FOREAGING EFFICIENCY AND PARENTAL CARE IN *COLIBRI CORUSCANS*

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An important increase in the demand for energy and nutrients occurs during reproduction. Eggs and sperm must be produced and united, development must take place with energy for growth and maintenance, and the young must be provided for until they achieve independence (Ricklefs 1974). As a result, it has been hypothesized that food quality or quantity may influence such aspects of bird breeding biology as the pair bond (Lack 1968, Orians 1969a), clutch size (Lack 1966, 1968), mode of development (Lack 1968, Ricklefs 1974), synchronization of breeding in colonial species (Emlen and Demong 1975), and the period required for care of fledged young (Orians 1969b). Also, priorities in the allocation of energy may change during reproduction. For example, energy could become a focal point for parent-offspring conflict during the period of parental care of fledged young (Trivers 1974).

Hummingbirds generally do not form pair bonds, and males do not contribute to rearing the young (Lack 1968). However, reports of pair cooperation (*Panterpe insignis*, Wolf and Stiles 1970), and apparent male contribution to incubation and/or care of the young (Schafer 1952) exist. This report deals with time and energy budgets and foraging efficiency of a Sparkling Violetear (*Colibri coruscans*) caring for two recently fledged young. The results suggest that the post-fledging period of parental care may not involve a substantial increase in time or energy expenditure by the parent relative to non-breeding periods and that it may be characterized by negative energy budgets perhaps forcing independent foraging by the young.

MATERIALS AND METHODS

Fieldwork was conducted near the village of Tamboraque, Peru, 99 km east of Lima on the Central Highway. Observations were made on a hillside at 3,009 m elevation between 11 August and 30 September, 1974, during the dry season. The hillside vegetation was composed primarily of *Mutisia accuminata* shrubs with occasional cacti.

THE FLOWER

Mutisia accuminata (Compositae) is a common perennial shrub throughout the central Andes at elevations from 2,000–3,200 m. A given plant may produce flowers for 4–8 weeks. In the study area, *Mutisia* was at peak bloom from mid-August to mid-September and had ceased blooming by mid-October. Each inflorescence had 7–9 florets, and nectar was located at the base of each in a sealed chamber. The chamber wall was thick except at the top, and to obtain nectar a hummingbird had to pierce the chamber at the top with the lower mandible. This produced characteristic longitudinal slits which could be reproduced by piercing the nectar chambers with the lower mandible of a museum specimen; using the entire bill resulted in enlarged holes which were never observed.

The nectar chambers contained an average of 15.1 μl when full (range 11.6–18.2 μl) with a nectar concentration equivalent to 0.77 molar sucrose measured by a temperature-compensated refractometer (Hainsworth and Wolf 1972a). It was not possible to measure nectar production rates for individual florets to estimate nectar extraction rates by the hummingbirds (Hainsworth and Wolf 1972b, Wolf et al. 1976). However, all extraction rates that have been measured for hummingbirds (Hainsworth and Wolf 1972b, Wolf et al. 1972, 1976) and sunbirds (Wolf 1975, Gill and Wolf 1975, Wolf et al. 1975) are linear with a positive intercept. To estimate extraction rates for this flower, 260 probes by *Colibri coruscans* were timed with a stopwatch, and the average of the 20 shortest times was used for 0 μl intake and the average of the 20 longest times for 15.1 μl intake. The straight line connecting these values was the estimate of seconds required to extract a volume of nectar.

THE BIRD

Colibri coruscans is a common hummingbird of upper tropical to temperate zones from Venezuela south to Bolivia and northwestern Argentina (Meyer de Schauensee 1970). The sexes are monomorphic and could not be distinguished except by inference from behavior. The recently fledged young are easily distinguished by their buffy coloration. *C. coruscans* is a relatively large hummingbird with a mass of 0.076–0.087 Newton (N) (Ruschi in Greenwalt 1962, D. Tallman, pers.

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TABLE 1. Time budgets for individual *Colibri coruscans* expressed as percentage of time observed in each activity.

