

Scaling of Nectar Foraging in Orchid Bees

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ABSTRACT: Morphology influences the rate at which foraging bees visit nectar flowers, the quantity of nectar they must consume to fuel their activities, and, consequently, the profitability of flower species. Because feeding time is a major determinant of visitation rate, I used a biomechanical model to examine how energy intake rate (E) varies with sucrose concentration, body mass (M), and proboscis length in orchid bees (Apidae: Euglossini). Under geometric scaling, the optimal sugar concentration (S_{\max}) should be largely independent of body size, and $E \propto M^{1.0}$. In a comparative study of 30 orchid bee species ranging from 50 to 800 mg, S_{\max} fell between 35% and 40% w/w, but $E \propto M^{0.54}$, significantly less than model predictions. Proboscis length and radius scale geometrically with body mass, but proboscis length exhibits substantial size-independent variation, particularly in small bees. One cost of a long proboscis is a reduction in both E and S_{\max} in accordance with the scaling model. This finding highlights a difference between the lapping mechanism used by bumblebees and the suction mechanism used by orchid bees. A field study confirms that orchid bees harvest nectars with between 34% and 42% sucrose, independent of body size.

Keywords: scaling, biomechanics, viscosity, Apidae, euglossini, proboscis.

Numerous insects fuel their daily activities by consuming floral nectars, and they imbibe these viscous fluids through a long, slender proboscis (Krenn et al. 2005). Whereas the diverse shapes and sizes of these mouthparts represent the evolutionary outcomes of historical contingency and ecological adaptation (Wiklund et al. 1979; Gilbert 1985; Harder 1985; Wasserthal 1993; Corbet 2000; Borrell 2005), the function of these structures is governed by a few physical principles (Kingsolver and Daniel 1995). Energy intake

rate during feeding may influence foraging efficiency (Wolf et al. 1972; Heinrich 1975; Whitham 1977; May 1988) and, potentially, reproductive fitness (Hainsworth et al. 1991). Accordingly, examining functional consequences of morphological variation will improve our understanding of the evolution of pollinator communities.

The radius and length of the proboscis, the mechanics of the suction pump, and the viscosity of floral nectars contribute to the energy intake rate during nectar feeding (Daniel et al. 1989). Owing to the effects of viscosity, intermediate sugar concentrations maximize energy intake rates (fig. 1; Baker 1975; Daniel et al. 1989). Much work has focused on elucidating the shape of this energy intake function and the value of this optimal nectar concentration within a single species (May 1985; Pivnick and McNeil 1985; Boggs 1988; Josens and Farina 2001). Over an evolutionary timescale, variation in morphology will influence both absolute values of energy intake rate and the position of this optimal nectar concentration. However, no study has addressed these predictions in a phylogenetic comparative framework.

Daniel et al.'s (1989) model of suction feeding makes two fundamental predictions about the influence of body size and tongue length on nectar feeding. The first prediction is that energy intake rates for all suction-feeding insects will be maximized when consuming nectars with sugar concentrations between 30% and 40% w/w sucrose and that this maximum will be largely independent of body size and morphology. The second prediction relates to the hypothesized cost of evolutionary increases in tongue length. The Hagen-Poiseuille equation predicts that the resistance to fluid flow is directly proportional to proboscis length. Insects with a long proboscis must compensate through changes in the radius of the proboscis or the size of the suction pump. Alternatively, they must bear this cost through a decrease in their rate of energy intake during feeding. While Daniel et al.'s (1989) model incorporates the Hagen-Poiseuille equation, compensatory properties of the suction pump should reduce the effects of proboscis morphology on nectar flow rates.

Neotropical orchid bees (Apidae: Euglossini) range over an order of magnitude in body mass from 50 to 1,000 mg and possess an equally impressive range of tongue lengths:

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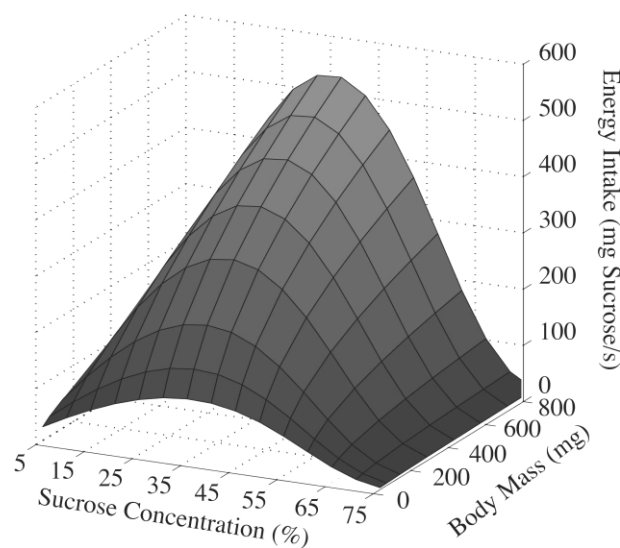


Figure 1: Predicted isometric scaling of energy intake rate with body mass at sucrose concentrations from 5% to 75%. In this simulation, muscle parameters are held constant as the proboscis and suction pump scale according to geometric similarity (case 2).

from 10 to more than 40 mm (Roubik and Hanson 2004). In this study, I measured intake rates for 30 species of euglossine bees feeding from unlimited nectar reservoirs and analyzed the relationship among body mass (M), tongue length (L), and energy intake rate (E) by using phylogenetically independent contrasts. In addition, I extracted crop contents from 25 species of euglossine bees to estimate the sugar concentration and intake rate of these bees in nature to partition morphological and habitat-related influences on nectar-foraging behavior.

