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Optimal sugar concentrations of floral nectars – dependence on sugar intake efficiency and foraging costs

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Summary. A model is developed to elucidate the determinants of sugar concentrations in flower nectars. This model analyses the efficiency of sugar intake, or energy flux, which for nectarivores closely approximates the rate of net energy gain. For both steady state and some non-steady flows of nectars, this energy flux is shown to be maximal at particular sugar concentrations referred to here as the maximum flux concentration. Higher concentrations actually yield lower energy intake rates because the concomitant rapid increase in viscosity sharply reduces the rate of fluid intake. For pure sucrose solutions, the maximum flux concentration is 22%. For flower nectars, which are chemically more complex, the maximum flux concentration is predicted to be closer to 26%, using the first viscosity measures obtained for flower nectars. This concentration is shown to be essentially independent of the pollinator's feeding organ morphology and of the type of potential inducing nectar flow. It is proposed that this concentration applies for virtually all pollinators that select nectars with maximal energy flux.

However not all pollinators are expected to select such nectars because this 26% concentration is not necessarily "optimal". The model predicts that optimal sugar concentrations vary for particular pollinators as a function of two primary factors: (1) the energy flux derived from the nectar, as discussed above, as well as (2) the relative contribution of transit costs to overall foraging costs. Relatively "dilute" nectars, with sugar concentrations close to the maximal flux value, are predicted for flowers pollinated by organisms that minimize feeding time to reduce high feeding costs, such as that of hovering or of exposure to enhanced predation while feeding. More concentrated nectars are predicted for flowers pollinated by nectarivores that incur high foraging transit costs relative to feeding costs.

Flowers pollinated by hovering pollinators, including many hummingbirds, hawkmoths and bats, have nectars with mean sugar concentrations in close accord with the 26% maximum flux concentration predicted. Moreover, these nectars have relatively low concentrations of non-sugar constituents, which increase viscosity and thereby decrease sugar flux. Over 75% of the flowers examined in this study, which are pollinated primarily by territorial hummingbird species, provide nectars that allow sugar uptake with an efficiency of 90% or greater of the maximal value. According to the model, these data suggest that feeding costs of these pollinators far outweigh foraging transit costs. In contrast, the model suggests that flower nectars taken by traplining hummingbirds and by bees, with sugar concentrations significantly above the maximum flux value, reflect the higher costs of foraging flight relative to costs of feeding for these pollinators.

Increasing temperature decreases nectar viscosity, and thereby increases absolute nectar uptake rates sharply. This leads to a number of predictions regarding foraging behavior as well as flower location, orientation, and color. However, the maximum flux concentration is shown to be practically invariable over a wide range of temperatures – increasing by only 2% sugar from 10° C to 30° C. Thus, contrary to previous expectations, little change in average sugar concentrations of flowers pollinated by particular groups of nectarivores is expected from cooler to warmer regions.

Introduction

Background

Considerable interest has focused recently on the low sugar concentration of most hummingbird flower nectars relative to most bee flower nectars. As sugars in nectar provide the primary energy source for hummingbirds' high energetic requirements, the "dilute" nature of such nectars is unexpected, even paradoxical. Consequently, this property of hummingbird flower nectars was ignored by some early pollination biologists, as pointed out by Baker (1975). Recently, since Baker brought attention to the "problem" of sugar-poor hummingbird flower nectars, several studies have focused on elucidating the evolutionary basis of this phenomenon. Calder (1979) and Calder and Hiebert (1980) considered the possibility that these nectars are dilute to provide for hummingbirds' water needs, but concluded that even in hot dry climates such flower nectars provide more than adequate water. In fact, the birds' primary osmoregulatory problem appears to be elimination of excess water. Bolten and Feinsinger (1978) proposed that dilute nectars have evolved not to attract hummingbirds, but to deter nectar-robbing bees. On this basis they predicted that nectars protected from bee access by longer corollas would have higher sugar concentrations than those more easily accessible to bees. This trend holds for nine Trinidadian hummingbird pollinated species (Bolten and Feinsinger 1978), as well as for hummingbird pollinated flowers in other areas (Feinsinger, pers. comm.). It is proposed in this paper, however, that rather than reflecting the influence of nectar-robbing bees, this dichotomy in sugar concentrations primarily reflects differences in foraging costs of territorial and traplining hummingbirds. Pyke and Waser (1981), after considering the hypotheses that had been proposed to date to explain the dilute nature of hummingbird flower nectars, concluded that this phenomenon remains enigmatic.

Baker (1975) offered the first clear insight on this aspect of the relationship between plants and their hummingbird pollinators. He proposed that although energetic reward per unit nectar volume increases with sugar concentration, hummingbirds would experience increasing difficulty ingesting more concentrated nectars, which of necessity have higher viscosities. On this basis he suggested that the 20–25% range of sugar concentrations typical of hummingbird-pollinated flowers may be optimal insofar as it yields maximal *rates of sugar intake* to the birds. (Sugar concentrations referred to in this paper are % sucrose equivalents on a weight-to-weight basis, as recommended by Bolten et al. (1979)). Lower sugar concentrations enable more rapid fluid uptake but lower energy reward per unit volume, and higher concentrations enable slower uptake of energy-rich solutions.

The first quantitative analysis of nectar-feeding was developed by Kingsolver and Daniel (1979) specifically for butterfly feeding. They analysed the flow of aqueous sucrose solutions through a truncated cone representing a butterfly proboscis, and found a maximum sugar flux for sucrose concentrations between 20 and 25%. It was not stressed, however, that the existence and position of this flux maximum is relatively insensitive to several parameters in their analysis, including the specific geometry and size of the feeding organ beyond the range found in butterflies, the mechanism inducing nectar flow, and the energetic cost of ingesting sugar solutions. As shown in Appendix 1, this flux maximum emanates directly from a simple ratio of nectar properties (sugar concentration/viscosity), essentially as envisioned by Baker (1975).

Findings presented in this paper

This paper presents a generalized model of energy flux provided by flower nectars to nectarivorous pollinators. It treats flower nectars, which are produced by plants to attract pollinators, as solutions that evolve in response to the selective influence of these nectarivores, and assumes that constraints imposed on plants by other factors have negligible influence on nectar sugar concentrations. For ease of presentation, the model is developed for steady state (time-invariant) flow of nectar and, as shown in Appendix 1-C, it yields results analogous to those for non-steady (time dependent) flows of fixed volumes of nectar, which have been analyzed explicitly for hummingbirds by Kingsolver and Daniel (1983). The model presented here is referred to as an effectively-steady model because it is applicable to both steady flows and to flows that vary with time but have the same dependence on viscosity as steady flows. On the basis of the functional relationship between sugar flux and the key fluid properties of nectar – sugar concentration and nectar viscosity – the model predicts a sugar concentration that maximizes sugar (or equivalently, energy) flux to nectarivores, assuming nectar flow to be rate limiting. This concentration is referred to here as the "maximum flux concentration". Although morphological and mechanical aspects of feeding control absolute rates of sugar intake, the maximum flux concentration is shown to be independent of the particular potential that drives nectar flow, and of the geometry of the nectarivore's feeding organ. One can therefore avoid many poorly constrained assumptions about details of feeding inherent in more specific models of nectar feeding.

The maximum flux concentration is not, however, "optimal" for all pollinators. Rather than maximizing energy flux during the feeding period alone, an optimal foraging strategy for nectarivores is to maximize the rate of energy intake averaged over an entire foraging bout. When travel contributes increasingly to total foraging costs, it will be shown that the optimal sugar concentration rises increasingly above the maximum flux concentration. Thus, the optimum for a given nectar feeder depends on both the rate of energy intake, which varies with sugar concentration and viscosity, and on the costs of feeding relative to those of travel.

The energetics of nectar intake is modeled here using, for the first time, measured nectar viscosities. This contrasts with other studies (Kingsolver and Daniel 1979 and 1983; Sutherland, in prep.) in which nectar flow is modeled as flow of simple sucrose solutions. Explicit consideration of temperature effects on nectar feeding point to the advantages of feeding on relatively warm nectar, and to the non-intuitive virtual independence of the maximum flux concentration from temperature. These and related results lead to the discussion of a number of biological implications.

Concurrent research

In addition to the generalized model presented here, applicable to nectar feeders that maximize energy gain per unit foraging cost, Baker's predictions regarding optimal sugar concentrations stimulated the simultaneous and independent development of two other models of nectar feeding: by Sutherland for hummingbirds (in prep.), and by Kingsolver and Daniel, also for hummingbirds (1983).

Sutherland's quantitative model of steady state capillary flow of sucrose solutions along hummingbird tongue grooves shows that a concentration of about 22% maximizes the rate of sugar intake. Additionally, he presents data indicating that when a broad concentration range of *Agave parryi* nectar is available to Rufous Hummingbirds in the field, the hummingbirds exhibit a significant preference for intermediate-age flowers with 25% sugar nectars – near the 26% maximum flux concentration predicted in this paper.

