

RATES OF ENERGY PROCESSING BY BLOWFLIES: THE USES FOR A JOULE VARY WITH FOOD QUALITY AND QUANTITY

By F. REED HAINSWORTH, GWEN FISHER AND ELIZABETH PRECUP

*Department of Biology, Syracuse University, Syracuse,
New York 13244-1270, USA*

Accepted 18 December 1989

Summary

Data on the variation of crop volumes with time for blowflies (*Phormia regina* Meigen) fed various volumes and concentrations of fructose or sucrose (from Gelperin, 1966, and Edgecomb *et al.* 1987) were used to characterize energy processing rates to test the assumption of food energy additivity of optimal foraging theories. Six regression models (linear, square root, cube root, hyperbolic, inverse cube root and exponential) were compared for data from Edgecomb *et al.* (1987) with measurements of crop volumes from 10 min to 5 h after blowflies were fed 9.7 or 14.5 μl of 0.25 mol l^{-1} sucrose. Only the hyperbolic regression could be discriminated as statistically different, and the linear model was selected as most parsimonious for examining rates of energy processing. About the same volume bypassed the crop for flies fed 9.7 or 14.5 μl . Volume rates of crop emptying (from Gelperin, 1966) did not change at intermediate concentrations but decreased from lowest and to highest concentrations. Energy processing patterns indicate that long-term storage rates increase with meal size and at intermediate concentrations and decrease (3.0 mol l^{-1} fructose) or remain constant (2.0 mol l^{-1} sucrose) at high concentrations, so the uses for a unit of energy are not additive across concentrations and meal sizes. Animals that process energy in this way should attempt to maximize meal size and include high-energy foods in their diet out of proportion to the amount of energy gained for the time spent foraging.

Introduction

Many optimal foraging theories, based on the assumption that animals maximize their long-term rate of net energy gain during foraging (e.g. Pyke, 1984; Stephens and Krebs, 1986), consider energy from different amounts and qualities of food to be additive in its effects on fitness. Some recent studies stress that different foods of the same gross energy value can yield different amounts of net energy because of variations in digestive assimilation (McClintock, 1986; Speakman, 1987; Karasov and Diamond, 1988), an observation that can be used to refine

Key words: allocation, blowflies, crop function, digestion, energy, feeding, food choice, meals, nectar, optimal foraging, storage rates.

measurements of achieved rates of net energy gain during foraging. However, after accounting for differences in assimilation, is a unit of energy from different amounts and qualities of food used equivalently?

Dynamic models of foraging attempt to integrate gains from feeding with short- and long-term requirements for energy (e.g. Mangel and Clark, 1988). If there is more than one use for assimilated energy, which is often likely to be the case, the allocation of this to different functions could produce variation in the use of a unit of energy from foods of different quality. For example, consider two uses for assimilated energy: one for short-term maintenance and the other for long-term storage or reproduction. If storage or reproductive use becomes saturated as food quality increases, a larger fraction of total assimilated energy could be allocated for short-term maintenance, and a food of high quality could be used for a longer time per unit of assimilated energy. Alternatively, the rate of energy storage or reproductive use could increase with food quality. In either case the two uses for a unit of assimilated energy would not be additive across foods, and foods of high quality should be preferred even though the long-term rate of net energy gain prior to assimilation may be lower for them. Similar arguments and predictions can be made for the amount of food consumed during foraging if there is a relationship between meal size and long-term rates of energy use.

Many animals consume meals of foods of variable quality. While they are foraging their intakes of energy can exceed their expenditures, and food accumulates in digestive structures (stomachs or crops). After they cease feeding, energy is supplied from these internal reservoirs. There is evidence that the use of assimilated energy influences the supply from stomachs or crops. Crop emptying rates vary with food utilization in fifth-instar locusts (*Locusta migratoria*) (Simpson, 1983). Increasing the quality of food slows the rate of stomach or crop emptying in humans (*Homo sapiens*) (Hunt, 1983), monkeys (*Macaca mulatta*) (McHugh and Moran, 1979), laboratory rats (*Rattus norvegicus*) (McCann and Stricker, 1986), cockroaches (*Periplaneta americana*) (Treherne, 1957), several species of hummingbirds (Wolf and Hainsworth, 1977) and blowflies (*Phormia regina*) (Gelperin, 1966; Edgecomb *et al.* 1987). However, only for monkeys and laboratory rats fed glucose, where rate of stomach emptying is constant within a concentration, has digestive supply rate been quantitatively related to rate of use of assimilated energy.