Date	Foraging	Sitting	Flycatching	Chasing	Changing perches	Gone	Total time (min)
18 Aug.[a]	25.0	65.4	0.8	2.1	1.2	5.5	170
21 Aug.	35.5	56.6	1.6	1.5	0.5	4.3	130
30 Aug.	36.1	57.5	1.3	1.7	0.9	2.5	64
2 Sept.[b]	28.0	60.5	6.7	0.8	1.8	2.2	190
4 Sept.	26.7	62.0	5.5	0.5	0.9	4.4	173
6 Sept.	30.2	61.0	5.4	1.2	1.1	1.1	188
8 Sept.	28.5	63.8	3.8	0	0.9	3.0	95
9 Sept.	29.3	63.0	2.4	2.9	1.1	1.3	149
11 Sept.	36.8	52.0	1.8	5.3	0.9	3.2	49
13 Sept.	39.2	52.9	1.1	0.8	1.2	4.8	183
15 Sept.	24.5	73.1	0.6	0.9	0.9	0	174
18 Sept.	33.5	56.5	0.6	2.3	2.1	5.0	191
20 Sept.	28.7	64.8	0.3	2.7	1.7	1.8	152
22 Sept.	42.0	49.7	1.7	3.5	1.9	1.2	155
25 Sept.	18.5	79.3	0.3	1.1	0.8	0	112
29 Sept.	37.1	59.6	0.5	2.6	0.2	0	76
30 Sept.	25.2	71.8	1.2	1.2	0.6	0	74

[a] Data for August are for one individual.
[b] Data for September are for a parent bird. In all instances the parent was caring for young.

comm.), a wing length of 74–84 mm ($n = 7$), and a bill length of 27–32 mm ($n = 7$) measured from gape to tip (collections of M. Koepke, Museo Historia Natural "Javier Prado," Lima, Peru).

Time budgets were obtained as described previously (Wolf and Hainsworth 1971, Wolf et al. 1976) using a stopwatch and tape recorder to time the categories of foraging, flycatching, perch changes, chases, and "gone." Time sitting was total observation time minus time in other categories. Individual foraging bouts were defined by intervals of at least 120 sec during which the birds were engaged in activities other than foraging or "gone." Ambient temperatures (±1.0°C) were measured in the shade at intervals, and a maximum-minimum thermometer was used to obtain minimum overnight temperatures.

Time budgets were obtained for 1–4 h continuous periods between 08:00 and 15:00 for two *Colibri coruscans.* The first was studied for 6 h over three days in mid- to late August. This bird subsequently left its territory. On 2 September, 1974 I discovered that the bird in the adjacent territory was caring for two recently-fledged young. The young were initially sedentary, and I could observe each parental feeding of the young while obtaining time budgets for the adult. The parent chased all other *Colibri*, *Metallura*, *Patagona*, or *Diglossa* that entered the territory. During 30 h of observation while the young were being cared for, I never observed a second *Colibri* care for the young or enter the territory without being chased, and I assumed that the parent was a female.

Several empirically derived prediction equations were related to obtain a direct estimate of the energetic efficiency of foraging bouts (achieved foraging efficiency, Wolf et al. 1975). Foraging bouts were timed, the number of flowers visited were counted and the percentage of time spent probing flowers on foraging bouts was measured. After accounting for the time spent moving between flowers, the seconds per flower (estimated from regression equations of total foraging time as a function of number of flowers visited) was used to calculate μl of nectar obtained per flower from the estimates of rate of nectar extraction.

I converted the times to energetic expenditures using two levels of expenditure for foraging and assuming a mass of 0.083 N. A cost of 27.03 watts/N was used for that portion of a foraging bout spent hovering while probing flowers. This is the sea level cost of hovering flight (Lasiewski 1963, Wolf and Hainsworth 1971, Berger and Hart 1972) increased by 6% to account for increased expenditures at 3,000 m altitude (Berger 1974). For that portion of a foraging bout spent in forward flight the cost of hovering was reduced by 15% to account for lower expenditures (Wolf et al. 1975). Energy intake was estimated from the calculated nectar volume intake times the energy value of *Mutisia* nectar (4.35 J/μl).

It is also possible to estimate foraging efficiencies indirectly from energy budgets (required foraging efficiency, Wolf et al. 1975). The calculated total daily energy expenditure divided by the cost for foraging is an estimate of the energy intake required per

TABLE 2. Energy budgets for the individual *Colibri coruscans* of table 1. All energetic values are in joules.