Kingsolver and Daniel approach hummingbird feeding much as they did butterfly feeding, with a detailed mechanical model of nectar uptake. They consider two non-steady feeding modes that depend on the timing of hummingbird tongue immersion. When a constant volume is taken per lick, regardless of concentration, a 22% sucrose solution is predicted to maximize energy flux – the same predicted by "steady state" models (Kingsolver and Daniel 1979; Sutherland, in prep; and the model presented here). As shown in Appendix 1-C, this agreement stems from the fact that the time averaged sugar flux for the steady model has the same dependence on viscosity and sugar concentration as Kingsolver and Daniel's constant-volume non-steady feeding mode. However, if the duration of tongue immersion is taken to be constant – such that smaller volumes are taken of more concentrated and therefore viscous solutions – a higher concentration of about 35% sucrose is predicted to maximize sugar flux. To determine which of these predictions is realistic for hummingbirds, a more detailed understanding of their technique of nectar ingestion is required. Although most laboratory choice tests indicate hummingbirds prefer relatively high sugar concentrations, the average nectar concentrations of hummingbird-pollinated flowers, and Sutherland's field choice data corroborate predictions of the steady state, or time-averaged constant-volume non-steady model for nectarivores that minimize feeding time. Moreover, as discussed in a later section, it will be proposed that Kingsolver and Daniel's (1983) model that yields a 35% maximum flux concentration is not applicable unless the viscous property of nectar controls only the initial infilling of the hummingbird tongue tip. More generally, when including other phases of nectar ingestion that involve nectar flow that may limit ingestion rates, the predicted maximum flux concentration for sucrose solutions would be closer to the 22% value predicted by the effectively-steady state model.

Model of nectar intake

Maximum flux concentration

Appendix 1 explicitly details the model presented here.

The rate of sugar intake by a nectar feeder, or equivalently the rate of energy intake, is proportional to the product of nectar flux and sugar concentration, as illustrated schematically in Fig. 1. There is a point beyond which an increase in sugar concentration actually decreases the rate of energy yield to the nectar feeder. This point represents the sugar concentration at which energy flux to the pollinator is maximized – the maximum flux concentration.

The dependence of energy flux on both sugar concentration and viscosity, and the independence of the maximal flux concentration from the particular feeding mechanism of the pollinator can be demonstrated quantitatively by considering a generalized relation for steady flow of fluid, with viscosity μ, in a conduit of arbitrary shape. The fluid flux is:

$$Q=\frac{\alpha}{\mu}\frac{dP}{dl}, \tag{1}$$

where α is a constant based on the conduit size and geometry. For steady laminar flow through a cylinder it becomes the Poiseuille-Hagen equation with $\alpha=\pi r^4/8$, r being the internal radius of the cylinder (Bird et al. 1960). The driving potential dP/dl represents the nectarivore's ability to induce nectar flow and may involve muscularly induced suction, gravity, capillarity, osmotic pressure, or any combination of these factors (see Appendix 1-A and 1-B). Equation (1) is strictly correct for steady flows in which case α and dP/dl are taken to be constant values characteristic of the nectarivore. It also adequately represents time-averaged properties of non-steady state flows involving fixed nectar volumes, which have been analyzed in the context of hummingbird feeding by Kingsolver and Daniel (1983). For such non-steady flows the time-averaged nectar flux $\bar{Q}$ can be computed, assuming now that α and/or dP/dl vary over a fixed interval characteristic of a particular nectarivore, independently of sugar concentration (Appendix 1-C). Implicit in Eq. (1) are two assumptions reasonable for nectar feeding: flow is laminar (the Reynold's number, which is on the order of 30 for hummingbirds – based on data from Ewald and Williams (1982) – and less for smaller organisms, does not approach the value of 2300 at which point flows in cylinders become turbulent) and nectar behaves as a linear viscous fluid (Barber 1966).

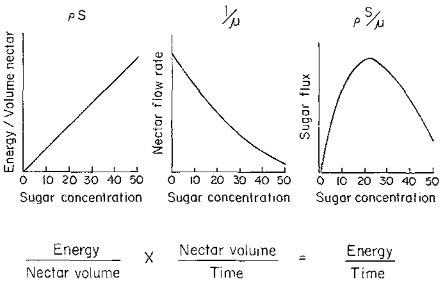

Fig. 1 A–C. Sugar flux (sugar mass/time) is the product of sugar concentration and nectar flux. With increasing concentration, two competing trends – a nearly linear increase in energy per unit volume of nectar **A** and a decrease in nectar flow rate inversely related to the increasing viscosity **B** – result in a maximum energy flux at an intermediate sugar concentration **C**

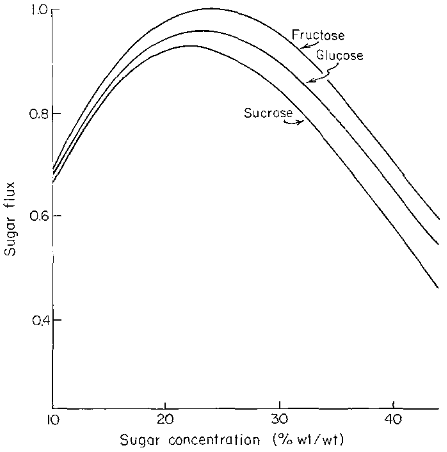

Fig. 2. Sugar flux as a function of sugar concentration for pure sucrose, glucose, and fructose solutions at 20° C. The flux is parameterized by the ratio S/μ, concentration to viscosity, and normalized with respect to the largest flux value, which is for 24% fructose. Concentrations are reported in % sucrose equivalents, on a weight-to-weight basis

The sugar flux is ρSQ where ρ is the fluid density and S is the concentration in % sucrose equivalents on a weight to weight basis. In solving for the sugar concentration that maximizes sugar flux, it is convenient to group all factors independent of, or weakly dependent on sugar concentration S in a proportionality factor K that represents fluid density, geometry of the feeding apparatus, and mechanism driving nectar flow for a particular nectarivore. The average sugar flux $\bar{E}$ can then be expressed as

$$\bar{E}=K\frac{S}{\mu}. \tag{2}$$

Thus the rate of sugar intake is effectively proportional to the ratio of sugar concentration to nectar viscosity – a parameter dependent on nectar composition and temperature. The ratio S/μ, representing sugar flux as a function of concentration, is shown in Fig. 1 for sucrose and in Fig. 2 for the three sugars most common in nectars. The concentration that maximizes sugar flux, as well as the rate of net energy gain (see Appendixes 1-C and 1-F), is represented by the maximum value of S/μ. The central importance of the S/μ ratio was also recognized independently by Sutherland in his consideration of hummingbird feeding (in prep.).

For single-sugar aqueous solutions this maximum flux concentration can be found using tabled viscosity values (Weast 1976, p D-261), as seen in Figs. 1 and 2. Sucrose viscosity data indicate that sugar flux is greatest for solutions with about 22% sugar. The monosaccharides glucose and fructose, also important components of most nectars (Baker and Baker 1982a), have lower viscosities than does the disaccharide sucrose. Maximum flux concentrations for these sugars are only slightly higher, however, than for sucrose – about 24% for both glucose and fructose. Maximum flux concentrations for mixtures of sucrose with glucose and/or fructose are likely to range between 22 and 24% sugar, because viscosities for such solutions are probably intermediate (Reid and Sherwood 1958; Heyneman, unpub. data).

Despite the pronounced effect of temperature on viscosity, the maximum flux concentration is shown here to be insensitive to temperature (Fig. 3), as was suggested by Kingsolver and Daniel (1979). The maximum flux concentration for pure sucrose solutions increases from 20% to only 23% sugar with a rise in temperature from 0° to 30° C. This virtual temperature independence of the concentration that yields maximal energy flux, in marked contrast with previous expectations (Hainsworth 1973; Baker 1975; Calder 1979), stems from the functional relationship between fluid viscosity and temperature (Appendix I-D).

Thus, for pure aqueous sugar solutions, over a wide range of both sugar compositions and temperatures, the concentration predicted to maximize energy flux is essentially constant between 21 und 24% sugar.

Optimal sugar concentration

Nectars with the maximum flux concentration minimize feeding time by offering maximal rates of energy reward per unit feeding cost. However, when this energy reward is compared with foraging costs associated with both feeding *and* transit, the benefit to cost ratio is clearly reduced. This effect is best visualized from a plot of energy cost versus benefit similar to that used by Charnov (1976) in his application of the marginal value theorem to optimal foraging. The curve in Fig. 4 shows the energetic cost and benefit of ingesting a certain volume of nectar for a series of sugar concentrations. In the absence of foraging transit costs, the benefit/cost ratio for a particular sugar concentration equals the slope of the straight line that passes from the origin through the concentration of interest on the curve. The maximum benefit/cost ratio is, therefore, the slope of the steepest line passing through the origin that intersects the curve. Thus it equals the slope of the tangent (OA), which contacts the curve for pure sucrose solutions at a concentration of 22% sugar (point A), the maximum flux concentration. When transit time is included, the slope of another tangent (for example BC) gives the highest benefit/cost ratio. The inclusion of transit costs reduces the maximum benefit/cost ratio, as indicated by the lower slope of BC, and shifts it to significantly higher concentrations.

Thus, the concentration that maximizes the benefit/cost ratio increases from 22% when transit cost is negligible (and energy flux is maximal) to higher concentrations as travel costs contribute more importantly to total foraging costs. The dependence of this optimal concentration on the "relative transit cost", taken to be the transit-feeding cost ratio, is shown in Fig. 5. The influence of foraging transit costs is significant; for example, when transit costs equal those of feeding, the optimal concentration for sucrose solutions is shifted from 22% to over 35% sugar.