The question considered here is whether digestive processing of energy together with rate of use of energy for maintenance by blowflies provides evidence for variation in the uses for a unit of energy as the quantity and quality of food varies.

Materials and methods

Sources of data

Drs Alan Gelperin and Robert Edgecomb kindly provided individual data from their detailed studies of crop emptying in blowflies (Gelperin, 1966; Edgecomb *et al.* 1987). The data used from the experiments by Edgecomb *et al.* (1987) were

for flies starved for 4 days, immobilized and fed 9.7 or 14.5 μl of 0.25 mol l^{-1} sucrose. Crop masses were measured at 0.17, 0.5, 1, 2 and 5 h after the start of feeding. Masses were corrected for the average mass of a crop prior to feeding (0.2 mg), and volumes were calculated by dividing corrected masses by the specific gravity of 0.25 mol l^{-1} sucrose.

The data from the experiments by Gelperin (1966) were for newly emerged male flies immobilized by taping their wings to a piece of plastic. They were fed several concentrations of X-ray-dense food of constant volume (10 μl for sucrose, 15 μl for fructose), and X-ray photographed at intervals following the meal. The area of the crop was measured from the photographs to estimate crop volumes.

Analysis of crop emptying

Model comparisons

Six regression models were used to search for the best depiction of crop emptying. These are based on studies with other species or physical models of elastic emptying structures (Stubbs, 1977; Smith *et al.* 1984; Jobling, 1986). The models involve: (1) a linear, (2) an exponential, (3) a square root, (4) a cube root, (5) a hyperbolic and (6) an inverse cube root change in volume with time.

The linear model has been suggested to apply when negative feedback influences emptying to produce a rate of energy supply to equal the rate of use (McHugh and Moran, 1979; Hunt, 1983), and it has been used to characterize stomach emptying of glucose by monkeys (McHugh and Moran, 1979) and laboratory rats (McCann and Stricker, 1986). The exponential model could apply when feedback for rate of energy supply is minimal, and it has been suggested to characterize stomach emptying of non-nutritional fluids in humans (Smith *et al.* 1984). The square root model is based on elastic structures following Laplace's law (tension = pressure \times radius) where the structure approximates an elastic cylinder (volume proportional to square of radius), and it has been used to characterize stomach emptying of some foods by humans (Hopkins, 1966) and laboratory rats (Booth, 1978). The cube root model involves Laplace's law with spherical emptying structures (volume proportional to cube of radius). The hyperbolic model has been used to describe stomach emptying in humans (Stubbs, 1977), and the inverse cube root model involves Laplace's law and Poiseuille's equation (for flow) applied to human stomachs (Stubbs, 1977).

There is evidence that some ingested food bypasses the crop and enters the midgut (Knight, 1962; Simpson *et al.* 1989; see below), so initial crop volumes are likely to be less than the amount fed to blowflies. This may be the case particularly for the first meal, when the mid- and hindguts contain no food. The fit of non-linear regressions will be influenced by changes in crop volumes immediately after feeding, so the data from Edgecomb *et al.* (1987) were used to compare regression models. These data include measurements of crop volumes 10 min after the start of feeding with 15 samples measured for each of five periods completely spanning

crop emptying. The first sample times in the experiments of Gelperin (1966) were sufficiently long after feeding for model fits to be biased by missing data.

Data were transformed and analyzed by linear, least-squares regressions. Models were compared for fit to the emptying data using squared residuals for untransformed data (Smith *et al.* 1984; Jobling, 1986). An analysis of variance (ANOVA) of squared residuals for untransformed data with multiple comparison (Scheffe's test) was used to determine which model(s) best characterized the emptying pattern.