Date	Foraging[a]	Sitting	Non-foraging flight[b]	Overnight[c] no torpor/torpor	RFE[d] no torpor/torpor
18 Aug.	21,174	14,755	3,064	22,953/3,936	2.93/2.03
21 Aug.	30,067	13.742	2,692	22,953/3,936	2.31/1.68
30 Aug.	30,573	12,975	2,843	22,953/3,936	2.27/1.65
2 Sept.[e]	23,715	13,650	6,955	22,953/3,936	2.84/2.03
4 Sept.	22,614	13,989	5,087	22,953/3,936	2.86/2.02
6 Sept.	25,578	13,763	5,757	22,953/3,936	2.66/1.92
8 Sept.	24,146	14,374	3,362	22,953/3,936	2.68/1.90
9 Sept.	24,825	14,215	4,781	22,953/3,936	2.69/1.92
13 Sept.	33,211	11,937	2,315	22,953/3,936	2.12/1.55
15 Sept.	20,754	16,493	1,792	22,953/3,936	2.99/2.07
18 Sept.	28,379	12,749	3,437	22,953/3,936	2.38/1.71
20 Sept.	24,314	14,621	3,437	22,953/3,936	2.69/1.90
22 Sept.	35,581	11,213	5,230	22,953/3,936	2.11/1.57
25 Sept.	15,668	17,895	1,570	22,953/3,936	3.71/2.49

[a] 70% time hovering and 30% in forward flight.
[b] At 85% of cost of hovering flight.
[c] For 12.5 hours at an ambient temperature of 5°C.
[d] RFE = Required Foraging Efficiency or 24 h energetic costs divided by the cost for foraging (Wolf et al. 1975).
[e] All September data refer to the parent caring for young.

unit of energy expended in foraging to provide a neutral budget (Wolf et al. 1975). The values used to calculate energy budgets have been discussed in detail elsewhere (Wolf et al. 1975). Briefly, the calculations for flight categories were the same as given above. Overnight costs were calculated from a thermal conductance of 52.38 J/h × °C (Kleiber 1972) using an average overnight temperature of 5°C for 11.5 h for both homeothermic (body temperature of 41°C, Wolf and Hainsworth 1972) and torpid conditions (body temperature of 11°C and neglecting the costs of entry and arousal, Wolf and Hainsworth 1972, Wolf et al. 1976). Sitting costs during the day also were estimated from thermal conductance and were increased by a factor of 1.7 to account for the increased expenditure of postural effects in alert birds (Wolf and Hainsworth 1971).

RESULTS

TIME AND ENERGY BUDGETS

Most time categories for the *C. coruscans* caring for young varied little from those not caring for young (table 1). The exception was time spent flycatching which was higher for the parent during the first week of observations while she cared for young; this activity subsequently decreased.

Foraging time varied from 18.5 to 42.0% of total time within three days toward the end of the period of parental care. During the last day of care the parent may have fed only one young per visit and at a decreased visitation rate (see below). Other variations in the foraging time budgets presumably reflected variations in nectar availability on the territory; very slight changes in foraging efficiencies can result in considerable changes in time budgets for foraging at the measured foraging times (Wolf et al. 1975).

Conversion of time budgets to energy budgets allowed for similar comparisons. Variation in daily calculated expenditures for non-foraging flight was due primarily to variation in flycatching activity and chases (table 2). As with other nectar-feeding birds (Wolf and Hainsworth 1971, Wolf 1975a, Wolf et al. 1976), most variation in energy expenditures resulted from differences in the costs of foraging and sitting. Total calculated daily energy expenditures varied from 58,086 to 47,977 joules, assuming no torpor, and from 39,069 to 55,959 joules, assuming torpor at night. These values are 5.6–7.2 and 3.7–5.4 times standard metabolic rate, respectively (Lasiewski and Dawson 1967).

Calculations of required foraging efficiencies (RFE) are given in table 2. To provide a balanced, 24 h energy budget, these hummingbirds would need to consume 6.49 to 10.43 joules for every joule expended in foraging if they were torpid at night and 8.83 to 15.53 joules for each joule foraging if they were not.