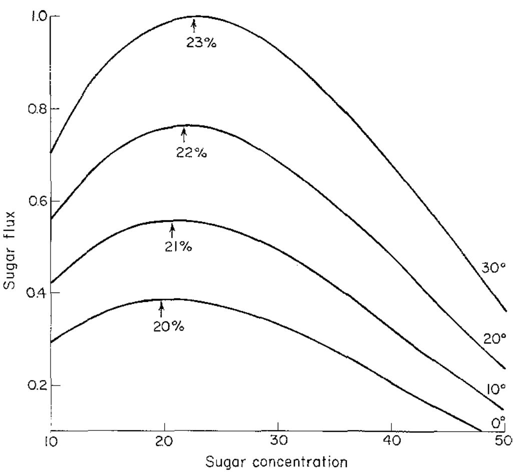

Fig. 3. Sugar flux as a function of concentration of sucrose solutions at temperatures of 0, 10, 20, and 30° C. Because all values are normalized with respect to the largest possible value of the effective flux, which for the range of conditions considered is 23% sugar at 30° C, the vertical axis can be interpreted as sugar intake efficiency

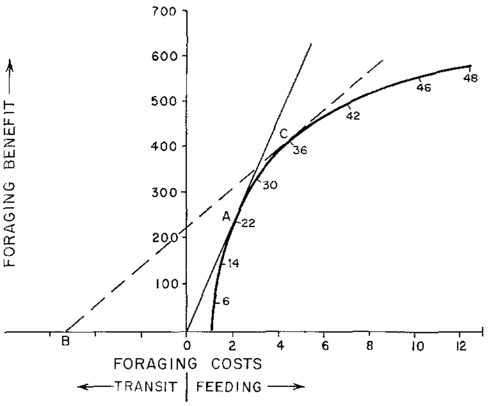

Fig. 4. The curve represents the energetic benefit and cost of ingesting a fixed volume of pure sucrose solution for a series of sugar concentrations (% sugar concentrations are indicated along curve). The benefits and costs are scaled respectively with sugar concentration (in kg/m^3) and with ingestion time, which is proportional to viscosity (in g/m-s). Maximal benefit/cost ratios are given by slopes of tangents to the curve that pass through the appropriate abscissa values. As expected, vanishing transit costs correspond to the highest possible benefit/cost ratio. The optimal concentration, given by the concentration at the point of tangency, shifts to higher values as transit costs increase

Data collection

To characterize the energy content and viscosity of actual floral nectars, field studies were carried out in December 1978 and 1980 in the highlands of central Mexico. The

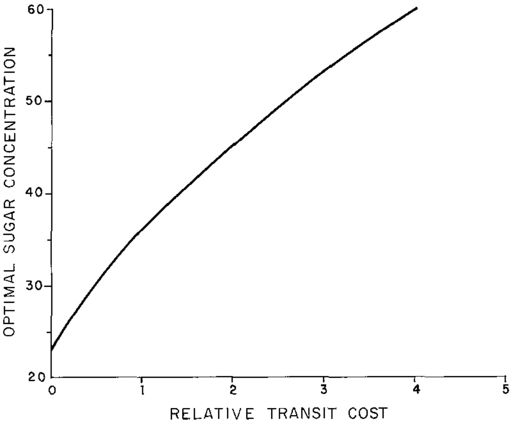

Fig. 5. Dependence of the optimal concentration (maximum benefit/cost ratio) on the relative transit cost, defined as the ratio of transit to feeding costs. This relationship is derived in Appendix 1-C [Eq. (A-10)]. When feeding costs for outweigh transit costs associated with foraging the relative transit cost is near zero, and a pollinator is expected to select sucrose solutions with sugar concentrations close to 22% – which maximize energy flux. High theoretical optimal concentrations may be unrealistic, as water needs or other physiological constraints may place an upper limit on the concentration of nectars ingested by pollinators

main study site was 170 km south of Guadalajara on the slopes of Volcan Colima, at elevations ranging from 2,000 to 2,500 m. The upper slopes of this active volcano are a primary wintering site for migrant Rufous Hummingbirds, *Selasphorus rufus*. The site also supports an extremely high concentration of hummingbirds representing twenty other species. In winter, a profusion of hummingbird pollinated shrubs, herbs, and vines flower in light gaps in the pine-oak forest. For a detailed description of the site and hummingbirds, refer to DesGranges (1977, 1978). Data were also collected at about 3,600 m in light gaps in pine-oak forest on the flanks of Iztaccihuatl, an inactive volcano south-east of Mexico City. A third study site was established at about 1,600 m on the semi-arid central plateau near San Miguel de Allende – midway between Guadalajara and Mexico City.

Nectar samples were generally collected early in the day from previously bagged, freshly opened hummingbird-pollinated flowers. Nectar characteristics measured in the field included total sugar concentration, viscosity, surface tension, volume, and pH. Total sugar concentration was measured with a standard Bellingham and Stanley pocket refractometer, calibrated to read percent sugar in grams sucrose equivalents per 100 grams solution. Readings were temperature compensated and reduced by 2% sugar units, as suggested by Inouye et al. (1980) to compensate for the effect of non-sugar components on the index of refraction. Maximum error, after corrections, should not exceed about 2% of the reading, which is generally less than the 1% resolution limit of the refractometer. Capillary rise, a measure of the surface tension of the solution, was determined by measuring the ascent of pooled nectar up a 5 μl VWR capillary tube.

A simple and effective technique to measure nectar viscosity in the field was devised. Details of this method and estimates of error are reported separately (Heyneman and Hallet, in prep.). Briefly, viscosity was estimated by accurately timing the descent of 2 μl nectar down a standard distance (50 mm) along the central section of a vertical 10 μl VWR capillary tube. Timed intervals ranged from about 1 second for pure water, to over 20 seconds for nectars with more than 50% sugars. Measures, repeated ten or more times for each sample, were reproducible within a few hundredths of a second, or with a standard deviation usually less than 5% of the mean. Data were corrected for differences in ambient temperature by normalizing values to 15° C, following Fasman's data (1975) on the temperature dependence of viscosity for aqueous sucrose solutions. Descent times t_d were converted to viscosity μ, using the following equation derived from well known expressions (e.g., Bird et al. 1960) for steady laminar flow in a vertical tube under the influence of gravity:

$$\mu=\frac{g r^2}{8 h} \rho t_d, \qquad (3)$$

where r is the internal radius of the capillary (2.44×10^{-1} mm), g the acceleration due to gravity, h the test distance traversed by the nectar in time t_d, and ρ the fluid density, assumed to be equal to the density of a pure sucrose solution of the same concentration (Fasman 1975). Complex flow patterns near the liquid/air interfaces at both ends of the solution in the capillary tube probably slowed the descent, resulting in a slight over-estimation of viscosity. This end effect, as well as other factors that would perturb flow, such as time required for acceleration of nectar, imperfectly clean capillary walls, bubble nucleation, and possible impurities such as pollen grains are discussed separately (Heyneman and Hallet, in prep.). The total effect of these flow complications on viscosity was assessed empirically by comparing field viscosity measures for both pure water and aqueous sucrose, glucose, and fructose solutions with published viscosities at comparable temperatures. The comparison supports the validity of this technique, and indicates that it overestimates true viscosities by about 7%. Thus, nectar viscosity measures were corrected for this overestimate.

Nectar samples were also collected for subsequent laboratory analyses, to determine relative abundances of the constituent sugars, and concentrations of the most abundant non-sugar components – including free amino acids, proteins, lipids, alkaloids, and phenols. Analytic techniques employed were those of Baker and Baker (1982a) for sugars; Baker and Baker (1976a, 1976b) as modified in Baker et al. (1978) for amino acids; Baker and Baker (1975) for lipids, organic acids, alkaloids, and proteins; and Smith (1969) for phenolics.

Results

Data are presented in Appendix 2.

Measured viscosities of nectars from hummingbird pollinated flowers increase nonlinearly with increasing sugar concentration (Fig. 6), and are significantly higher than values for pure sucrose solutions of equal concentrations. A strong linear correlation ($r^2=0.96$) between viscosities of nectars and of sucrose solutions of equivalent concentrations indicates that the viscosity variation in nectar is due primarily to variation in total sugar concentration. Over the range of sugar concentrations of interest, measured nectar viscosities tend to systematically exceed corresponding sucrose solutions by an average 0.8 centipoise (g/m-s) (standard deviation = 0.4). When compared with the sucrose/glu-

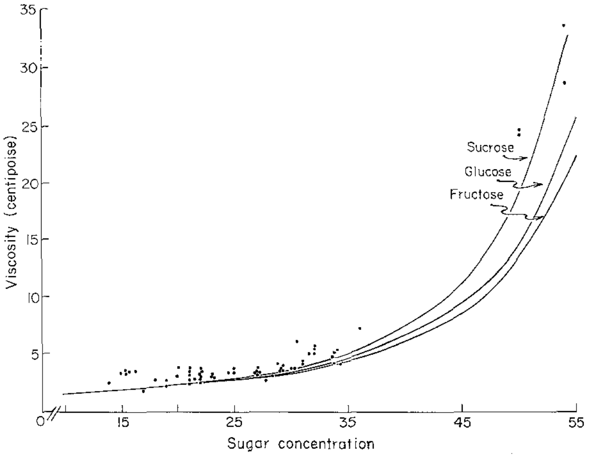

Fig. 6. Viscosity measurements of nectars of hummingbird-pollinated flowers. These field determinations were normalized to 15° C (see text). Viscosity curves for pure sucrose, fructose and glucose solutions at 15° C are included for comparison

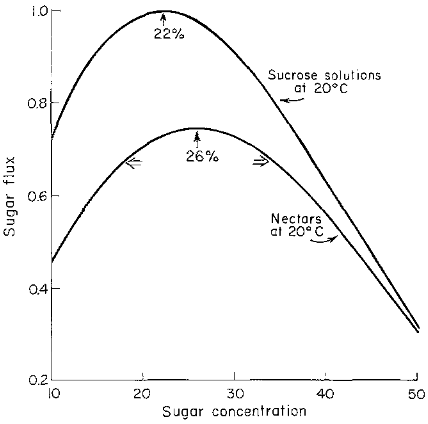

Fig. 7. Normalized sugar flux for a pure sucrose solution and for idealized nectar, taken to be uniformly more viscous than an equivalent pure sucrose solution by 0.8 cp. Double arrows point to the concentration range over which birds can ingest nectar with an efficiency within 10% of maximum

cose/fructose mixtures typically found in nectars, which could be as much as 6–7% less viscous than pure sucrose solutions (Fig. 6, and Reid and Sherwood 1958), an even greater viscosity excess is evident.

