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Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees

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Summary. Fluid viscosity only affected ingestion rates of bumble bees (*Bombus*) for solutions greater than 35–40% sucrose (mass of solute per mass of solution). This contrasts with previously published models based on fluid dynamics which predicted continuous depression of ingestion rates with increasing viscosity. Individual bees maintained constant lapping rates regardless of sucrose concentration (up to at least 70%). The decline in ingestion rates at higher concentrations apparently resulted from the tongue not contacting liquid long enough to become saturated due to reduced capillary flow. Increasing flower depth similarly decreased the volume of liquid ingested per lap, and did not affect lapping rate. Morphologically dissimilar bees drank at different rates because glossa length affects lapping rate and volume ingested per lap, and body mass affects lapping rate. An additional species-specific component to lapping rate also influenced ingestion rates. Deviations from a regression model derived to explain ingestion rates as a function of glossa length, body mass, flower depth and liquid viscosity suggest mechanistic and behavioral aspects to flower probing time. Because of the relation between ingestion rate and liquid viscosity, the sucrose concentration maximizing a bee's rate of net energy uptake should lie between 50–65%, depending primarily on specific conditions of nectar volume, inflorescence size and flight time between inflorescences.

Nectar concentration simultaneously affects the costs and benefits of foraging for nectar-feeding animals through correlations with viscosity and the energy content of a given nectar volume. Because the relative contributions of nectar concentration to foraging costs and benefits can influence flower choice by nectarivores, the depressive effect of nectar viscosity has recently attracted considerable attention (Waller 1972, Hainsworth 1973, Pouvreau 1974, Baker 1975, Hainsworth and Wolf 1976, Heyneman 1983, Kingsolver and Daniel 1983, Montgomerie 1984, Roubik and Buchmann 1984, May 1985, Pivnick and McNeil 1985). Unfortunately theoretical analyses have provided conflicting predictions (compare Pyke and Waser 1981, Heyneman 1983 and Kingsolver and Daniel 1983) which are not supported by empirical results (see May 1985, Pivnick and McNeil 1985). For example, based on fluid dynamics, Heyneman (1983; Fig. 1b) and Kingsolver and Daniel (1983; Fig. 1) predicted that ingestion rates for hummingbirds should decrease continuously with increasing concentration. In contrast, observations by Hainsworth (1973; Fig. 1) and Montgomerie (1984; Table 3) indicate that ingestion rate varies little for concentrations below 40% (sucrose equivalents = percent mass of solute per mass of solution).

This paper expands an earlier description (Harder 1983a) of the duration of flower visits by nectar-feeding bumble bees (*Bombus*). As with other bees, bumble bees drink by lapping with their hairy tongues (Snodgrass 1956, Harder 1982, 1983b), so that the rate of nectar ingestion depends jointly on lapping rate and the volume ingested per lap. My previous study (Harder 1983a) demonstrated positive correlations between ingestion rate and bee tongue (= glossa) length and body mass. Increasing flower depth reduced ingestion rates, but the effect of flower depth was greatest when bees visited flowers deeper than the lengths of their tongues.

The revised description of flower handling time presented here is based on three experiments that considered the influence of nectar concentration. The first experiment dealt with the dependence of ingestion rate on concentration when bees had ready access to nectar (i.e. flower depth = 0 mm). To understand the mechanism of nectar ingestion, the second experiment considered the influence of bee and flower characters on lapping rates and the volume ingested per lap. In the third experiment I directly assessed the combined effects of flower depth and nectar concentration on ingestion rates for queens and workers of morphologically different species. I tested the utility of a regression model describing the results of this experiment as a predictor of probing time by comparing the observed and expected probing times of bees visiting artificial flowers containing small nectar volumes. Development of this probing time model allowed me to consider nectar concentrations that maximize a bee's rate of net energy uptake, a feature which could affect foraging decisions.

