

Mechanical determinants of nectar feeding strategy in hummingbirds: energetics, tongue morphology, and licking behavior

Joel G. Kingsolver¹ and Thomas L. Daniel^{2,*}

¹ Department of Zoology, University of California, Berkeley CA 94720, USA

² Department of Zoology, Duke University, Durham NC 27706, USA

Summary. To explore the mechanical determinants of feeding strategies for nectar feeders, we develop a fluid dynamical and behavioral model describing the mechanics and energetics of capillary feeding in hummingbirds. Behavioral and morphological data for *Calypte* and *Archilochus* are used to test and illustrate this model. We emphasize the important differences between capillary and suction mechanisms of fluid feeding. Model predictions of nectar intake rates and nectar volumes per lick are consistent with observed values for *Calypte anna*. The optimal nectar concentration maximizing rate of energy intake depends on tongue morphology and licking behavior. For hummingbirds exhibiting optimal licking behavior, the optimal nectar concentration is 35–40% sucrose for feeding on large nectar volumes. For small nectar volumes, the optimal concentration is 20–25%. The model also identifies certain tongue morphologies and licking frequencies maximizing energy intake, that are consistent with available observations on licking behavior and tongue design in nectar feeding birds. These predictions differ qualitatively from previous results for suction feeding in butterflies.

The model predicts that there is a critical food canal radius above which suction feeding is superior to capillary feeding in maximizing the rate of energy intake; the tongues of most hummingbirds and sunbirds fall above this critical radius. The development of suction feeding by nectarivorous birds may be constrained by the elastic properties of their flexible tongues. Our results show that, in terms of morphology, scaling, and energetics, different mechanisms of feeding on the same food resource can lead to qualitatively different predictions about optimal design and feeding strategies.

Introduction

In a previous paper on the mechanics of fluid feeding, we developed and evaluated a model for the mechanics and energetics of nectar feeding by suction mechanisms (Kingsolver and Daniel 1979). This model, based on a form of Poiseuille's relation for continuous, steady-state

fluid flow, yielded to major predictions. 1) At any given pressure drop, there is a unique optimal nectar concentration of 20–25% sucrose maximizing the net rate of energy gain that is independent of temperature, metabolic rate, and the size and shape of the feeding tube within the range found in butterflies. This result follows from the exponential relationship of viscosity to nectar concentration, as noted by Baker (1975). 2) There are upper limits on the feeding and energy intake rates attainable by suction feeding, which are particularly important for organisms with feeding tubes of small radius. Although these results apply to a variety of insects, including butterflies, bombyliids, and sphingids, there are other nectar feeders, such as bumblebees and hummingbirds, which do not feed by simple suction mechanisms.

Recently, Sutherland (in prep.) has suggested that mechanical constraints also determine the optimal nectar concentration for feeding by hummingbirds, and presented a model and field results in support of this. Heyneman (1983) has independently proposed a related model for all pollinator types. Both of these investigators also use forms of Poiseuille's relation for continuous, steady-state flow to suggest that the concentration maximizing energy intake rate during feeding is 20–25% sucrose for hummingbirds as well as suction feeding insects. At issue is whether such models based on continuous and steady-state fluid dynamics adequately describe the feeding process for all nectar feeders.

The tongues of hummingbirds consist of open grooves that cannot sustain a pressure differential due to suction across their lengths (Weymouth et al. 1964). Thus, suction feeding cannot occur. Instead, fluid movement results from the action of capillarity, a physical phenomenon driven by surface tension; for this reason, we call hummingbirds "capillary feeders". There are three important differences between capillary feeding in hummingbirds and suction feeding. First, fluid movement during capillary flow is induced by surface tension, which is a function of nectar concentration. Second, capillarity-induced flow is not at steady-state, so that the results of previous steady-state models do not necessarily apply. Third, the rapid tongue licking movements of hummingbirds result in a discontinuous flow process, in contrast to the continuous flow process considered in previous models.

* Present address: 104-44, California Institute of Technology, Pasadena CA 91125, USA

Offprint requests to: J.G. Kingsolver

In this paper, we develop a model for the mechanics and energetics of capillary feeding. We use the morphological and behavioral data of Ewald and Williams (1982) to test the model. We use this model to address three topics:

- 1) The existence and mechanical determinants of optimal nectar concentrations in capillary feeding;
- 2) The effects of tongue morphology, nectar volume, and licking behavior in maximizing rates of energy intake; and
- 3) The consequences of and constraints on capillary and suction mechanisms for nectar feeders.

By comparing capillary and suction mechanisms of feeding on fluids, our results emphasize the potential importance of feeding mechanisms for foraging strategies.

Tongue morphology and the feeding cycle

Anatomical studies in several hummingbird and sunbird species (Hainsworth 1973, Weymouth et al. 1964) reveal a pair of open grooves in the tongue that extend for the distal half of the tongue. The cross-sectional area of each groove is roughly constant over most of the length of the groove, but is smaller at the proximal and distal ends of the groove (Hainsworth 1973, Schlammowitz et al. 1976).

Movie film analysis of hummingbirds on artificial feeders has been used to examine feeding kinematics. Early studies used film speeds that were too slow to observe the details of tongue movement during feeding, but recent high speed (70 frames/s) movies clarify several aspects of feeding mechanisms (Ewald and Williams 1982). There are several phases of a single licking cycle of tongue movement. First, the distal part of the tongue is extended beyond the tip of the bill, and the tongue tip penetrates the fluid source. Fluid flows into the grooves by capillary action. The tongue is then retracted inside the bill. The bill is closed slightly and the tongue extruded from the bill; the constriction of the tongue by the bill during extrusion removes the fluid from the grooves. The tongue tip again penetrates the fluid source, and the cycle is repeated. It is not known how the fluid removed from the grooves by the bill is moved into the esophagus.

Ewald and Williams (1982) reported a mean licking rate (ω) of 13.8 Hz for Anna (*Calypte anna*) hummingbirds on artificial feeders. Their results show that the volume of fluid per lick is less than the volume of the tongue grooves, and that the volume of nectar adhering to the tongue outside of the grooves is less than 7% of the nectar transported. These observations confirm that capillary action is a primary mechanism for nectar removal in hummingbirds.

The results of Ewald and Williams (1982) apply to feeding in which repeated licks on a single nectar source are used. Feinsinger and associates (Bolten and Feinsinger 1978; Feinsinger et al. 1982; Feinsinger, unpubl. data) have documented that the volume of nectar available in hummingbird flowers varies from less than 1 μ l to more than 60 μ l. This variation indicates that on some nectar sources only a single tongue lick may be required to remove the entire nectar volume, while on other sources repeated licks are required. Our model will consider both of these feeding situations.

In the present study, we shall consider the licking cycle in two phases: a capillary phase C , in which the fluid moves into the tongue grooves by capillary action, and an unloading phase M , in which the tongue is retracted into the bill, and then extended again to penetrate the fluid source. Our analysis will focus on the mechanics of the capillary phase, and on the relative duration of the two phases.

Using artificial feeders, several workers have documented that licking rates for hummingbirds decrease as the length of the (artificial) 'corolla' increases (Hainsworth 1973), and as the distance between the bill tip and the nectar source (which we assume is related to corolla length under natural feeding conditions) increases (Ewald and Williams 1982). It is not known whether the duration of the capillary phase changes with 'corolla' length. Indeed, even at a fixed corolla length, one can envision at least two possible licking behaviors with respect to capillary phase duration. First, the capillary phase could be fixed at some constant duration T , regardless of (say) nectar concentration or the volume of nectar obtained during T . We call this behavior " \dot{E}_T behavior" (see The model). Alternatively, the volume of nectar obtained could be fixed, regardless of nectar concentration (\dot{E}_L behavior), such that the duration of the capillary phase might vary. These different licking behaviors lead to somewhat different model formulations and predictions.

The model

In this section, we present two levels of models for hummingbird feeding. First, we develop an energy balance to describe the capillary phase of feeding, and indicate how this model for capillary feeding differs from suction feeding. Second, we incorporate this model for capillary flow into a model describing the licking cycle. Finally, we evaluate the necessary parameters for the model simulations, using data available in the literature.

We shall consider models for three different tongue and flow orientations: horizontal, vertical upwards, and vertical downwards. Throughout the paper, we shall define optimal as maximizing the average rate of energy intake under certain constraints, as is customary in many foraging models. In the present situation, there are two natural measures of the mean rate of energy intake during the capillary phase. We could consider the average rate of energy intake (termed \dot{E}_T) for some specified time period T . Alternatively, we could consider the average intake rate (\dot{E}_L) over a variable time period required to fill a tongue groove to a distance L . These two average rates of energy intake correspond to the two behavioral modes of licking suggested earlier.