Because of their higher viscosities, sugar flux for nectars is substantially lower than for pure sugar solutions with comparable concentrations. As seen in Fig. 7, the mean viscosity increase of 0.8 cp reduces energy flux to 26% below the level for pure sucrose solutions near the maximum flux concentration, but shifts the maximum flux concentration only slightly, from 22% for sucrose solutions to 26% for nectars.

This higher viscosity of nectars relative to sugar solutions is presumed to result from non-sugar components such as amino acids, proteins, lipids, phenols and alkaloids. Indeed, non-sugar compounds are sufficiently abundant in hummingbird flower nectars to affect significantly the index of refraction (Inouye et al. 1980; Hiebert and Calder, in press), suggesting that viscosity could be similarly affected. Chemical analyses indicate, however, that no single factor clearly accounts for the viscosity excesses or the variation in viscosities measured for the 10 species in Appendix 2. Viscosity tends to increase as expected with proportion of sucrose relative to glucose and fructose, but this trend is not statistically significant. Preliminary experiments with free amino acids, generally the most abundant non-sugar nectar constituent, indicate a viscosity increase of only 3% results from addition of 0.25 mM histidine (the highest concentration of free amino acids found in flower nectars, according to Baker and Baker 1982b) to a 22% sucrose solution. And within the relatively narrow free amino acid concentration range typical of flowers pollinated by hovering nectarivores (hummingbird, hawkmoth and bat flowers in Table 1), histidine enhances viscosity less than 1%. Amino acids with greater molecular weights or mixtures of amino acids may, however, have greater effects. Larger molecules such as proteins and lipids presumably affect viscosity more strongly than equivalent concentrations of amino acids, but typically these compounds are undetectable or are present in very low concentrations in hummingbird pollinated flowers (Appendix 2; Baker 1977a). It seems unlikely that nectar viscosities are affected importantly by phenols (common), alkaloids (rare), and pH differences (small: mean for 10 species in this study = 6.0, with a standard deviation of 0.4); refer to data in Appendix 2. Hence the chemical basis for the relatively high and variable viscosity of actual nectars in comparison with simple sugar solutions remains enigmatic.

Differences in the surface tension of nectars requires further investigation. Within-sample variation of capillary rise measures overshadowed between-sample differences. Washburn (1921) suggests a dynamic method using horizontal capillaries that may give more accurate measures of surface tension than the static technique with vertical capillaries used here.

Discussion

Model predictions and empirical implications

The model of effectively-steady nectar ingestion presented here predicts that for pure aqueous sugar solutions sugar flux to nectarivores is maximal for concentrations of 21% to 24% sugar. For actual flower nectars this concentration is somewhat higher – about 26% sugar – because of their high viscosity relative to pure sugar solutions. This maximum flux concentration defines the "optimum" for pollinators with a premium on minimized feeding time, whether because feeding costs are high or foraging transit costs are low. More generally, the model predicts that the optimal sugar concentration is higher for pollinators whose transit costs contribute substantially to their total foraging costs (Figs. 4 and 5). However, in nature costs associated with feeding and transit are often complex, relatively intangible, and difficult to express quantitatively in common terms, for example in energy units. As a result, it is difficult to make precise predictions of optimal sugar concentrations for particular pollinators. It is possible, however, to make broad comparative predictions based on pollinators' primary energetic costs of foraging. And, perhaps more importantly, this model provides a framework for interpreting differences in sugar concentrations as well as other aspects of nectar chemistry between plants pollinated by different pollinator types.

Table 1. Mean concentrations of sugars and amino acids in floral nectars. This table summarizes the sugar concentration data gleaned from the literature by Pyke and Waser (1981), and incorporates more recent data on sugars as well as amino acids, reported by Baker and Baker (1982a, b)

Pollinator	Sugar concentration		Amino acid concentration	
	Sample size	Mean (% wt/wt)	Sample size	Mean (μM/ml)
Hummingbirds	(222)	23	(150)	0.45
Bats	(11)	17	(23)	0.31
Hawkmoths	(44)	19	(65)	0.54
Settling moths	(11)	22	(78)	1.06
Butterflies	(85)	25	(118)	1.15
Bees	(224)	35	(715)	0.62

A consideration of bee foraging in light of this model lends insight on the relatively concentrated nectars typical of flowers they pollinate. Because bees often travel long distances to flowers, and perch while imbibing nectar, flight to and between flowers constitutes the most energetically costly phase of their foraging (Heinrich 1979). On this basis the model would predict an optimal sugar concentration significantly higher than the maximum flux concentration (Figs. 4 and 5). This prediction is in accord with the observation that bee pollinated flower nectars average 35% sugar (Table 1), about 50% above the maximum flux concentration. Although bees might be expected to favor even more concentrated nectars, according to Fig. 5, their water needs may effectively set an upper limit on acceptable sugar concentrations. This inference is supported by observations that bees select flowers with more dilute nectars when their water needs are high (Southwick and Pimentel 1981). In contrast, Kingsolver and Daniel (1979) have suggested that the relatively high sugar concentration of bee pollinated flowers is a consequence of the particular suction mechanism bees employ to imbibe nectar. It is shown in Appendix 1C of this paper, however, that although differences in mechanisms inducing nectar flow affect absolute rates of nectar intake, they do not influence maximum flux or optimal sugar concentrations.

The relative importance of foraging transit costs versus feeding costs for other nectarivores is not generally as evident as it is for bees. A consideration of hummingbirds, for example, reveals numerous factors that contribute to their relative foraging costs. These factors include, for example, the high energetic cost per unit time of hovering while feeding relative to that of flight to and between flowers (Pennycuick 1968; Hainsworth 1981, Fig. 3), as well as the relative duration of these two modes of flight. More subtle factors may also be important. For example, risk of nectar loss to intruders constitutes a feeding cost that may lend advantage to those territorial birds that minimize time spent away from prominent surveillance positions to feed. To minimize feeding time, such birds would be expected to select nectars that provide maximal sugar flux. Similarly, intruders would maximize energetic gain in the limited feeding time available before discovery by territory owners by selecting nectars with maximal sugar flux. In contrast, traplining hummingbirds expend a greater proportion of foraging energy in transit relative to feeding. Such species may therefore be expected to maximize benefits by selecting more concentrated nectars. Clearly, obtaining a precise measure of feeding versus travel costs is complex for these pollinators.

The preponderance of hummingbird flower nectars with sugar concentrations that yield near-maximal energy flux and contain extremely low concentrations of non-sugar constituents (Baker 1975) imply effective natural selection for nectars that offer maximum rates of energy intake, and suggest, according to the model presented here, that feeding costs of hummingbirds generally far outweigh travel costs. The hummingbird pollinated species summarized in Table 1 ($n = 222$) average 23% sugar – within 3% of the 26% maximum flux concentration predicted for nectars with viscosities typical of hummingbird pollinated species (Fig. 7). In addition, the 10 plant species examined in this study average 27.6% sugar (standard deviation = 7% sugar; Appendix 2) – within 2% of this concentration. This match is particularly notable in view of the fact that (as seen in Fig. 7) birds could ingest nectar at 90% or greater of the maximum efficiency over a relatively broad range of sugar concentrations, from 17% to 33%. Bolten and Feinsinger (1978; Feinsinger, pers. comm.) have pointed out, however, that the distribution of sugar concentrations for hummingbird pollinated flowers tends to be bimodal, with flowers pollinated by short billed birds having significantly lower sugar concentrations than those pollinated by long billed species. This dichotomy in sugar concentrations would be predicted by this model on the basis of differences in hummingbird foraging costs. Short billed species, generally territorial (Feinsinger 1976; Feinsinger and Colwell 1978), have lower relative transit costs than long billed, traplining species. Because optimal sugar concentrations rise with increased transit to feeding costs (Fig. 5), long corolla flowers, generally pollinated by trapliners, are expected to contain more concentrated nectars than short corolla flowers. Feinsinger (pers. comm.) has found that, for hummingbird pollinated species, nectars of long corolla flowers average close to 35% sugar – similar to concentrations typical of bee pollinated species – whereas short corolla flowers average around 25%. As the hummingbird pollinated plants considered here (Appendix 2) are primarily short corolla species, according to Bolten and Feinsinger's categorization (1978), it is not surprising that their flower nectar concentrations average about 25% sugar – close to the maximum flux concentration.

Additional field data collected in northern Arizona by S. Sutherland (in prep.) also suggest that in nature short billed hummingbirds select nectars with sugar concentrations predicted to maximize energy flux. Rufous Hummingbirds (*Selasphorus rufus*) feed in that region on *Agave parryi* nectar, which increases from 15% sugar at flower opening to nearly 60% after several days. A significant preference is exhibited for those intermediate-age flowers with near-maximum flux concentration (average 25% sugar) nectars.

That hummingbirds are capable of selecting nectars on the basis of energy flux is evidenced by their preference for artificial feeders with shorter "corollas", which yield greater nectar flux than feeders with longer "corollas" filled with the same sucrose solution (Hainsworth and Wolf 1976). Several laboratory studies also indicate preference by hummingbirds for sugar solutions with maximal energy flux. Ruschi (1953 – cited in Stiles 1976) found that several Brazilian hummingbird species prefer sucrose solutions in the range of 15 to 25%, over both lower and higher concentrations. More recently, hummingbird choice tests by Hainsworth and Wolf (1976) with 5 to 30% sucrose solutions indicate a preference for the more concentrated member of each pair of solutions offered below the maximum flux concentration predicted here; above this value the preference for higher concentrations disappears.