General Model of Nectar Intake

The nectar-feeding apparatus of suction-feeding insects may be divided into two components: the elongate proboscis and the suction pump. The flow rate in the proboscis, Q (m^3/s), depends on the radius, R (m), length, L (m), and viscosity, μ ($\text{Pa} \times \text{s}$), of nectar:

$$Q = \frac{\pi R^4 P}{8\mu L}, \quad (1)$$

where P (Pa) is the driving pressure gradient (Daniel et al. 1989). The expansion of the suction pump or pumps produces this pressure gradient. Bees have a single suction pump, the cibariopharyngeal chamber (henceforth, cibarium), which is expanded via a group of pump dilator muscles that attach to the clypeus and frons on the interior

dorsal surface of the head (Paul et al. 2002). In contracting muscle, the force of contraction, F_{muscle} (N), is inversely proportional to the shortening velocity, V (m/s), as described by the Hill equation (Hill 1938). We can use this relationship to calculate the pressure gradient produced by the suction pump by dividing F_{muscle} by the cross-sectional area of the cibarium, A_{cib} (m^2):

$$P = \frac{F_{\text{muscle}}}{A_{\text{cib}}} = \frac{T_0(V_{\text{max}} - V)}{A_{\text{cib}}(V_{\text{max}} + 4V)}, \quad (2)$$

where T_0 is the maximum isometric tension of the pump dilator muscle (N) and V_{max} is the maximum shortening velocity (m/s). Because the rate of flow into the cibarium must equal the rate of volume change in the cibarium chamber, we can substitute equation (2) into equation (1) to produce a general expression for the mechanics of suction feeding:

$$Q = \frac{\pi R^4 [T_0(V_{\text{max}} - Q/A_{\text{cib}})]}{8\mu L [(A_{\text{cib}}(V_{\text{max}} + 4Q/A_{\text{cib}}))]}, \quad (3)$$

The solution to this quadratic equation was presented by Daniel et al. (1989). Energy intake rate during feeding, E (W), is

$$E = eS\rho, \quad (4)$$

where e is the energy equivalent of nectar, 15.4 J/mg, S is sucrose concentration (% w/w), and ρ is nectar density (kg/m^3). The value of S that maximizes E is termed S_{max} .

Material and Methods

Scaling of Model Parameters

The most fundamental null scaling model is that of geometric similarity, where organisms are simply scaled versions of one another: linear morphological variables scale as $M^{1/3}$, areas as $M^{2/3}$, and volumes as M^1 (LaBarbera 1989). Alternatively, organisms may scale allometrically, where relative sizes of component parts change with body size, owing to ontogenetic constraints or functional demands. Because it was not obvious how muscle parameters should scale with body size, null scaling predictions for E and S_{max} were estimated from simulations under three cases (table 1): geometric scaling of the proboscis only (case 1), geometric scaling of the proboscis and pump volume (case 2), and geometric scaling of the proboscis, pump volume, and pump musculature (case 3). The first two simulations may be considered allometric because the relative size of the component parts of the nectar-feeding system vary with body size, while the third case is an example of geo-

Table 1: Summary of the results from simulations for the scaling of energy intake rate as a function of body mass (50–750 mg), proboscis length (5–25 mm), or proboscis radius (0.02–0.1 mm)

Case	Simulation	Model	b (35%)	S_{\max}
1	Allometric	Proboscis only	.50	32% \Rightarrow 42%
2	Allometric	Proboscis and pump	.56	37%
3	Geometric	Proboscis, pump, and muscle	.97	36% \Rightarrow 39%
4	Proboscis	Length change	-.56	36% \Rightarrow 32%
5	Proboscis	Radius change	2.12	27% \Rightarrow 47%

Note: The scaling exponent, b , is provided for a 35% sucrose solution, along with the predicted shift in the optimal nectar sugar concentration, S_{\max} . Model estimates were derived using values for V_{\max} and A_{muscle} , which provide the best fit to the observed data. Arrows indicate the shift in S_{\max} with increasing body size.

metric scaling. Muscle parameters were estimated by minimizing the sum-of-squares error between each model and the data. Under case 3 scaling, in which the suction pump scales with body size, it was assumed that $V_{\max} \propto M^{-0.12}$, while P_0 was held at 8 kPa (Medler 2002).

Two simulations were conducted to examine the effects of independently varying proboscis length from 5 to 25 mm and radius from 0.03 to 0.09 mm (table 1, cases 4 and 5). To develop null predictions of regression coefficients of M and L , a full factorial multiple regression model was fitted to data simulated from actual species body masses and tongue lengths. After eliminating nonsignificant interaction terms, these regression coefficients could be estimated.

Study Sites and Organism. Male bees were captured at chemical baits of cineole, skatole, methyl salicylate, eugenol, and vanillin at field sites throughout Costa Rica (table A1 in the online edition of the *American Naturalist*) and Panama (Barro Colorado Island, Pipeline Road, in Soberania National Park, Altos de Campana National Park, and Nusagandi Biological Station in the Kuna Yala Province). Intake rate was recorded for 751 individuals in 30 species between June 2002 and June 2004 (fig. 2). An additional 663 individuals in 25 species were captured at these same field sites for measurements of sucrose concentration and volume of crop nectars. All individuals were identified to species, except the sister species *Eulaema meriana* and *Eulaema bombiformis*, which were combined in this analysis, owing to difficulties in distinguishing these bees in the field. *Eulaema meriana* is about 80% as massive as *E. bombiformis* (Darveau et al. 2005) and three to four times more common (Roubik 2001).

