TESTS OF A MODEL OF FOOD PASSAGE RATES IN HUMMINGBIRDS

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ABSTRACT.—I calculated food passage rates for caged hummingbirds (*Amazilia saucerottei* and *Chlorostilbon canivetii*), after *ad libitum* feeding and after single meals. Daytime excretion rates for both species conformed to a negative exponential function and were positively correlated with meal size. This supports a negative exponential model, rather than a linear model, of crop emptying rates and confirms that crop emptying rates parallel passage rates in the digestive tract.

Active birds fed *ad libitum* cleared all excess water from their crops and gastrointestinal (GI) tracts in less than 25 min after food deprivation. In daytime trials both species had a statistically significant linear relationship between the size of a meal and the time required to excrete excess water. In 30 min, active birds can pass crop contents that are more than twice the volume of an average meal. This allows the use of 30-min deprivation periods to obtain body-mass measurements that are not subject to water content error. *Ad libitum* feeding rates were only 45% (*Amazilia*) and 67% (*Chlorostilbon*) of estimated maximum food passage rates. Although *Chlorostilbon* may be feeding at rates closer to its physiological limit, both species seem capable of processing food considerably faster than their *ad libitum* intake rates.
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HUMMINGBIRDS have extremely high mass-specific metabolic rates and an energetically expensive foraging mode (hovering flight). Thus, they must consume relatively large amounts of energy-rich food, usually nectar (Hixon et al. 1983, Karasov et al. 1986). Many ecological, morphological, and behavioral factors can impose limits on the food intake rate of hummingbirds. Early studies on how hummingbirds process their meals dealt primarily with crop function (Hainsworth and Wolf 1972) and assimilation efficiency (Hainsworth 1974). Recently the digestive physiology of hummingbirds has been investigated as another possible constraint on energy intake. By examining the rates at which food empties from the crop and is assimilated in the intestinal tract, Diamond et al. (1986) and Karasov et al. (1986) demonstrated that the crop volume in *Selasphorus rufus* and *Calypte anna* decreased (following a 100-μl meal) as a negative exponential function of time. They proposed that crop emptying time was set by two digestive processes: acidification of the meal in the stomach and absorption of sugars in the small intestine. Finally, they suggested that these physiological constraints on food passage rates limited rates of food intake. Thus, the large amount of time hummingbirds spend perching instead of feeding (Stiles 1971, Wolf and Hainsworth 1971, Ewald and Carpenter 1978, Hixon et al. 1983) may be required for the crop to empty sufficiently to accommodate the next meal.

The first goal of my study was to test four predictions based on the Karasov et al. (1986) model. If waste is not stored in appreciable amounts, then (1) excretion rates should follow a negative exponential decline over time, and (2) maximal crop emptying rates (and thus maximal excretion rates) should be positively correlated with meal size. If crop and gastrointestinal (GI) passage rates limit food intake rates, then (3) maximal excretion rates should correspond closely to intake rates of normally active birds, and (4) species with feeding rates closer to their maximal passage rates should spend more time perching than those with lower feeding rates.

The second goal was to determine how rapidly hummingbirds pass the contents of their crops and GI tracts after feeding. Birds that are digesta-free should be at a relatively "stable weight" (unbiased by excess water weight), with additional weight loss at a minimal baseline rate determined by metabolic expenditures and evaporative water loss (EWL). If relatively short deprivation periods can yield reliable stable weights without undue stress to birds, this could

provide a means for measuring fat production (and hence net energy gain) during the daily foraging period.

METHODS

I measured rates of food intake, excretion, and time to reach a stable weight in two hummingbird species that differ markedly in body size and foraging mode. I mist-netted six *Amazilia saucerottei* (body mass = 3.98 ± 0.55 g) and six *Chlorostilbon canivetii* (2.12 ± 0.19 g) near Monteverde, Costa Rica, and kept them in a 13 m^3 communal aviary on a diet of sucrose solution (20% by weight) and *Drosophila, ad libitum*. At the end of the experiment I released all birds at the site of capture. For each of 15 trials per species I moved birds to individual 1 m^3 cages with *ad libitum* 20% sucrose solution (but no *Drosophila*) for 2 h. I then deprived each subject of food for 75 min and recorded its mass from a perch-balance (±0.001 g) every 5 min (the "ad lib" runs). I then offered each bird a vial of 20% sucrose solution for 60 s. To ensure an adequate range of meal sizes across the 15 trials, the contents of the vial varied from 100 to 500 μl. I weighed each vial before and after feeding, and recorded meal size (±0.001 g). I again deprived each bird of food for another 75 min and recorded body mass every 5 min (the "single-meal" runs). At the end of each trial I fed birds *ad libitum* on 20% sucrose solution for 10 min and returned them to the communal aviary. I conducted the daytime trials between 0730 and 1635. I used subjects for one trial per day, for a total of two or three trials per bird.

