Energetics of Foraging: Rate and Efficiency of Nectar Extraction by Hummingbirds

Abstract. *The efficiency with which several species of hummingbirds extract nectar was estimated by converting the rate of extraction of nectar volumes to the energy expended and the energy obtained from the nectar. The extraction rates depend on corolla and bill morphologies, and the extraction efficiencies depend, in addition, on the bird weight and nectar concentration. Differential extraction efficiencies can be exploited by plants to increase pollinator specificity.*

Basic to an understanding of the feeding ecology of consumer organisms is the relation between the caloric uptake in food and the caloric expenditure in obtaining that food. There is considerable information on food uptake and foraging rates (*1–3*) and increasing information on the energetic costs of various activities by consumer organisms (*4, 5*). However, there has been little attempt to unite these lines of research to provide a complete picture of foraging energetics. For most consumer organisms, it is difficult to measure foraging efficiency under natural conditions because of problems associated with observing foraging or measuring the caloric value of different food items, or both.

Hummingbirds feeding on flower nectar constitute a system in which all of the variables necessary to determine the efficiency of nectar extraction are relatively easy to measure. Foraging usually involves hovering flight which is relatively easy to observe and to quantify energetically (*5, 6*). Hummingbirds feed almost exclusively on small arthropods and flower nectar, and most hummingbirds visit flowers only for nectar (*7*). The rate of secretion and the caloric value of the nectar can be determined easily so that the energy available per foraging bout or per unit of energy expenditure in foraging can be calculated.

The energy used in foraging can be calculated from the cost of hovering, the amount of time spent foraging, and the body weight. Measured costs of hovering for a 3-g and a 10-g hummingbird are 42.4 and 43.4 ml of oxygen per gram per hour, respectively (*5, 8*). Moreover, theoretical estimates of hovering costs for a variety of hummingbird species suggest that the per gram cost of hovering does not vary with body weight (*9*). We use 43 ml of oxygen per gram per hour or 215 cal per gram per hour (respiratory quotient = 1.0) in calculating hovering costs. To measure foraging costs in the field we timed the length of individual visits of hummingbirds to numbered flowers with a stopwatch and analyzed films of foraging birds. We timed only the interval during which the bird had its bill inserted into the flower corolla, not considering, at this stage, the time the bird spent between flowers. Therefore, the data presented here refer only to the efficiency of actual nectar extraction.

We measured the nectar extraction efficiency of three species of hummingbirds at flowers of three species of *Heliconia* at Finca La Selva in the Caribbean lowlands of northeastern Costa Rica during July 1971. The relevant characteristics of the hummingbirds and flowers studied are given in Tables 1 and 2.

To estimate the amount of nectar taken, we recorded the time of each visit to individual flowers. We thus knew the length of time between visits to individual flowers. From previously measured rates of hourly nectar production for these *Heliconia* species we could calculate the amount of nectar secreted since the last visit. By sampling the nectar remaining in several flowers immediately after a visit by a hummingbird we confirmed that the amount left is constant for a given species of hummingbird.

We measured the refractive indices of the nectar to convert the volume of nectar taken into calories (Table 2). Chromatographic analysis of the nectar of all three *Heliconia* species confirmed that they contained only sucrose, glucose, and fructose (this composition is typical of the nectar of most flowers) (*10*). The refractive index of the nectar (correlated to 20°C) could be used to estimate the nectar concentration, expressed as an equivalent sucrose concentration, which could then be converted to calories (*11*).

The equations relating the volume of nectar uptake and the time spent in foraging at different flowers are presented in Table 3. A low slope indicates a high rate of nectar extraction. Two types of comparisons can be made. First, a given hummingbird species (for example, *Phaethornis superciliosus*) shows different rates of nectar extraction at different flowers. *Phaethornis* extracted nectar significantly faster from *H. rostrata* than from *H. tortuosa* (*t*-test; $P < .05$). The rate of nectar extraction from *H. imbricata* was intermediate and not significantly different from that from either *H. tortuosa* or *H. rostrata*. Second, nectar from a given flower (*H. imbricata*) can be extracted at different rates by different hummingbirds. *Thalurania furcata* males extracted nectar significantly faster than *Amazilia tzacatl* or *P. superciliosus* ($P < .02$), whereas the rates of nectar extraction for *A. tzacatl* and *P. superciliosus* were not significantly different.

The results can be expressed in energetic terms by converting nectar volumes and foraging times to calories. The equations relating nectar intake in calories and foraging costs in calories are presented in Table 4; a low slope indicates a high energy extraction efficiency. Two comparisons, similar to the time-

Table 1. Characteristics of hummingbirds studied ($N = 10$ for each species).

Bird species	Weight* (g)	Bill length (mm)	Foraging costs‡ (cal/sec)
Phaethornis superciliosus	6.0 (5.3–6.7)	37.0	0.36
Thaluranía furcata (male)	4.5 (3.9–5.3)	19.0	0.27
Amazilia tzacatl	5.0 (4.3–6.1)	20.0	0.30

* The range appears in parentheses; single values are means. † Based on a value of 43 ml of oxygen per gram per hour for mean weights and a respiratory quotient of 1.0.

Table 2. Characteristics of *Heliconia* flowers studied ($N = 15$ for each species).