Concentration comparisons

Results of model comparisons indicated that the linear model described crop emptying with relatively low residual variation (see Results). It could only be discriminated statistically as different from the hyperbolic model, a common feature of analyses of emptying patterns (Smith *et al.* 1984; Jobling, 1986), and it was considered sufficient and most parsimonious for comparing crop emptying with the data from the experiments of Gelperin (1966).

The regressions of crop volume did not include volumes fed to flies. Zero values were included but, to minimize sampling error effects, data for long times following feeding were not used if more than 50% of the crops were empty. The averaged data in Gelperin (1966) excluded zero values and this produces considerable artificial curvature in the emptying functions as volumes approach zero.

Assimilation assumption

Animals that have evolved to consume foods without sucrose may lack sufficient sucrase for effective sucrose digestion (Martinez del Rio *et al.* 1989), but it is assumed that blowflies, like other nectar-feeders, assimilate essentially all ingested sucrose, glucose and fructose, regardless of concentration. Glucose is absorbed within the first two-thirds of the midgut of honeybees (*Apis mellifera*, Crailsheim, 1988), and their excreted fluid contains virtually no sugars (Pasedach-Poeverlein, 1941). Hummingbirds assimilate 97–99% of ingested sucrose and glucose regardless of concentration ($0.5\text{--}2.0\text{ mol l}^{-1}$ sucrose) (Hainsworth, 1974; Karasov *et al.* 1986). Cockroaches assimilate 95–98% of ingested glucose regardless of concentration ($0.04\text{--}1.0\text{ mol l}^{-1}$; Treherne, 1957). Humans digest and absorb essentially all ingested simple sugars (Low, 1988). Measurements of the refractive index of excreted fluid for painted lady butterflies (*Vanessa cardui*) indicate 96–98% assimilation for $0.5\text{--}1.5\text{ mol l}^{-1}$ sucrose (F. R. Hainsworth, in preparation). Also, blowflies fed 1.0 mol l^{-1} glucose showed no excretion of sugar detectable by paper chromatography (Hudson, 1958) and complete assimilation of crop energy as glucose was necessary to account for total energy expenditures during flight (Hudson, 1958; Clegg and Evans, 1961).

Overall energy processing rates

We were interested in comparing rates for processing amounts consumed

(including what may have bypassed the crop) and we wished, therefore, to identify a criterion for the time between meals to calculate energy processing rates between meals. There is evidence that in locusts (Simpson and Ludlow, 1986) and in hummingbirds (Wolf and Hainsworth, 1977) feeding following a meal is related to emptying of the crop. Tarsal thresholds for proboscis extension in blowflies are also related to crop emptying in a manner suggesting that feeding may be associated with emptying of the crop (Dethier, 1976; Edgecomb *et al.* 1987). However, recent experiments with the Australian sheep blowfly (*Lucilia cuprina*) show that higher crop volumes occur at feeding when food is more concentrated ($2.2 \mu\text{l}$ with 1.0 mol l^{-1} vs $1.4 \mu\text{l}$ with 0.1 mol l^{-1} glucose) (Simpson *et al.* 1989). If a higher crop volume also occurs in *Phormia regina* it could influence calculated energy processing rates from regressions, depending on the model used and the time to the next meal. Using linear regressions to calculate overall energy processing rates has the advantage of producing constant emptying rates over time but overall energy processing rates could still vary, depending on the amount of energy that bypasses the crop together with the time to the next meal.

Slopes and intercepts of linear regressions from the data of Gelperin (1966) were compared across food concentrations. Overall energy processing rates were calculated for the time to reach a crop volume of 0.5, 1.0, 2.0, 3.0 or $4.0 \mu\text{l}$ by subtracting these volumes from the volume fed and using the heats of combustion of the sugar solutions (16.48 J mg^{-1} sucrose, 15.69 J mg^{-1} fructose). The consequences of varying crop volumes associated with feeding for overall energy processing rates could thus be examined.