To determine if short deprivation periods could also be used to obtain stable weights at the end of the foraging day, I conducted a second set of trials on six individuals of each species just prior to roosting. The protocol was as described above, except that after the experimental meal (offered at ca. 1800, the normal roosting time), I turned off the lights, and birds roosted. I recorded body masses for a minimum of 100 min.

Changes in mass before reaching a stable level could be due to excretion, evaporative water loss (EWL), changes in RQ, or all of these. Because I recorded mass after meals (while sucrose was being processed), RQ was probably constant at ca. 1. Birds consumed more than sufficient water to compensate for EWL and maintain tissue water balance, as evidenced by high rates of water excretion. Thus, were this water not lost to evaporation, it would be excreted as excess. For purposes of analysis, I included EWL with excretion and equated weight-loss rate with excretion rate.

Analysis.—I analyzed data from each run individually by nonlinear regression (BMDP program PAR, Dixon 1985) to fit parameters of the model:

$$\Delta wt = P1 + P2 \cdot e^{P3 \cdot \Delta t}, \quad (1)$$

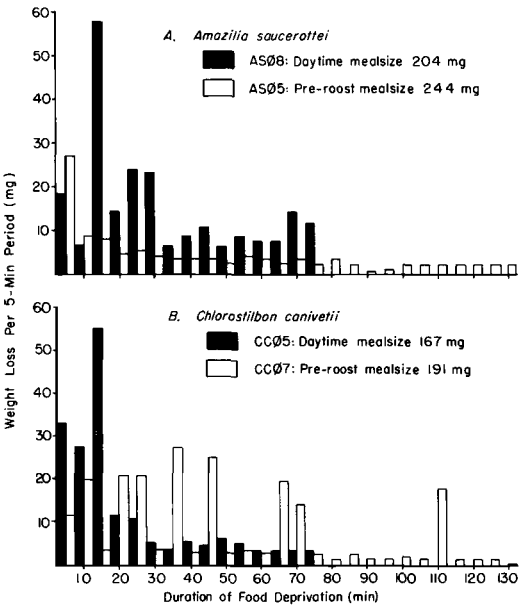

Fig. 1. Mass-loss rates after a single meal for active vs. roosting birds. Active birds during the day exhibited a short lag time before a sharp peak followed by exponential decline. Roosting birds exhibited a range of responses, from virtually no weight loss following a meal (top), to very intermittent and irregular weight loss (bottom). Daytime birds had smaller meals, but passed food much more rapidly during the first hour than did the roosting birds.

where Δwt is weight loss during the 5-min period ending at Δt, Δt is time (min) since deprivation began, and P1–P3 are unknown parameters solved by iteration.

In preliminary experiments both species reached stable rates of weight loss in 40–45 min (H. Tiebout unpubl. data). I calculated the baseline rate of weight loss for each run as the mean of the last six weight loss measurements (Δt = 50 to 75 min). Then I calculated the time at which this decay curve (Eq. 1 for each run) intersected the 95% confidence interval for the baseline rate. This point represented the end of the first 5-min measurement period for which the rate of weight loss was equivalent to the baseline rate. I subtracted 5 min from this time to obtain the time to first reach stable mass. I used the maximum weight loss during any 5-, 10-, and 15-min time block (MAX5, MAX10, and MAX15, respectively) to determine the effects of meal size on excretion rate.