General Feeding Methodology. Immediately following capture, bees were transported to a shaded, screened enclosure for feeding trials. Bees were maintained in this enclosure until they depleted nectar stores such that they were willing to consume artificial nectars. Nectar intake rate was mea-

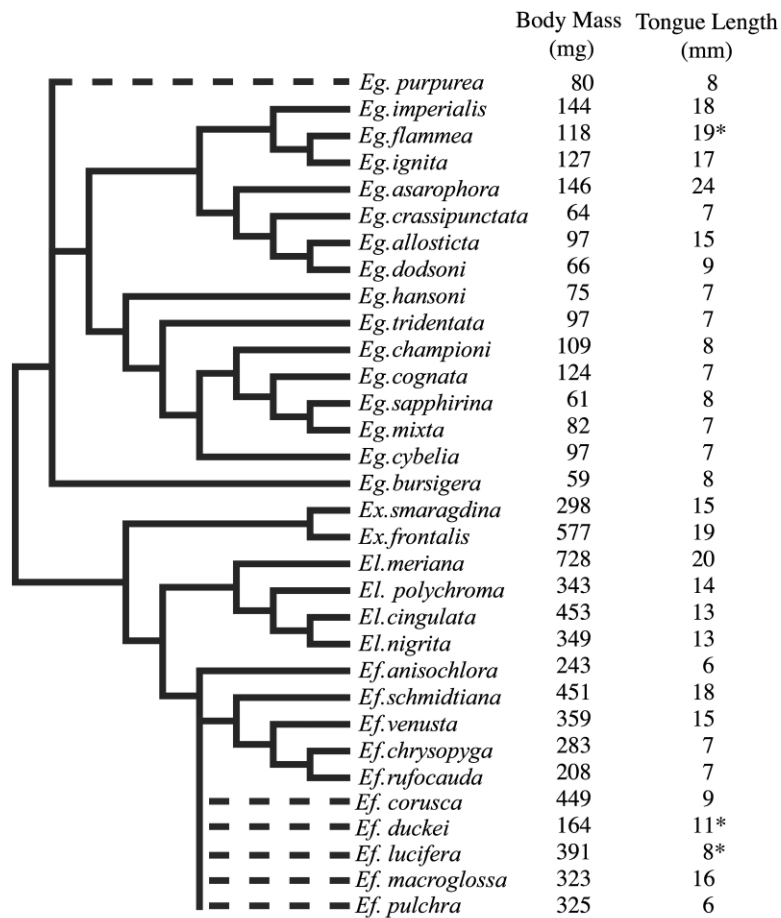
sured via standard methods (Borrell 2004). In short, the mass gain of the bee (± 1 mg) was divided by the time spent feeding. Nectar solution temperature was controlled between 27.5° and 32.5°C by warming it before and during feeding trials using a 15-W halogen lamp or a hot-water bath. Ambient temperature could not be controlled, and only trials in which ambient temperature was within 2°C of the experimental nectar solution were included in these analyses.

Following each trial, folded tongue length, body length, and wing length of each bee were measured to ± 0.01 mm using digital calipers. Mean proboscis radius was estimated from digital images of proboscis components from 11 species. Extended tongue lengths for all bee species were obtained from Roubik and Hanson (2004), except that of *Eufriesea macroglossa*, which was measured by the author. For three species, folded tongue length was estimated from extended tongue length using a linear regression.

Head dimensions (width and height) and clypeus width, height, and breadth were measured for 20 species of bees. Clypeus volume (in arbitrary units) was calculated as width \times height \times breadth. Clypeus volume is directly related to the size of pump musculature in the Homoptera (Novotny and Wilson 1997), but because pump dilator muscles in bees also have attachments on the frons, the correlation is less clear (Paul et al. 2002).

Nectar Foraging in Nature

Nectar stored in a bee's crop is not diluted or modified in any way (Blatt and Roces 2002) and should be representative of nectars actually collected during foraging (Roubik et al. 1995). Nectar was extracted into 25- or 100- μ L capillary tubes by gently squeezing abdomens of bees arriving at chemical baits at six study sites in Costa Rica (table A1). For examination of allometric trends, additional data were collected at Cerro Campana, Panama (600–800 m), where *Eufriesea* are abundant in the early wet season. Digital calipers were used to estimate the vol-



*Estimated from Roubik and Hanson (2004)

Figure 2: Phylogenetic relationships among 32 species of euglossine bees used for nectar-feeding experiments or morphological measurements. Character values presented for body mass (mg) and tongue length (mm). Extended tongue length is about twice these tongue length measurements.

ume of the nectar column in the capillary tube, and equivalent sucrose concentrations were determined using a temperature-corrected pocket refractometer (0%–62%; samples >62% were diluted). Floral nectars collected by long-tongued bees are sucrose dominant, but they often contain a significant fraction of fructose and glucose (Baker and Baker 1983). Additionally, owing to the presence of amino acids in floral nectars, refractometer readings may be several percentage points higher than true sugar concentrations (Inouye et al. 1980) and are correlated with the slight increase in viscosity of floral nectars as compared with pure sucrose solutions (Heyneman 1983). Nectar energy, E_{crop} , was calculated from nectar volume and sucrose concentration. Elevation was recorded using a barometric altimeter, and air temperature, T_{air} , was recorded using either a handheld thermocouple or a mercury thermometer shielded from direct sunlight.