A. The capillary phase

(1) *Horizontal feeding.* Let us consider flow in a single tongue groove of constant radius r and length D . We model the tongue groove as a thin-walled cylindrical tube. At time $t=0$, fluid is at a distance $l=0$ from the distal end of the groove. For horizontal flow there is a force balance between a capillary force, and a viscous force opposing the flow. The pressure drop due to the capillary force is

$$\Delta P = \frac{2\gamma \cos \theta}{r}. \quad (1)$$

All symbols are defined in Appendix A. The pressure drop that induces fluid movement is thus a function of the groove radius (r) and the surface tension characteristics of the fluid (γ, θ). We modify Poiseuille's relation for flow in a cylindrical tube to a time dependent relation that describes the volumetric flow rate $Q(t)$:

$$Q(t) = A \frac{dl}{dt} = \frac{\pi r^4 \Delta P}{8\mu l(t)}. \quad (2)$$

Note that $l(t)$, and thus the flow rate $Q(t)$, vary with time. Substituting Eq. (1) into (2) and integrating, we find that

$$t(l) = \frac{2\mu l^2}{r\gamma \cos \theta}, \quad (3a)$$

$$l(t) = \left[\frac{r\gamma \cos \theta t}{2\mu} \right]^{\frac{1}{2}}. \quad (3b)$$

Equations (3a) and (3b) specify the relation of the fluid distance and time to the viscosity (μ) and surface tension characteristics of the fluid. Substituting Eq. (3b) and (1) into (2) we obtain the volumetric flow rate at time t ,

$$Q(t) = \frac{\pi}{4} \left[\frac{2r^5 \gamma \cos \theta}{\mu t} \right]^{\frac{1}{2}}. \quad (4)$$

Then the instantaneous rate of energy intake at time t , $\dot{E}(t)$, is

$$\dot{E}(t) = \varepsilon \rho S Q(t) = \varepsilon \rho S \frac{\pi}{4} \left[\frac{2r^5 \gamma \cos \theta}{\mu t} \right]^{\frac{1}{2}}. \quad (5)$$

Let \dot{E}_T be the mean rate of energy intake over the time interval 0 to T . Then

$$\dot{E}_T = \frac{1}{T} \int_0^T \dot{E}(t) dt = \varepsilon \rho S \pi \left[\frac{r^5 \gamma \cos \theta}{2\mu T} \right]^{\frac{1}{2}}. \quad (6)$$

The fluid density (ρ) and surface tension coefficient (γ) are linearly increasing functions of nectar concentration S , while viscosity (μ) increases exponentially with concentration (Eq. (14)).

There are two points of interest here. First, $Q(t)$ and $\dot{E}(t)$ are decreasing functions of time: as fluid moves up the groove the viscous force opposing the flow decreases the flow rate. Second, $Q(t)$, $\dot{E}(t)$, and \dot{E}_T are all increasing functions of r , so that the rate of energy intake is maximized at $r = \infty$.

The above model describes the mean rate of energy intake for some fixed time T . Let us now consider the time required to move fluid some fixed distance L . Let t_L be the time at which $l=L$. Then the mean energy intake rate \dot{E}_L is simply

$$\dot{E}_L = \frac{1}{t_L} \int_0^{t_L} \dot{E}(t) dt = \frac{L A \varepsilon \rho S}{t_L}. \quad (7)$$

Substituting Eq. (3a) into (7) for when $l=L$, we obtain

$$\dot{E}_L = \frac{\pi r^3 \gamma \cos \theta \varepsilon \rho S}{2\mu L}. \quad (8)$$

Note that, for small nectar volumes requiring single licks, the volume of nectar obtained is determined by the volume within the flower or nectar source. Thus, E_L is the appropriate measure of energy intake rate for feeding on small nectar volumes. Also note that \dot{E}_T and \dot{E}_L , our two measures of mean rate of energy intake, differ in their dependence on the surface tension coefficient and viscosity of the fluid. Both measures, however, are increasing functions of r .

This model differs from models of continuous, steady-state flow under suction in several ways. 1) For suction feeding, the pressure differential inducing flow is produced by a pump mechanism, and is independent of fluid properties; for capillarity, ΔP is a function of both r and the surface tension coefficient, a fluid property dependent on concentration. 2) Equations (2) and (5) show that the instantaneous rates of flow and energy intake are not constant with time. We can write the analogous equation to (5) for the instantaneous rate of energy intake by suction ($\dot{E}_s(t)$) based on Poiseuille (Kingsolver and Daniel 1979):

$$\dot{E}_s(t) = \frac{\varepsilon \rho S \pi r^4 \Delta P_s(t)}{8\mu L} \quad (5')$$

where $\Delta P_s(t)$ is the instantaneous pressure drop due to suction. Note that Eq. (5') applies even if ΔP_s is a function of time. The energy intake rates for suction (5') and capillary (5b) feeding differ in their dependence on both food canal morphology and on fluid properties that are functions of concentration. 3) Because flow during suction is continuous, Eq. (5') describes the energy intake rate at any time during suction feeding on a single nectar source. The discontinuous nature of feeding by hummingbirds, due to the rapid tongue movement during licking, requires several definitions of mean energy intake rate (Eq. (6) and (8)) that depend on the behavioral determinants of licking.

(2) *Vertical feeding.* First consider vertical feeding with upwards flow. Now there is an additional term in the energy balance due to gravity, such that the total pressure drop (see Eq. (1)) is

$$\Delta P = \frac{2\gamma \cos \theta}{r} - \rho g l(t) \equiv a - b l(t) \quad (9)$$

where $a = 2\gamma \cos \theta / r$ and $b = \rho g$. The relations for instantaneous and average rates of flow and energy for vertical upwards and vertical downwards orientations are derived in Appendix B. Here we point out several important qualitative differences between horizontal and vertical feeding orientations.

For vertical upwards flow, the pressure drop ΔP decreases with time (Eq. (9)). Because flow rate approaches zero as ΔP approaches zero (Eq. (2)), there is an equilibrium height \bar{L} to which fluid will rise (Eq. (B.3)). Conversely, for any given L , there is a maximum groove radius r_m above which fluid will not flow to the height L (Eq. (B.7)). Because of this constraint on the

radius for vertical upwards flow, it can be shown (see Appendix B) that there is some finite radius r that maximizes the average rate of energy intake \dot{E}_L . This is in contrast to the horizontal feeding case, for which \dot{E}_L increases monotonically with r .

The vertical downwards feeding model is simply obtained by substituting $g = -g$ in the second term of the RHS of Eq. (9); the relations for flow and energy intake rates for this model are given in Appendix B. In this case, the pressure drop (Eq. (B.8)) is an increasing function of time and of distance l . As a result, there is no equilibrium height or maximum radius less than ∞ . Thus, for vertical downwards feeding, the average rates of energy intake are maximized at radius $r = \infty$, in contrast to vertical upwards feeding.

B. The licking cycle

In this section we incorporate the above models for capillary flow into a model that describes feeding on large nectar volumes requiring repeated licks. As discussed earlier, the licking cycle consists of a capillary phase of duration t_c , and an unloading phase of duration t_m . The total feeding time per lick is simply

$$t_f = t_c + t_m. \quad (10)$$

We define the licking frequency $\omega = 1/t_f$. The rate of energy intake during licking is then

$$\dot{E} = \frac{t_c \dot{E}_{t_c}}{t_f} \quad (11)$$

where \dot{E}_{t_c} is the mean rate of energy intake during a capillary phase of duration t_c . Note that the duration of the capillary phase may either be fixed at $t_c = T$, such that $\dot{E}_{t_c} = \dot{E}_T$, or variable such that $\dot{E}_{t_c} = \dot{E}_L$, depending on the licking behavior of the hummingbird. Also note that t_c is constrained: $t_c \leq T$.

We now consider the role of T in maximizing \dot{E} . Let t_m be a constant, and allow t_c to vary. For horizontal feeding, we can write t_c in terms of the fluid level l_c at t_c , using Eq. (3a). Using the definition of \dot{E}_T given by Eq. (7), we can rewrite Eq. (11) as

$$\dot{E} = \frac{SA l_c \varepsilon \rho}{t_m + t_c}. \quad (12)$$

By substituting Eq. (3b) into (12), differentiating \dot{E} with respect to t_c , and setting $d\dot{E}/dT = 0$, it can be shown that \dot{E} is maximized when

$$t_c = t_m. \quad (13a)$$

Thus, for horizontal feeding, the rate of energy intake is maximized when the durations of the capillary and unloading phases are equal.

By a similar process it can be shown that the optimal fluid level l_c for maximizing \dot{E} is

$$l_c = \frac{r \gamma \cos \theta t_m}{2\mu}. \quad (13b)$$

Note that whereas the optimal t_c depends only on t_m , the optimal l_c also depends on γ and μ — that is, on

fluid properties which are functions of concentration. This difference in their dependence on concentration relates to the two definitions of mean rate of energy intake during the capillary phase.

In summary, there are three main analytical results.

1) For both the horizontal and vertical downward feeding orientations, the mean rate of energy intake is maximized at a groove radius of $r = \infty$. For the vertical upward orientation, there is an optimal finite radius maximizing the mean rate of energy intake.

2) For vertical upward feeding, there is an upper limit on the groove radius and a maximum height that is possible using capillary feeding.

