THE DYNAMICS
OF HUMMINGBIRD FLIGHT

by

LARISSA MAE CHATTERS

B.Sc., The University of British Columbia, 1991

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS OF THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming
to the required standard.

THE UNIVERSITY OF BRITISH COLUMBIA

April 1996

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Department of Zoology
The University of British Columbia
Vancouver, Canada

Date Apr. 25/96
ABSTRACT

Using rufous hummingbirds (*Selasphorus rufus* Gmelin) as test subjects, this paper addresses issues surrounding the energetic cost of acceleration. Hummingbirds have been the subjects of extensive aerodynamic and energetic studies, but current aerodynamic theory ignores acceleration as an energy expenditure during flight. Using four experiments, this thesis explores acceleration as an important part of the daily energy expenditures of rufous hummingbirds (*Selasphorus rufus*).

In experiment 1, I estimate velocity and acceleration continuously in hummingbirds. This experiment indicates that for short flights (< 3.5 m), hummingbirds accelerate for 100% of the flying time. For longer flights, a section of constant maximum velocity is inserted between two "acceleration envelopes" (one positive; one negative). These envelopes are independent of the length of the flight. Since most of hummingbirds' daily flights are less than 2 metres long (patch to patch and between flowers in patches), this suggests that most of the foraging time of hummingbirds is spent accelerating. This experiment shows that hummingbirds actively accelerate and may passively decelerate.

Experiment 2 is a preliminary theoretical exploration of the possible energetic costs of acceleration. Using current aerodynamic theory, a thought experiment was performed to assess this cost. Current aerodynamic theory predicts a high cost for accelerating flights. However, due to its steady-state assumptions and small range of applicable velocities around $V_{mp}$, aerodynamic theory probably underestimates the cost of acceleration.

In experiment 3, I estimate the power required for acceleration by measuring the acceleration of hummingbirds in relation to the inclination of flight. This experiment indicates that hummingbird flight is energy limited and acceleration may cost as much as 3 times that of steady-state flight. It also shows that the power required for acceleration is close to the maximum sustainable power output estimated in other studies.
In experiment 4, I estimate the power required for acceleration by measuring total power input and mass changes and by estimating energy expenditures from a complete time budget. Since the costs of all other component activities have been measured previously, the only term unknown is the cost of acceleration. This experiment supports the conclusion that acceleration is an expensive activity approximating the cost of maximum sustainable power output.
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ACKNOWLEDGMENTS

I would like to thank the following people for their help and support:

Dr. Lee Gass for his patience and his pep talks,

Alistair Blanchard and Alan Boulton for help with parallax error reduction,

Neil Dryden and Mark Halpern for general science and physics advice,

Lance Bailey for programming and computer support,

Mohammed Darwish for setting up a new server for our lab,

Dan Fandrich for setting up balances and thermisters and for general programming and computer support,

Drs. John Gosline, Mark Halpern, Robert Blake and Horacio de la Cueva for reading earlier drafts,

Dr. Al Lewis for his patience and understanding about missed deadlines,

And my parents and Dan Fandrich for their unwavering support and encouragement.
Chapter 1: General Introduction

Locomotion is an important part of all mobile animals' lives. Whether by walking (running), swimming or flying, they must locomote to forage for food, find mates, avoid predators, etc. Walking on a two-dimensional plane is in a class by itself; but swimming and flying are similar as they involve three-dimensional locomotion through a fluid medium. Various aerodynamic theories describe the motion of swimming and flying animals (Brown 1963; Pennycuick 1969, 1972, 1975, 1989; Tucker 1971, 1974, 1975; Webb 1971, 1975; Wu 1971; Weis-Fogh 1973; Ellington 1975, 1984a-f; Greenewalt 1975; Lighthill 1975; Alexander 1977; Rayner 1979a-c, 1989; Norberg 1990). Aerodynamic theory attempts to relate locomotory performance and energetics to morphology and it is successful in many, but not all ways. A comprehensive theory should explain the phenomenon under all circumstances.

