	P = 0.001	P = 0.834	P = 0.900
% Lipid (of dry mass)	F = 0.661	F = 2.672	F = 1.635
	P = 0.522	P = 0.110	P = 0.208

pooled sexes. Butterflies on fructose and sucrose diets added mass during the experimental period, and this was partially due to accumulation of lipids in the sucrose group, whereas individuals fed glucose or nothing lost mass and apparently depleted metabolic reserves present at emergence. The greatest mass loss was in the nonfed butterflies (Table 2); these data, however, were not statistically analyzed with the other treatment groups.

Estimated changes in lipid stores (Table 4) should be interpreted with caution because of estimation errors in emergence lipid masses introduced by the use of regression as described above. Standard errors in Table 4 reflect only variance in the lipids actually measured at the end of the experimental period; estimation errors from calculation of emergence lipid mass were not carried through to these figures. Two-way ANOVAs showed no significant differences among treatments in estimated emergence lipid weights ($F = 0.176$, $P = 0.839$), although females had significantly more lipid ($F = 8.8$, $P = 0.005$). Lipid change did not differ significantly among treatments ($F = 3.025$, $P = 0.06$), although the probability level is close. There was no difference in lipid change between sexes ($F = 0.03$, $P = 0.865$). According to these estimates, individuals on sucrose accumulated fat, those on fructose lost a small amount, and those on glucose or no food lost more lipid. Multiple comparison tests (Fisher PLSD) showed that significant differences existed between the sucrose and glucose treatments, between fructose and glucose treatments, but not between sucrose- and fructose-fed butterflies.

TABLE 4. Lipid mass and energy utilization as a function of treatment in *Agraulis vanillae*. Figures indicate mean ± SE; sample size in parentheses. N/A = not applicable.

	Treatment			
	Sucrose	Fructose	Glucose	Not fed
Initial lipid (mg)	17 ± 1 (17)	17 ± 2 (17)	18 ± 1 (18)	17 ± 1 (8)
Lipid change (mg)	−3 ± 2 (13)	1 ± 1 (15)	5 ± 2 (15)	8 ± 2 (5)
Energy use ratio	0.80 ± 0.11 (13)	0.62 ± 0.06 (15)	1.40 ± 0.30 (15)	N/A
Total energy use (J)	974 ± 66 (13)	1060 ± 53 (15)	657 ± 69 (15)	307 ± 85 (5)

Energy Use Ratio and Total Energy Expenditure differed significantly among treatments (Table 4). Two-way ANOVAs of these indices used treatment and sex as classifying variables, and excluded individuals that did not feed. Both indices showed significant differences among treatments, but not between sexes (Use ratio: $F_{treat} = 9.3$, $P = 0.0005$, $F_{sex} = 0.407$, $P = 0.53$; Expenditure: $F_{treat} = 12.19$, $P = 0.0001$, $F_{sex} = 0.20$, $P = 0.655$). Multiple comparison tests (Fisher PLSD) showed for both that the sucrose and fructose groups differed significantly from the glucose group but not from each other ($P < 0.05$). These estimates suggest that a) per unit of energy ingested as an adult, the butterflies fed glucose had relatively greater amounts of energy stored as lipid at the end of the experiment than did individuals in the fructose and sucrose groups, and b) the glucose-fed individuals had significantly lower total energy budgets than did the fructose- and sucrose-fed individuals.

As a test of the hypothesis that individuals with low emergence weights (and therefore low lipid reserves; correlation between emergence weight and lipid weight for pooled sexes, $r = 0.70$, $df = 18$, $P < 0.01$) ingest more food to supplement lipid reserves from larval feeding, I sought correlations between forewing length or emergence weight and volume of nectar imbibed on each day of the feeding trial as well as total volume imbibed. If correct, this hypothesis would predict a negative correlation between emergence weight and the volume of nectar taken. Because many correlations were performed in this analysis, I used the Systat software package (Systat, Inc., Evanston, Indiana) and a sequential Bonferroni technique (Rice 1989) to ensure that the probability of type I error was less than 0.05 for all correlations. Considering both individuals within treatment groups and all treatments pooled together, no consistent relations between body size and nectar consumption were found (Table 5). Although most correlations were not significant, the nature of the body size vs. volume consumed relationship differed among treatments, and between days within some treatments. Body size indicators and volume consumed were negatively correlated in some cases, though never significantly, and positively in

TABLE 5. Correlation coefficients between body size traits and nectar consumption. Correlations significant at the 0.05 level are in bold type.

Nectar consumption	Body size trait, by treatment							
	Sucrose		Fructose		Glucose		All treatments	
	Wt.*	FW**	Wt.	FW	Wt.	FW	Wt.	FW
Day 1	0.227	0.319	−0.207	0.232	−0.498	−0.051	−0.077	0.284
Day 2	0.209	0.537	−0.036	−0.106	−0.242	0.374	0.032	0.277
Day 3	0.190	0.428	0.311	0.278	0.081	0.224	0.149	0.352
Total	0.372	0.664	0.037	**0.620**	−0.359	0.053	0.023	0.431

* Wet weight at emergence.
** Forewing length.

others. The only significant correlation coefficient was opposite of what was predicted, i.e., butterflies with larger forewings consumed more nectar over the three-day feeding period in the fructose group.