3) In horizontal feeding, the rate of energy intake during repeated licking (\dot{E}) is maximized when the durations of the capillary and unloading phases are equal, regardless of nectar concentration. In contrast, the optimal distance l_c maximizing \dot{E} depends on the duration of the unloading phase, groove radius, and nectar concentration.

C. Model parameters and assumptions

The following parameters are required in the model.

1. Fluid dynamical properties: Viscosity (μ), density (ρ), and surface tension coefficient (γ) for sucrose solutions are generally available (e.g. Stokes and Mills 1965). Based on such values, we derived the following regressions relating sucrose concentration (in %) for use in the simulations:

$$\rho = 1000 + 5.37 S \quad [\text{kg m}^{-3}], \quad (14a)$$

$$\gamma = 7.18 \times 10^{-2} + 7.11 \times 10^{-5} S \quad [\text{N m}^{-1}], \quad (14b)$$

$$\mu = \exp[0.00076 S^2 + 0.012 S - 6.892] \quad [\text{kg m}^{-1} \text{s}^{-1}]. \quad (14c)$$

In each case the regression explains over 90% of the total variance.

2. Contact angle, θ : Precise estimation of contact angles is generally difficult (Adamson 1963). Since many wettable surfaces have contact angles near zero (Adamson 1963), we set $\theta = 0^\circ$ as a limiting case for all simulations. This assumption may lead to overestimates of the surface tension forces and flow rates.

3. Groove radius (r) and length (G): Hainsworth (1973) and Schlamowitz et al. (1976) have taken serial cross-sections of tongues of *Archilochus colubris* hummingbirds and three species of *Nectarina* sunbirds, respectively, and estimated the cross-sectional area $A(l)$ of the groove along the tongue's length. We use the middle part of the groove for which $A(l)$ is constant to define the area A , and define the groove radius as $r = (\bar{A}/\pi)^{1/2}$. For *Archilochus* we obtained a radius of 1.32×10^{-4} m. Hainsworth (1973) gave a value for length of 1.1×10^{-2} m. Ewald and Williams (1982) measured the depth, width, and length of a *Calypte anna* hummingbird tongue, and estimated that the groove radius was about 1.4 times, and length 1.8 times, larger than that measured for *Archilochus*. We used these factors in computing r and G for *Calypte*.

4. Durations of the capillary (t_c) and unloading (t_m) phases of licking: Ewald and Williams (1982) measured

t_c and t_m as a function of the distance between the bill tip and the nectar source for *Calypte*, and have kindly made their original data available to us.

The following assumptions are made in developing the model, or in deriving the analytical results.

1. The groove acts as a tube of uniform radius. The fact that the groove is not enclosed may affect the effective radius of the groove for capillary flow (Davies and Rideal 1979), but will not affect the structure or qualitative results of the model.

2. The flow is laminar and Newtonian. See Kingsolver and Daniel (1979) for a discussion of nectar flow.

3. The inertial forces resulting for acceleration of the fluid are small relative to viscous and capillary forces. The Womersley number (Wo) describes the relative effects of inertia and viscosity in periodic flows (Vogel 1981):

$$Wo = r \left[\frac{2\pi\omega\rho}{\mu} \right]^{\frac{1}{2}} \quad (15)$$

Our calculations for hummingbirds show that Wo is less than one, for which inertial forces may be safely neglected. For this reason, nectar flow is technically considered to be quasi-steady-state: although flow rate changes with time (i.e., is time-dependent), at any instant in time the flow is sufficiently near steady-state. The contrasts to unsteady flows for which fluid acceleration is important. Thus, the start-up phase of flow, before the development of quasi-steady-state flow, may be safely neglected. Our calculations indicate that the duration of this start-up flow is less than 5–10% of the duration of the capillary phase (see Bird et al. 1960, pp 126–130).

4. The relationship between t_c and t_m is not determined by the mechanics of tongue movement – that is, by the material properties of the tongue. If, for example, storage of elastic energy in the tongue during the licking cycle produced certain ‘resonant’ licking frequencies, t_c and t_m would not be independent. This assumption of independence is required in identifying the optimal t_c and l_c during licking (Eq. (12) and (13)).

Model verification and simulation results

A. Testing the model

Ewald and Williams (1982) have collected data that yield estimates of t_c , t_m , licking frequency, and nectar intake rates for *Calypte anna* hummingbirds. Using their estimates of groove radius and t_m , we can predict t_c , nectar volume per lick V , and the rate of nectar intake Q (Table 1). The prediction of V is within 15% of the observed value, and the predicted Q is within 3% of the mean observed value, while the observed value of t_c is within 40% of the optimal predicted value (see also Fig. 6).

Figure 1 gives predicted maximal rates of nectar intake for *Archilochus* (Hainsworth 1973) and *Calypte* (Ewald and Williams 1982) as a function of nectar concentration, assuming a licking frequency of 13.8 Hz

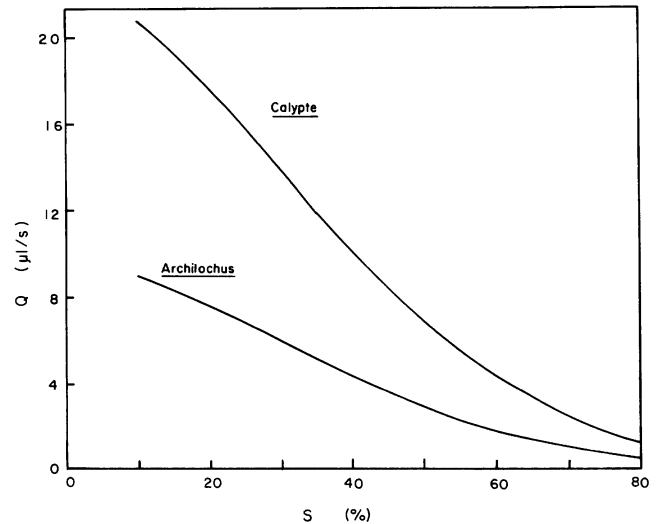


Fig. 1. Maximum rate of fluid intake Q (in $\mu\text{l/s}$) as a function of nectar concentration S (in % sucrose) for *Calypte anna* and *Archilochus colubris*. Calculations assume a licking frequency $\omega = 13.8$ Hz (Ewald and Williams 1982), and $t_c = t_m$ (Eq. (13a)). See Model Parameters

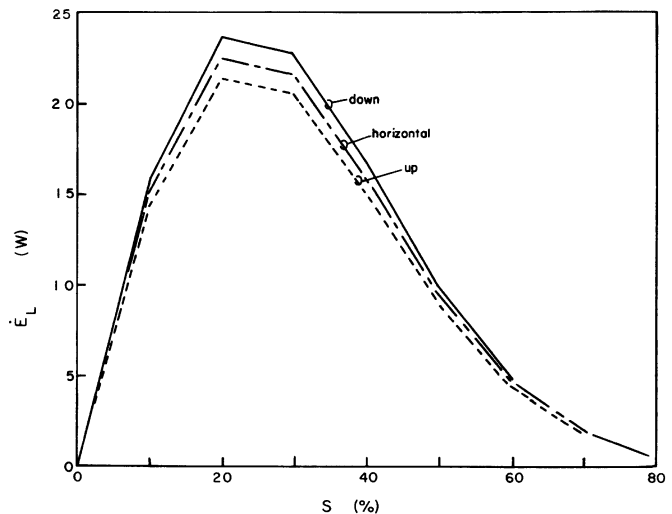


Fig. 2. Mean rate of energy intake during the capillary phase E_L (in W) as a function of nectar concentration S for three flow orientations: horizontal, vertical upward (up), and vertical downward (down). Parameters: $r = 0.1$ mm; $L = 1.0$ cm

Table 1. Model predictions for *Calypte anna*, based on observations from Ewald and Williams (1982). Parameters: $r = 1.848 \times 10^{-4}$ m; $D = 2.9 \times 10^{-2}$ m; $S = 24\%$ sucrose; $t_m = 0.03$ s.

| | t_c (s) | V ($\mu\text{l}/\text{lick}$) | Q ($\mu\text{l}/\text{s}$) |
|-----------|-------------------|-----------------------------------|--------------------------------|
| Observed | 0.05 | 1.2 | 15.0 |
| Predicted | 0.03 ^a | 1.05 | 17.6 |

^a Based on the predicted optimum at $t_c = t_m$ (Eq. 21a)

(Ewald and Williams 1982). For a concentration typical of hummingbird flowers (25% sucrose), predicted intake rates are $6.8 \mu\text{l/s}$ for *Archilochus* and $15.7 \mu\text{l/s}$ for *Calypte*, within the ranges reported for a variety of hummingbirds (Hainsworth and Wolf 1976).