The close correspondence between mean sugar concentrations of hummingbird pollinated flower nectars and values predicted to maximize energy flux, together with Sutherland's field observations and a number of choice tests demonstrating hummingbird preference for nectars that minimize feeding time provide considerable motivation for understanding why most laboratory experiments with short billed species paradoxically indicate that these hummingbirds favor more concentrated sugar solutions offered to them (eg. Stiles 1976; Pyke and Waser 1981; Gass, pers. comm.). This divergence suggests that hummingbirds behave differently in the laboratory than in the field. Incentives that may set a premium on minimized feeding time in the field, such as reduced ability for a territory owner to perceive intruders while feeding, feeding discreetly and quickly in another bird's territory, or enhanced exposure to predation while feeding are absent in the laboratory. Choice tests carried out by L. Gass (pers. comm.) indicate that over a period of 2–3 days field-caught *Selasphorus rufus* gradually shift their preference upward to concentrations of over 50%. In the absence of competition and predation, Gass (pers. comm.) suggests that hummingbirds may maximize sitting time by feeding infrequently on sugar-rich solutions. Studies designed to evaluate differences between such laboratory experiments and natural nectar feeding promise to be most instructive.

Although data collected for this study are from nectars primarily used by hummingbirds, the theoretical model is general and predictions regarding optimal nectars apply to other nectarivores as well. Other pollinators that use energetically expensive feeding techniques are perhaps most likely to benefit significantly from minimized feeding time. Available data appear to support this expectation for hovering pollinators in general. Average nectar sugar concentrations for flowers pollinated by most hummingbirds, hawkmoths and bats fall close to or lower than values predicted to minimize feeding time by providing maximal energy flux (Table 1).

Butterflies and moths, although they do not hover while feeding, also pollinate flowers with nectar sugar concentrations close to the maximum flux value (Table 1). Increased risk of predation during feeding rather than high energy expenditure during feeding, for example, may provide an evolutionary incentive for minimized feeding time. Though sugar concentrations approach the maximal flux value, the absolute rate of energy intake from butterfly-pollinated flower nectars may be relatively low. The high concentration of amino acids (Table 1), plus evidence of further amino acid enrichment of nectars by "pollen dunking" observed for some species (Gilbert 1972; Dunlop-Pianka et al. 1977) and by pollen dislodgement from the introsely-dehiscing anthers typical of butterfly flowers (Baker and Baker 1975; Willmer 1980) would tend to increase nectar viscosity, and thereby decrease flux. Viscosity measures for butterfly pollinated species would disclose this decrease in sugar flux undetected by pocket refractometers. The significant increase in viscosity above that attributable to sugar concentration revealed for hummingbird pollinated species in this study, and the large concomitant decrease in sugar flux indicates that it is insufficient to measure sugar concentration alone. To carefully compare energy flux of nectars used by different pollinators, and the effect of nectar chemistry on the maximum flux concentration, nectar viscosity should be measured as well – particularly for nectars such as those taken by butterflies, which tend to be rich in non-sugar constituents.

Stability of the maximum flux concentration

A particularly notable aspect of the maximum flux concentration is its stability over a wide range of both environmental (Appendix 1D) and compositional variables. Ambient temperature, sugar composition, and the low concentrations of non-sugar nectar constituents typical of hummingbird, bat, and hawkmoth pollinated flowers have little effect on the concentration predicted to maximize energy flux – despite their important influences on both nectar viscosity and sugar flux, as is considered subsequently. As has been noted, the maximum flux concentration for aqueous sugar solutions shifts upward by only 3% sugar with an increase in temperature of 0° C to 30° C (Fig. 3). Similarly, the non-sugar constituents typical of hummingbird flower nectars analyzed in this study (Appendix 2) shift the 22% maximum flux concentration of pure sucrose solutions upward by only 4% for nectars (Fig. 7).

Flower inclination may also shift the maximum flux concentration slightly if the weight of nectar is significant relative to other forces driving nectar flow. A nectarivore visiting upward-facing flowers must take nectar against gravity, whereas gravity actually enhances nectar intake from pendulous flowers. The maximum flux concentration is likely to be rather insensitive to flower inclination, but would tend to shift to lower concentrations for upright flowers and higher concentrations for pendulous flowers, as shown in Appendix 1E. This leads to the prediction, assuming minimized feeding time, that hawkmoth flowers (which tend to face upward) should be slightly more dilute than hummingbird flowers (which tend to be pendulous), which is corroborated by data in Table 1. However bat flowers, which tend to be pendulous, also have lower mean sugar concentrations than hummingbird flowers.

Possible shifts in the maximum flux concentration

Because the predicted maximum flux concentration depends on fundamental nectar properties and is independent of feeding morphology and of the potential used to draw up nectar, it is applicable to virtually all nectarivores that minimize feeding time. However, differences may arise when considering organisms that use complex feeding techniques, for example involving discontinuous nectar flow. In their model of nonsteady nectar ingestion by hummingbirds, Kingsolver and Daniel (1983 and outlined in Appendix 1-C) have shown that different modes of feeding could result in significantly different maximum flux concentrations. The average energy flux can be calculated for single feeding events in which the tongue tip is filled either to a fixed volume or for a fixed time period. These distinct feeding modes yield maximum flux concentrations of 22 and 35%, respectively. However, differences in energy intake efficiency between these modes of feeding must be viewed cautiously because they yield *identical* sugar fluxes [Eq. (A-4) and (A-5)] when expressed in common and comparable terms. Moreover, it is stressed that the effect of nectar flow properties on ingestion rate may not be limited to the short duration time-dependent capillary filling of the tip of a hummingbird tongue alone, which is the subject of Kingsolver and Daniel's analysis. Ingestion also involves nectar transport from the bill tip, where it is presumably extruded from the tongue (Ewald and Williams 1982), to the mouth and eventually to the crop of the bird. Because this transport involves a particular volume of nectar determined by the amount ingested, and hence a relatively constant viscous resistance, any fixed driving potential induced by the nectarivore would tend to induce flow that could be treated as effectively-steady. Models of nectar feeding would, therefore, ideally include both a time-dependent infilling phase and an effectively-steady state phase, which is likely to be relatively long because of the relative length of the corresponding transport distance. The inclusion of effectively-steady state flow as an integral and important part of feeding favors the fixed-volume model that maximizes both steady and non-steady phases. This is the model presented here, which yields a maximum flux sugar concentration of about 26% for nectar flows involving both phases. Careful experimental investigation of nectar uptake rates versus concentration, similar to preliminary experiments by L. Gass (pers. comm.), could yield valuable insight on the relative importance of the short duration infilling phase and the effectively-steady phase.

Implications of reduced sugar flux

Although environmental and compositional variables have been shown to affect the maximum flux concentration only slightly, these factors strongly influence nectar viscosity, and consequently energy flux. This variation in energy flux leads to interesting predictions regarding nectar feeding behavior. The impact of temperature is particularly striking. It is evident from Fig. 3 that within the 10 to 45% range of sugar concentrations it is often energetically beneficial to feed at higher temperatures, even if this entails taking nectars with concentrations that yield sub-maximal energy flux. Energy flux is higher, for example, for a 10% sucrose solution at 30° C than for the 22% maximum flux concentration at 15° C. Yet hummingbirds are abundant in many cool regions – such as the tropical highlands where data for this study were collected – where temperature effects on sugar flux are exacerbated by increased metabolic demands for thermoregulation. On this basis hummingbirds and other nectarivorous pollinators would be expected to feed at the highest temperatures possible, wherever or whenever sugar flux is high and metabolic costs are low. When flowers are available in cooler areas, hummingbirds will (1) first visit flowers in the sun; (2) if physiologically possible, warm nectar, possibly using counter-current exchange circulation (Schmidt-Neilsen 1964) to keep the tongue warm; (3) if available, select plant species with warmer-than-ambient flowers [some bee and beetle pollinated species are known to maintain flower temperatures as much as 20° C above ambient (Lamarck 1778; Meeuse 1978; Knutson 1979)]; and (4) feed during the warmest part of the day. Many constraints are involved, of course – physiological (inadequate circulatory system in tongue to warm nectar?), mechanical (inadequate tongue-nectar contact time to transfer heat?), energetic (hummingbirds must forage throughout the day, including cool morning hours), and evolutionary (hummingbird flowers with the ability to warm nectars have not evolved?). There is evidence, however, that hummingbirds preferentially visit sunlit flowers (Willmer and Corbet 1981), and that some hummingbird-pollinated flowers sun-track, presumably to control intrafloral temperatures (Kevan 1975; Corbet and Willmer 1981).

The predominant red color of hummingbird flowers may also affect nectar temperatures by controlling the radiative heating of flowers. Analyses of the spectral reflectance of flower petals, as well as other plant tissues indicate that reflectance and transmittance typically rise from very low values through the visible part of the spectrum to much higher values in the infra-red past the "reflectance edge" (Gates 1980). A slight shift of the reflectance edge to shorter wavelengths would result in reflected red light. Further shifts would yield other visible colors but would also further decrease the overall absorptance of the flowers. It is apparent that within the constraints of the plant reflectance spectra, possibly imposed by available pigments (Gates 1980), red colored flowers would maximize absorption of nectar-warming solar energy while reflecting light brightly in the visible spectrum – apparently essential for attracting bird pollinators.