Methods

Ingestion rate, lapping rate and volume per lap

To determine the relation of ingestion rate and its components (lapping rate and volume ingested per lap) to flower depth and nectar concentration, bees were placed in a test chamber (13 cm × 8 cm × 7 cm) with access to a feeder consisting of two nested tubes. The shorter outer tube projected almost horizontally through a chamber wall so that the

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end available to the bee (proximal end) was flush with the box's inner surface. Within this tube lay a longer tube (inside diameter = 1.39 mm) positioned with its proximal end recessed a specific distance from the proximal end of the outer tube. Bees' heads were too broad to fit inside the outer tube so that bees had to reach with their tongues to drink sucrose solution from the inner tube. The distance between the proximal ends of the two tubes will be referred to as feeder depth.

During each feeding trial I measured the length of the nectar column in the inner tube, allowed a bee to feed for a timed period of 10–15 s and then withdrew the tube and remeasured the nectar. Many bees were not fully active at the beginning of a trial, so this procedure was repeated up to five times in rapid succession for each experimental treatment. I used the fastest rate of uptake to represent a bee's capability. Bees were starved for several hours before each trial. This basic protocol was used in three different experiments, which were conducted at ambient temperatures of 20–22° C.

The first experiment considered only the effect of nectar concentration on ingestion rate. I measured each bee's feeding rate on six different sucrose solutions (10, 20, 30, 40, 50 and 65%) from the feeder with depth = 0 mm.

To aid interpretation of the results of this and a subsequent experiment, I conducted a second experiment assessing the influence of both concentration and flower depth on lapping rates and the volume ingested per lap. The test chamber wall through which the feeder projected was replaced with a thin paper card so that the motion of the bee's tongue during feeding could be observed. I recorded the lapping of sugar solution during each feeding trial of this experiment on videotape. By replaying this record at slow motion (1/6 normal speed) I could count the number of laps during 5 s of real time. The volume ingested per lap was calculated by dividing the observed overall ingestion rate by the lapping rate. This experiment included two workers of three species selected to include large bees with long tongues (*B. fervidus*), small bees with medium tongues (*B. vagans*), and large bees with medium tongues (*B. impatiens*: see Harder 1985, Fig. 1b). I observed the feeding rate of each bee in response to six treatments: all combinations of three sucrose concentrations (20, 55 and 70%) chosen because they represent equal intervals of log(viscosity); and two feeder depths, 4 mm and a depth estimated to be greater than the length of the bee's glossa.

The third experiment involved two queens and two workers of four species and two workers of two additional species to incorporate extensive variation in bee morphology. Each bee experienced nine treatments: all combinations of three sucrose concentrations (20, 55 and 70%); and three feeder depths, 0 mm, medium depth (4 mm for workers, 5 mm for queens), and deep (greater than the bee's glossa length). I recorded only ingestion rate during this experiment.

At the end of each experiment all bees were starved overnight before being weighed, killed and stored in 70% ethanol. I later measured glossa length as described in Harder (1982).

Probing time

Regression analysis of the third experiment provided an overall description of ingestion rate in terms of bee tongue length, body mass, flower depth and nectar viscosity. To test whether this description could be incorporated into an accurate predictive model of probing time, I conducted a final experiment with artificial flowers. Each flower was made of a 1.8 cm × 1.8 cm × 1.3 cm block of Plexiglas with a 1.2 cm disk of blue tape on its upper surface. A 1.6 mm diameter hole centered on this disk was drilled through the block and then filled with paraffin. I then removed wax from the upper end of the hole using a drill bit with a depth stop to produce a well of desired depth.

During each trial a marked worker from a captive *B. impatiens* colony entered a screen cage with one glass side (30 cm × 30 cm × 30 cm) which contained 48 of these flowers, all of the same depth. This array included a random arrangement of 12 empty flowers and six flowers of each of six additional treatments; three volumes (0.5, 1.0 and 3.0 µl) of two concentrations (30 and 50%) of sugar solution. The four bees examined experienced this array twice for each of two flower depths (3 and 6 mm) chosen to be shorter and longer than their tongues (range = 4.3–5.8 mm). I recorded each flower visit on video tape and later timed feeding with a stopwatch at slow motion.