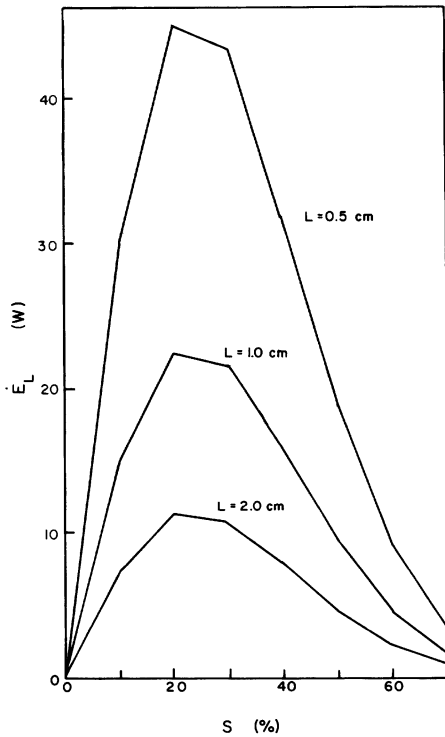


Fig. 3. Mean rate of energy intake during the capillary phase \dot{E}_L (in W) as a function of nectar concentration S (in %) for the horizontal orientation, for three distance values L (in cm). Parameters: $r = 0.1$ mm

B. Energetics of the capillary phase

Figure 2 gives mean rate of energy intake \dot{E}_L as a function of nectar concentration S (% sucrose) for three feeding orientations. For all orientations, \dot{E}_L is maximized at $S = 20\text{--}25\%$. Bill orientation has a small effect ($\pm 5\%$) on energy intake. Further simulations indicate that the optimal S is independent of r . Because \dot{E}_L is the appropriate measure of energy intake rate for feeding involving a single tongue lick, the optimal concentration for feeding on small nectar volumes is 20–25%.

The effects of varying L on \dot{E}_L for horizontal feeding orientation are shown in Fig. 3. Mean rate of energy intake decreases rapidly as L increases (see Eq. 8). This result is independent of orientation and radius. Note that varying L does not vary the optimal S .

Figure 4 shows the relationship of \dot{E}_T , our other estimate of mean rate of energy intake, to nectar concentration. In contrast to \dot{E}_L , \dot{E}_T is maximized at $S = 35\text{--}40\%$, independent of T , r , L , and orientation. Thus, the optimal concentration depends upon the behavioral licking response of the hummingbird, as summarized by E_L and E_T . Note that E_T decreases with increasing T ; this is due to the fact that the instantaneous flow (Eq. (4)) and energy intake (Eq. (5)) rates are decreasing functions of time.

The relationship between the mean rate of energy intake \dot{E}_L and food canal radius r reveals the potential importance of feeding orientation (Fig. 5). For both horizontal and vertical downwards feeding orientations, \dot{E}_L increases monotonically with r . For vertical upwards feeding, however, there is an optimal r maximiz-

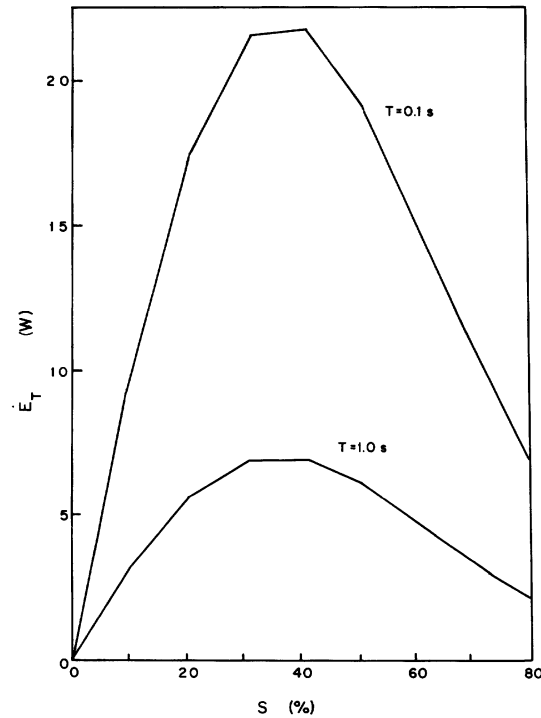


Fig. 4. Mean rate of energy intake during the capillary phase \dot{E}_T (in W) as a function of nectar concentration S (in %) for the horizontal orientation, for two time values T (in s). Parameters: $r = 0.105$ mm

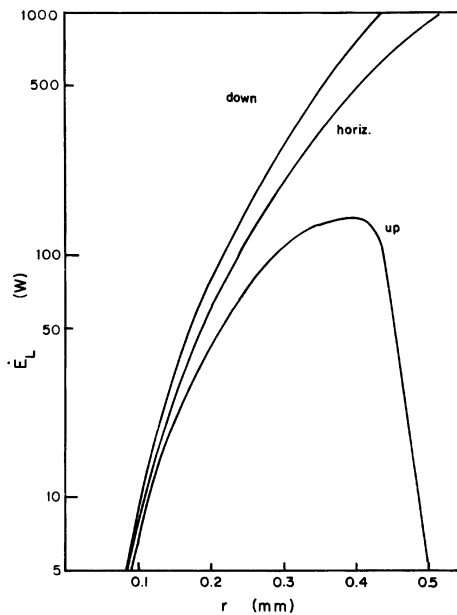


Fig. 5. Mean rate of energy intake during the capillary phase \dot{E}_L (in W) as a function of groove radius r (in mm), for three flow orientations: horizontal (horiz), vertical upward (up), and vertical downward (down). Parameters: $L = 3.0$ cm; $S = 20\%$ sucrose

ing \dot{E}_L . In addition, there is a maximum r_m at which $\dot{E}_L = 0$. These results reflect the constraint on the product rL identified earlier (Eq. (B.7)). However, this constraint appears at values of rL much larger than those observed for hummingbirds and sunbirds.

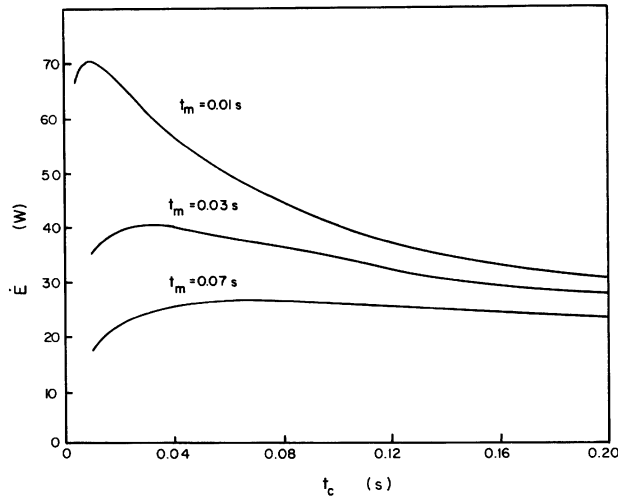


Fig. 6. Rate of energy intake during licking \dot{E} (in W) as a function of the duration of the capillary phase t_c (in s), for three different values of the duration of the unloading phase t_m (in s). Parameters: $r=0.14$ mm; $t_G=0.22$ s; $S=30\%$

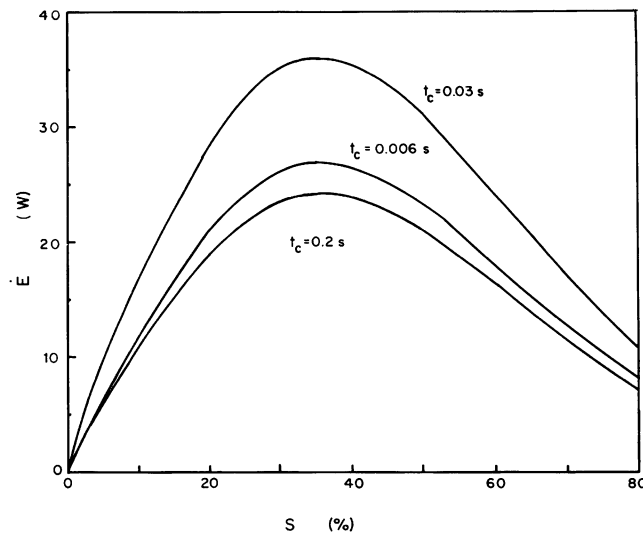


Fig. 7. Rate of energy intake during licking \dot{E} (in W) as a function of nectar concentration S (in %), for different values of duration of the capillary phase t_c (in s). Parameters: $r=0.132$ mm; $t_m=0.03$ s

C. Energetics and licking behavior

For large nectar volumes requiring repeated licks, the rate of energy intake during the licking cycle \dot{E} is a function of the durations of both the capillary (t_c) and the unloading (t_m) phases (Fig. 6). As indicated by Eq. (10), \dot{E} is maximized when $t_c=t_m$; this relationship holds regardless of nectar concentration (Fig. 7). If t_c is held constant at some value, then energy intake rate during licking \dot{E} is maximized at a concentration of 35–40% (Fig. 7). This result follows from the fact that, for t_c constant, \dot{E}_T is the appropriate mean rate of energy intake during the capillary phase. Thus, \dot{E} is maximized when both 1) $S=35\text{--}40\%$, and 2) $t_c=t_m$.