Results

Regression analyses

Multiple comparisons of untransformed residual squared variation for blowflies fed 9.7 or $14.5 \mu\text{l}$ of 0.25 mol l^{-1} sucrose showed that only the hyperbolic regression consistently produced significant variation (Table 1). Because the other regressions produce predictions that are statistically the same, the linear regression was selected as most parsimonious, sufficient, and most tractable for comparisons of statistical features.

Fig. 1 shows the original data with linear regression lines. The equations are: for $9.7 \mu\text{l}$, volume (in μl) = $5.11 - 0.83t$ (where t is time in hours), and for $14.5 \mu\text{l}$, volume = $9.82 - 1.54t$. Slopes were relatively high (see below), and the higher volume was emptied faster. Comparison of intercepts with the amount fed indicates that about the same volume (4.6 – $4.7 \mu\text{l}$) bypassed the crop for each volume fed to the flies, although the intercept may underestimate the average volume in the crop for flies fed $14.5 \mu\text{l}$ (Fig. 1).

Concentrations and volume emptying rates with linear regressions

Multiple comparisons of squared residuals for untransformed data from the experiments of Gelperin (1966) showed that most regressions could not be

Table 1. Scheffe's *F*-values for model comparisons for crop emptying of different volumes of 0.25 mol l⁻¹ sucrose

| | \sqrt{V} | $\sqrt[3]{V}$ | $\frac{1}{V}$ | $\frac{1}{\sqrt[3]{V}}$ | lnV |
|-------------------------|----------------------|----------------------|---------------|-------------------------|----------------------|
| 9.7 μ l | | | | | |
| V | 2.9×10^{-6} | 1.8×10^{-6} | 24.1* | 4.1×10^{-4} | 1.1×10^{-6} |
| \sqrt{V} | | 9.2×10^{-6} | 24.1* | 4.8×10^{-4} | 4.5×10^{-7} |
| $\sqrt[3]{V}$ | | | 24.1* | 3.6×10^{-4} | 5.6×10^{-6} |
| $\frac{1}{V}$ | | | | | |
| $\frac{1}{\sqrt{V}}$ | | | | 23.9* | 24.1* |
| $\frac{1}{\sqrt[3]{V}}$ | | | | | 4.6×10^{-4} |
| 14.5 μ l | | | | | |
| V | 0.09 | 0.15 | 5.42* | 2.71* | 0.28 |
| \sqrt{V} | | 0.008 | 6.91* | 1.81 | 0.05 |
| $\sqrt[3]{V}$ | | | 7.39* | 1.58 | 0.02 |
| $\frac{1}{V}$ | | | | | |
| $\frac{1}{\sqrt{V}}$ | | | | 15.8* | 8.15* |
| $\frac{1}{\sqrt[3]{V}}$ | | | | | 1.25 |

Data from Edgecomb *et al.* 1987.

Crop volume (*V*) is measured in μ l.

* $P < 0.05$.

statistically discriminated as different within a concentration for either fructose or sucrose (Scheffe's *F*-tests, $P > 0.05$). The hyperbolic regression gave significantly higher variation compared with other regressions for 0.3, 0.5 and 1.0 mol l⁻¹ fructose and 2.0 mol l⁻¹ sucrose and predicted negative initial volumes at most concentrations. The exponential regression predicted high initial volumes and produced significantly higher residual squared variation for some concentrations, but this is probably due to the lack of data for crop volumes close to zero time.

Slopes of linear regressions decreased as concentration increased for both sugars, but the changes in slope did not precisely reflect changes in concentration (Table 2). Slopes decreased significantly from the lowest and to the highest concentrations for each sugar, but at intermediate concentrations there were no significant changes in slope despite twofold (sucrose) and threefold (fructose) changes in concentration (Table 2).