Using relevant morphological parameters (whether of airplane, bird, bat, or insect) and the physical laws of fluid dynamics, aerodynamic theory simplifies and quantifies the output power required for overcoming the drag due to wings, body and lift at given velocities and air densities. It accurately describes the power required for level flight at a constant velocity (Welham 1994). If the calculated power is plotted for various velocities, a U-shaped curve results, defining two characteristic velocities (Pennycuick 1989; Fig. 1). The minimum power velocity ($V_{mp}$) minimizes power per unit time and the maximum range velocity ($V_{mr}$) minimizes power per unit distance. Thus the theory predicts flight speeds for birds maximizing time or distance per unit fuel, respectively.

Unfortunately, the assumptions that underlie this theory become unrealistic at speeds much below $V_{mp}$ or much above $V_{mr}$ (Pennycuick 1989). This means that aerodynamic theory breaks down at very low or very high speeds. Independent theories have been developed for hovering
Figure 1: Power output for forward horizontal flight as a function of velocity. Vmp is the minimum power velocity at which energy expenditure per time is minimized. Vmr is the maximum range velocity at which energy expenditure per distance is minimized. It occurs where the power:velocity ratio is the lowest (J/s / m/s = J/m). The dotted line indicates the common assumption that aerodynamic theory predicts costs for velocities below Vmp.
flight at zero forward velocity (Weis-Fogh 1972; Ellington 1984a-f; Norberg 1990). Currently, there is no theory to describe flight at velocities between zero and $V_{mp}$. However, many papers include a version of Figure 1 with the power curve continuous to a very low velocity (Wolf and Hainsworth 1978; Hainsworth 1981; Blake 1985; McLaughlin and Montgomerie 1985; May 1991; Hedenstrom and Alerstam 1995).

There is a major problem with applying aerodynamic theory to real animal situations. Aerodynamic theory and the U-shaped power curve were developed for constant velocity situations. The power output for a flight (in W, or J/s) depends on that flight being at a constant velocity for a length of time. However, any change in velocity involves acceleration. Thus acceleration is not described by current aerodynamic theory.

Nectar-feeding birds are ideal subjects for energetic studies (Wolf and Hainsworth 1978). Hummingbirds (for example) are small homeotherms with expensive locomotion which results in rapid accumulation of the energetic consequences of actions (Gass and Montgomerie 1981). This allows us to calculate costs for activities over a short time frame. Their floral "prey" are stationary, self-renewing, and easily quantified by energy value. As well, hummingbirds exhibit relatively few activity states (e.g., sitting, hovering, flying forward), which simplifies converting time budgets to energy budgets. Hummingbirds are also relatively easy to keep in captivity (Lasiewski 1962). This is important as energetic studies become more difficult outside a controlled laboratory environment where variables can be kept relatively constant and food intake and time and energy budgets can be measured accurately (Gass 1978). As well, the energetics of the various activities of hummingbirds have been studied extensively. The energetic costs of perching (Lasiewski 1963; Epting 1980; Suarez et al. 1990), sleeping and torpor (Hainsworth and Wolf 1970; 1978a,b; Hainsworth, et al. 1977; Hiebert 1990; 1991; 1992; 1993), and hovering (Lasiewski 1963; Suarez et al. 1990) have been measured in laboratory situations but the cost of forward flight remains under some question and the cost of acceleration is completely unknown.

The cost of acceleration has only recently and rarely been taken into account in flight energetics studies. May (1991) reported acceleration values for dragonfly flight and calculated
the cost of accelerating flight as the force multiplied by the velocity at each time interval. In reporting flight speeds of black terns, Welham and Ydenberg (1993) calculated a cost for acceleration by dividing the kinetic energy by the metabolic conversion efficiency. This calculation was an overall cost of accelerating to some airspeed and assumed constant acceleration. I will explore the correlation of these calculations to actual data in later chapters.

Using Rufous hummingbirds (*Selasphorus rufus*) as test subjects, this thesis will address issues surrounding the energetic cost of acceleration. Does acceleration have a separate cost from steady-state flight? Is it possible to measure or estimate this cost? Is acceleration more expensive than steady-state flight and how does this influence the daily energetics of hummingbirds? How does wing morphology affect acceleration performance and energetics? Specifically, do the shorter, narrower wings and higher wing disc loading of males afford greater aptitude for high speed and acceleration (Feinsinger and Chaplin 1975; Feinsinger et al. 1979; Collins and Paton 1989; Norberg 1995) or lesser aptitude (Pennycuick 1975; Kodric-Brown and Brown 1978; Norberg and Rayner 1987; Webb, et al. 1992)?