One consequence of the relationship between \dot{E} and t_c is that both the optimal licking frequency ω and the

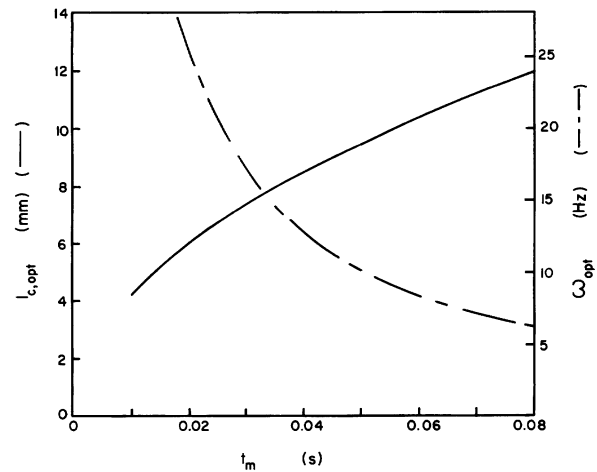


Fig. 8. The optimal fluid distance during the capillary phase $l_{c,opt}$ (in mm, left ordinate), and the optimal licking frequency ω_{opt} (in Hz, right ordinate), as a function of the duration of the unloading phase t_m (in s). Optimal values are those maximizing \dot{E} . Parameters: $r=0.14$ mm; $S=30\%$

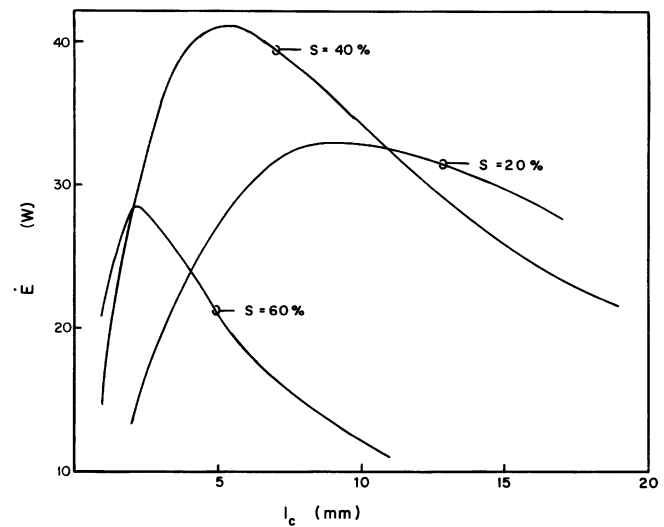


Fig. 9. Rate of energy intake during licking \dot{E} (in W) as a function of fluid distance during the capillary phase l_c (in mm), for three values of nectar concentration S (in %). Parameters: $r=0.14$ mm; $t_m=0.03$ s

optimal distance l_c change with t_m (Fig. 8). Because t_m is directly proportional to the distance between the bill tip and the nectar source (data base of Ewald and Williams 1982), and thus to corolla length, our model predicts that as corolla length increases, 1) licking frequency will decrease, and 2) nectar volume per lick V (which is linearly related to l_c) will increase.

Figure 9 shows the relationship of \dot{E} to l_c , the fluid distance moved during the capillary phase, for several nectar concentrations. In contrast to t_c , the l_c maximizing \dot{E} is a function of S : as S increases, the optimal l_c decreases. Similarly (Fig. 10), for any fixed t_m , as l_c increases the optimal S maximizing \dot{E} decreases. We can locate the maximum \dot{E} evaluated over all values of l_c and S ; Figs. 9 and 10 show that this optimum occurs at $S=36\%$ and $l_c=6.0$ mm. Using Eq. (3a), we observe

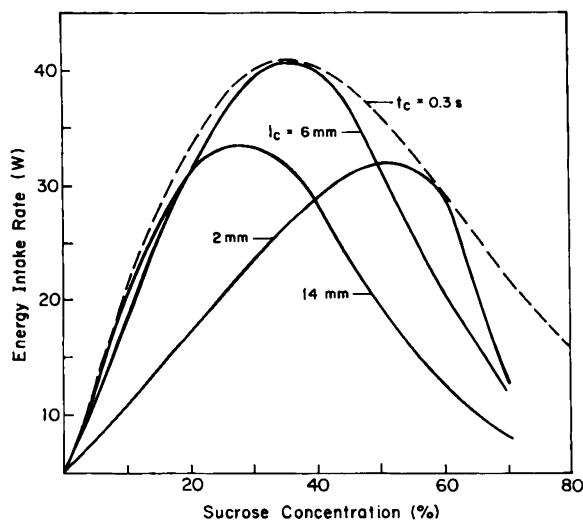


Fig. 10. Rate of energy intake during licking \dot{E} (in W) as a function of nectar concentration S (in %), for three values of fluid distance during the capillary phase l_c (in mm) (\dot{E}_L behavior, solid lines). The relation of \dot{E} vs. S is also given for a fixed capillary phase duration t_c (\dot{E}_T behavior, dashed line), showing that this \dot{E}_T behavior is equivalent or superior to \dot{E}_L behavior at all concentrations. Parameters: $r=0.14$ mm; $t_m=0.03$ s

that this value of l_c is equivalent to the conditions $S=36\%$ and $t_c=t_m$ — the equivalent of maximizing \dot{E} with respect to S and t_c (Fig. 6 and 7).

These considerations of the optimal t_c and l_c unify our earlier distinction between \dot{E}_T and \dot{E}_L , the two measures of mean rate of energy intake during the capillary phase. Let us define the optimal licking behavior as that behavior which maximizes \dot{E} over all possible values of l_c , t_c , and S . For a hummingbird exhibiting optimal licking behavior, l_c must change as a function of S . Thus, \dot{E}_L will not be the appropriate mean measure of intake rate, and licking behavior in which l_c is fixed regardless of concentration (\dot{E}_L behavior) is not the optimal licking behavior. On the other hand, licking behavior in which t_c is fixed (\dot{E}_T behavior) can maximize \dot{E} regardless of concentration; for such behavior, the optimal nectar concentration is 35–40%. This effect is clearly shown when \dot{E}_T and \dot{E}_L behaviors are considered simultaneously (Fig. 10): at all concentrations, energy intake rate is higher for the \dot{E}_T behavior than for any of the \dot{E}_L behaviors. Thus \dot{E}_T behavior is always equivalent or superior to \dot{E}_L in maximizing the rate of energy intake during licking, and the optimal licking behavior occurs when $t_c=t_m$ and $S=35$ –40%.

In summary, we emphasize seven main numerical results, in addition to the analytical results summarized earlier.

1) The model predicts rates of nectar intake within the ranges reported for *Archilochus* and *Calypte*.

2) The optimal nectar concentration maximizing mean rates of energy intake during the capillary phase, \dot{E}_L and \dot{E}_T , are 20–25% and 35–40%, respectively.

3) \dot{E}_L and \dot{E}_T decrease with increasing distance L and time T during the capillary phase, respectively, because of the time-dependent nature of capillary flow.

4) As corolla length and the duration of the unloading phase (t_m) increase, the model predicts that the optimal licking frequency will decrease, and the optimal nectar volume per lick will increase. For the ranges of t_m measured thus far in hummingbirds, the model predicts that nectar volume per lick will be less than the total volume of the tongue grooves.

5) For feeding on small nectar volumes (single licks), the optimal concentration maximizing energy intake rate (\dot{E}_L) is 20–25%. For large nectar volumes (repeated licks), the overall optimal concentration is 35–40%.

6) For birds exhibiting \dot{E}_L behavior during repeated licking, the optimal nectar concentration varies with l_c . For birds exhibiting \dot{E}_T behavior, the optimal nectar concentration is 35–40%, regardless of t_c .

7) \dot{E}_T behavior is equivalent or superior to \dot{E}_L behavior in maximizing the rate of energy intake during repeated licking \dot{E} . Optimal licking behavior maximizing \dot{E} occurs when both a) the durations of the capillary and unloading phases are equal and b) the nectar concentration is 35–40%.

Discussion

A. Application of the model

Our model assumes that capillary flow of nectar into the tongue grooves is an essential feature of hummingbird feeding. We believe that the film analyses of Ewald and Williams (1982), and the design of the tongue itself (Weymouth et al. 1964, Hainsworth 1973), strongly support the assumption that capillary flow is the dominant mechanism of feeding for hummingbirds on inflorescences. There may be feeding situations, however, for which this is not the case. For example, if the tongue were to be fully extended into a nectar source, such that the grooves were completely filled by this movement, capillarity would play a negligible role in feeding, and the above model would not apply.

As suggested by Sutherland (in prep.), this latter situation may hold for hummingbirds for certain types of open and gravity flow feeders (Hainsworth and Wolf 1976) for which the entire tongue could be inserted into the nectar source. In this case, fluid intake rates would be determined not by viscosity and surface tension, but by the rates of tongue movement alone. We would expect energy intake rates, then, to be maximized by fluids with high energetic content per volume — that is, by concentrated nectars near saturation, as suggested by Sutherland (in prep.). Note that gravity itself has quite small effects on flow and energy intake rates (Fig. 2); the issue is whether the bird completely immerses the tongue grooves in the nectar source.

