OXYGEN CONSUMPTION DURING HOVER-FEEDING IN FREE-RANGING ANNA HUMMINGBIRDS

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SUMMARY

Rates of oxygen consumption during hover-feeding of wild, unrestrained, adult male Anna hummingbirds (*Calypte anna*) were measured with an artificial outdoor feeder converted into a respirometer mask. A computer sampled changes in O_2 concentration in air drawn through the mask, automatically detecting the presence of a hummingbird from a drop in the O_2 concentration, and photoelectrically timing the duration over which the feeder functioned as a mask. Birds coming to the feeder were weighed on a trapeze perch suspended from a force transducer. Feeding bouts consisted of sallies which carried the head in and out of the feeding mask about once a second. The volume of O_2 consumed per feeding sally was linearly related to the length of the sally. The energy cost of hover-feeding in five hummingbirds, mean mass 4·6 g, was $41·5 \pm 6·3 \, \text{ml} \, O_2 \, \text{g}^{-1} \, \text{h}^{-1}$.

INTRODUCTION

Since the pioneering studies of Pearson (1950), the energy cost of hummingbird hovering flight has been measured by a number of investigators using either small containers (Lasiewski, 1963; Wolf & Hainsworth, 1971; Schuchmann, 1979; Epting, 1980), feeders modified to function as masks (Berger & Hart, 1972; Berger, 1974; Epting, 1980), or masks (Berger, 1985). As the investigators themselves have often pointed out, all these methods have technical deficiences related to the tunnel and ground effects associated with powerful movements of air within the confines of the respirometer chamber, problems of constraint on the flight movements of the birds associated with masks and tubing, unnatural durations and patterns of hovering, and the uncertain 'training condition' of the captive birds being measured – in captivity, Anna hummingbirds (*Calypte anna*) stabilize at 80–90 % of their mass at capture and spend only half as much time flying as they do in the wild (Stiles, 1971).

In view of the variety of techniques and calculations that have been employed and the variety of taxa that have been studied, it is not surprising that a wide range of values for the energy cost of hovering flight in hummingbirds has been reported. However, the consensus is that at air temperatures near 20 °C hummingbirds

weighing 3–10g consume between 40 and $50 \text{ ml } O_2 \text{g}^{-1} \text{h}^{-1}$ while hovering. This range of values, which is equivalent to about 1 W for a 4-g hummingbird, exceeds the metabolic rates of all other vertebrates, but it is far from the maximum of which hummingbirds are capable (Berger, 1974; Epting, 1980). The reasonable value of $43–44 \text{ ml } O_2 \text{g}^{-1} \text{h}^{-1}$ for the cost of hovering has often been used in ecological studies and foraging models despite the fact that methodological difficulties exist in all of the procedures upon which it is based.

Although in theory it would be desirable to separate the cost of imbibing nectar from the cost of hovering, the data presently available do not allow this distinction to be made.

From a strictly technical point of view, the most satisfactory measurements of the cost of hummingbird hovering are probably those of Berger & Hart (1972), in which birds hovered for 20s or more at a feeder-mask housed in a 1 m^3 cage, and those of Epting (1980), in which measurements were made using a feeder-mask and a carefully calibrated photoelectric timing system. However, many species feed inter-mittently for periods of less than 1s, even while remaining at a single food source, advancing and retreating many times in the course of a single feeding bout.

Because hummingbirds, as a consequence of their feeding habits, are often the animals of choice for foraging studies and foraging models, and also because their capacity for hovering flight is unparalleled in any other bird, it is of interest to test and evaluate this consensus value for cost of hovering (approx. $43 \text{ ml } O_2 \text{g}^{-1} \text{h}^{-1}$) by making measurements on free-living hummingbirds under conditions that closely approximate those in which they normally operate. We report such an effort here. To our knowledge, this is the first direct measurement of the oxygen consumption during flight of wild birds in the field.

MATERIALS AND METHODS

We measured the rate of O_2 consumption ($\dot{V}_{O_2}$) of unrestrained, wild Anna hummingbirds (*Calypte anna*) which had learned to use a sugar water feeder that was instrumented to function as a respirometry mask. The feeder-mask was available to the birds in an area in which they are native and in an environment where they regularly breed (Rustic Canyon, Santa Monica Mountains, Los Angeles County, California, altitude approx. 30 m). The area is characterized by extensive stands of native vegetation (soft chapparal) adjacent to eucalyptus trees and ornamental plantings.