Sucrose yields about twice the energy of an equimolar fructose solution, so slopes for sucrose solutions should be about half those for fructose solutions after adjusting for equimolarity. The 0.5 and 1.0 mol l⁻¹ sucrose solutions were emptied at half the rate of the equimolar fructose solutions (Table 2). The 0.3 mol l⁻¹ fructose solution would be similar in energy content to a 0.15 mol l⁻¹ sucrose solution and the 0.1 mol l⁻¹ sucrose solution to 0.2 mol l⁻¹ fructose. Reducing the slope for 0.3 mol l⁻¹ fructose by one-third or increasing the slope for 0.1 mol l⁻¹

sucrose by half produces the same rate of emptying as for the other sugar (Table 2). However, similar comparisons between slopes for 3.0 mol l^{-1} fructose and 2.0 mol l^{-1} sucrose show the fructose is emptied at a rate twice that of the

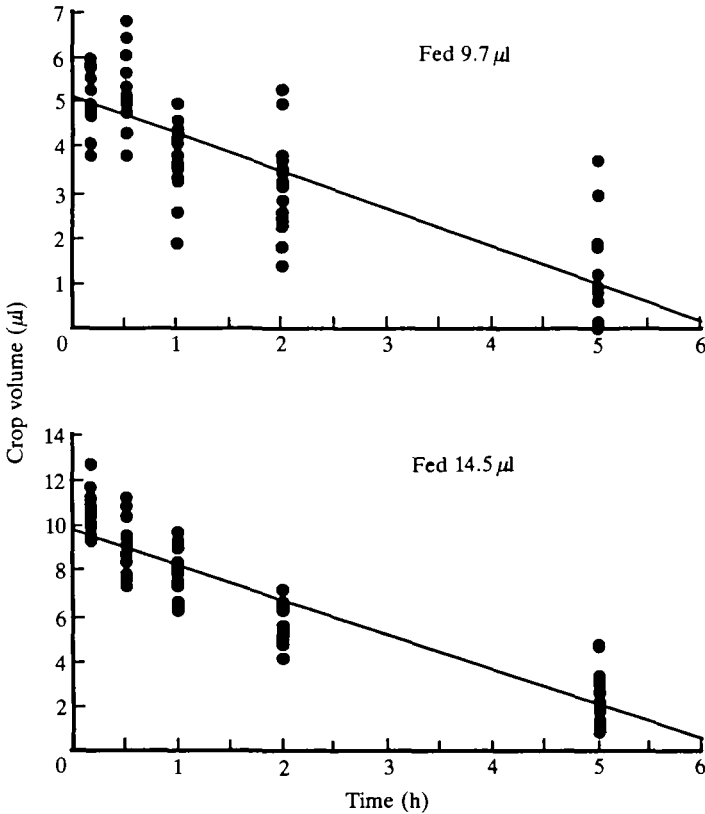


Fig. 1. Individual data for crop volume vs time for 0.25 mol l^{-1} sucrose (from Edgecomb *et al.* 1987). Lines are linear regressions (see text for equations).

Table 2. Intercepts, slopes and \pm their 95% confidence intervals for linear regressions of crop volumes (μl) vs time (h)

| Sugar | Concentration (mol l^{-1}) | Intercept | Slope |
|----------|--|------------------|------------------|
| Fructose | 0.3 | 9.10 ± 2.50 | -0.89 ± 0.45 |
| | 0.5 | 8.25 ± 1.52 | -0.34 ± 0.09 |
| | 1.0 | 7.77 ± 0.84 | -0.30 ± 0.05 |
| | 1.5 | 10.11 ± 1.10 | -0.35 ± 0.05 |
| | 3.0 | 11.85 ± 0.88 | -0.18 ± 0.02 |
| Sucrose | 0.1 | 9.35 ± 0.90 | -0.60 ± 0.10 |
| | 0.5 | 6.85 ± 0.65 | -0.16 ± 0.03 |
| | 1.0 | 6.97 ± 0.95 | -0.17 ± 0.04 |
| | 2.0 | 7.91 ± 1.0 | -0.10 ± 0.03 |

sucrose. This may be due to the higher initial crop volume (intercept) for fructose at the highest concentration (Table 2) because increasing crop volume increases volume rate of emptying (Fig. 1; Gelperin, 1966). Despite the different volumes of fructose (15 μl) and sucrose (10 μl) fed to flies, intercepts for linear regressions were similar except at higher concentrations (Table 2).