These considerations suggest that care must be used in the design of and interpretation of behavioral data from artificial feeders (Sutherland in prep.). Previous results indicating that hummingbirds behaviorally choose more concentrated nectars, and suggesting that energy intake rate increases monotonically with nectar concentration (Hainsworth 1973; Pyke and Waser 1981), must be evaluated in terms of whether the open artificial feeders used in these experiments accurately reflect the

feeding process on real inflorescences. In addition, our model makes different predictions of optimal concentrations depending on nectar volume; all experimental results to date using artificial feeders apply only to large nectar volumes.

Our capillary model of hummingbird feeding makes predictions of nectar intake rates that are consistent with observed values for *Calypte* hummingbirds, based on estimates of groove radius, t_m , and the fluid mechanical properties of sucrose solutions. More data on groove radii, nectar intake rates, and nectar concentration, combined with high-speed cinematography of hummingbirds at appropriately designed feeders, will be needed for more rigorous tests of the model. We emphasize that the questions of whether the model adequately describes fluid and energy transfer during feeding, and whether hummingbirds exhibit characteristics identified as optimal by the model, are quite separate.

It is important to note that the qualitative predictions from the model, including those about optimal nectar concentrations, optimal licking behaviors, and licking frequencies, are insensitive to changes in model parameters such as the radius and length of the tongue grooves. Further, the assumption of a circular tube of uniform radius to describe the tongue groove will not affect these results, because an effective radius may be defined to describe more complex geometries (Davies and Rideal 1979). This insensitivity to geometry occurs for the same reasons that the optimal nectar concentration of 20–25% for steady-state, continuous flow is insensitive to food canal geometry (Kingsolver and Daniel 1979).

B. Mechanics, energetics, and feeding behavior

Baker (1975) first suggested that the exponential relationship between nectar viscosity and concentration might affect the preferred concentration of nectar feeders. Kingsolver and Daniel (1979) formalized this idea for suction feeders, and identified the optimal nectar concentration of 20–25% for continuous, steady-state feeding. Here we have extended this approach to capillary mechanisms of feeding. In both cases, the optimal concentrations are due in part to the exponential relationship which Baker noted.

Our results indicate that the dependence of the surface tension coefficient of the nectar on nectar concentration is trivial relative to the effects of concentration on density and viscosity (Fig. 2). This is consistent with the result of Heyneman (1983) that the optimal concentration of 20–25% is independent of an assumed steady driving potential producing fluid flow – whether by suction, capillarity, or osmotic potential. However, the assumption that flow and energy intake are continuous and at steady-state is violated in all non-suction nectar feeders, including hummingbirds. It is precisely the time-dependent and discontinuous nature of flow during hummingbird feeding which leads to the new model results presented here.

In an appendix (I.C), Heyneman (1983) shows that her steady-state model yields identical predictions to our fixed volume, time-dependent model for the capillary phase (E_T). As Heyneman notes for all of the

steady-state models and the fixed volume model during the capillary phase, the energy intake rate is proportional to $\rho S/\mu$, yielding an optimal sucrose concentration of 20–25% (Eq. (8); Fig. 2, 3). However, when this fixed volume model for the capillary phase is incorporated into the overall licking cycle, the optimal concentration varies in a complex manner, and the 20–25% optimum does not hold (Fig. 10). For the fixed time (E_T) model, the energy intake rate both during the capillary phase and during repeated licking is proportional to $\rho S/\mu^{\frac{1}{2}}$, yielding an optimal concentration of 35–40% (Eq. (6); Fig. 4, 7).

One new prediction from the present model is that the optimal nectar concentration depends on the temporal behavioral response of the hummingbird to nectar concentration: stated more generally, the optimal diet depends on the behavioral mechanism by which food intake is averaged over time. Because of the time-dependent and discontinuous nature of hummingbird feeding, there are (at least) two different responses in licking behavior to nectar concentration, which yield different relationships between energy intake rate and concentration. This is in contrast to continuous modes of feeding, which yield a single optimal concentration of 20–25% sucrose. We emphasize that the differences in optimal concentration for different licking behaviors are due not to different flow processes, but rather to differences in the constraints imposed by behavior on the flow process. It is the combination of these constraints with the non-linear and discontinuous flow during feeding that yield these results. This interaction between feeding mechanics and behavior has not been explicitly considered in previous models of optimal foraging (Schoener 1971; Pyke et al. 1977) or of nectar feeding; we suggest that an adequate description of foraging strategy must incorporate such mechanical considerations.

For continuous suction feeding, energy gain is maximized at the highest pressure drop which can be maintained by the suction pump, regardless of food canal morphology, nectar concentration, or corolla length. For capillary feeding, there are certain optimal licking behaviors which may depend on each of these factors. The model predicts that energy intake is maximized at $t_c = t_m$; data for *Calypte* indicate that t_c is about 1.4 times larger than t_m (Table 1), but that the predicted energy intake would be 95% of the predicted maximum gain (Fig. 6). This optimum is formally identical to previous results in foraging theory concerning movement among resource patches, such as the marginal value theorem (Charnov 1976) and related microeconomic results; here the time spent in a 'patch' corresponds to the duration of the capillary phase, t_c .

The present model also predicts that t_c will be much less than t_m , the time required to completely fill the tongue grooves (Fig. 6), so that the nectar volume per lick V will be much less than the total groove volume, as observed by Ewald and Williams (1982). Further, the model predicts that both t_c and V will increase with increasing corolla length, for hummingbirds exhibiting optimal licking behavior.

For feeding on large nectar volumes requiring repeated licking, the two modes of licking considered here yield qualitatively different predictions with re-

spect to nectar concentration choice. Fixing t_c regardless of nectar concentration (\dot{E}_T behavior) is the behavior that maximizes the rate of energy intake during licking. For this behavior, the optimal nectar concentration is 35–40%. The alternative behavior of fixing L regardless of concentration (\dot{E}_L behavior) results in lower energy intake rates than those for the optimal \dot{E}_T behavior. For \dot{E}_L behavior, the optimal concentration varies with l_c in a complex manner. Whether hummingbirds exhibit \dot{E}_T or \dot{E}_L behavior during feeding is not known; as a result, we cannot identify the optimal nectar concentration for hummingbirds. Our model does predict that energy intake rate during repeated licking is maximized over all possible behaviors and concentrations when 1) nectar concentration is 35–40% and 2) the durations of the capillary and unloading phases are equal.

Regardless of behavior, our model prediction of an optimal concentration of 35–40% only applies when feeding involves multiple licks during feeding on a single nectar source. This is the case for hummingbirds feeding on flowers with large nectar volumes and on artificial feeders. For nectar sources with nectar volumes less than the volume of the tongue grooves, the entire nectar volume can be obtained in a single lick. In this case the fixed volume model for flow during a single capillary phase applies, for which the optimal concentration is 20–25% sucrose (Eq. (8); Fig. 2, 3). Thus, the model predicts that the optimal concentration may change with nectar volume: 20–25% for small volumes, and 35–40% for large volumes.

These predictions are consistent with present evidence on the nectar concentrations in flowers visited by hummingbirds (e.g., Baker 1978; Baker and Baker 1982; Pyke and Waser 1982). The work of Feinsinger and associates (Bolten and Feinsinger 1978; Feinsinger et al. 1982) indicates that short-tongued hummingbirds feed on flowers with short corollas, small standing nectar volumes (often $<1-2 \mu\text{l}$), and dilute nectars (15–25% sucrose equivalent). Long-tongued hummingbirds, in contrast, feed on flowers with long corollas, large standing nectar volumes, and more concentrated nectars (31–38%). Previous attempts to explain mean concentrations in hummingbird flowers (27% sucrose; Pyke and Waser 1981) have thus obscured important biological phenomena by such averaging. It is in this transition from nectar volumes requiring a single lick to multiple licks in which we move from continuous (Kingsolver and Daniel 1979; Heyneman 1983) to discontinuous (Eq. (10–13)) feeding models, with the resultant change in optimal nectar concentration.

Present evidence for nectar concentration choice in hummingbirds is conflicting. Natural choice experiments with *Calypte* hummingbirds on *Agave* showed that these birds preferred concentrations of 20–25% (Sutherland in prep.). More controlled laboratory experiments with *Archilochus* involving choice tests between pairs of available concentrations showed that hummingbirds consistently chose the higher concentration available at lower concentrations, but failed to discriminate for concentrations above 30% (Hainsworth and Wolf 1976). On the other hand, the results of Pyke and Waser (1981) indicate that *Selasphorus* on artificial feeders chose nectars in excess of 75% (but see

earlier discussion). We emphasize that factors other than foraging energetics, such as water balance (Calder 1979) and plant-pollinator coevolution (Pyke and Waser 1981), may also affect the observed patterns of nectar choice in pollinators and concentration in plants; models that consider several of these factors – for example, the combined water and energy balance – may be more appropriate than the single factor hypotheses proposed and tested previously (Pyke and Waser 1981).

In contrast to both hummingbirds and butterflies, bumblebees and honeybees appear to use a combination of capillary and suction forces during nectar feeding. The presence of numerous setae on the glossal ‘tongue’ of bees (Snodgrass 1954) will greatly affect fluid movement during feeding; capillary and viscous forces through such porous structures may be qualitatively different from simple tube flow (Davies and Rideal 1979). For this reason, we believe that the results concerning optimal nectar concentration presented here and in previous steady-state models don’t apply to nectar feeding in bees.