To compare predictions of the previously derived regression model of ingestion rate with these observations of probing time, I calculated ingestion rates during visits to artificial flowers as follows. The average probing time for empty flowers by a given bee was taken as the average time to enter and leave all flowers of that depth (access time). Ingestion rate equals the inverse of the difference between probing time for a flower containing sugar solution and access time.

Results

Ingestion rate and concentration

Increasing sucrose concentration from 10 to 40% had no significant effect on the ingestion rates (µl/s) of 22 bees of 9 species; however, these bees ingested 50 and 65% solutions much less quickly (Fig. 1). To assess the influence of nectar viscosity (μ; in centipoises (cp)), and a bee's glossa length (G; in mm) and body mass (W; in g) on ingestion rate (I), I fit the regression model

$$\log(I) = b_1 d + b_2 d \log(\mu) + b_3 \log(G) + b_4 \log(W) \quad (1)$$

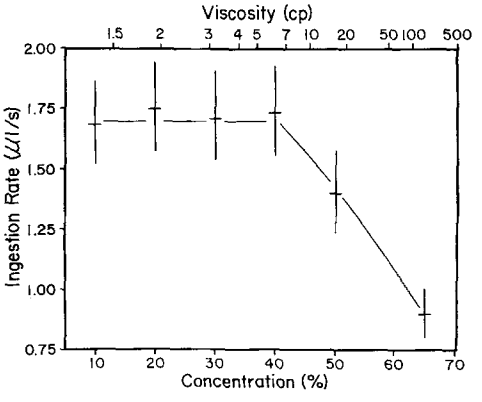

Fig. 1. Relation of ingestion rates of 22 bumble bees to concentration and viscosity of sucrose solutions at 20° C. Mean and standard error are presented for each concentration examined. See text for regression statistics

Table 1. Average (±SE) lapping rates and volumes of sucrose solution ingested per lap for workers of three bumble bee species (*B. fervidus, B. impatiens* and *B. vagans*) in relation to concentration and feeder depth. Statistics for volume per lap are based on log transformed data, hence the asymmetrical standard errors

	Lapping rate (laps/s)	Volume ingested per lap (μl)	Lower standard error (μl)	Upper standard error (μl)	Sample size
Sucrose concentration					
20%	4.7±0.19	0.271	0.255	0.288	12
55%	4.8±0.20	0.186	0.174	0.199	12
70%	4.9±0.19	0.099	0.090	0.109	12
Feeder depth					
4 mm	4.8±0.13	0.187	0.169	0.208	18
>glossa	4.8±0.18	0.156	0.133	0.177	18

to these observations. I considered viscosity rather than concentration because this fluid characteristic affects the capillary flow (Kingsolver and Daniel 1983) involved in loading the tongue with liquid (Harder 1982). In Eq. 1, d is a binary variable indicating whether viscosity is less than ($d=0$) or greater than ($d=1$) the critical viscosity (μ_c) at which ingestion rate begins to decline. To implement the regression model, d was set to one for concentrations greater than 30%. The actual value of the critical viscosity is

$$\log(\mu_c) = -b_1/b_2.$$

The results of this analysis indicate that

$$\hat{I} = G^{0.710}\, W^{0.558}$$

below the critical viscosity of 6.49 cp, which is equivalent to a sucrose concentration of 40.5% at 20° C. In other words, below about 40% sucrose, ingestion rate is determined by the size of the bee and the length of its tongue when the bee feeds from a completely open flower. In particular, large bees and bees with long tongues ingest nectar most rapidly. Above the critical concentration of 40.5%

$$\hat{I} = 1.466\, \mu^{-0.205}\, G^{0.710}\, W^{0.558},$$

indicating the depressive effect of viscosity on ingestion rate. Note that because of the exponential relation between viscosity and concentration, the critical viscosity is about five times greater than the viscosity of a 10% sucrose solution, whereas a 65% solution is 22 times more viscose than the critical viscosity (Fig. 1). Overall this regression model explained 86.0% of the observed variation in ingestion rate ($P<0.001$).