Like low temperatures, non-sugar components of nectars reduce sugar flux significantly (Fig. 7). Several lines of evidence indicate that nectars with substantial quantities of non-sugars are indeed selected against. Hainsworth and Wolf (1976) showed that hummingbirds select against 10 and 20% concentration sucrose solutions containing large quantities of free amino acids in favor of comparable solutions with no amino acids. Although they interpret this as selection against "bad tasting" amino acids, birds may well select against more viscous solutions in favor of those with greater energy flux. This preference disappeared when tested against more concentrated sucrose solutions in which non-sugars have comparatively less influence on viscosity. Interestingly, Hainsworth and Wolf (1976) also report that when glycine is enriched to 150 times the total amino acid level typical of hummingbird flower nectars (Baker and Baker 1982b), captive birds cease feeding on the sucrose/amino acid solution altogether, and increase their rate of *Drosophila* capture. Similarly, by means of a series of choice tests Sheithauer (1967) found that hummingbirds prefer pure, non-"enriched" sugar solutions. Another line of evidence comes from nectar analyses, which reveal extremely low concentrations of non-sugar components, including free amino acids, proteins, and lipids, for flowers with sugar concentrations near the maximum flux value pollinated by hummingbirds, bats, and hawkmoths (Baker 1977a; Baker and Baker 1982a; Table 1 and Appendix 2). Certain non-sugar nectar components may be nutritionally important to pollinators. However, the cost of selecting a nutritionally complete *nectar* diet, in terms of reduced sugar intake rates due to increased viscosity (Fig. 7), may be severely constraining for hovering nectarivores. Careful observations by Sheithauer (1967, pp 133–134) suggest that a hummingbird would have to consume over 800 ml nectar each hour (equivalent to the weight of more than 250 White-Eared Hummingbirds!) to fulfill its protein requirements, determined by calculating the protein equivalent of *Drosophila* consumed by a captive *Hylocharis leucotis* freely supplementing a pure sucrose solution diet. Similar estimates indicate that at least a five-fold increase in a bat's normal nectar intake would be required to account for its protein requirements (Scogin 1980). It is apparent, therefore, that nectars primarily supply the energetic needs of bats and hummingbirds, but do not nearly satisfy their other nutritional needs. The protein-rich pollen ingested by bats (Howell 1974), and insects and pollens (S.M. Hiebert unpub. data) ingested by hummingbirds are undoubtedly essential supplements to their energy-rich nectar diets. That low levels of nonsugar constituents are nonetheless present in hummingbird, bat and hawkmoth pollinated flowers may indicate that physiological and/or taxonomic constraints limit the abilities of plants to secrete pure sugar solutions.

Conclusions

In conclusion, the effectively-steady model predicts that nectars with concentrations of about 26% sugar maximize sugar or energy flux, and the rate of net energy gain to nectarivorous pollinators. This concentration is virtually independent of variation in temperature, constituent sugars, and the low concentrations of non-sugar constituents typical of hummingbird, bat, and hawkmoth pollinated species. Because highest sugar flux is provided by maximum flux concentration nectars with low viscosities, feeding time minimizers would tend to select the warmest available near-26% sugar nectars with the lowest concentrations of non-sugar constituents. Increased foraging transit cost relative to feeding cost reduces the importance of minimized feeding time for nectarivorous pollinators, and shifts the optimum to higher sugar concentrations. As this foraging cost ratio increases, the optimal sugar concentration climbs until other constraints, such as water needs, moderate the influence of foraging transit costs. These findings provide a theoretical framework to interpret the evolution of "dilute" as well as sugar-rich floral nectars. Predictions forwarded by the model suggest numerous paths for future laboratory and field research to further our understanding of the coevolution of plants and their pollinators.

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Appendix 1

Generalized model of nectar ingestion

A. Introduction. A general analysis of the ingestion of sugar by a nectarivore is presented in this appendix. Possible determinants of nectar ingestion are assumed to include:

- sugar concentration and viscosity of nectar
- size and shape of the feeding organ
- flower inclination, nectar density, and gravity
- muscularly induced pressure gradients
- pressure gradients induced by surface energy effects, including those associated with any of several interfaces: nectar-air, nectar-corolla, and nectar-feeding organ.
- osmotic pressure gradients
- time variations in pressure gradients.

As most of these parameters will be shown to be effectively independent of sugar concentration in nectar, the concentration that allows maximal sugar intake rates can be calculated with little regard to parameters other than nectar viscosity and concentration. Moreover, net energy gain of a nectarivore is shown to be essentially equal to energy intake because the energetic cost of nectar ingestion is negligibly small.

This analysis is applicable to all types of nectar feeding techniques for which nectar flow is rate-limiting, as they all involve the same general relationship between nectar viscosity and sugar flux. This would include conduit-type flows (butterflies, moths and bees), as well as those induced by rapid tongue motions (hummingbirds), lapping (bats) or other methods. By modeling nectar flow into the grooves of a hummingbird tongue or into the proboscis of an insect as flow in a conduit of arbitrary cross-section, the primary determinants can be considered simply and systematically. The liquid flux for steady laminar flow can be expressed as:

$$Q=\frac{\alpha}{\mu}=\frac{d}{dl}[\rho g Z+(m_n-m_f)+(\sigma_n-\sigma_f)+(o_n-o_f)]. \qquad \text{A-1}$$

Here, α represents the conduit size and geometry. For example, for a cylinder of circular cross-section with radius r, $\alpha=\pi r^4/8$; and for two parallel plates with a separation s, Q is the flow per unit width for which $\alpha=s^3/12$. The $\rho g Z$ term represents gravitational effects on flow in an inclined conduit where nectar density is ρ, acceleration due to gravity is g, and the elevation drop along the nectar flow path is Z. The terms in parentheses represent other parameters that could affect the potential that induces nectar flow. The derivative of the potential with respect to distance l in the flow direction is the driving pressure gradient (dP/dl in Eq. (1) in the text). In addition to the gravity term, it involves pressure differences induced 1) by muscular contractions m, 2) by surface energy differences σ between the flower nectar pool and the feeder's mouth, and 3) by osmotic pressure differences o due to differences in ionic strength between nectars and fluids in the nectarivore. Subscripts n and f represent conditions in the nectar pool and in the mouth of the nectarivore, respectively. For example, nectar pressure σ_n may be affected by curvature of the nectar pool meniscus or by adsorption onto plant tissues. Non-steady flows with low Reynolds numbers can also be well represented by Eq. A-1 after replacing the relevant parameters, usually dP/dl, by the corresponding time-dependent variable (eg. Washburn 1921).

B. Parameter dependence on sugar concentration in nectars. To calculate how nectar flux varies with sugar concentration it is necessary to identify all variables dependent on concentration: μ, ρ, σ and o. The relative importance of the first three can be assessed by noting how much each varies over a range of sugar concentrations. Using data for pure sucrose solutions (Browne and Zerban 1941), increasing sugar concentration from 10% to 30% results in a 140% increase in viscosity, an 8.5% increase in density, and a 2% increase in surface tension, which is reflected in σ. The viscosity rise, which greatly surpasses increases in the other parameters, dominates increasingly with increasing concentration. Hence, to first order, the influence of flower inclination, which depends on ρ, and the effects of surface energy, which control capillarity or fluid adhesion, can be assumed to be effectively independent of sugar concentration. It follows that, with the exception of possible cases for which nectar flow is controlled by osmotic pressure differences, the pressure differential dP/dl inducing flow will depend on the organism but will be effectively independent of sugar concentration.

C. Maximal flux concentration and optimal concentration for steady and non-steady nectar flows. The steady state model presented here will be shown to arrive at results identical to those of the non-steady fixed-volume model proposed by Kingsolver and Daniel (1983) for hummingbird feeding. For non-steady flows, particularly the filling of a conduit, average sugar flux will depend on the duration of nectar intake because the effective length of the flow path l, and hence the pressure gradient dP/dl, vary with time. The choice of an appropriate averaging interval is critical and, ideally, both the steady and non-steady nectar flows should be modeled using compatible assumptions. For steady-state flows, the effect of sugar concentration on nectar feeding by a particular organism is analysed by taking a fixed dP/dl, which is characteristic of the nectarivore and is independent of sugar concentration. Similarly, for non-steady state conditions the dependence of sugar flux on concentration can be analyzed by considering a fixed range of dP/dl. This is well exemplified by considering the slow penetration of liquid into a circular capillary tube induced by a fixed pressure difference ΔP; in this case the fixed range of dP/dl corresponds to a fixed range of l. The Washburn (1921) equation describes approximately the relation between ΔP and the meniscus speed u,

$$u=\frac{r^2\,\Delta P}{8\,\mu l}, \qquad \text{A-2}$$

where l is the length of liquid penetration. This constitutes a generalization of Kingsolver and Daniel's (1983) analysis for a fixed l; in contrast with their analysis, limited to capillarity, Eq. (A-2) is valid for all types of driving potentials. As u is also equal to the mean speed of the fluid, the instantaneous flow rate Q is simply u (πr^2), which is precisely equal to the rate of steady state laminar flow through a circular tube (Eq. A-1). Noting that u is simply dl/dt, and taking $l=0$ initially, Eq. (A-2) can be integrated to yield:

$$l^2=\frac{r^2\,t_f\,\Delta P}{4\,\mu}. \qquad \text{A-3}$$

The nectar flux $\bar{Q}$ averaged over the duration of the flow period, t_f, can be obtained from the instantaneous flux Q, which equals $\pi r^2\,\frac{dl}{dt}$.

$$\bar{Q}=\frac{1}{t_f}\int_0^{t_f} Q\,dt=\frac{\pi r^3}{2}\left(\frac{\Delta P}{\mu t_f}\right)^{1/2}. \qquad \text{A-4}$$

As expected, nectar flux decreases with time because the effective pressure gradient driving flow decreases as one moves over the liquid penetration distance l. To satisfy the fixed $\Delta P/l$ constraint, t_f must satisfy Equation A-3, which leads to

$$\bar{Q}=\frac{\pi r^4\,\Delta P}{4\,\mu l}, \qquad \text{A-5}$$

which is exactly twice the steady state fluid flux driven by a pressure gradient $\Delta P/l$ through a circular cylinder. Hence it is clear that the dependence of the mean sugar flux on S/μ applies for both steady flow and for this type of non-steady flow; such flows are termed here effectively-steady flows. This result can be extended, for example, to the "start-up" flow in a circular tube (Bird et al. 1960) and probably to all other unsteady flows involving fixed nectar volumes, because for these problems time invariant dP/dl is simply replaced by a properly averaged effective value.