C. Mechanics, morphology, and scaling

For continuous suction feeding, the rate of energy intake always increases with increasing food canal radius, regardless of nectar concentration or feeding orientation (Kingsolver and Daniel 1979). For capillary feeding in the vertical upwards orientation, there is an upper limit on the groove radius – more precisely, a constraint on the product rL – such that there exists an optimal r maximizing energy intake (Eq. (15), Fig. 5). Our simulations suggest that this upper limit is considerably larger than the groove radii measured thus far for hummingbirds and sunbirds. In addition, recall that L , the distance in the tongue groove to which nectar is drawn, is determined by the licking rate, and not necessarily by tongue morphology. For these reasons, the constraint on rL is probably not of ecological importance for these nectar feeding birds.

The mechanical and behavioral factors influencing L do, however, have important consequences for tongue morphology. Because \dot{E}_L and \dot{E}_T decrease as more and more nectar enters the tongue grooves, it is energetically unprofitable to use more than the distal portion of the grooves for nectar transport during licking. Accordingly, the grooves extend only over the distal half of the tongue in hummingbirds. In sunbirds the two distal grooves fuse into a single groove over the proximal part of the tongue; we predict that this proximal groove is not used for nectar transport. The fact that larger nectarivorous birds such as honeyeaters and white eyes have highly divided tongues, instead of grooves of larger radii, may also relate to these mechanical constraints on capillary flow.

Because the relationship between energy intake and tube radius differs for suction and capillary feeding (see Eq. (5) and (5')), we can compare how these two mechanisms of feeding scale with food canal size. Consider a canal of radius r and length L , and consider the rate of energy intake during the time required to fill the canal with nectar. Let \dot{E}_n be the energetic advantage of capillary feeding over suction feeding. Then the condition

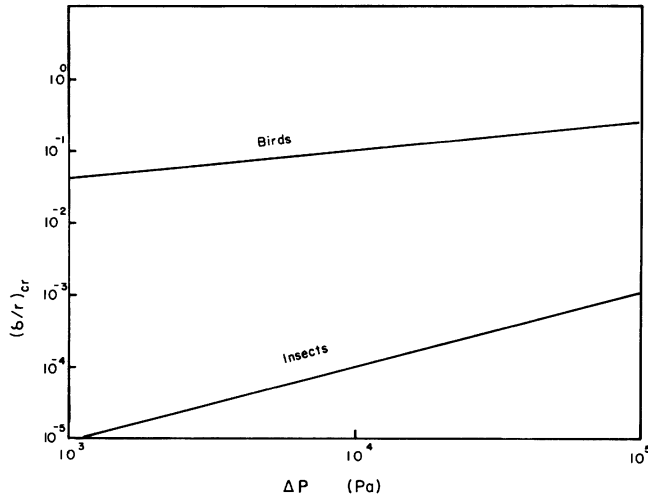


Fig. 11. The critical wall thickness to radius ratio $(\delta/r)_{cr}$ as a function of the pressure drop due to suction ΔP_s (in Pa). The lines indicate points at which tube fracture (for insect cuticle) or tube collapse (for bird tongues) would occur: see Eq. (17a) and (17b). See text for parameter values

for $\dot{E}_n > 0$ is (Appendix C)

$$r < \frac{2\gamma \cos \theta}{\Delta P_s} \quad (16)$$

Estimates of ΔP_s for blood-sucking insects (Daniel and Kingsolver in press) and for butterflies and bees (Schmitt and Kingsolver unpubl.) give values of 1–50 kPa; this means that $E_n > 0$ for $r < 0.0028$ – 0.14 mm, values of r which are generally less than those measured for sunbirds and hummingbirds. This simple result provokes the question: Why do these nectar feeding birds utilize capillary rather than suction feeding?

One possible constraint on the development of suction feeding in nectar feeding birds is the low elastic modulus of flexible, vertebrate tongues. Consider a hollow tube of radius r and wall thickness δ , to which a suction ΔP_s is applied. Let Y be the elastic modulus of the wall material in the circumferential and transverse directions. For rigid materials such as insect cuticle, there is a critical thickness:radius ratio, $(\delta/r)_{cr}$, below which the tube will fracture:

$$\left(\frac{\delta}{r}\right)_{cr} = \frac{\Delta P_s}{Y_c} \quad (17a)$$

(Alexander 1968; Kingsolver and Daniel 1979), where Y_c is the ultimate strength of the material. Using a value of $Y_c = 95$ MN m⁻² (Wainwright et al. 1976), we can show that the critical ratio for insect feeders is always less than 0.001 (Fig. 11). Measured values for δ and r show that such mechanical failure is probably never of importance for nectar feeding insects which use simple, suction tubes (Kingsolver and Daniel 1979).

The situation for flexible tubes is quite different. Here there is a critical $(\delta/r)_{cr}$ ratio below which the tube begins rapidly to collapse (but not fracture):

$$\left(\frac{\delta}{r}\right)_{cr} = \left[\frac{3.53 \Delta P_s}{Y}\right]^{\dagger} \quad (17b)$$

(Kresch and Noordergraaf 1972). Using a value of $Y = 25$ MN m⁻² for vertebrate tendon (Crisp 1972), we can show that the critical ratio for vertebrate feeders using suction would be as high as 0.24 (Fig. 11), more than two orders of magnitude greater than for insects. These calculations suggest that vertebrates using simple suction tubes for nectar feeding would require reinforced or very thick walls to prevent collapse of the tube. This constraint due to mechanical failure might make the advantages of using suction tubes of large radius for feeding (Eq. (16)) unattainable for vertebrate nectar feeders.

These results show that, in terms of morphology, scaling characteristics, and energetics, different mechanisms of feeding on the same food resource can lead to qualitatively different predictions about optimal design and feeding.

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Appendix A

Nomenclature

| Symbol | Quantity | Units |
|-----------------|---|---------------------------------|
| A | groove cross-sectional area | m ² |
| $A(l)$ | groove cross-sectional area at position l | m ² |
| C | the capillary phase | - |
| G | groove length | m |
| \dot{E} | rate of energy intake during the licking cycle | W |
| $\dot{E}(t)$ | instantaneous rate of energy intake | W |
| \dot{E}_L | mean rate of energy intake during fluid movement to a distance L (capillary phase) | W |
| $\dot{E}_{L,c}$ | mean rate of energy intake during fluid movement to a distance L due to capillarity | W |
| $\dot{E}_{L,m}$ | mean mechanical work to suck fluid to a distance L | W |
| $\dot{E}_{L,s}$ | mean rate of energy intake during fluid movement to a distance L due to suction | W |
| \dot{E}_n | net energetic advantage of capillary over suction feeding | W |
| \dot{E}_{tc} | mean rate of energy intake during a capillary phase of duration t_c | W |
| \dot{E}_T | mean rate of energy intake during fluid movement for a duration T (capillary phase) | W |
| g | gravitational constant | m ⁻¹ s ⁻² |

| Symbol | Quantity | Units |
|---------------|--|---------------------------------|
| $l, l(t)$ | fluid position at time t (variable) | m |
| l_c | fluid distance moved during the capillary phase | m |
| L | fluid position (fixed) | m |
| \hat{L} | fluid position at equilibrium | m |
| M | the unloading phase | - |
| ΔP | pressure drop | Pa |
| ΔP_s | pressure drop due to suction | Pa |
| $Q(t)$ | volumetric flow rate at time t | $\text{m}^3 \text{s}^{-1}$ |
| Q | steady-state rate of volumetric flow | $\text{m}^3 \text{s}^{-1}$ |
| r | groove radius | m |
| r_m | maximum groove radius | m |
| S | nectar concentration | % sucrose (mass/mass) |
| t | time (variable) | s |
| t_c | duration of the capillary phase | s |
| t_G | duration to fill the groove to length G | s |
| t_f | time per lick | s |
| t_L | time for fluid movement to a distance L (capillary phase) | s |
| t_m | duration of the unloading phase | s |
| T | time (fixed) | s |
| V | fluid volume per lick | m^3 or μl |
| W_o | Womersley number | - |
| Y | elastic (Young's) modulus of the tube wall | MN m^{-2} |
| Y_c | ultimate strength of the tube wall | MN m^{-2} |
| δ | wall thickness | m |
| ε | energy content of sucrose | J g^{-1} |
| η | muscular efficiency | - |
| μ | dynamic viscosity of the fluid | $\text{g m}^{-1} \text{s}^{-1}$ |
| γ | surface tension coefficient of the fluid | N m^{-1} |
| θ | surface contact angle | radians |
| ρ | fluid density | g m^{-3} |
| ω | licking frequency | $\text{Hz} (= \text{s}^{-1})$ |