The feeder-mask consisted of an inverted, 100-ml graduated cylinder filled with a sugar solution (1 part sucrose and 3 parts water by volume) and equipped with a feeding tube surrounded by a red artificial corolla. The orifice of the feeding tube was positioned 40 mm inside a mask consisting of a transparent cylinder (21 mm i.d.) into which a hummingbird had to insert its entire head to feed (Fig. 1A). Air was drawn at a rate of 1016 ml min^{-1} through the mask, through a Drierite-Ascarite $H_2O–CO_2$ scrubber, through a Brooks Rotameter flowmeter, and then through the sensor of
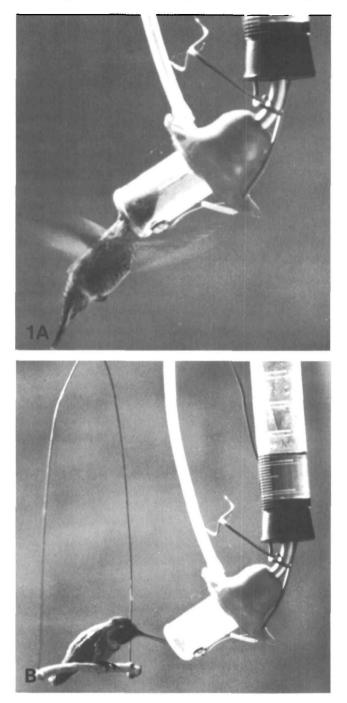
Fig. 1. (A) Wild male Anna hummingbird, mass 4·8 g, at the feeder-mask. (B) The same hummingbird perched on the weighing trapeze.

an Applied Electrochemistry S-3A O_2 analyser. The pressure at the flowmeter, measured with a water manometer, was about 1·5 Torr below ambient barometric pressure, and this difference was ignored.

The rotameter was calibrated against a modified version of the bubble flowmeter described by Levy (1964), which consisted of a vertical precision bore glass tube (47 mm i.d.) across which a soap film was introduced and through which the film was swept at a rate determined by the air flow through the tube. The passage of the film up the tube was detected at two precisely measured points by optical detection systems consisting of light-emitting diodes (LED) and light-dependent resistors (LDR) at opposite sides of the tube. Passage of the soap film past the LED caused a fluctuation in the resistance of the LDR which was detected and timed to an accuracy of 0·01 s by a computer. The volume of the tubing between the two optical detecting units was precisely known, allowing the flow rate to be computed from the time taken for the film to sweep this volume as described by Levy (1964). Calibration took place at an ambient temperature of 24°C and a pressure of 752 Torr. Using the error budget of Levy (1964) and allowing for the high accuracy of the computerized timing system, the absolute accuracy of the primary calibration was better than 0·25 %. In practice we were able to maintain flow rates constant to better than 1 % during a given run.

The O_2 analyser was calibrated against dry, CO_2-free outside air (fractional concentration of $O_2 = 0·2095$). Because the system measured outside air continuously except when a bird visited the feeder, base lines were readily established before and after each visitation. Depletions in O_2 fractional concentration caused by the birds were measured with a resolution of 0·001 %.

An LDR, cemented to the underside of the feeder mask, was used to detect the presence of the head of the bird while it was feeding. The outputs of the O_2 analyser and the LDR system were fed into an Acorn BBC computer and sampled 10 times s^{-1}. The computer sampled the airstream until it detected an oxygen depletion of $\geqslant 0·05$ %. Upon being triggered by this oxygen depletion, it retained the previous 140 samples in memory and then recorded the next 500 samples. The signals from the LDR system and the O_2 analyser were plotted on the monitor in real time and automatically saved to disc after sampling was complete. The computer immediately resumed monitoring. The software was devised by JRBL and was a modification of that described in Lighton (1985).

To determine the mass of the birds, we attached a hummingbird-sized trapeze to a Biocom model 1030 force transducer and suspended it immediately in front of the feeder-mask. Birds coming to feed perched on the trapeze (Fig. 1B) and were automatically weighed to the nearest 0·05 g. The output from the transducer was monitored either with a computer or with a digital voltmeter. The system was calibrated with weights of known mass over a range from 1 to 6 g after each weighing.

All measurements were made during July and August, 1985, between 15.00 and 19.00 h. The feeder-mask was located outdoors in open shade 2 m from the wall of the room in which our instrumentation was located and 1·75 m above the ground. Air temperatures varied from 20 to 25°C.

The bird's head had to be completely within the mask for the light striking the photoresistor to be occluded. In this situation the mask was fully functional. As the bird moved into and out of the feeding position, the period during which the feeder functioned as a mask was accurately detected by the photoresistor and automatically timed by the computer. Birds hovering in the immediate vicinity of the feeder did not cause measurable depletions of O_2 in the airstream pulled through the mask.