Results are reported as $\bar{x} \pm SD$. I performed statistical tests between groups using one-way ANOVA (BMDP program 7D; in cases of unequal variances, I used the Brown-Forsythe ANOVA [Dixon 1985]). I analyzed data from daytime and nighttime trials sep-

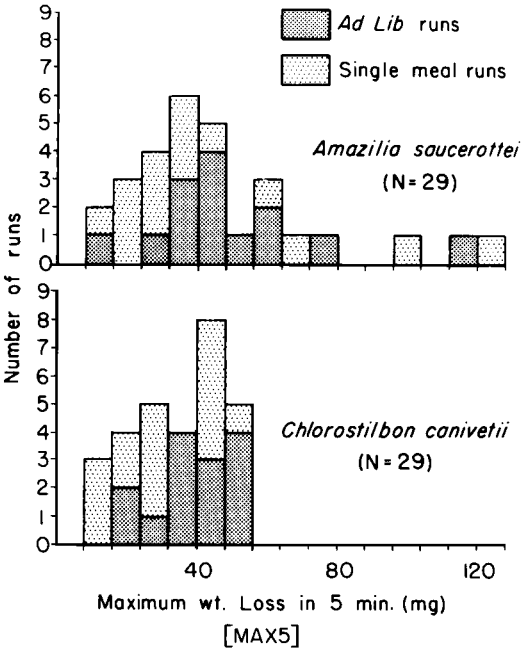

Fig. 2. Maximum weight loss in 5 min (MAX5) after *ad libitum* feeding and single meals during daytime runs. The distribution for *Amazilia saucerottei* is approximately normal, while that for *Chlorostilbon canivetii* is sharply truncated at 56 mg.

arately. One daytime ad lib run for each species was lost due to feeder malfunction.

Results

For both species, daytime excretion rates conformed to negative exponential functions. Ad lib runs showed this response as soon as deprivation began (with one exception), whereas single-meal runs usually showed a brief lag time before a peak followed by exponential decline (Fig. 1, daytime trials). For both species, excretion rates were highly positively correlated with meal size (Table 1). In all cases the coefficient of correlation increased with increasing time period.

For the ad lib runs, MAX5 did not differ significantly between species (50.1 ± 24.3 and 41.6 ± 12.1 mg/5 min; *Amazilia* and *Chlorostilbon*, respectively). The distribution for *Chlorostilbon*, however, was strongly truncated on the right, with no MAX5 values >56 mg (Fig. 2). Within each species there was no significant difference in the maximum MAX5 value for *ad libitum* (118 vs. 56 mg/5 min; *Amazilia* and *Chlorostilbon*, respectively) compared to single-meal runs (125 vs. 55 mg/5 min; *Amazilia* and *Chlorostilbon*, respectively). In each case *Amazilia* exhibited maximum excretion rates more than twice as great as did *Chlorostilbon* ($P < 0.05$).

Table 1. Correlations between meal size and excretion rate for *Chlorostilbon canivetii* and *Amazilia saucerottei* during daytime and post-roosting nighttime trials.[a]

	5 min (MAX5)	10 min (MAX10)	15 min (MAX15)
Daytime			
Amazilia	0.9244**	0.9574**	0.9676**
Chlorostilbon	0.6915**	0.8448**	0.8672**
Combined	0.8417**	0.8988**	0.9246**
Nighttime			
Combined	0.3356 NS	0.4676 NS	0.5651 NS

[a] ** = $P < 0.01$; NS = not significant.

For the daytime single-meal runs, the relationship between meal size in mg (MSIZE) and the time (min) after deprivation to reach a stable mass (TSTABLE) fit a linear model.

Amazilia: TSTABLE = 0.0971(MSIZE) + 5.048 (2)
($r = 0.608$, $P < 0.05$)

Chlorostilbon: TSTABLE = 0.1001(MSIZE) + 10.34 (3)
($r = 0.709$, $P < 0.01$)

Birds fed *ad libitum* reached stable weights very quickly after deprivation began (17.9 ± 9.3 and 24.4 ± 8.2 min; *Amazilia* and *Chlorostilbon*, respectively).

Excretion rates for birds roosting after single meals fit neither linear nor nonlinear models consistently. Thus, it was impossible to calculate TSTABLE for roosting birds. Both species exhibited variable responses (Fig. 1). In some instances birds passed very little, if any, of their pre-roost meals (Fig. 1A). Although body masses "stabilized," most of the water from the last meal was retained for >2 h. In other instances roosting birds exhibited intermittent peaks of excretion with no clear stabilization (Fig. 1B). Roosting excretion rates were low compared to daytime rates (MAX5 values: 34.7 ± 16.0 and 23.3 ± 10.9; *Amazilia* and *Chlorostilbon*, respectively) and showed no significant correlation with the size of meal eaten before roosting (Table 1).