Statistical Analysis of Species Data

Raw data were preprocessed in Matlab (MathWorks 2004) to calculate species means for parameters of interest. Allometric slopes were estimated in JMP (SAS Institute 2001) using ordinary least squares (OLS) regressions of log-transformed variables. Because OLS minimizes the sum-of-squares error in the dependent variable (i.e., energy intake), error in the measurement of the independent variable (i.e., body mass) leads to an underestimate of the functional slope (McArdle 2003). Reduced major axis has been championed in the scaling literature (LaBarbera 1989), but it requires the improbable assumption that the error variance ratios (both measurement error and equation error) of the dependent and independent variables be equal (McArdle 2003). Carroll and Ruppert (1996) recommend using the method of moments estimator (MM)

to correct the OLS slope for attenuation because it requires only an estimate of measurement error. The MM for interspecific regressions on body mass can be estimated by comparing intraspecific variance in body mass (error variance, EV) with interspecific variance in body mass (total variance, TV). For the euglossine bee data set, $MM = TV/(TV - EV) = 7,483/(7,483 - 225) = 1.031$. Thus, conventional OLS regression slopes presented throughout this article should be revised upward by 3.1% to compensate for measurement error in body mass. Unfortunately, this technique cannot readily be applied to independent contrasts, although it may be feasible in the future through the use of a phylogenetic ANOVA or some other simulation method (Garland et al. 1993).

A multiple regression approach was employed to analyze the effects of sucrose concentration and the possible interaction between sucrose concentration and body mass on *E*. The null hypothesis of isometry was tested by comparing 95% confidence intervals of *b* with scaling predictions listed in table 1. Functional equivalence for S_{\max} is achieved if $S_{\max} \propto M^0$. Therefore, a significant interaction between body mass and sucrose concentration indicates that S_{\max} changes with body mass or tongue length. For eight species, nectar intake rate was measured across the entire range of sucrose concentrations, and a species-specific S_{\max} was derived from each of these independent data sets. Thus, an alternative approach to testing tongue length and body mass trends uses these estimates of S_{\max} .

Standardized phylogenetic independent contrasts (PIC) were calculated from the log-transformed character data (Garland et al. 1992). These analyses were conducted using the PDAP module in Mesquite (ver. 1.0; Maddison and Maddison 2003; Midford et al. 2003), incorporating a species-level phylogeny (fig. 2) based on maximum likelihood analysis of *cyt b* sequence information from 36 euglossine species and five outgroup taxa (Darveau et al. 2005). Analyses were also performed using hypothesized trees obtained from other analyses (neighbor-joining, Bayesian, and maximum parsimony), and the results varied by no more than 5%. The phylogenetic placement of *Euglossa purpurea* and four *Eufriesea* species examined in this study are uncertain. Consequently, I calculated *P* values for the relationship between *E* and body mass for the 35% solution using several approaches: 1,000 genus-level phylogenies in which the relationships among lower taxa were randomly resolved, 1,000 phylogenies in which the relationships among *Eufriesea* were randomly resolved, and finally with *E. purpurea* shuffled within the *Euglossa* clade. None of these permutations significantly affects the conclusions of this study. To ensure that branch lengths were adequately standardized, the absolute values of standardized independent contrasts were plotted against their standard deviation (Garland et al. 1992). For visualization

and calculation of *y*-intercepts, independent contrast regression equations were mapped back into the data space of the raw species data using estimates of character data at the root node (Garland and Ives 2000).

Results

Predicted Scaling of Feeding Mechanics

Scaling exponents vary substantially depending on the scaling model, ranging from 0.50 to 1.0 (table 1). Under case 3 scaling, S_{\max} shifts upward slightly with body mass ($S_{\max} \propto M^{0.02}$), while under case 2 scaling, it is independent of body mass ($S_{\max} \propto M^0$). Under case 1 scaling, S_{\max} shifts upward by 10% over the observed body mass range ($S_{\max} \propto M^{0.12}$).

When proboscis radius and length are varied independently of body size, the model predicts intake rate to decline as $L^{-0.56}$ or increase as $R^{2.1}$ (table 1). Using the length-mass covariance structure of the actual data, the case 1 model predicts intake rate to scale as $M^{0.72}$ and $L^{-0.54}$, and S_{\max} should shift up slightly with body mass and tongue length. The case 2 model predicts intake rate to scale as $M^{0.67}$ and $L^{-0.52}$, with S_{\max} shifting down from 36% to 31% sucrose as tongue length increases from 5 to 24 mm. The case 3 model predicts intake rate to scale as $M^{1.11}$ and $L^{-0.52}$. This model predicts significant interactions between all pairs of variables.

Scaling of Feeding Morphology

With the exception of head width, no morphological variable scaled with exponents significantly different from expectations of geometric similarity ($P > .05$; table A2 in the online edition of the *American Naturalist*). However, for both tongue length and extended tongue length, size-independent variation was substantial, particularly for smaller bees (fig. 3). There was no relationship between size-corrected values of tongue length and radius ($P > .05$).

Scaling of Nectar Intake

Energy intake rate depends on both body mass and sucrose concentration (fig. 4; conventional: $R^2 = 0.745$, $F = 89.59$, $df = 3, 92$, $P < .0001$; PIC: $F = 15.05$, $df = 2, 88$, $P < .0001$). Using a conventional OLS regression, energy intake rate scales as $M^{0.55}$ (OLS confidence interval [CI] = 0.47–0.64; MM slope = 0.57). Using PIC, intake rate scales as $M^{0.54}$ (CI = 0.28–0.79). The interaction between body mass and sucrose concentration was not significant ($P > .05$). Thus, case 1 is not supported because S_{\max} does not increase with body mass, and case 3 may be