The first order expression for the average sugar flux $\bar{E}$ for effectively-steady flows, as a function of sugar concentration S, can thus be written as:

$$\bar{E}=\bar{Q}\rho S=K\frac{S}{\mu}, \qquad \text{A-6}$$

where K, which includes characteristics of the feeding apparatus, nectar density, and pressure gradient, is independent of concentration.

$$K=\alpha\rho\,\frac{d}{dl}\,[\rho gZ+(m_n-m_f)+(\sigma_n-\sigma_f)+(o_n-o_f)]. \qquad \text{A-7}$$

Sugar flux is maximal when $d\bar{E}/dS=O$. Using this condition, together with A-6, leads to the following simple equation for S_m, the sugar concentration that will maximize the average sugar flux:

$$S_m=\mu\left(\frac{d\mu}{dS}\right)^{-1}. \qquad \text{A-8}$$

This relation indicates that the maximum flux concentration S_m depends only on viscosity and its variation with concentration, regardless of the details of feeding.

The analysis is readily extended to calculate the optimal sugar concentration for cases where foraging transit costs are significant. It is convenient to express all transit and feeding costs as time equivalents, such that cost per unit time of transit is directly comparable to that of feeding. Sugar intake can then be averaged over the sum of the effective transit time t_t and effective feeding time t_i to yield:

$$\bar{E}^*=\frac{v\rho S}{t_t+t_i}, \qquad \text{A-9}$$

where v is the volume of nectar ingested. It is reasonable to assume that t_i, which includes all feeding costs, is proportional to the time period t_f during which nectar is ingested. For effectively-steady flows, t_f, and hence t_i, scale with viscosity μ [e.g. Eq. (A-3)]. The optimal sugar concentration S_o is calculated by setting $d\bar{E}^*/dS=0$, which yields

$$S_o=\frac{(1+C)\,\mu}{d\mu/dS}, \qquad \text{A-10}$$

where the relative cost ratio C equals t_t/t_i. Note that for negligible transit costs $C=0$ and A-10 reduces to A-8, thereby rendering $S_o=S_m$. Thus, it is apparent from Eq. (A-10), which is illustrated in Fig. 5, that the benefit/cost ratio is maximized for sugar concentrations S_o that depend only on viscosity and its variation with concentration, and on the relative cost ratio. To evaluate this quantitatively, the transit and feeding costs, which can be numerous and diverse, must be expressed in comparable terms such as in time or energy.

Although results of the effectively-steady model presented here have been shown to converge with those of Kingsolver and Daniel's non-steady fixed-volume flow model, they contrast with those they derive for non-steady feeding constrained to arbitrary time periods. They show that the nectar flow rate averaged over a flow period of fixed duration scales with $\mu^{-1/2}$ [as can be seen in Eq. (A-4)]. This contrasts with the μ^{-1} dependence characteristic of both steady state and non-steady fixed volume models [seen in Eq. (A-5)], and gives rise to a different relationship between energy flux and sugar concentration. Applying a time limitation on feeding for all sugar concentrations requires that amounts of nectar ingested decrease with increasing concentration. This constitutes a constraint distinct from the fixed dP/dl constraint used in this paper for both steady and non-steady state flows, and leads to different results. The apparent difference in the models represented by Eq. (A-4) and (A-5) must be interpreted with caution, however, because the sugar fluxes are identical when expressed in common and comparable terms.

D. Temperature effects. The maximum flux concentration S_m can be shown to vary only slightly with temperature by explicitly considering the temperature dependence of nectar viscosity, approximated adequately by a simple Arrhenius expression (Bird et al. 1960)

$$\mu=\mu_o \exp\left(\frac{\Delta F}{RT}\right), \qquad \text{A-11}$$

where μ_o is a viscosity coefficient dependent on composition, generally taken to be independent of temperature. ΔF is the activation energy for viscous flow essentially independent of concentration, R is the gas constant and T is the absolute temperature. By substituting A-11 in A-8, it is clear that the temperature-dependent viscosity term *exp* $(\Delta F/RT)$ cancels out. Therefore, despite the exponential decrease in viscosity with increasing temperature (A-11), the maximum flux concentration is virtually temperature independent. The independence is not complete, however, because μ_o varies slightly with temperature (Barber 1966) and induces a slight shift in S_m (Fig. 3).

E. Flower inclination effects. Flower inclination also may influence S_m as seen by refining the analysis of Eq. A-1. The terms in parenthese in A-1 representing non-gravitational contributions to the driving potential can be conveniently grouped as dP_o/dl to express sugar flux $\bar{E}$ as follows:

$$\bar{E}=\frac{\alpha\rho S}{\mu}\left(\rho g \sin\beta+\frac{dP_o}{dl}\right), \qquad \text{A-12}$$

where β is the flower inclination; $\beta=0$ when the flower is horizontal and increases as the flower tilts downward ($\sin\beta=dZ/dl$). The maximum sugar flux can be obtained directly by setting $d\bar{E}/dS=0$ and by assuming now that density ρ, as well as viscosity μ, are the only parameters that vary significantly with concentration. Solving for the concentration S_m where sugar flux is maximal yields:

$$S_m=\frac{\mu}{\frac{d\mu}{dS}-\frac{\mu}{\rho}\frac{d\rho}{dS}\left(\frac{\rho g\sin\beta}{\rho g\sin\beta+dP_0/dl}+1\right)}. \qquad \text{A-13}$$

Note that $\sin\beta$ is positive for pendulous flowers, and that because nectar density increases with concentration, $d\rho/dS$ is also positive. A-13 implies that as a pendulous flower hangs more steeply, the denominator would decrease because of an increase in the term in parentheses. Thus, S_m would increase with $\sin\beta$. It follows, therefore, that the optimum concentration would tend to be lower for upright flowers and higher for pendulous flowers. In cases where gravity negligibly affects nectar intake, A-13 is simplified by letting $g=0$, which yields:

$$S_m=\frac{\mu}{\frac{d\mu}{dS}-\frac{\mu}{\rho}\frac{d\rho}{dS}}. \qquad \text{A-14}$$

For negligible variation in nectar density with concentration $d\rho/dS$ can be set to zero and A-14 then reduces to A-8.

F. Energetic costs of ingestion are negligible. As Kingsolver and Daniel (1979) have pointed out, the net energy benefit to a nectarivore, the key element in the energetics of nectar feeding, is the *difference* between the rates of energy intake and of energy spent drawing in nectar. This energy cost will now be evaluated. Although the precise mechanisms of nectar intake are not generally well understood, the energy required for ingestion can be estimated adequately.

Considering a unit time and ignoring energy expenditures unrelated to sugar concentration in nectars, the net energy gain is:

$$E_{\text{net}}=E_{\text{in}}-E_{\text{mech}}, \qquad \text{A-15}$$

with E_{in} being the energy equivalent of nectar ingested and E_{mech} the energy cost of ingesting this nectar due to viscous resistance (Kingsolver and Daniel 1979). According to Ewald and Williams (1982), a typical ingestion rate is 17 ± 3 μl/s for *Calypte anna* feeding on a 20% sucrose solution. This corresponds to approximately $E_{\text{in}}=60$ J/s, using 1.6×10^4 J/g for the caloric value of sugar in nectar (Heinrich 1975, p 141). It is worth noting that although nectar may flow passively up a hummingbird tongue due to surface tension, as suggested by Kingsolver and Daniel (1983), the ultimate source of energy for ingestion must be the hummingbird. The work required to empty the tongue and to transport nectar to the crop is likely to scale as E_{mech}.

To estimate conservatively the energy expended on taking in nectar, the flow of nectar in the grooves of a hummingbird tongue is modeled as flow in a cylindrical conduit of equivalent cross-sectional area. The energy dissipated per unit time for a viscous fluid moving in a conduit is

$$E_{\text{mech}}=(\bar{Q})\ (\Delta P)\ \eta, \qquad \text{A-16}$$

where $\bar{Q}$ is the fluid flux, ΔP is the driving potential, and η is the effective muscular efficiency (Kingsolver and Daniel 1979). For effectively steady laminar flow in a cylindrical conduit of equivalent radius r and length l,

$$\Delta P=\frac{8\,\mu l\,\bar{Q}}{\pi\,r^4}, \qquad \text{A-17}$$

where μ is the nectar viscosity. Combining Eq. A-16 and A-17 yields:

$$E_{\text{mech}} = \frac{8\,\mu l\,\bar{Q}^2\,\eta}{\pi\,r^4}. \qquad \text{A-18}$$

Reasonable values for the relevant parameters are: μ is 2.0 cp (centipoise = g/m-s) for a 20% solution at 20° C; l is 11 mm and the mean effective radius is 0.11 mm on the basis of Hainsworth's (1973) measures of the grooves in a hummingbird tongue; $\bar{Q} = 17$ µl/s (Ewald and Williams 1982), and η is of order unity. Substitution of these values in A-18 yields a value for the energy required to ingest nectar per unit time on the order of 5×10^{-5} J/s, about one million times smaller than, and hence negligible relative to the energy benefit of 60 J/s for hummingbirds. It is clear, therefore, that maximizing E_{in} for hummingbirds is equivalent to maximizing E_{net}. It is worth stressing that if nectar flows into the feeding conduit through a lateral slit, as in the twin grooves on hummingbird tongues, the energetic costs of this nectar intake would be even less than estimated above.