NECTAR EXTRACTION AND FORAGING BOUT EFFICIENCY

Using the two point method to define the extraction rate equation gave:

$$\text{Seconds probing} = 0.5 + 0.59\ (\mu l)$$

with about 0.5 sec required to probe an empty floret. While the *C. coruscans* were foraging the following relationship was found:

$$\text{Time in flowers} = -0.89 + 0.69\ (\text{Total time})$$

TABLE 3. Achieved foraging efficiencies calculated for bout lengths of different duration.[a]

Bout length (sec)	Cost/bout (joules)	No. of flowers	μl	Joules intake	Achieved efficiency (intake/cost)
67.8	154.9	15.0	63.6	276.8	1.78
75.5	171.7	16.8	71.2	309.8	1.80
106.0	238.7	23.8	100.9	439.2	1.85
111.8	251.2	25.1	106.4	463.1	1.85
137.3	305.6	31.0	131.4	571.5	1.88
167.0	368.5	37.8	160.3	697.5	1.89
192.1	422.9	43.6	184.9	804.7	1.90
221.5	485.7	50.3	213.3	928.3	1.91
223.1	489.9	50.7	214.9	935.0	1.91
248.6	535.9	56.6	240.0	1,044.2	1.92

[a] Data for 8 September, 1974. Each bout includes 5 sec round trip time from perch to first flower visit.

with N = 40, r = 0.98; $S_{yx} = \pm 1.819$. The intercept was not different from zero ($P > 0.05$), and the slope was significant ($P < 0.05$). The proportion of time spent probing flowers was high compared with other nectarivore-flower systems (49–53%, Wolf 1975, Wolf et al. 1976). However, as in other systems, the proportions of time in and between flowers were the same regardless of flower characteristics such as nectar availability and spacing, which were not controlled in the measurements.

On 8 September the following relationship was obtained between total time foraging and number of flowers visited:

$$\text{Total time (sec)} = 2.51 + 4.35\ (\text{No. of flowers})$$

with N = 21, r = 0.97, $S_{yx} = \pm 3.094$. The intercept of 2.51 sec represented approximately the time from a perch to the flowers and was increased to a round trip of 5.0 sec for energetic calculations. The 4.35 sec/flower was reduced by 31% to account for time spent moving between flowers to give 3.0 sec/flower. From the extraction rate estimate, the average flower visited for this time on this day would yield about 4.2 μl of nectar or 18.0 J.

From measurements of the lengths of individual foraging bouts for this day, the numbers of flowers visited were calculated along with the energy intake, assuming that each flower provided the estimated 4.2 μl. Energy intakes were divided by the cost of each bout to calculate foraging efficiencies (table 3; assuming 70% hovering and 30% in forward flight based on the measurements of proportions of a bout spent probing and moving between flowers and assuming 100% assimilation of nectar energy, Hainsworth 1974). The increase in efficiency with length of foraging bouts (table 3) resulted from the decreasing impact of the round trip cost of getting to and from the flowers (Wolf 1975).

CARE OF YOUNG

The frequency of feeding the young remained relatively constant until the last day of parental care. Prior to this time an average of 2.9 ± 1.1 (95% confidence interval) to 4.9 ± 1.5 trips/h were made to feed young. On the last day the rate decreased to 2.0 ± 1.9 trips/h. Before 13 September each trip to feed the young involved feeding both fledglings. Subsequently, the young began to fly more, and some feedings involved only one young. The parent fed the young at only one site within the territory. The decreased rate of feeding on the last day of parental care was accompanied by increased mobility of the young. Occasionally during the last day the parent visited the feeding site when both young were absent.

Except for two days of parental care (including the last day), foraging bouts prior to feeding of the young were significantly ($P < 0.05$) longer than those when young were not fed. Also, the average lengths of foraging bouts for each day prior to feeding young were positively related to percent time foraging; bout lengths when young were not fed were not related to percent time foraging (fig. 1). There was no relationship between average number of foraging bouts per hour ($\bar{x} = 6.5$; R = 5.4–7.5) and percent time foraging prior to feeding young and when young were not fed ($r_s = 0.28$, $P > 0.30$). This indicates that most adjustments to changes in resource availability were made before feeding young through the length of feeding bouts rather than their frequency.