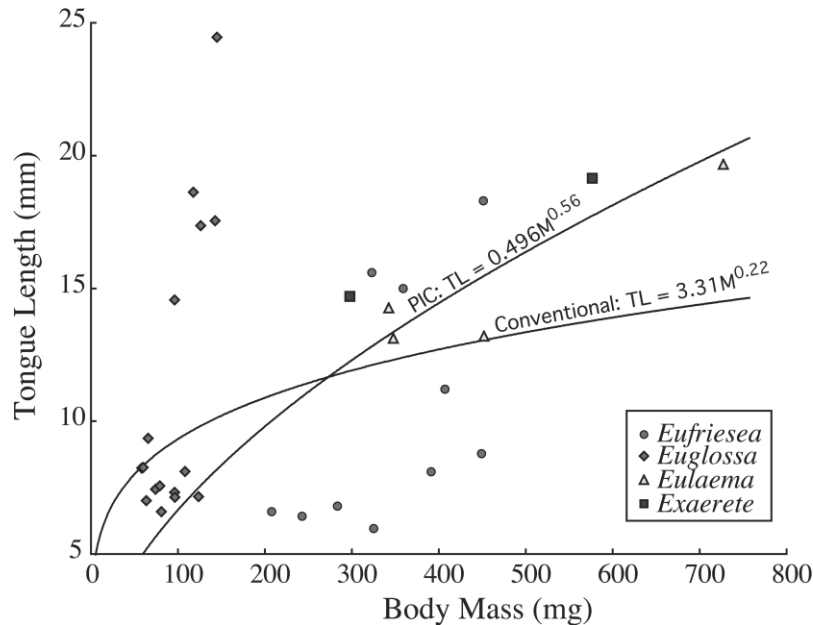


Figure 3: Scaling of tongue length with body mass for 32 species of euglossine bees from 50 to 800 mg. Conventional ordinary least squares (OLS) regression is shown, along with an OLS regression based on phylogenetically independent contrasts (PIC) mapped back into the species data space using a root node estimate of body mass and intake rate.

rejected because the predicted exponent lies outside of the confidence interval for the actual data.

A multiple regression of independent contrasts incorporating sucrose concentration, body mass, tongue length, and all two-way interactions was conducted to test the significance of the hypothesized interactions in the scaling models. Because the interactions between body mass and sucrose and between tongue length and body mass were nonsignificant under all possible models using conventional statistics and PIC ($P > .5$), these terms were dropped. This lack of significance is at odds with predictions of both the case 1 and the case 3 models. Under conventional regression, there was an interaction between tongue length and sucrose concentration, but using PIC, the interaction was not significant ($P = .1043$).

A final model containing the significant parameters was used to estimate scaling exponents (table 2). Using phylogenetically independent contrasts, intake rate scales as $M^{0.67}$, which is again consistent with negative allometry of the suction pump. Intake rate declines as $L^{-0.32}$, which is significantly less than predicted by any of the three models.

Values for S_{\max} could be estimated independently for eight species and range from 31.4% to 42.1% (fig. 5); S_{\max} was not related to body mass ($P > .05$), but I chose to analyze it using both raw values of tongue length and S_{\max} and using residuals from regressions of those variables on body mass. Using both conventional regression and PIC,

S_{\max} declines significantly in both cases ($P < .05$). Values for S_{\max} decline by about 0.6% for an increase in 1 mm of tongue length, which is consistent with predictions from the multiple regression.

Nectar Foraging in Nature

Nectar sugar concentration (NSC) ranged from 5% to 75% sucrose, but half of all observations fell between 33.6% and 41.0% sucrose (fig. 5). Only 10% of observations fell below 29.6% sucrose or above 46.2% sucrose. The distribution of NSC was similar among bees of all body sizes, and there was no support for a trend in mean NSC with body size ($P > .05$).

In the six most widespread bee species, site was a significant predictor of NSC (ANOVA: $F = 8.322$, $df = 4, 384$, $P < .0001$; table A1), but species was not ($P = .3135$). NSC at sites on Pacific slopes was about 5% greater than sugar concentrations at sites on Atlantic slopes (linear contrast: $F = 25.1155$, $df = 1, 384$, $P < .0001$). Monteverde was excluded from this analysis because of low species sampling, but incorporating it only strengthens statistical findings (table A1). Nectar volume and nectar energy increase with body mass with exponents not significantly different from 0.75 or 1 (table A2).

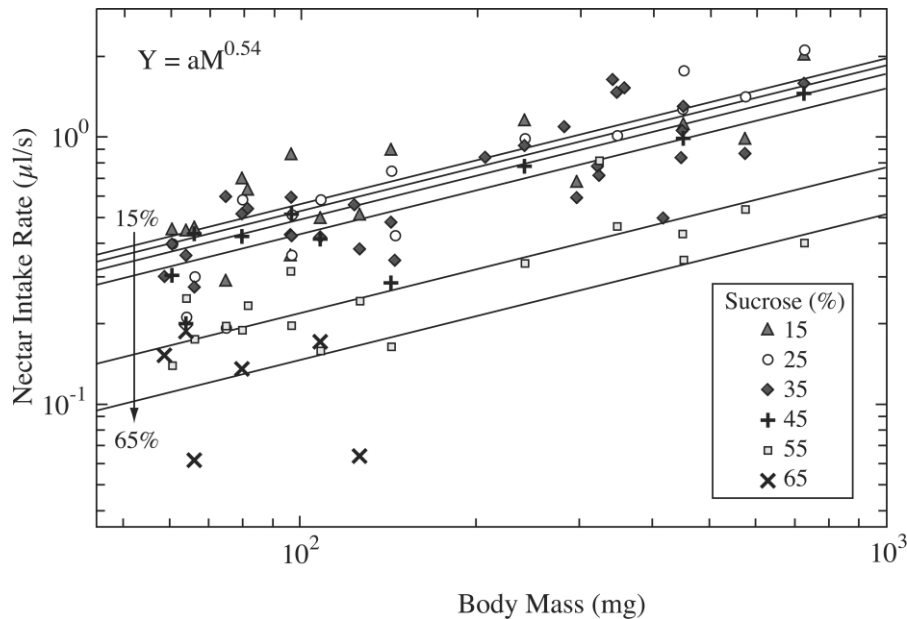


Figure 4: Scaling of nectar intake rate with body mass for 30 species of euglossine bees and six sucrose concentrations. The fitted lines are based on a multiple regression of phylogenetically independent contrasts mapped back into the species data space using root node estimates of intake rate and body mass for each concentration data set. Energy intake rate (E) was transformed to volumetric intake (Q) for graphical clarity.