Lapping rate and volume per lap

Even though flower depth (Harder 1983a) and viscosity (Fig. 1) significantly depressed ingestion rate, they had no significant effect on the lapping rates of six bees of three species (concentration, $F_{2,2}=15.14$, $P>0.05$; depth, $F_{1,3}=0.38$, $P>0.5$; concentration × depth interaction, $F_{2,2}=0.61$, $P>0.5$: Table 1). Lapping rates did differ significantly between species ($F_{2,3}=37.86$, $P<0.01$). To determine the role of glossa length and body size in these differences, I considered the regression between these variables and the lapping rates for nine bees (including the six examined at three concentrations) drinking 55% sucrose solution (depth = 4 mm). A negative effect of glossa length and a positive effect of body mass together accounted for 68.6% of the observed variation in lapping rate ($P<0.05$). However, simply knowing that a bee was a *B. impatiens* rather than *B. vagans* or *B. fervidus* explained 88.0% of lapping rate variation ($P<0.005$), suggesting that there was a species-specific component to lapping rates in addition to glossa length and body mass.

In contrast to lapping rate, the volume of sucrose solution ingested per lap did not differ between the three species ($F_{2,3}=3.33$, $P>0.1$), but it was negatively affected by both sucrose concentration ($F_{2,2}=72.23$, $P<0.025$) and feeder depth ($F_{1,3}=32.74$, $P<0.025$; concentration × depth interaction, $F_{2,2}=8.01$, $P>0.1$: Table 1). For the nine bees whose feeding was observed on 55% sucrose solution, volume per lap was not significantly correlated with glossa length ($r=0.511$, $P>0.1$) or body mass ($r=0.492$, $P>0.1$) by themselves. However, volume per lap (V) and glossa length (G) were significantly correlated when lapping rate (L) was held constant ($r_{VG.L}=0.973$, $P<0.01$).

Concentration and depth effects on ingestion rate

I analyzed the added effect of flower depth on ingestion rates by including the term

$$b_5 \log(1.41 - C/G)$$

in the regression model described by Eq. 1. This term standardizes the effect of flower depth by expressing depth (C) as a proportion of the bee's glossa length (G) and subtracting that term from the maximum standard depth from which a bumble bee can ingest nectar (1.41 times the glossa length or the total length of the labium: Harder 1983a).

Regression analysis of the observed ingestion rates of 20 bees to all combinations of three sucrose concentrations (20, 55 and 70%) and three feeder depths (1 mm, 4 mm (workers) or 5 mm (queens), and depth greater than glossa length) indicate a critical viscosity of 4.50 cp which is equivalent to a 35.5% sucrose solution at 20° C. For solutions less viscose than this critical value

$$\hat{I} = G^{0.611}\, W^{0.410} (1.41 - C/G)^{0.221}; \quad (2a)$$

for more viscose solutions

$$\hat{I} = 1.403\, \mu^{-0.225}\, G^{0.611}\, W^{0.410} (1.41 - C/G)^{0.221} \quad (2b)$$

($R^2=0.853$, $P<0.001$), hence increasing flower depth decreases ingestion rate. To examine the effects of species and caste on ingestion rate, I used Eq. 2 to describe the covariates in an analysis of covariance with species and caste as the main effects. Significant differences in ingestion rates remained between species ($F_{5,8}=19.23$, $P<0.001$), but not between castes ($F_{1,8}=0.15$, $P>0.5$: species × caste interaction, $F_{3,8}=1.11$, $P>0.25$) after removal of the covariate effects. The overall linear model, including covariates and estimates of species and caste effects, explained 96.0% of the variation in ingestion rates.