The slopes for emptying 0.1–0.5 mol l^{-1} sucrose (Table 2) are less than the slope for emptying 0.25 mol l^{-1} sucrose based on the data from Edgecomb *et al.* (1987). This should not be due to differences in initial crop volumes because crop volumes were no larger for flies fed 9.7 μl of 0.25 mol l^{-1} sucrose (Fig. 1; Table 2). Starving flies for 4 days prior to their first meal could perhaps have increased crop emptying rates. If this is the case, it would suggest a feedback mechanism between energy stores and digestive processing of food.

Overall energy processing rates

Energy processing rates incorporating the amount that bypassed the crop were calculated for each linear regression over the time to reach a crop volume of 0.5, 1.0, 2.0, 3.0 or 4.0 μl (Table 3). As expected from the comparisons of slopes for linear regressions (Table 2), intermediate concentrations of each sugar (0.5–1.5 mol l^{-1} fructose, 0.5–1.0 mol l^{-1} sucrose) produced increasing rates of energy processing within a minimum crop volume category. At the highest concentrations, overall energy processing rates either remained the same (sucrose) or decreased (fructose) compared with the next lower concentrations. Increasing the volume remaining in the crop when a new meal is consumed would increase overall energy processing rates (Table 3) because the fraction passing to the mid- and hindgut becomes an increasing proportion of the total amount processed.

Table 3. Overall energy processing rates (in J h^{-1}) for blowflies calculated from linear regression equations for the time to empty the crop to variable volumes

| Fructose (mol l^{-1}) | 0.3 | 0.5 | 1.0 | 1.5 | 3.0 |
|----------------------------------|------|------|------|------|------|
| Empty to: 0.5 μl | 1.27 | 0.90 | 1.69 | 2.24 | 1.95 |
| 1.0 μl | 1.30 | 0.93 | 1.75 | 2.28 | 1.97 |
| 2.0 μl | 1.38 | 0.99 | 1.92 | 2.38 | 2.01 |
| 3.0 μl | 1.49 | 1.10 | 2.13 | 2.51 | 2.07 |
| 4.0 μl | 1.63 | 1.24 | 2.47 | 2.67 | 2.14 |
| Sucrose (mol l^{-1}) | 0.1 | 0.5 | 1.0 | 2.0 | |
| Empty to: 0.5 μl | 0.36 | 0.67 | 1.41 | 1.45 | |
| 1.0 μl | 0.36 | 0.69 | 1.45 | 1.47 | |
| 2.0 μl | 0.37 | 0.74 | 1.54 | 1.53 | |
| 3.0 μl | 0.37 | 0.82 | 1.69 | 1.61 | |
| 4.0 μl | 0.38 | 0.95 | 1.93 | 1.73 | |

Energy is standardized for volumes fed minus the volume to which the crop empties account for food that did not enter the crop (based on data from Gelperin, 1966).

Discussion

Variation in crop volumes did not permit discrimination between models for crop emptying except for the hyperbolic model. Studies of stomach emptying in other species have also found it difficult to distinguish between models (Smith *et al.* 1984; Jobling, 1986). The problem may be resolved by attempting to obtain more precise measurements of volumes. Nevertheless, the statistical similarity between regressions suggests that there may be little difference between predictions, even if a 'best' model could be identified. This may be the case particularly when rates are predicted to low crop volumes where regressions may converge along slightly different paths.

Rate of energy processing increased with meal size for the blowflies fed 9.7 or 14.5 μl of 0.25 mol l^{-1} sucrose. They passed about the same volume to the mid- and hindgut, the linear regression was of lower slope for the smaller volume, and both regressions approached zero volume at about the same time (Fig. 1), so overall rate of energy processing increased in proportion to the amount consumed. If this pattern occurs for foraging flies, it would suggest an important role for meal size in optimal foraging. Thus, to maximize the rate of energy processing a fly could be predicted to forage where meal sizes would be higher, even when rate of net energy gain while foraging may be low (such as when food is widely dispersed). However, the overall rate of energy processing across meal sizes may depend on the condition of the fly, so the importance of meal size may depend on how much a fly has consumed prior to foraging.