Discussion

Scaling of Nectar Intake Rate

Insofar as tongue morphology reflects ecological relationships among bees (Inouye 1980; Ranta and Lundberg 1980; Harder 1985), their evolutionary relationships can also be traced through such morphological variation (Michener and Brooks 1984). Bees have traditionally been divided into two functional types: long-tongued bees (Apidae, Anthophoridae, Ctenoplectridae, Fideliidae, and Megachilidae) and short-tongued bees (Colletidae, Oxaeidae, Andrenidae, Halictidae, Melittidae, and Stenotritidae; Harder 1983*b*). Although some short-tongued bees exhibit adaptations for feeding from deep flowers (Laroca et al. 1989), these bees are so named because the distal components of the proboscis (glossa, galeae, and labial palps) are typically shorter than the proximal components (stipes and prementum). The situation is reversed in long-tongued bees, which can have effective tongue lengths of up to 18 mm in the bumblebees and 44 mm in the euglossines.

Morphological differences translate to functional differences in the mechanics of nectar feeding in long- and short-tongued bees. In both bee groups, the glossa reciprocates in order to transfer nectar to the mouth (lapping), but in short-tongued bees, the prementum must rock back and forth in concert with these lapping motions (Harder

1983*b*). Euglossines have experienced a second functional shift in feeding modality: from lapping to sucking (Borrell 2004). In suction feeding, the glossa is completely static, and fluid transport is achieved solely via contraction of the cibarial dilator muscles. Just as the short-tongued condition sets an upper limit to tongue length, the lapping modality may be effective only for bees with tongues shorter than 20 mm. Lapping depends on closely spaced hairs on the glossa, but these hairs will increase the resistance of fluid flow during the suction phase of feeding (Kingsolver and Daniel 1995). If, at longer tongue lengths, the relative contribution of the suction pump exceeds that of mechanical reciprocation, then we may expect an evolutionary reduction in glossal hairs and, ultimately, the loss of lapping.

The magnitude of E within bee groups depends on both tongue morphology and the modality of fluid feeding. Harder (1983*b*) demonstrated that E varies linearly with body mass in short-tongued bees but is exponential in long-tongued bees; E in euglossines is no more than one-fifth of that expected for a lapping, long-tongued bee of similar body size (Harder 1983*b*; Roubik and Buchmann 1984). Moreover, within the Apidae, size-corrected values of E are much greater in the three clades of lappers (Meliponini, Apini, and Bombini) than in suction-feeding Euglossini.

The relative reduction in E observed in euglossine bees

Table 2: Log energy intake rate in 30 species of euglossine bees as a function of log body mass, log tongue length, and sucrose concentration, using both a conventional ANCOVA and an ANCOVA of phylogenetically independent contrasts (PIC)

Effect	Conventional				PIC			
	Coefficient	95% CI	<i>t</i>	<i>P</i>	Coefficient	95% CI	<i>t</i>	<i>P</i>
Intercept	1.11	.91–1.32	10.67	<.0001	Zeroed			
Sucrose	.0048	.0030–.0066	5.17	<.0001	Zeroed			
Sucrose ²	–.00051	–.00063–.00039	–8.22	<.0001	Dropped			
Body mass	.633	.537–.730	13.02	<.0001	.669	.419–.919	5.31	<.0001
Tongue length	–.295	–.479–.111	–3.19	.0019	–.321	–.516–.008	–3.27	.0016
Tongue length × sucrose	–.0168	–.0274–.00633	–3.18	.0020	–.014	–.014–.008	–1.64	NS

Note: Conventional: $R^2 = 0.791$, $F = 67.96$, $df = 5, 90$, $P < .0001$. PIC: overall $F = 11.73$, $df = 4, 86$, $P < .0001$. Because independent contrasts are mapped through the origin, the sucrose concentration effect is zeroed. NS = not significant. CI = confidence interval.

is a direct result of the shift in feeding modality rather than a correlate of an increase in tongue length. Energy intake rate increases with proboscis length in bees that lap (Harder 1983a, 1983b), while this study shows that it decreases with proboscis length in euglossine bees. Even if we take proboscis length differences into account, such variation cannot explain the fivefold decline in E incurred by suction-feeding bees. Harder (1983b) hypothesized that the increase in E associated with the long-tongued condition was part of the reason these bees tend to dominate bee communities in temperate regions. Exact numbers are not available for the tropical communities that euglossine bees inhabit, but a low E is obviously not limiting their ecological success.

Although one may expect the modality of feeding to influence the scaling of E , there are no differences in scaling exponents among bee groups. A direct comparison of the scaling exponents in various taxa is confounded by methods of data collection and a lack of phylogenetic controls, but a qualitative assessment is feasible. In five species of short-tongued bees in two families (Halictidae and Andrenidae), $E \propto M^{0.61}$ (Harder 1983b), and in the three clades of apid lappers, $E \propto M^{0.6}$ (Harder 1983b; Roubik and Buchmann 1984). For comparison, total handling time for 13 species of Hymenoptera visiting *Lavandula latifolia* scales as $M^{-0.80}$ (estimated from Herrera 1989). It seems that in spite of differences in feeding modality, the estimated scaling in lappers does not differ substantially from the scaling in euglossine bees ($\propto M^{0.54}$).