DISCUSSION

Tests of excretion rate predictions.—Daytime excretion rates after deprivation followed a negative exponential decline over time. This is consistent with the Diamond et al. (1986) and Karasov et al. (1986) model that digestive processes set crop emptying rates, which also conform to a negative exponential function (see also Hainsworth 1978). The strong positive correlation between meal size and maximum excretion rate, however, seems inconsistent with the suggestion that digestive processes set crop emptying time. Although this correlation would be predicted from a negative exponential model of crop emptying (but not from a linear model), I believe that the regulatory mechanism functions in the crop rather than the GI tract. If processes in the GI tract constrained crop emptying rates, then there should exist a crop volume threshold above which excretion rate would not increase. This was not found. Similarly, if gastric acid or some digestive enzyme were limiting, then its exhaustion at high rates of food passage would result in a sharp peak in excretion rates after large meals, followed by depressed rates. The increasing coefficients of correlation from MAX5 to MAX15 (Table 1) indicate this is not the case.

Application to experimental design.—To use short deprivation periods (DPs) to obtain reliable stable weights, periods must be long enough to allow passage of excess water, yet short enough so that birds do not incur an irreversible energy debt (see Tooze and Gass 1985). Hainsworth and Wolf (1972) found that fluid passes through a hummingbird's digestive tract in about 0.5 h. Accordingly, Hainsworth et al. (1977, 1981) used 30-min DPs to minimize the effects of water exchange on mass measurements. During my daytime ad lib runs, both species reached stable weights after a mean deprivation time of <25 min. After 45 min, however, some birds began to show signs of entering daytime torpor (see Tooze and Gass 1985), and one *Chlorostilbon* had to be revived by hand. This further supports the use of a 30-min DP as a conservative but reliable method.

From the regression equations for MSIZE vs. TSTABLE, I estimated the largest meal each species could consume and still reach a stable weight within 30 min. Potentially, in 30 min *Amazilia* could process a meal of about 257 mg of 20% sucrose solution (Eq. 2), compared to its mean meal size of 112.1 ± 42.0 mg (n = 6 birds measured for 2 days each; Tiebout in prep.). *Chlorostilbon* could process about 196 mg (Eq. 3), compared to its normal meal of 69.5 ± 19.8 mg (n = 6 birds measured for 2 days each; Tiebout in prep.). If crop contents equal the average meal size (Karasov et al. 1986), or even if they exceed twice the average meal size, these figures provide independent theoretical support that stable weight should be reached within 30 min after deprivation.

Finally, because passage rate is a negative exponential function of time, small errors in estimating the actual time to reach stable weight will result in relatively small errors in estimating true stable weight. For example, one *Amazilia* during daytime deprivation after *ad libitum* feeding reached stable weight in 15 min, after losing 74 mg. The time to lose one-half of this mass was only 4.7 min. This agrees closely with the figure reported by Karasov et al. (1986) and Diamond et al. (1986), based on a negative exponential model, of 4.1 min to empty one-half of a 100-μl meal of 20% sucrose solution from the crop (a 100-μl meal consists of 86.4 mg H_2O).

Roosting *Amazilia* and *Chlorostilbon* processed crop contents differently from active birds. For these species, reliable stable weights could not be obtained using standard 30-min post-roost DPs (or any other duration <2 h), as was done for *Archilochus alexandri* (Hainsworth et al. 1977) and *Eugenes fulgens* and *Lampornis clemenciae* (Hainsworth et al. 1981). The irregular weight loss curves (Fig. 1) could reflect changes in crop emptying rates, digestion and assimilation rates, waste-water storage and excretion rates, and substrates metabolized. For example, roosting birds might exhibit reduced crop emptying rates if they metabolize carbohydrates directly rather than convert sugars to fat that is then metabolized. Because energy is lost when sugars are stored as fat, the former would be energetically more efficient. Kruger et al. (1982), however, found that for 17 species of hummingbird, RQ changed from daytime values of 1.0 (carbohydrate metabolism) to 0.8 (fat metabolism) within 40 min after roosting. Roosting birds may process meals in essentially the same way as active birds, except that waste water may be retained longer. This might serve to protect against excessive evaporative water loss during the night.