Flower species	Corolla length* (mm)	Nectar concentration* (cal/μl)
H. rostrata	40 (37–42)	1.28 (1.15–1.43)
H. tortuosa	48 (45–52)	1.35 (1.32–1.43)
H. imbricata	25 (23–27)	0.88 (0.77–0.98)

* The range appears in parentheses; single values are means.

Table 3. Equations for the rate of nectar extraction by three hummingbird species at three species of *Heliconia* flowers; X values are microliters of nectar available; Y values are in seconds of foraging; N is the number of observations for each bird-flower combination.

Hummingbird	*Heliconia* sp.	Least-squares equation	N	S_{YX}
Phaethornis superciliosus	*H. tortuosa*	$Y = 1.26 + 0.39\,X$	55	± 3.21
P. superciliosus	*H. rostrata*	$Y = 1.30 + 0.25\,X$	53	± 2.65
P. superciliosus	*H. imbricata*	$Y = 0.80 + 0.27\,X$	23	± 2.26
Thalurania furcata (male)	*H. imbricata*	$Y = 1.11 + 0.13\,X$	36	± 1.70
Amazilia tzacatl	*H. imbricata*	$Y = 0.70 + 0.23\,X$	33	± 1.57

Table 4. Equations relating foraging costs in calories (Y) to energy uptake in calories (X) for three species of hummingbirds foraging at three species of *Heliconia* flowers; N is the number of observations for each bird-flower combination.

Hummingbird	*Heliconia* sp.	Least-squares equation	N	S_{YX}
Phaethornis superciliosus	*H. tortuosa*	$Y = 0.45 + 0.10\,X$	55	± 1.15
P. superciliosus	*H. rostrata*	$Y = 0.47 + 0.07\,X$	53	± 0.95
P. superciliosus	*H. imbricata*	$Y = 0.29 + 0.11\,X$	23	± 0.81
Thalurania furcata (male)	*H. imbricata*	$Y = 0.30 + 0.04\,X$	36	± 0.47
Amazilia tzacatl	*H. imbricata*	$Y = 0.21 + 0.08\,X$	33	± 0.48

volume results from Table 3, can be made, with differing results due to the variable input of flight costs as a function of body size, and of nectar quality as a function of sugar concentration. First, *P. superciliosus* is more efficient at extracting nectar from *H. rostrata* than at extracting nectar from either *H. tortuosa* or *H. imbricata* ($.10 > P > .05$). The extraction efficiency of *P. superciliosus* at *H. tortuosa* is not significantly different from that at *H. imbricata* ($P > .50$). The importance of the nectar concentration is apparent since the rates of nectar extraction at *H. rostrata* and *H. imbricata* do not differ significantly, but the extraction efficiencies at these two plants do differ significantly for *P. superciliosus*. Second, the extraction efficiency at *H. imbricata* is significantly higher for *T. furcata* than for *A. tzacatl* or for *P. superciliosus* ($P < .01$); this result is similar to the data on the rate of extraction. The importance of flight costs as a function of body size is apparent since *A. tzacatl* and *P. superciliosus* were similar in their rate of nectar extraction at *H. imbricata*, but the larger species (*P. superciliosus*) has a lower caloric extraction efficiency ($.10 > P > .05$) because of its higher foraging costs.

From these data it is clear that results of time comparisons may be different from the results of energetic comparisons of efficiency, and these differences must be kept in mind when one analyzes the strategy of resource exploitation by a consumer organism (*12*). The foraging strategy that is finally used depends on the richness of the reward, the predictability of a reward in time, and the cost of foraging. For a hummingbird the energetic costs of nectar foraging (assuming hovering is used) are high per unit time but the time used in search can be short because of the stationary, visible character of the flowers. The small prey of many small insectivorous birds may be relatively less predictable in time and space so that the total time required to capture a given prey item is higher. In general, small insectivores forage by hopping and short flights (*1, 3*) which are less expensive than hovering flight. For species that must spend long time periods to locate one energy unit of prey the search costs should be less than for species that can find one energy unit of prey in short time periods, if the species are to have the same foraging efficiency.

Theoretical considerations of predator-prey relationships suggest that, as the availability of prey decreases, the selectivity of the predators will also decrease (*12, 13*). The data in Table 4 suggest an analogous situation in hummingbirds: namely, a decreased advantage for flower selectivity when nectar availability is low. The similarity of the Y-intercepts at the several flowers indicates that major differences in foraging efficiency probably do not occur until the birds are exploiting relatively large caloric reservoirs at a foraging visit. Thus, under conditions of low nectar production or frequent visits to the flowers it should be unprofitable for a bird to discriminate between flower species.

In hummingbird-pollinated flowers, adaptations affecting foraging efficiency may be an important part of the plant's reproductive strategy. In hummingbird-flower interactions, nectar serves as an energy source to attract pollinators. There are strong selective pressures on obligately outcrossed flowers to maximize appropriate movement of pollen by increasing the probability that a pollinator will consecutively visit individuals of the same flower species (*14*). One method of achieving this may be to evolve differences in flower characteristics, such as nectar concentration and corolla length, than can affect the extraction efficiency of hummingbird species. Differences in corolla morphology probably affect mainly the rate of nectar extraction, but extraction efficiency also depends on nectar concentration. The efficiency with which pollinators can harvest the nectar of different flowers probably affects the regularity with which they visit specific plant species.

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