As a general rule, then, larger bees drink nectars relatively more slowly than smaller bees. The suction-feeding model (Daniel et al. 1989) explains about 65% of the variation in nectar intake rate, regardless of scaling assumptions. However, the sum-of-squares error between the model and the data was minimized when only the proboscis and the cibarial pump volume were allowed to scale geometrically with body mass (case 2). Because flow rate depends on the square of radius, most of the increase in flow rate with body size is explained by the geometric

increase in proboscis radius. This result suggests that pump volume and pump musculature increase, in absolute terms, only slightly with body size. However, clypeus volume (a presumed correlate to cibarial pump musculature) scaled geometrically, which contradicts this inference. Regardless, although relative muscle volume may be larger in small bees, it is unlikely to limit the lower size range of euglossines, as it may in xylem-feeding insects (Novotny and Wilson 1997).

The scaling of E in other suction-feeding taxa ranges from negative allometry to functional equivalence. In the nectar-feeding ant *Camponotus mus*, E scales as $M^{0.56}$ (4–16 mg; Josens 2002). Data from seven species of Lepidoptera (May 1985; Pivnick and McNeil 1985; Boggs 1988; Hainsworth et al. 1991; Josens and Farina 2001) provide strong evidence for functional equivalence in this group, with $E \propto M^{1.06}$ (30–680 mg). Total handling time for 23 species of Lepidoptera visiting *L. latifolia* scales as $M^{-0.98}$ (estimated from Herrera 1989). Lepidoptera achieve functional equivalence, in part, via a positive allometry of proboscis radius with body mass ($M^{0.43}$), but more studies are needed to confirm this.

Foraging efficiency in the field is influenced not only by net energy intake rate during feeding but also by flight speed, resource density and accessibility, and foraging strategy. In two species of butterflies, differences in foraging efficiency were attributed to interspecific variation in floral accessibility (via proboscis length) rather than feeding energy intake rate or NSC (May 1988). Indeed, the number of *Costus* and *Calathea* species accessible to euglossines scales as $M^{0.35}$ and is thus proportional to tongue length (Borrell 2005). In studies of temperate bumblebees, researchers have also documented positive allometry to foraging efficiency (Goulson et al. 2002; Ings et al. 2005). It will be interesting to see how nectar density and nectar availability vary with body mass in order to develop a more comprehensive understanding of the partitioning of nectar resources.

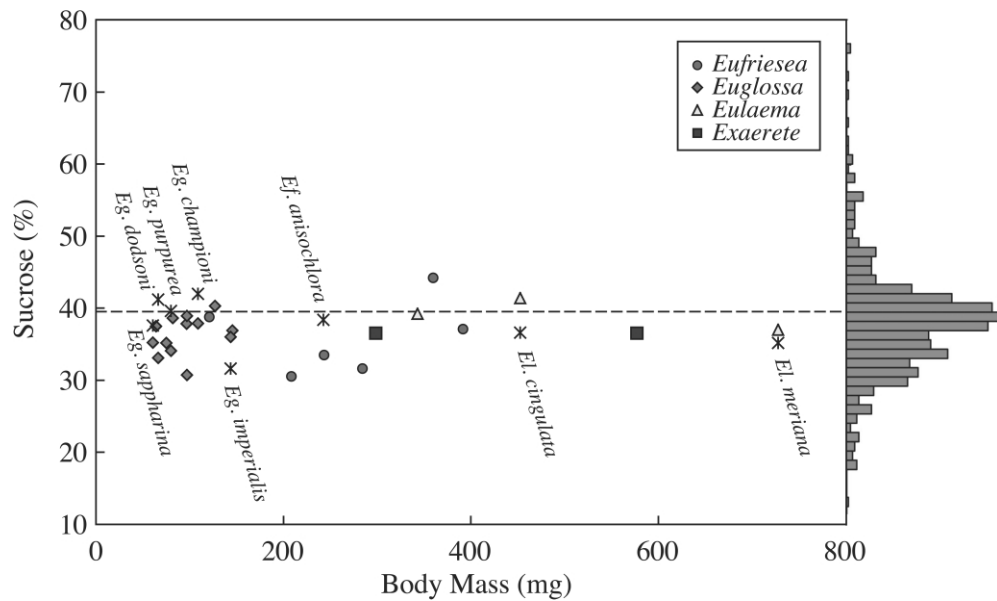


Figure 5: Optimal nectar sugar concentration (S_{\max}) and sugar concentration of nectars collected in the field are independent of body size in euglossine bees. Values of S_{\max} calculated from eight bee species are plotted (asterisks). Dashed line depicts the optimal nectar concentration calculated from the root node using data from all 30 species. The deviations of S_{\max} from the dashed line are due in part to differences in tongue lengths among bee species. The histogram to the right shows the distribution of 663 nectar samples taken from euglossine bees in the field (mean = 37.9 ± 0.6 , range = 12.6%–76.8%).

Optimal Nectar Sugar Concentration and Body Size

The NSC that maximizes energy intake rate, S_{\max} , ranges from 30% to 40% sucrose and is independent of body size in euglossine bees. Daniel et al. (1989) were the first to predict the universality of this optimal nectar concentration for suction feeders. Functional equivalence of S_{\max} means that large bees and small bees should prefer the same concentrations of nectars and that while nectar energy may have evolved to match pollinator body size (Brown et al. 1978), NSC should remain relatively constant with body size. The nectars foraged by euglossine bees ranged from 5% to 75% sucrose, but an overwhelming number of visits are made to flowers that produce nectars with between 30% and 40% sucrose throughout their geographic range (Roubik et al. 1995). All nectar flowers specialized for euglossine bee pollination produce nectars between 30% and 40% sucrose (Borrell and Krenn 2006). Euglossine bees visit the highest-concentration nectar available when solutions are offered in unlimited volumes (Kato et al. 1992), suggesting that in some settings, bees may maximize energy intake rates over a temporal scale longer than a single feeding visit (Gass and Roberts 1992). In the present data set, drier Pacific sites were associated with a slight increase in NSC; however, these differences were on the order of several percentage points, which may

not even be biologically significant to bees. It would be interesting to determine whether these plants compensate for increased evaporation by secreting more dilute nectars earlier in the day. Under conditions of drought stress, nectar volume tends to decline, whereas sugar concentration is maintained within a narrow range (Carroll et al. 2001).