Relationship between passage rates and feeding rates.—Assuming that maximum rates of weight loss during 5-min periods (MAX5) estimate ex-

cretion rates accurately and that assimilation efficiencies are ca. 100% (Hainsworth 1974), I estimated average and maximum potential rates of food intake from the daytime ad lib runs. These maximum potential rates apply only to hummingbirds under normal, nonstressed conditions. Maximum intake rates could increase above these estimates when birds are subjected to increased metabolic demand (H. Tiebout unpubl. data; L. Gass pers. comm.). Using the mean MAX5 for each species and assuming the excretion rate represents 80% of intake rate (for 20% sucrose solution), *Amazilia* and *Chlorostilbon* would consume 9,018 and 7,488 mg of food, respectively, over a 12-h foraging day. These figures agree well with measured *ad libitum* rates of 10,126 ± 1,686 for *Amazilia* and 6,731 ± 1,054 mg/day for *Chlorostilbon* (H. Tiebout pers. obs.). Using the maximum MAX5 value for each species to calculate maximum potential rates of food intake, I found estimates of 22,500 mg/day for *Amazilia* and 10,080 mg/day for *Chlorostilbon.*

If these latter estimates represent the physiological limits to food intake for unstressed birds under conditions when processing rates can be maximized (i.e. when birds can have either full crops, large meals, or both), then *Amazilia* appears to feed at less than one-half its potential rate (10,126/22,500 = 45%). *Chlorostilbon* may be closer to its intake limit (67%), as suggested further by the extremely truncated distribution of excretion rates during ad lib runs (Fig. 2). Diamond et al. (1986) argued that such a physiological constraint on feeding rate may explain the high percentage of time hummingbirds spend perching instead of foraging. If this is the case, then *Chlorostilbon* should spend more time perching than *Amazilia.* In cage studies, however, *Chlorostilbon* spent somewhat less time perching than *Amazilia* (68.2 vs. 73.9%, respectively, $P > 0.05$; H. Tiebout in prep.). This difference may be even greater in the wild. To exploit its typical array of widely dispersed resources (Feinsinger 1976, Feinsinger and Colwell 1978), *Chlorostilbon* may spend up to 75% of its waking time in foraging flight (P. Feinsinger pers. comm.). Under such conditions, birds may actually increase food intake rates to balance their energy budgets against increased foraging flight costs. Thus, they would be even closer to their physiological limits of nectar processing than when food is more easily obtained. The relationship between sitting time and physiological constraints on feeding rates seems tenuous at best. Perhaps some other process, such as minimizing energy expenditure, may explain perching time in hummingbirds. Furthermore, it has not been determined that any hummingbird species achieves intake rates in the field that are high enough to be constrained by the physiological processes of digestion.

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100 Years Ago in The Auk

From "Restoration of an Audubonian form of *Geothlypis trichas* to the American avifauna" by E. M. Hasbrouck (1889, Auk 6: 167)

"More than a year ago while comparing specimens of the genus *Geothlypis*, one in particular arrested my attention as being materially different from any in my collection, and from any I had seen. It is numbered 442 and was taken by myself at Big Lake George, Florida, March 18, 1886. I carried it to Mr. Ridgway who, after comparing it with the series in the Smithsonian, declared it different from anything he had seen, and probably a new race, but advised me to say nothing concerning it until I secured more of the same variety. In accordance with his counsel I visited Florida in December of the past year for the purpose of securing as many as possible, and although unable to reach the scene of the first capture, I was successful in finding the bird abundant in Putnam County in the vicinity of Palatka, and was fortunate in obtaining seven more; three males and four females, all of which (the males) were nearly exact counterparts of the type with the exception of one immature male referred to later. On reaching Washington I submitted the entire series of eight to Mr. Ridgway, and with the assistance of Dr. Stejneger, compared them a second time; we found them differing considerably from the true *trichas* in possessing the larger size and more extended yellow beneath of *occidentalis*, together with an extremely narrow and paler ashy band behind the mask, and from *occidentalis* by the paler yellow throat and less orange of *trichas*. Audubon (Orn. Biog., Vol. I, 1832, p. 124, pl. 24) describes an *immature* specimen of the Yellow-throat taken in Mississippi, to which he gives the name *Sylvia roscoe*, and afterwards refers it to *trichas*: the description tallies almost exactly with mine above mentioned, while specimens in the Smithsonian collection from the Gulf States and Mississippi Valley agree closely with mine, thus leaving little room for doubt that it is a valid race between *Geothlypis trichas* and *Geothlypis trichas occidentalis*. I therefore have the pleasure of restoring a long neglected form to the American fauna, giving to it the name *Geothlypis trichas roscoe* (Aud.)."