The mechanism suggested to control crop emptying in blowflies involves blood osmotic concentration (Gelperin, 1966). Raising blood osmotic concentration decreases the rate of crop emptying. Assimilation of sugar into the blood will increase blood osmotic concentration and decrease rate of crop emptying. As sugar is removed from the blood for various uses, osmotic concentration will decrease and crop emptying rate will increase (Gelperin, 1966). Thus, the rate of crop emptying should reflect an interplay between gain to the blood from assimilation and loss from the blood for maintenance or storage uses. The concentration of food has to change by a factor of two or three to change crop emptying rate, which suggests a differential rate of loss from the blood compared with assimilation gains as food concentration changes.

It could be argued that the lack of change in volume rate of emptying at intermediate concentrations is because of changes in percent assimilation of sugars. Thus, if percent assimilation decreases as concentration increases, the same amount of sugar could be assimilated as concentration changes, and blood osmotic concentration would not vary as food concentration changed. Two observations argue against this interpretation. First, blowflies have been shown to assimilate essentially all sugars at an intermediate concentration (1.0 mol l^{-1} glucose, Hudson, 1958). Second, the volume rate of emptying decreases significantly at the highest sugar concentrations (Table 2). If this reflects an increased assimilation, why should it be restricted to high concentrations?

Blowflies process the energy in foods of different amounts and concentrations so

the uses for a unit of energy vary. They use energy for at least two purposes: short-term maintenance and long-term storage. Because the blowflies were immobilized, short-term maintenance was relatively fixed and should not have varied appreciably with food. Based on measurements of resting rates of oxygen consumption for insects (assuming $RQ=1.0$), a 25 mg blowfly would expend about 0.5 J h^{-1} for maintenance at rest (Bartholomew and Casey, 1978; Gromysz-Kalkowska and Hubicka, 1988). Rates of energy processing exceed this except for 0.1 mol l^{-1} sucrose (Table 3). Excess rates of processing would represent the rate at which blowflies allocate energy for long-term storage. This rate increased with meal size and with food concentration at intermediate concentrations and reached a plateau or decreased at the highest concentrations for both sugars (Table 3).

Increasing the volume in the crop at the start of a meal increased overall energy processing rates (Table 3). Experiments with the Australian sheep blowfly indicate that concentrated foods empty to somewhat larger crop volumes at the start of a meal (Simpson *et al.* 1989). Thus, overall energy processing rates for concentrated foods may be higher than the rates calculated assuming the same crop volume. This would make the disparity in overall energy processing rates even greater among foods of different concentrations.

Many optimal foraging theories involve additive ranking of food by the amount of energy gained for the time spent foraging (e.g. Stephens and Krebs, 1986). When the value of assimilated energy varies, as measured here by how animals process the energy, it should influence how they rank food. The inclusion of items of high energy value in a diet could reflect a greater use for energy from the foods. When this is the case, animals should search for and select foods of high energy value out of proportion to the amount of energy gained for the time spent foraging.

A number of nectar-feeding animals select concentrated sugar solutions even though these foods produce a lower rate of net energy ingestion while they are feeding. They include hummingbirds (Hainsworth and Wolf, 1976; Montgomerie *et al.* 1984), blowflies (Dethier and Rhoades, 1954) and painted lady butterflies (Hainsworth, 1989). It has been suggested that this preference occurs because it produces a greater net gain of energy from a meal (Hainsworth, 1990). The way blowflies process energy suggests that the selection of energy-rich foods can be advantageous not only because of the large net energy gains from feeding but also because of the relationship between energy gains and use for these foods.

This work was supported by a grant from the Whitehall Foundation. We thank Drs Alan Gelperin and Robert Edgecomb for sharing their data and two anonymous referees for comments on the manuscript.

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