The volume of oxygen consumed was calculated by integrating, using a trapezoidal algorithm, the oxygen depletion envelope over time (in s), and converting the integral to STP:

$$ml\,O_2 = [(I \times 60 \times F)/(1 - 0.2095)] \times (273.15/T) \times (760/P),$$

where I is the integral (in s), F is flow rate (in $ml\,min^{-1}$), T is air temperature (in K) at the flowmeter, and P is barometric pressure (in Torr). The value 0.2095 is the fractional oxygen concentration in dry, CO_2-free air. The rate of O_2 consumption was obtained by dividing $ml\,O_2$ by the length of time during which the bird's head was completely inside the mask:

$$ml\,O_2\,h^{-1} = (ml\,O_2/S) \times 3600,$$

where S is the summed feeding time (in s).

In the case of a hummingbird which fed for long periods, it was also possible to determine $\dot{V}_{O_2}$ for individual feeding sallies by using the 'instantaneous' response computation described by Bartholomew, Vleck & Vleck (1981). This allowed us to correct for the damped response caused by the washout characteristics of the system, and to calculate O_2 depletion volumes caused by discrete feedings.

Unless otherwise specified, data are presented as mean ± S.D.

RESULTS

Satisfactory data were obtained from five males *Calypte anna*, of which three successively maintained territorial dominance over the area in which the feeder-mask was located, and two were persistent interlopers. All of the birds were accustomed to using man-made feeders, and habituated to the feeder-mask without difficulty.

The feeding bouts of four of the birds were characterized by frequent 'sallies' which carried the head in and out of the feeding mask about once a second (Fig. 2). One individual fed for much longer intervals (Fig. 3). The volume of O_2 consumed per feeding sally was linearly related to the length of the sally (Fig. 4). The linear regression of O_2 consumed *versus* time extrapolates to zero at a feeding interval of 0 s. From this we infer that the respirometry system allowed accurate measurement of $\dot{V}_{O_2}$, independent of the period during which the bird's head was inside the mask.

We obtained measurements of 49 entire feeding bouts from five unambiguously identified individuals of known mass (Table 1). Their mean mass, $4.6 \pm 0.4\,g$, did not differ significantly from the $4.4 \pm 0.3\,g$ reported by Stiles (1973) for 36 wild-caught male Anna hummingbirds from the Santa Monica Mountains.
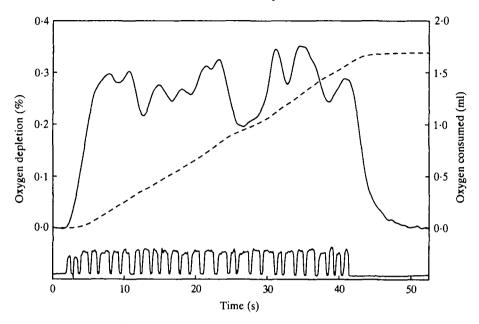
Fig. 2. Percentage O_2 depletion (solid line), cumulative O_2 consumption (dashed line) and photoelectric record of feeding sallies (bottom trace) of a 4·4-g male Anna hummingbird. Air temperature, 22 °C. Duration of feeding bout, 39·5 s; feeding time, 30·9 s. The oxygen values are plotted 6·1 s to the left to compensate for the lag time between feeder and O_2 sensor and synchronize the O_2 values and the feeding record.
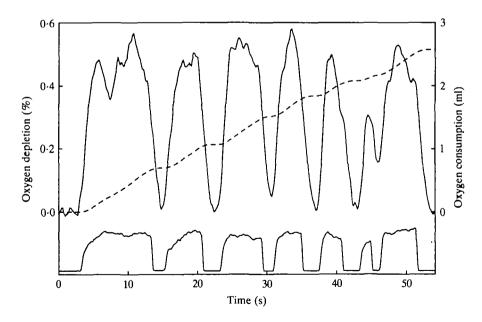