Laboratory studies of hummingbird feeding suggest that the time between two foraging bouts is related to the time spent foraging on the initial bout. At the same rate of

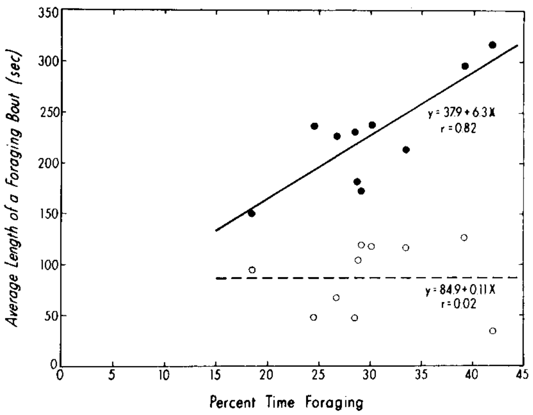

FIGURE 1. Average foraging bout length as a function of percent time foraging (table 1) for *C. coruscans* prior to feeding young (closed circles) and when young were not fed (open circles).

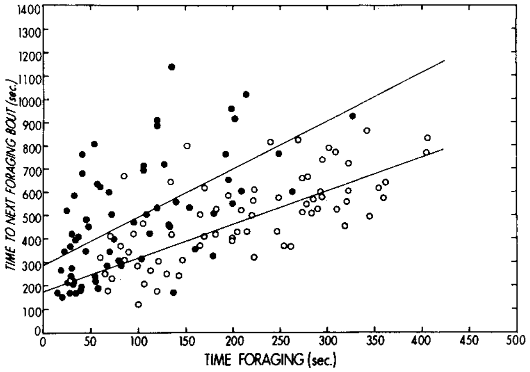

FIGURE 2. Time to next foraging bout as a function of time foraging. Each point represents an individual foraging bout. Closed circles and upper line are for bouts prior to not feeding young; open circles and lower line are for bouts when young were fed.

intake, longer foraging bouts should yield more nectar; likewise, energy expenditure between bouts should determine when the next foraging episode is initiated (Wolf and Hainsworth 1977). If the parent were delivering nectar to the young, the relationship between time foraging and the time to the next foraging bout should be different for bouts before feeding young and those after which young are not fed. This was the case (fig. 2). For a given time foraging, the parent spent less time before the next bout when she fed young (slopes significantly different, $P < 0.01$) suggesting that part of the nectar she had consumed was delivered to the young.

FLYCATCHING

Because flycatching presumably contributed to the nutritional and energetic requirements of the recently fledged young, it deserves to be examined in more detail. The average number of times the parent left its perch to flycatch (flycatch attempts/min) was positively related to percent time flycatching ($r = 0.98$, $P < 0.001$) such that:

$$\text{Flycatch attempts/min} = 0.09 + 0.20\ (\%\ \text{Time flycatching})$$

with $N = 10$; $S_{yx} = \pm\ 0.0787$. The slope was significant ($P < 0.05$), and the intercept was not significantly different from zero ($P > 0.05$). This would give 360 flycatch attempts per hour if the hummingbird were to spend 30% of its time foraging for insects instead of nectar. If each insect had a dry mass of 0.0000147 N (about the size of *Drosophila*, Scheithauer 1967, Wolf 1975) and the digestive efficiency was 70% (Hainsworth 1974, Wolf 1975), with 2,304,770 J/N (Golley 1961) and one insect per attempt, the birds could obtain 98,285 J in 11.5 h. I have no information on the efficiency of flycatching attempts by hummingbirds, but even if it were as low as 40%, the birds could achieve their total required energy intake if they engaged in flycatching for 30% of the time instead of nectar feeding.

DISCUSSION

With the need to provide for her own costs and the maintenance costs of two fledged young, a parent *C. coruscans* might be expected to have high energy demands. Time and energy budgets were somewhat higher, and estimated required foraging efficiencies were lower, than for males of three hummingbird species visiting flowers in a highland, tropical habitat in Costa Rica (range of required efficiencies: 2.51–5.57 with torpor, and 3.26–7.93 without torpor, Wolf et al. 1976). However, most comparisons with other nectar-feeding birds suggest that energy from nectar could be obtained without a substantial increase in foraging time during the period of parental care. For example, most of the time budget measurements for foraging were similar to the larger values within the range measured for a number of nectar feeding birds (10–35%; table 1, Pearson 1954, Wolf and Hainsworth 1971, Wolf 1975, Wolf et al. 1976). The question remains, however, whether the parent bird was providing all of the energy required for maintenance of the group.