I tested the predictive ability of Eq. 2 in two ways. The first involved predicting ingestion rates for eight bees that

Table 2. Incidence of correct [0] and incorrect (overestimation [+], underestimation [−]) predictions of ingestion rates by Eq. 2 for four *B. impatiens* workers in relation to sucrose concentration, depth of artificial flowers and nectar volume. Assessment of the validity of predictions was based on *t*-tests comparing observed and predicted ingestion rates (see text)

Sucrose concentration (%)	Flower depth (mm)	Nectar volume (µl)		
		0.5	1.0	3.0
30	3	0 0 0 0	0 0 0 0	0 + 0
	6	0 + + +	+ + + 0	0 0 0 +
50	3	− 0 − 0	0 0 − 0	0 0 0 0
	6	− − 0 0	0 0 0 0	0 0 0 0

were originally included in the experiment on which Eq. 2 is based, but which died before completing all nine treatment combinations. Equation 2 explained 89.6% of the variation in observed ingestion rates for these bees and the observed rates of all 57 trials fell within the 95% prediction intervals associated with Eq. 2.

Prediction of probing time

The second test of Eq. 2 as a predictive model involved predicting the ingestion rates of four bees that fed from artificial flowers containing volumes similar to those bees encounter naturally. For each treatment combination (volumes = 0.5, 1, or 3 µl; concentration = 30 or 50%; depth = 3 or 6 mm) for each bee, I calculated the observed mean ingestion rate (see Methods) and its standard error, and the predicted mean (based on Eq. 2) and the standard error for this prediction given a sample of the same number of observations that contributed to the observed mean (Neter and Wasserman 1974). Observed and predicted means were then compared with *t*-tests.

Thirty-four of the 47 predicted mean ingestion rates did not differ significantly from the average observed ingestion rates (Table 2). The 13 significant deviations occurred in response to a limited number of treatment combinations. In particular, all eight cases in which bees visited flowers more briefly than expected involved flowers with 30% sucrose solution. This overestimation was especially prevalent for 6 mm flowers, which were deeper than the bees' tongues. Longer visits than expected occurred only when bees visited flowers containing 50% sucrose solution, especially those with only 0.5 µl.

Discussion

Influences on ingestion rates

The effect of viscosity on ingestion rates is not continuous for lapping nectarivores. Below 35–40%, sucrose solutions are not sufficiently viscose to affect the ingestion rates of bumble bees (Fig. 1), stingless bees (*Melipona* spp.), honey bees (*Apis mellifera*: Roubik and Buchmann 1984) or hummingbirds (Hainsworth 1973, Montgomerie 1984). Above this concentration, rapidly increasing viscosity depresses ingestion rates.

At least for bumble bees, this discontinuity can be explained by the constant lapping rate regardless of viscosity (Table 1). As long as the tongue contacts liquid for a sufficient period to become saturated, the volume of liquid ingested per lap will remain constant. However, at some point viscosity begins to reduce the volume ingested per lap, resulting in a lower ingestion rate. Two mechanisms could cause this decline: either viscosity depresses capillary flow so that the tongue ceases to contact liquid long enough to become saturated; or the tongue ceases to be completely cleaned of liquid on each protraction of the glossa (see Harder 1982).

The models of Heyneman (1983) and Kingsolver and Daniel (1983) do not represent this discontinuous function because they are based on Poiseuille's description of the mechanics of flow through a cylindrical tube which only contacts liquid at one end. In contrast, during ingestion hummingbirds carry nectar in grooves on either side of the tongue (Hainsworth 1973, Ewald and Williams 1982), and bees carry nectar on the outer surface of their hairy tongues (Snodgrass 1956, Harder 1982, 1983b). In both cases movement of liquid onto the tongue's fluid-bearing surface can occur at any point along that surface. Therefore capillary flow of liquid onto the tongue when the tongue is partially or totally immersed would be much more rapid than the process modelled by Heyneman (1983) and Kingsolver and Daniel (1983). This immersion effect may be quite common because nectar is often contained in slender channels and nectar spurs. Insertion of the tongue into these channels would tend to displace nectar and increase the area of contact between nectar and tongue.