Appendix B

Capillary flow for vertical feeding

First consider vertical feeding with upwards flow. Now there is an additional term in the energy balance due to gravity, such that the total pressure drop (see Eq. (1), (9)) is

$$\Delta P = \frac{2\gamma \cos \theta}{r} - \rho g l(t) \equiv a - bl(t) \quad (\text{B.1})$$

where $a = 2\gamma \cos \theta / r$ and $b = \rho g$. Substituting Eq. (B.1) into (2), integrating, and rearranging, we obtain

$$t(l) = \frac{8\mu}{r^2} \left[\frac{a}{b^2} \ln \left[\frac{a}{a-bl} \right] - \frac{l}{b} \right]. \quad (\text{B.2})$$

Note that $Q=0$ when $\Delta P=0$ (Eq. (B.1)). The equilibrium height \hat{L} to which fluid will rise is

$$\hat{L} = \frac{2\gamma \cos \theta}{r \rho g}. \quad (\text{B.3})$$

We cannot obtain an explicit expression for $l(t)$ for the vertical flow model. The energy intake rate at time t is

$$\dot{E}(t) = \frac{\varepsilon \rho S \pi r^4 [a - bl(t)]}{8\mu l(t)} \quad (\text{B.4})$$

and the mean rate of energy intake over a period T is

$$\dot{E}_T = \frac{\varepsilon \rho S \pi r^4 l(T)}{8\mu \left[\frac{a}{b^2} \ln \left[\frac{a}{a+bl(T)} \right] - \frac{l(T)}{b} \right]} \quad (\text{B.5})$$

where $l(T)$ is given implicitly by Eq. (B.2).

We can get an explicit relation for \dot{E}_L . Using Eq. (7) and substituting Eq. (B.2) for $l=L$, we obtain

$$\dot{E}_L = \frac{\varepsilon \rho S \pi r^4 L}{8\mu \left[\frac{a}{b^2} \ln \left[\frac{a}{a-bL} \right] - \frac{L}{b} \right]} \quad (\text{B.6})$$

Note that t_L is constrained (Eq. (8.2)): L must be less than \hat{L} for $t_L < \infty$. Thus, for a given L , r is constrained by

$$r < \frac{2\gamma \cos \theta}{\rho g L} \equiv r_m. \quad (\text{B.7})$$

Because $t_L \rightarrow \infty$ as $r \rightarrow r_m$, it follows that there must be some finite radius r that maximizes \dot{E}_L . This is in contrast to the horizontal feeding case, for which \dot{E}_L increases monotonically with r .

The vertical downward feeding model is simply obtained by substituting $g = -g$ throughout the above derivation (Eq. (B.1-6)). The relations for ΔP , $Q(t)$, \dot{E}_T , and \dot{E}_L for the vertical downwards model are

$$\Delta P = \frac{2\gamma \cos \theta}{r} + \rho g l(t) = a + bl(t), \quad (\text{B.8})$$

$$Q(t) = \frac{\pi r^4 [a + bl(t)]}{8\mu l(t)}, \quad (\text{B.9})$$

$$\dot{E}_T = \frac{\varepsilon \rho S \pi r^4 l(T)}{8\mu \left[\frac{a}{b^2} \ln \left[\frac{a}{a+bl(T)} \right] + \frac{l(T)}{b} \right]}, \quad (\text{B.10})$$

$$\dot{E}_L = \frac{\varepsilon \rho S \pi r^4 L}{8\mu \left[\frac{a}{b^2} \ln \left[\frac{a}{a+bL} \right] + \frac{L}{b} \right]} \quad (\text{B.11})$$

Note that because ΔP is an increasing function of $l(t)$ and of t , there is no equilibrium height $\hat{L} < \infty$ and no constraint of t_L or r . In addition, as r approaches ∞ the numerators of Eq. (B.10) and (B.11) approach ∞ faster than their denominators. As a result, \dot{E}_T and \dot{E}_L are maximized at $r = \infty$.

Appendix C

Scaling of capillary and suction feeding

Consider the horizontal feeding orientation. We wish to examine the energetic advantage of capillary *vs* suction feeding. We compute \dot{E}_L , the mean rate of energy intake during filling the groove or tube to a distance $l = L$. Define $\dot{E}_{L,c}$ and $\dot{E}_{L,s}$ as \dot{E}_L for capillary and suction feeding, respectively. From Kingsolver and Daniel (1979) it can be shown that

$$\dot{E}_{L,s} = \frac{\Delta P_s \pi r^4 S \rho \varepsilon}{4 \mu L}. \quad (C.1)$$

The mechanical work required to suck, $\dot{E}_{L,m}$ is given by (Kingsolver and Daniel 1979)

$$\dot{E}_{L,m} = \Delta P_s \bar{Q} / \eta \quad (C.2)$$

where \bar{Q} is the mean volumetric flow rate, and η is the muscular efficiency. Then it can be shown that

$$\dot{E}_{L,m} = \frac{[\Delta P_s]^2 \pi r^4}{4 \mu L \eta}. \quad (C.3)$$

We define the advantage in rate of energy intake of capillary *vs* suction feeding as

$$\dot{E}_n = \dot{E}_{L,c} - \dot{E}_{L,s} + \dot{E}_{L,m}. \quad (C.4)$$

Substituting Eq. (8), (C.1), and (C.3), and rearranging, we obtain

$$\dot{E}_n = \frac{\pi r^3}{2 \mu L} \left[\gamma \cos \theta S \rho \varepsilon - \frac{\Delta P_s}{2} [S \rho \varepsilon - \Delta P_s / \eta] \right]. \quad (C.5)$$

For $S \geq 1\%$ sucrose, $S \rho \varepsilon \gg \Delta P_s / \eta$. Using this simplification, the condition for $\dot{E}_n > 0$ is

$$r < \frac{2 \gamma \cos \theta}{\Delta P_s}. \quad (C.6)$$

References

- Adamson A (1963) *Physical Chemistry of Surfaces*. John Wiley and Sons, New York
- Baker HG (1975) Sugar concentration in nectars from hummingbird flowers. *Biotropica* 7:37-41
- Baker HG (1978) Chemical aspects of the pollination biology of woody plants in the tropics. In: *Tropical Trees as Living Systems*. Cambridge U. Press, Cambridge, pp 57-82
- Baker I, Baker HG (1982) Some constituents of floral nectars of *Erythrina* in relation to pollinators and systematics. *Alberonia* 4:25-37

- Bird RB, Stewart WE, Lightfoot EN (1960) *Transport Phenomena*. John Wiley and Sons, New York
- Bolten AB, Feinsinger P (1978) Why do hummingbird flowers secrete dilute nectars? *Biotropica* 10:307-310
- Calder WA (1979) On the temperature-dependency of optimal nectar concentrations for birds. *J Theor Biol* 78:185-196
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Pop Biol* 9:129-136
- Crisp JD (1972) Properties of tendon and skin. In: *Bio-mechanics: Its Foundations and Objectives*. Prentice-Hall, New Jersey, pp 141-179
- Daniel TL, Kingsolver JG (in press) Feeding strategy and the mechanics of blood sucking in insects. *J Theor Biol*
- Davies JT, Rideal EK (1979) *Interfacial Phenomena*. Academic Press, New York
- Ewald PW, Williams WA (1982) Function of the bill and tongue in nectar uptake by hummingbirds. *Auk* 99:573-576
- Feinsinger P, Wolfe JA, Swarm LA (1982) Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology* 63:494-506
- Hainsworth FR (1973) On the tongue of a hummingbird: its role in the rate and energetics of feeding. *Comp Biochem Physiol* 46:65-78
- Hainsworth FR, Wolf LL (1976) Nectar characteristics and food selection by hummingbirds. *Oecologia (Berlin)* 25:101-113
- Heyneman A (1983) Optimal sugar concentrations of floral nectars- dependence on nectar energy flux and pollinator foraging costs. *Oecologia (Berlin)* 60:198-213
- Kingsolver JG, Daniel TL (1979) On the mechanics and energetics of nectar feeding in butterflies. *J Theor Biol* 76:167-179
- Kresch E, Noordergraaf A (1972) Cross-sectional shape of collapsible tubes. *Biophysical Journal* 12:274-294
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Quart Rev Biol* 52:137-154
- Pyke GH, Waser NM (1981) The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* 13:260-270
- Schlamowitz RF, Hainsworth FR, Wolf LL (1976) On the tongues of sunbirds. *Condor* 78:104-107
- Schoener TW (1971) Theory of feeding strategies. *Ann Rev Ecol Syst* 2:369-404
- Snodgrass RF (1954) *Principles of Insect Morphology*. McGraw-Hill, New York
- Stokes RH, Mills R (1965) *Viscosity of Electrolytes and Related Properties*. Pergamon Press, Oxford
- Sutherland S (in prep) Nectar concentration in hummingbird flowers: maximizing the instantaneous rate of energy intake
- Vogel S (1981) *Life in Moving Fluids*. Willard Grant Press, Boston
- Wainwright SA, Biggs WD, Currey JD, Gosline JM (1976) *Mechanical Design in Organisms*. Halsted Press, New York
- Weymouth R, Lasiewski R, Berger A (1964) The tongue apparatus in hummingbirds. *Acta Anat* 58:252-270

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