Currently, there are few measurements of the velocity of hummingbirds and these are all time-averaged velocities (Hayes 1929; Allard 1934; Gill 1985) for long flights (~40 m). The only estimations of hummingbird acceleration were taken during the last tenth of a second during docking at flowers (Lee, et al. 1991). Chapter 2 fills this gap in the literature by providing continuous measurements of velocity and acceleration for rufous hummingbirds as obtained from video recordings. Here, I control bird morphology and experimentally manipulate one aspect of habitat: the foraging flight distance between a perch and a feeder. Male and female hummingbirds are sexually dimorphic in wing length and wing shape and there are conflicting predictions (above) about how this affects their velocity and acceleration performance. I also manipulated the distance of foraging flights. Since hummingbirds perform straight, direct flights while foraging, they may decide where to fly before leaving the perch. This means that they have some foreknowledge of the flight (i.e. distance from the perch; Gass 1974; Gass and Sutherland 1985). Given this foreknowledge, do hummingbirds accelerate at different rates depending on the
expected length of the flight, or do they accelerate at the same rate regardless? The answers will have implications for the energetics of foraging and thus for foraging strategy (Feinsinger and Chaplin 1975).

Chapter 3 is a preliminary theoretical exploration of the possible energetic costs of hummingbird acceleration using steady-state assumptions from the literature. I estimate the costs under various conditions and speculate on the significance of that cost for hummingbird time and energy budgets under realistic field conditions. Using steady-state assumptions, I calculate a cost for a hypothetical accelerating flight, add the cost for accelerating the mass (paying Newton) and then compare this to the energetic cost of a steady-state flight. I expand this analysis to include the dimorphic flight performance reported in Chapter two and relate it to current aerodynamic theory. The chapter does not address acceleration directly but uses steady-state assumptions to show that current aerodynamic theory is insufficient to accurately predict the energetic cost of acceleration; empirical data will be required. Chapter 4 and 5 attempt to supply these data using separate methods.

One way to estimate the power required for acceleration would be to observe the acceleration of birds who are loaded in some way. A backpack of some sort could be used to change the mass of a hummingbird but this method would add extra drag factors, would likely change the centre of mass of the bird and therefore alter the geometric relationship between forces in unknown ways (Cuthill and Kacelnik 1990). Another way to load the bird is by adding a component of the acceleration due to gravity. In Chapter 4, I manipulate the effect of gravity and measure acceleration as a function of the inclination of flight. This experiment determines whether acceleration or energy is the more important commodity on individual flights of hummingbirds. If accelerating at a certain rate is more important for some reason and if power is not limiting, then birds should expend the power to achieve this; acceleration should not depend on inclination. But if power available for acceleration is limiting, or if for some reason it is important to expend power at a certain rate, then acceleration should vary predictably with inclination. In this case, the average power put into a flight of a certain length will remain
constant and be insensitive to the load put on the bird. In effect, I manipulate the power required by the bird for acceleration at a given rate and infer the energetic cost of acceleration from the bird's responses.

Another way to estimate the energetic cost of acceleration is to actually measure its consequences. Since there is currently no way to directly measure the energetic cost of forward flight, in Chapter 5, I estimate it by comparing the overall energy balance of birds in situations requiring different amounts of acceleration. By manipulating the food available on individual foraging flights, I adjusted the activity budgets of birds in short (2.5 m, 100% acceleration) and long (7.5 m, ~50% acceleration) tunnels to the same proportion of time spent flying. But because the proportion of forward flight time spent accelerating in short and long flights differs greatly, birds in short tunnels should expend more energy for the same flight time to the extent that acceleration is energetically expensive. If so, then over several days, they should eat more, lose more mass (or gain less mass), and/or spend more time in nocturnal torpor than those in long tunnels.