Capillary uptake of nectar along the fluid-bearing surface of the tongue probably also determines the effect of flower depth on ingestion rates, a subject not addressed by Heyneman (1983) or Kingsolver and Daniel (1983). Ingestion rates decline with increasing flower depth for both hummingbirds (Hainsworth and Wolf 1976, Montgomerie 1984) and bumble bees (Harder 1983a, this study). For hummingbirds this decline accompanies a parallel decline in lapping rate (Ewald and Williams 1982). In the case of bumble bees, lapping rate remains constant with increasing flower depth, but the volume ingested per lap declines (Table 1). Two factors probably contribute to this decline: a reduced period of contact between the tongue and nectar, because the tongue must travel farther to the liquid surface; and a decreased area of contact between the tongue's fluid-bearing surface and the nectar.

Both glossa length and body mass affect ingestion rates of bumble bees. Glossa length is particularly important because it determines the maximum flower depth from which a bee can feed (Harder 1983a), the volume of liquid ingested per lap, and lapping rate. In contrast, body mass only influences lapping rate. In addition to these morphological influences, an unidentified species-specific component also affects lapping rate and, consequently, ingestion rate.

Probing time

The regression model (Eq. 2) calculated to explain the influences of glossa length, body mass, nectar viscosity and flower depth on the ingestion rates of bees drinking from a feeder with a large volume of sucrose solution also correctly predicted the ingestion rates of bees feeding from artificial flowers with limited volumes, in most cases (Table 2). Departures of the observed ingestion rates from the regression

model followed a particular pattern: several bees visited flowers 6 mm deep with 30% sucrose solution for shorter periods than expected; and they visited flowers with small volumes (0.5 µl) of 50% solution for longer than expected. These deviations may represent a failure of the model to describe ingestion of small volumes, but the particular pattern of deviations suggests behavioral and mechanistic components of probing time.

Bees are sensitive to their rate of energy uptake and they modify their feeding patterns in response to variation in this rate (Pyke 1978, Hartling and Plowright 1979a and b, Heinrich 1979, Morse 1980). Bitterman (1976) found that experience with a 40% sucrose solution reduced the acceptability of 20% solution to honey bees. Hodges (1981, 1985) demonstrated that bumble bees feed as though they form specific expectations for the rate of energy uptake realized from each inflorescence. Bumble bees even leave nectar in flowers they are visiting when their rate of net energy uptake drops below the average rate expected from the flower population as a whole (Whitham 1977, Hodges and Wolf 1981).

Because the bees I observed on artificial flowers had access to all six concentration-volume combinations for a given flower depth during a single trial, they could have left flowers suppling low rates of return before they were empty, with the expectation of finding a more rewarding flower. Half of the flowers with sucrose solution contained 50% solution, so that a bee had a high probability of finding a richer flower when feeding on a flower with 30% solution. Leaving a partially emptied flower to search for more concentrated sucrose solution would be especially likely when the bees fed from 6 mm flowers, because of the reduced ingestion rate associated with feeding from deep flowers. Furthermore, flowers with small nectar volumes are less attractive in terms of the rate of net energy uptake they provide (see below, especially Fig. 3d), hence a bee's tendency to leave these flowers prematurely should be greater than for flowers with larger volumes (see Table 2).

The longer than expected visits to flowers with 50% sucrose solution (Table 2) could result from bees taking an additional lap before leaving the flower to ensure removal of all liquid. The effect of an additional lap on probing time would be greatest for flowers containing small volumes.

If Eq. 2 adequately represents nectar ingestion from flowers with limited volumes, then the duration of a flower visit (probing time: T_p) can be characterized by

$$T_p = T_a + V/I; \tag{3}$$

where T_a is the time required to enter and leave the flower (access time), V is the volume of nectar, and I is the ingestion rate for the specific bee and flower characteristics as represented by Eq. 2. Figure 2 illustrates the expected probing time of a 0.2 g bumble bee with a 6 mm glossa as a function of flower depth for four nectar volumes and two concentrations, based on a linear relation between flower depth and access time (Harder 1983a). This figure illustrates that nectar viscosity mainly changes the elevation of the probing time function (Eq. 3), whereas interaction between flower depth and nectar volume changes its shape. In particular, for flowers deeper than the length of the bee's tongue, probing time increases most rapidly with increasing flower depth when flowers contain large nectar volumes.