The energetic cost of nectar intake could approach the order of magnitude of the energetic reward only for nectarivores with a $\bar{Q}^2/r^4$ ratio at least ten thousand times larger than the value used here for hummingbirds ($\bar{Q}^2/r^4 = 2\ \text{m}^2\ s^{-2}$). This would imply organisms with an r less than 10 µm or $\bar{Q}$ greater than 1.7 ml/s, taking the complementary variable to have the values used here for hummingbirds.

In conclusion, the rate of net energy gain associated with nectar flow for most if not all nectar feeders will effectively equal the rate of energy intake.

Appendix 2

Chemical and physical properties of nectars from hummingbird pollinated flowers

Each group of numbers includes: mean, followed by sample size (n) in parentheses (upper); range (middle); and standard deviation (lower). " – " indicates constituent is not detectable

Plant species	% sugar (wt/wt)	Viscosity (cp, @ 15° C)	Relative sugar flux (S/μ)	Nectar μ-suc. soln. μ (cp)	pH	Volume (µl)
(1) *Campsis sp*	23.2 (11) 16–32 5.8	2.8 (5) 1.9–3.8 0.8	7.9 (5) 5.5–9.3 1.3	0.2 (5) −0.1–0.8 0.3	6.8 (11) 6.2–7.1 0.3	4.7 (5) 3–8.9 2.2
(2) *Castilleja integrifolia*	33.4 (14) 23–41.5 5.4	5.4 (6) 4.3–7.3 1	6 (6) 4.9–7.2 0.7	1.1 (6) 0.3–1.8 0.5	6.1 (10) 5.6–6.2 0.2	1.6 (27) 0.05–3.2 1.0
(3) *Castilleja tenuiflora*	41.6 (16) 28–56 9.8	19.7 (6) 2.9–33.5 11.8	4.1 (6) 1.6–8.9 3.2	1.2 (6) −3.2–5.1 2.9	6.4 (10) 6–6.8 0.2	2.9 (14) 0.5–7.1 1.6
(4) *Leonotus nepetaefolia (?)*	16.1 (14) 12–18.3 1.5	3.4 (5) 3.3–3.6 0.1	4.6 (5) 4.4–4.7 0.1	1.6 (5) 1.4–1.6 0.1	5.7 (14) 5.6–5.8 0.1	4.7 (12) 3–5.9 0.8
(5) *Lobelia laxiflora*	23.1 (8) 19–27 2.6	3.2 (8) 2.3–3.9 0.5	6.7 (8) 5.2–9 1.2	0.9 (8) 0–1.6 0.5	5.9 (10) 5.6–6.5 0.3	28.8 (16) 0–45 14.1
(6) *Loeselia mexicana (?)*	29.9 (7) 21–35.8 5.2	4.6 (8) 2.4–6.2 1.3	6.8 (8) 4.9–9 1.2	0.7 (8) −0.4–2.3 0.8	5.9 (5) 5.7–6.1 0.1	1.1 (20) 0.3–2.8 0.5
(7) *Salvia fulgens*	24.1 (9) 20–28 2.2	3.2 (4) 3.1–3.5 0.2	6.7 (4) 6.4–7.1 0.3	0.8 (4) 0.6–1 0.1	5.6 (3) 5.6–5.7 0.1	23.2 (7) 7.2–45 15
(8) *Salvia iodantha*	25.3 (12) 21–29 2.1	3.2 (9) 2.8–3.8 0.3	7.6 (9) 7.1–7.9 0.3	0.4 (9) 0.2–0.6 0.1	5.8 (12) 5.6–6.5 0.3	2.1 (24) 0–4.1 1.2
(9) *Salvia* sp	28.7 (9) 23–31 2.8	4 (3) 3.2–5.1 0.8	6.5 (3) 6.2–6.7 0.2	0.9 (3) 0.8–0.9 0.04	5.8 (6) 5.7–5.9 0.1	12.6 (3) 12.2–13.1 0.4
(10) acanthaceae	30.6 (8) 29–32 0.9	3.5 (8) 2.7–4.2 0.4	8.2 (8) 6.9–10.2 1	0.4 (8) −0.6–3.3 1.1	5.8 (7) 5.6–6.1 0.2	1.6 (14) 0.3–3 0.8
Mean of above 10 species	27.6 16.1–41.6 6.9	5.3 2.8–19.7 5.1	6.5 4.1–8.2 1.3	0.8 0.2–1.7 0.4	6.0 5.6–6.8 0.4	8.3 1.1–28.8 10.0

Appendix 3

Definitions of symbols

C	relative transit cost; t_t/t_i
$\bar{E}$	sugar flux averaged over duration of flow period t_f
$\bar{E}^*$	benefit to cost ratio; sugar intake divided by sum of effective feeding period t_i and effective foraging transit period t_t
E_{in}	energy equivalent of nectar ingested
E_{mech}	energetic cost of ingesting nectar due to viscous resistance
E_{net}	net energy gain from ingesting nectar
ΔF	activation energy for viscous flow
g	gravitational constant
h	timed distance traversed by nectar in vertical capillary
l	distance in the flow direction
m	pressure induced by muscular contractions
o	osmotic pressure
ΔP	pressure differential inducing nectar flow; may include suction, gravity, capillarity, and osmosis
P_o	pressure differences induced by muscular contractions, by surface energy, and/or by osmosis; $P_o=(m_n-m_f)+(\sigma_n-\sigma_f)+(o_n-o_f)$
Q	instantaneous or steady state fluid flux
$\bar{Q}$	fluid flux averaged over duration of flow period t_f
R	gas constant
r	internal radius
S	sugar concentration (% sucrose equivalents on a weight to weight basis)
S_m	maximum flux concentration; concentration for which sugar flux $\bar{E}$ is maximal
S_o	optimal sugar concentration; concentration for which benefit to cost ratio $\bar{E}^*$ is maximal
s	separation between two parallel plates
T	absolute temperature
t	time
t_d	nectar descent time
t_f	duration of nectar flow period
t_i	time equivalent of total feeding costs, such that cost per unit time of feeding is directly comparable to that of transit
t_t	time equivalent of total transit costs, such that cost per unit time of transit is directly comparable to that of feeding
u	meniscus speed
v	volume of nectar ingested
Z	elevation drop along the nectar flow path
subscript $_n$	conditions in nectar pool

	Proportion sugars				Ratio S/G+F	Amino acids (mM)	Lipids (mg/ml)	Proteins (mg/ml	Phenols[a] (brightness)	Alkaloids[a]
n	SUC	GLU	FRUC	others						
1:	11	35	51	3	0.1		−(1)	−(1)	+++(1)	−(1)
8:	56	8	28	8	1.7	0.43 (11)	−(3) and 4 (3)	−(6)	++(3) and +++(4)	−(7)
	35–73	5–15	19–41	2–12	0.6–2.9	0.1–0.9				
	10	3	7	3	0.7	0.3				
1:	55	8	28	9	1.5			−(1)	+++(1)	−(1)
3:	31	29	36	4	0.5	0.5 (2)	−(2)	−(2)	++(2) and +++(1)	−(3)
	14–36	26–33	28–42	0–11	0.2–0.8	0.4–0.6				
	13	3	6	5	0.3	0.1				
9:	56.5	5.5	36.5	1.5	1.4	0.16 (12)	−(7)	−(11)	−(2) and +(2) and ++(4) and +++(1)	−(9)
	49–66	2–14	27–44	0–4	1–1.9	0–0.4				
	6	3	6	1.3	0.3	0.12				
1:	37	27	36	–	0.6	3.5 (2)	−(1)	0.075 (1)	++(2)	−(2)
						2.3–4.7				
						1.2				
4:	69	7	21	3	2.5	0.28 (6)	−(3)	−(3)	−(2) and +(1)	−(3)
	65–74	2–20	11–27	1–5	2.1–3.1	0–0.8				
	3	7.5	6	1.6	0.4	0.3				
9:	53	18	27	2	1.2	0.25 (10)	−(7)	−(6)	−(3) and ++(4)	−(7)
	41–60	14–21	21–39	0–4	0.7–1.6	0.1–0.8				
	6	2	5	1	0.3	0.2				
4:	57	8.5	31	3.5	1.5	0.31 (6)	−(3)	−(4)	−(2) and ++(1)	−(3)
	50–67	4–13	25–41.5	0–5.5	1–2.3	0–0.8				
	6	3	6	2	0.5	0.2				
3:	52	20	26	2	1.1	0.23 (3)	−(1)	−(1)	++(2)	−(1) and trace? (1)
	45–55	19–23	22–33	0–3	0.9–1.3	0.2–0.3				
	5	2	5	1.4	0.2	0.05				
	48	16.5	32	3.5	1.2	0.71 (8)	1 of 9	1 of 9	9 of 10	1? of 10
	11–69	7–35	21–51	0–9	0.1–2.5	0.2–3.5				
	17	11	8	3	0.7	1.1				

[a] Relative abundances are indicated as follows: − = not detectable, and + to +++ = present, as indicated by increasing intensity of the test reaction. Sample sizes are indicated in parentheses

subscript $_f$	conditions in mouth of nectar feeder
α	constant based on conduit size and geometry
β	flower inclination
K	proportionality factor representing geometry of feeding apparatus and mechanism driving nectar flow
η	effective muscular efficiency
μ	dynamic viscosity of nectar
μ_o	viscosity coefficient dependent on nectar composition and relatively independent of temperature
ρ	nectar density
σ	pressure induced by surface tension

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