The ability of the adult to provide for herself and two young is best determined from the more direct estimates of achieved foraging efficiency obtained for 8 September (table 3). Young were fed after relatively long foraging bouts where the highest efficiency was 1.92:1. If a young weighed 0.078 N, it would have a calculated sitting cost during a 11.5 h, 20°C day of 20,908 J and an overnight cost for 12.5 h at 5°C of 22,918 J without torpor and 3,820 J with torpor. If neither young was torpid at night, their combined daily maintenance requirements would be 87,653 J, and if they were torpid, daily requirements would be 49,456 J. The cost for the adult for 8 September 1974 was 64,836 J without torpor and 45,818 J with torpor at night. The maximum observed achieved foraging efficiency for this day (with 24,146 J expended foraging) would give a total intake of 46,361 J from nectar. This intake would barely be sufficient to provide for the costs of the adult if she were torpid at night, and several foraging bouts would have provided less efficient intake than the 1.92:1 value (table 3).

These calculations do not take into account the energy resulting from flycatching activities. Using the assumptions given earlier, the maximum percent time flycatching of 6.7% (table 1) would have yielded 21,605 J/day if every attempt provided one insect the size of a fruit fly. This would supply only part of the energy needed for maintenance of the young and only for the period after fledging when flycatching activity was high (table 1).

These considerations lead to the conclusion that the parent may have been operating on a negative energy budget relative to the requirements of all three birds. Energy in the form of nectar and insects was delivered to the young but apparently not enough to cover all costs on a daily basis. The parent probably assumed some of the total deficit as her behavior suggested compensations in foraging bout length to provide greater nectar intake before feeding the young. The young could also have reduced their requirements by entering torpor at night. However, they would eventually be forced to forage on their own or face starvation. By providing some energy to the young after fledging, the parent could delay independence and allow a degree of "practice" by the young (Orians 1969b), but failure to provide all energy requirements of the young could be important in forcing independence. Recent examinations of parent-offspring relationships suggest that parent-offspring conflict should increase during the period of parental care (Trivers 1974). In energetic terms this conflict may create a situation where the cost-to-benefit relationships are such that a negative energy budget for the offspring is an appropriate part of parental behavior.

That the parent may have exercised some degree of control over the energy deficit of the young is suggested from the observation that she did not forage as long as she could have before feeding the young. The crop of a 0.083 N hummingbird should hold about 1,000 μl (Hainsworth and Wolf 1972a), but the longest bout on 8 September 1974 yielded only a estimated 240 μl (table 3). An alternative explanation would be that the defended territory provided insufficient nectar, so that further extensions of foraging time would have proved inefficient.

Flycatching appeared to provide a significant portion of the energy given to the young and the behavior of the parent suggested that this could be as efficient in providing energy as foraging for nectar (assuming at least 40% success in insect captures). If flycatching is as efficient as the calculations suggest, the use of nectar as a primary energy source by most hummingbirds may be related to long term efficiency characteristics based on its stationary, predictable nature rather than a proximate ability of the birds to exploit nectar more efficiently than insects.

SUMMARY

Time and energy budgets and estimates of foraging efficiencies were obtained for two *Colibri coruscans*. One of these was caring for two recently fledged young while territorial at flowers of *Mutisia accuminata* at an elevation of 3,000 m in the Andes of Central Peru. Despite somewhat lower estimates of foraging efficiencies than for other nectarivores, parental care was accomplished without substantial increases in foraging time. Flycatching increased for the first week and subsequently declined; estimates of the efficiency of flycatching suggested values similar to using nectar as a food source.

Calculations based on achieved foraging efficiency for one day suggested that the parent was not meeting all the energy requirements of herself and the two young. Foraging behavior suggested increased nectar intake by the parent before feeding young and the delivery of some of this nectar to the young. Also, increased flycatching should have been important in supplying energy. However, failure by the parent to provide for all energy requirements of the young may have been important in forcing their independent foraging.

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