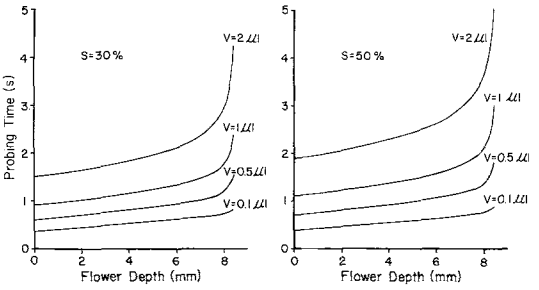

Fig. 2. Predicted relation of probing time for a 0.2 g bumble bee with a 6 mm glossa to flower depth, nectar volume (V) and concentration (S), based on Eq. 2 and 3

Preferred nectar concentration

Bumble bees feed in a manner that tends to maximize their rate of net energy intake (reviewed by Waddington 1983, Plowright and Laverty 1984). On a per inflorescence basis this rate (E) depends on the difference between the energy obtained from the n flowers visited and the energy expended on probing those flowers and flying between inflorescences, divided by the total probing and flight time. This rate can be represented by

$$E = \frac{ne\rho SV - W(nc_pT_p + c_fT_f)}{nT_p + T_f}, \tag{4}$$

where: e is the energy content of 1 mg of sucrose (15.48 J); ρ is the nectar density (mg/µl); S is the nectar concentration; V is the nectar volume; W is the bee's mass; c_p (0.034 J g^{-1} s^{-1}) and c_f (0.435 J g^{-1} s^{-1}: Heinrich 1975) are the mass-specific rates of energy expenditure during probing and flight; and T_p (see Eq. 2 and 3) and T_f are the probing and flight times, respectively. Because energetic benefits increase directly with nectar concentration and probing time is unaffected by increasing concentration below 35–40%, the concentration that maximizes a bee's rate of energy uptake must be greater than 40%.

Over a broad range of conditions a bee would maximize its rate of net energy uptake, as described by Eq. 4, by ingesting nectar with concentrations between 50 and 65% (Fig. 3: see Roubik and Buchmann 1984 for similar results with stingless and honey bees). Nectar of 50% sucrose maximizes this rate when it is available to bees in very large volumes, such as from *ad libitum* feeders (Fig. 3a). For more natural volumes the concentration that maximizes a bee's rate of energy uptake is closer to 60%, but it depends on the specific conditions the bee encounters. In particular, increasing foraging costs by increasing flight time (Fig. 3b) or decreasing inflorescence size (Fig. 3c) or nectar volume (Fig. 3d) increases this concentration. The most rewarding concentration is not affected by increasing flower depth for flowers shallower than the length of the bee's glossa: beyond that depth this concentration declines slightly. Preference for concentrated nectar in response to differences in energetic efficiency would coincidentally reduce the metabolic problem of minimizing water load (Bertsch 1984).

The results of choice experiments with honey bees (Woodrow 1968, Waller 1972) and bumble bees (Pouvreau 1974) generally agree with the expectations of Eq. 4, but the bees did not exhibit precise preferences. Woodrow found that honey bees collected a significantly greater mass of 40 and 50% sucrose solutions than less (20 and 30%)