DISCUSSION

Type of sugar present in nectar clearly affects feeding behavior and lipid dynamics in *Agraulis vanillae*, although the reason for this difference is not obvious. All three sugar solutions had equal sugar concentrations, and therefore equal absolute energy content per unit volume. Based on energy content alone, there is no adaptive reason to expect butterflies to prefer one sugar type over another, unless there are differences in metabolizable energy between sugar types. Further, the difference is not between monosaccharides and oligosaccharides, as responses to sucrose and fructose nectars were not significantly different in any of the measures examined, while both differed significantly from the response to glucose. Fructose and sucrose clearly are preferred by this butterfly as judged by average meal size. The sugar types also differed with respect to changes in daily meal size; this decreased from day 1 to 3 with sucrose and fructose nectars, but stayed constant in glucose-fed butterflies.

These differences in meal size and thus energy intake among treatments significantly affected body composition in five-day old adults. Sucrose- and fructose-fed butterflies had larger total mass and lean mass than glucose-fed butterflies. Although differences in lipid contents were not statistically significant, it is likely that differences in lipid storage account for some of the differences in mass change. Sucrose- and fructose-fed butterflies either accumulated lipids or depleted very little, while glucose- and nonfed butterflies depleted lipids. Lean-mass loss among these latter groups suggests these butterflies were metabolizing nonlipid body constituents as well.

The proportion of body mass allocated to lipid did not differ signif-

icantly among groups, suggesting that as butterflies metabolize lipid stores, they also metabolize a relatively constant proportion of nonlipid components, and that this is independent of sugar type in the adult diet. The differences seen in the indices of energy use derived here may be due to either a) physiological differences in sugar metabolism among sugar types (glucose-fed butterflies showed greater lipid reserves per unit of energy ingested) or more likely, b) dietary differences lead to behavioral differences in adult butterflies, with glucose-fed butterflies showing lower activity levels and therefore conserving stored lipids that are not replaced by adult dietary intake.

These findings are especially puzzling in light of the traditional view of insect carbohydrate metabolism, which holds that the primary sugar circulating in the hemolymph is trehalose, a disaccharide synthesized from glucose in a process that is apparently relatively expensive metabolically (Chapman 1979). Trehalose is presumably the carbohydrate that is the intermediate between ingested sugars and lipid storage in the fat body. Thus, ingested sucrose and fructose first must be modified to glucose and then trehalose, which would suggest that given equal-concentration solutions of glucose, sucrose, and fructose, glucose should be the most efficient in terms of conversion to trehalose. Other butterflies studied can metabolize all three of the sugars via carbohydrases (Watt et al. 1974, Ehrhardt 1991).

In light of the field foraging behavior of *Agraulis vanillae*, the results here are consistent with their failure to discriminate among flowers differing in energy content in natural situations. Given a choice between flowers of significantly different energy contents, they often fail to preferentially visit flowers with the highest energy contents, whereas another species (*Phoebis sennae* L., Pieridae) does selectively visit flowers with higher energy content (May 1992). In addition, there may be little selective pressure for butterflies to discriminate flowers on the basis of sugars, as it may be rare for flowers to produce nectars with only one type of sugar. For example, Baker and Baker (1983) found that in a sample of 765 nectars from a variety of pollination syndromes tested for sugar content, only nine had one type of sugar only. Seven nectars had sucrose only, two had glucose only, and none had fructose only. As most nectars apparently have some combination of all three sugars (649 in the Bakers' sample), butterflies may respond to relative sweetness or detectability, which is higher for sucrose and fructose than glucose.

These butterflies showed no clear relationship between emergence weight and amount of food taken by adults. The best indicator of fat reserves at eclosion, the emergence wet weight, showed no significant correlations with any measure of nectar consumption. These data thus

provide no support for the hypothesis that variation in adult feeding by this species can compensate for poor larval conditions by increasing adult intake in individuals with low metabolic reserves at emergence (May 1992), although the feeding opportunities available in this laboratory context are drastically different from feeding opportunities available to wild butterflies.

Whatever the reasons for the effect of different sugars on adult intake, these results are generally in accord with studies of nectar composition in butterfly-visited flowers, which are typically sucrose-rich (Baker & Baker 1975, 1979, 1982, 1983). Watt et al. (1974), however, showed that some *Colias* species (Pieridae) preferred flowers that have high proportions of glucose and fructose. Recent experimental studies of nectar preference by the butterfly *Battus philenor* L. (Papilionidae) showed a clear preference for sucrose and fructose over glucose, and a less dramatic preference for sucrose over fructose (Ehrhardt 1991, 1992). Sucrose-rich nectars have been suggested by other workers to be associated with high energy-demand pollinators such as hummingbirds (Hainsworth & Wolf 1976, Stiles 1976). Relative to most other pollinator groups, however, butterflies are probably one of the pollinator groups with the lowest energy demands, based on flight energetics (Heinrich 1975, Zebe 1954) and low nectar volumes in butterfly-visited flowers (Watt 1974, May 1988, 1992).

The differences among feeding response to different sugars seen here are also consistent with studies of sugar sensitivity and preference in some flies and orthopterans, which can detect sucrose at very low concentrations, fructose at slightly higher concentrations, and glucose only at much higher concentrations (Hansen 1978, Cook 1977). Ehrhardt (1991) suggests that these abilities and preferences may be general in insects.

Some caution needs to be exercised in interpreting these feeding differences in the context of foraging behavior in natural situations, as butterflies rarely if ever have the opportunity to feed uninterruptedly to satiation from a single source. However, the marked differences in responses to different types of sugars suggest that more detailed studies of sugar preferences and metabolism in a variety of insects might be fruitful.

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