Fig. 3. Oxygen consumption of a 4·8-g male Anna hummingbird with unusually long feeding sallies. Conventions as in Fig. 1. Oxygen values were processed using the 'instantaneous' computation (see text). Total duration of feeding bout, 48·4 s; feeding time, 38·7 s. Air temperature, 21 °C.
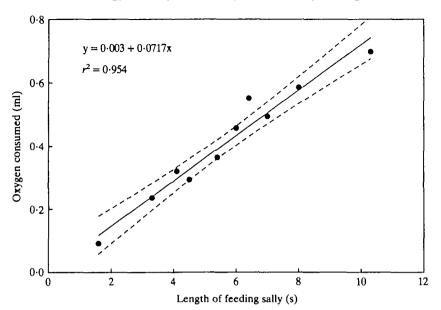
Fig. 4. The relationship between the volume of O_2 consumed per feeding sally and the length of the sally (see text). Data are from several feeding bouts of a 4·8-g male Anna hummingbird. Slope is in $ml\, O_2\, g^{-1}\, s^{-1}$, and is equivalent to $53·7\, ml\, O_2\, g^{-1}\, h^{-1}$. The 95 % confidence limits of the slope (dashed lines) include the mean $\dot{V}_{O_2}$ for this individual (Table 1, row 4).

Table 1. *Oxygen consumption rates and feeding patterns in five male Anna hummingbirds*

Mass (g)	N	$\dot{V}_{O_2}$ $(ml\, O_2\, g^{-1}\, h^{-1})$ Mean	S.D.	Time at feeder (s) Mean	S.D.	Time feeding (s) Mean	S.D.	No. of sallies Mean	S.D.
5·1	16	36·9	4·6	31·1	8·6	23·3	5·9	27·4	5·9
4·2	12	44·6	5·6	28·6	10·0	20·9	7·5	20·9	7·7
4·4	13	41·4	5·7	24·9	8·2	18·1	7·3	18·7	5·1
4·8	6	47·0	6·6	35·4	9·0	27·7	6·6	9·5	4·5
4·8	2	43·2	—	19·8	—	12·0	—	16·0	—

The overall mean $\dot{V}_{O_2}$ during hover-feeding was $41·5 \pm 6·3\, ml\, O_2\, g^{-1}\, h^{-1}$, with individual means ranging from $36·9$ to $47·0\, ml\, O_2\, g^{-1}\, h^{-1}$ (Table 1). Over the narrow size range of the sample, the energy cost for hovering was not affected by mass. Because the animals were not captive, we did not measure their wing areas or wing discs. However, the mean wing disc loading of five individuals with a mean mass not significantly different from our sample and captured in the same area was $3·94 \pm 0·36\, N\, m^{-2}$ (data from Epting, 1980; see below).

DISCUSSION

The data with which our measurements are most directly comparable are those of Epting (1980), who studied the energy metabolism of captive Anna hummingbirds captured in the same general area occupied by the birds used in the present study.

The three females and two males that he measured had a mean mass of $4\cdot7 \pm 0\cdot4$ g which does not differ significantly from that of the sample in the present study ($P > 0\cdot7$). However, the oxygen consumption of the hovering captive birds was $49\cdot99 \pm 4\cdot34$ mlO_2g^{-1}h^{-1}, which is significantly higher ($P < 0\cdot04$) than that of the free-ranging wild hummingbirds that we measured. This suggests that either the conditions of captivity, or the relatively confined system within which the captive birds were measured, resulted in an increase in the energy cost of their flight.

Despite the difference between free-ranging and captive birds described above, the value for the energy cost of hover-feeding obtained in the present study, $41\cdot5$ mlO_2g^{-1}h^{-1}, is bracketed by the values ($40\cdot8$–$45\cdot6$) for oxygen consumption of hummingbirds ranging in mass from 3 to 10 g during hovering under similar conditions of temperature and barometric pressure reported in the literature: Lasiewski (1963), Wolf & Hainsworth (1971), Berger & Hart (1972), Berger (1974, 1985). (We are at a loss to account for the extremely low values for hovering metabolism reported by Schuchmann, 1979.) From this concordance we infer that the problems associated with measuring the cost of hummingbird hovering in enclosed spaces may be partly self-cancelling.

It appears that the cost of hovering is very similar in the various species that have been measured. This supports the hypothesis that the power input for hovering is not correlated with body mass (Hainsworth & Wolf, 1972), but with wing disc loading (Epting & Casey, 1973; Epting, 1980).

A pattern of quick sallies during which the bird alternately feeds and hovers with its beak a few centimetres from the flower is characteristic of Anna hummingbirds, and many other species. Because of the rapidity of the bird's movements, accurate measurement of the time spent actually obtaining nectar is not possible by direct observation, or even when using a cumulative stopwatch. A model based on total time from beginning to end of a group of feeding sallies will overestimate the time spent in feeding *per se* by about 30 % (Table 1), which is substantial in view of the extremely high cost of hovering in these animals. However, the total duration of the feeding bout, not the cumulative duration of individual feeding sallies, is the proper unit to use when estimating the energy cost for obtaining nectar from a given food source.

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