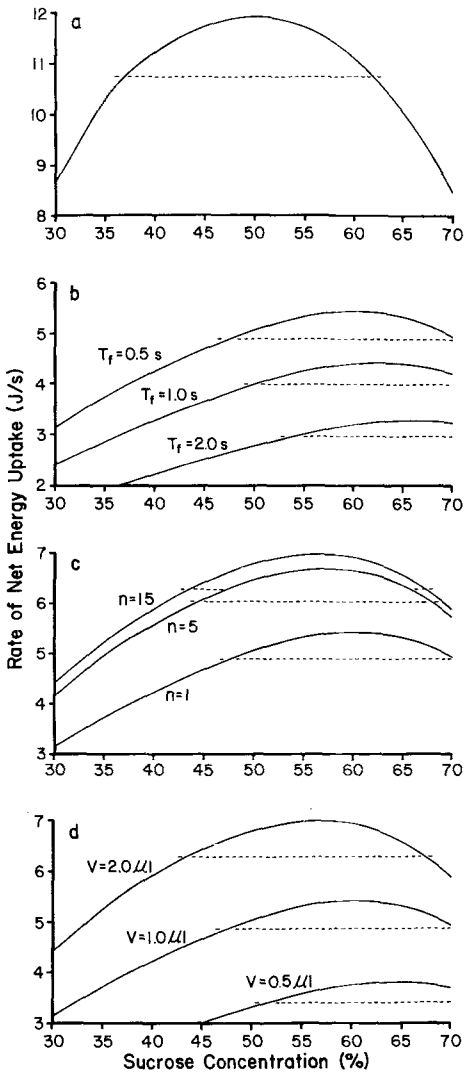

Fig. 3a–d. Influences of nectar volume **a** and **d**, flight time **b** and inflorescence size **c** on the relation of the rate of net energy uptake by a 0.2 g bumble bee with a 6 mm glossa to nectar concentrations, based on Eq. 4. For panel **a** flower depth (C) = 0 mm, nectar volume (V) = 200 µl, inflorescence size (n) = 1 flower, flight time (T_f) = 0.0 s. For panels **b–d**, C = 4.0 mm, V = 1.0 µl, n = 1 flower and T_f = 0.5 s, unless otherwise noted. Dashed lines indicate rates of net energy uptake 10% less than the maximum rate

or more (60 and 69%) concentrated solutions that were freely available in open dish-feeders. When drinking from feeders that simulated deep flowers these bees preferred the 60% solution over the others. In two tests during which honey bees had access to feeders containing six sucrose solutions (10–60%), Waller found that the bees drank: a significantly greater volume of 30 and 40% solutions than the remaining solutions in the first test; and equivalent volumes of 30, 40, 50 and 60% solutions and lesser volumes of 10 and 20% solutions in the second test. Pouvreau allowed colonies of three bumble bee species access to seven sucrose solutions (10–56%). After three to four hours these bees had removed similar volumes of 27, 35 and 43% solutions and less of the 10, 49 and 56% solutions. These experiments were not replicated so it is not possible to assess preferences statistically.

At least two factors could have contributed to the broad preferences observed during these studies. The first is the number of bees with simultaneous access to the feeders. Waller (1972) found that consumption of less preferred solutions increased when several bees visited a feeder. The second potential influence is the shape of the relation between concentration and the rate of net energy uptake during ingestion of large volumes (Fig. 3a). Because the rate of net energy uptake changes slowly in the vicinity of the most rewarding concentration (50%), bees feeding on 37% to 61% nectar ingest energy with less than a 10% reduction in efficiency. Even though the energetic motivation of bumble bee foraging has received considerable attention (reviewed by Waddington 1983, Plowright and Laverty 1984), the magnitude of differences in the rate of net energy uptake required to induce selective feeding has not been investigated. If these bees do not respond to a 10% difference in foraging efficiency, they would tend to feed equally on a broad range of concentrations, especially when nectar is available in large volumes.

Heyneman (1983) asserted that, on the basis of her model, the nectar concentration that maximized a nectarivore's rate of net energy uptake did not depend on the method of nectar ingestion. However, unlike bees, butterflies maximize their rate of net energy uptake by feeding on 35–40% nectar (May 1985, Pivnick and McNeil 1985). Apparently differences in the dynamics of lapping (bees) and suction feeding (butterflies) do determine the relation between nectar viscosity and ingestion rates. By governing ingestion rates, the mechanics of nectar ingestion can also influence foraging energetics and, by implication, flower choice.

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