In other nectar feeders, the match between S_{\max} and NSC is less clear, largely owing to competing physiological demands. Choice experiments have yet to demonstrate clear preferences for the intermediate nectar concentrations that maximize energy intake rate (Hainsworth and Hamill 1993). In nectar-feeding bats, mean NSC in flowers is much lower than S_{\max} (Tschapka 2004), indicating that water gain is a principal concern in these animals (Von Helverson and Reyer 1984; Roces et al. 1993). Because bees are in positive water balance at moderate temperatures, the benefits of reducing load by ingesting concentrated nectars may sometimes be more important than maximizing E (Bertsch 1984). NSC in hummingbird flowers is also lower than S_{\max} (Baker 1975; Roberts 1995), but hummingbirds do not appear to be as constrained by dietary water needs at moderate temperatures (Calder 1979). In hawkmoths and long-proboscid flies, NSC is also lower than S_{\max} (Haber and Frankie 1989; Manning and Gold-

blatt 1997), but in butterflies, there is some correspondence between the two values (Heyneman 1983; May 1988).

It is important to remember that the present distribution of NSC in plants was influenced not by the average pollinator but by the foraging decisions of the most efficient pollinator (Schemske and Horvitz 1984; Herrera 1987, 1989). Further studies are needed to clarify choice behaviors in foraging nectarivores and their consequences for plant reproductive fitness (Pyke and Waser 1981).

Costs and Consequences of Long Tongues

Rate of nectar intake declines with increasing tongue length in the euglossine bees. This trend contrasts with results from bumblebees, where intake rate increases in direct proportion to glossa length (Harder 1983a, 1986). The reasons for these differences are related to the different modalities of fluid feeding. In suction feeding, resistance to fluid flow increases with proboscis length, but in capillary-based lapping, the amount of nectar that can be extracted per lap is proportional to the surface area of the tongue (Harder 1983a, 1986; Kingsolver and Daniel 1983, 1995). As predicted by the suction-feeding model, the relationship between energy intake rate and proboscis length was less than the direct proportionality predicted by a simple analysis of the Hagen-Poiseuille equation. The reason for this difference is that the pressure drop developed by the cibarium depends on the resistance to flow (Daniel et al. 1989). The data also support the second prediction of the model that S_{\max} declines slightly with tongue length. This latter result is relevant from a biomechanical standpoint but not necessarily an ecological one.

An additional cost of long tongues is due to proboscis extension and handling time at flowers. Although I did not measure proboscis extension times for a range of euglossine bees, these times are likely to increase with both absolute tongue length and relative tongue length. Floral handling times, by contrast, are a result of a complex interaction among floral morphology, floral choice, tongue length, and body size (Harder 1983a, 1985, 1986; Goulson et al. 2002; Peat et al. 2005). The practical and theoretical aspects of collecting such data for all bee-flower combinations are daunting, but it is useful to consider that even for bumblebees visiting artificial flowers with just 1 μL of 37.5% honey solution, handling time is less than one-fifth of ingestion time (Harder 1983a). Two studies have reported that handling time is minimized when bees visit flowers matching their proboscis length, although these analyses did not consider fluid and floral handling times separately (Inouye 1980; Goulson et al. 2002). Harder (1983a) found that access time was a linear function of flower depth and that at shallow flowers, short-tongued

bumblebees appear to have an advantage over long-tongued bumblebees.

Effective proboscis length of euglossine bees varies by a factor of four, but the most remarkable aspect of this diversity is that some of the smallest bees have evolved the longest tongues. Consequently, a 150-mg *Euglossa asarophora* is able to access many of the same flowers as a 900-mg *Eulaema bombiformis*. Pyke (1978) used an energetic argument to demonstrate that large bees should specialize on low-density plants with large nectar rewards, and on a large scale, there is a correlation among large pollinators, large nectar reservoirs, and widely spaced flowers (Janzen 1971; Brown et al. 1978). However, the functional reasons for this specialization are not as straightforward as Pyke's (1978) model suggests. In most cases, in fact, it pays to be small. This is because the energetic cost of transport increases with body mass more steeply than fluid handling time declines (Darveau et al. 2005). Clearly, widely spaced flowers in the tropics require the services of large nectarivores for their outcrossing (Janzen 1971; Frankie et al. 1976), but the abundance of small bees in any local area will easily overwhelm a rich nectar resource (Brown et al. 1978). The plant's dilemma is to provide enough nectar to attract visitors of the appropriate size class but not to provide so much that the pollinator is satiated or fails to transfer pollen among plants (Klinkhamer and De Jong 1993).

Plants typically use two mechanisms to exclude small bees: elongation of the nectar spur and, less commonly, force-dependent access (Proctor et al. 1996). Force-dependent mechanisms may be less common because they require rather unique morphological features, whereas elongation of the nectar spur is achieved via directional selection on a quantitative trait (Nilsson 1988). Plant-pollinator interactions are typically diffuse or asymmetrical, and the evolution of an elongate nectar spur in any one plant species is unlikely to have exerted reciprocal selection on insect proboscis length (Nilsson 1998; Wasserthal 1998). Thus, the long tongues of small bees may have evolved so that bees could thwart these plants' defenses and visit a wide range of flower types (Wiklund et al. 1979; Borrell 2005). As this study shows, such ecological benefits come with a biomechanical cost.

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