By the use of theoretical analysis and empirical data, this thesis illuminates the problem of acceleration and its energetic cost. It should also provide a platform for the development of aerodynamic theory to include all aspects of forward flight at all velocities.
Chapter 2: Velocity and Acceleration of Rufous Hummingbirds in Straight Horizontal Flight

The flight speed of birds has been of interest for many years (Cooke 1933; Meinertzhagen 1955; McLaughlin and Montgomerie 1985, 1990). The earliest reported velocities, including those of hummingbirds (Hayes 1929; Allard 1934; Gill 1985), were estimated using vehicle speedometers (airplane, train, automobile) and stop watches. Neither method is accurate. At best, stop watches can estimate the average velocity of flights, but even slight inaccuracies in timing short flights result in inaccurate velocity estimates. On long flights, birds may not fly the straight paths necessary to estimate velocity accurately (Schnell 1965). In any case, flight duration can provide no information about maximum velocity or acceleration.

New technology has improved the accuracy of velocity and acceleration measurements. Doppler radar has been used to measure instantaneous velocity in many species of birds (Schnell 1965; 1974; Schnell and Hellack 1978; Larkin and Thompson 1980; Blake, et al. 1990; Hedenstrom and Alerstam 1992; Welham and Ydenberg 1993). Radar accurately measures instantaneous velocity but gives no information about the rest of the flight, including acceleration. Unfortunately, hummingbirds are too small to be measured accurately by radar (H. de la Cueva, pers. comm.). Using high-speed cinematography, velocity and acceleration measurements have been made on lions (Elliott, et al. 1977), fish (Webb 1976; 1983; 1988; Domenici and Blake 1991; Harper and Blake 1990), insects (Waloff 1972; May 1991), bats (Rayner and Aldridge 1985; Aldridge 1988; 1991) and many species of birds (Pennycuick 1968; Tucker and Schmidt-Koenig 1971). Pearson (1960) was the first to use film to measure velocity of hummingbirds and Lee et al. (1991) estimated acceleration by hummingbirds for the last tenth of a second of a flight. In this study, I use video recordings to obtain continuous velocity and acceleration measurements for rufous hummingbirds on foraging flights.

Foraging hummingbirds usually fly in straight paths from perch to patch (Gass 1985; Gass and Sutherland 1985) and from patch to patch and flower to flower within patches (Gass, 1974).
Since they fly directly to their destination, the entire path is likely determined when they leave the perch. How should this affect the timing and magnitude of acceleration? Birds with foreknowledge of their flights might optimize their acceleration and velocity to maximize efficiency, minimize energetic cost or achieve some other criterion, such as to maximize the time spent at cruising speed. For example, they could accelerate faster on shorter trips to maximize the time spent at $V_{mp}$ and thus the time spent at the lowest power output. However, the magnitude of acceleration may be limited by the ability of the flight muscles to deliver power. If so, the magnitude and timing of acceleration for flights of different distances should be equal. In this study, I will investigate these possibilities by comparing flight parameters from foraging flights of different distances.

Adult rufous hummingbirds are sexually dimorphic in many aspects. The most striking difference between males and females is in their plumage, the males being more brightly coloured (Stiles 1972; Ortiz-Crespo 1972). Sexually dimorphic bill length allows long billed females to feed at flowers with longer corollas and to feed more quickly than males (Temeles and Roberts 1993). Other aspects of sexual dimorphism affect the cost of flight and flight performance (Norberg 1995). For example, males have more pointed tail feathers with gaps between them and females have broader tail feathers (Stiles 1972; Norberg 1995). Females have longer, broader wings than males (Fig. 2; Collins and Paton 1989) which leads to differences in wing disc loading (the ratio of the mass of the bird over the wing disc area – the area swept out by the wings) and aspect ratio (the ratio of squared wing span to wing area).

Differences in wing morphology greatly affect flight performance and energetics (Lasiewski 1963; Epting and Casey 1973; Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979; Epting 1980; Norberg 1995). It is uncertain, however, what these effects should be. Many authors state that the higher wing disc loading of males should impart greater maneuverability and higher accelerations to the males' flight performance (Feinsinger and Chaplin 1975; Feinsinger et al. 1979; Rolseth et al. 1994). The longer wings of females should impede rapid acceleration because of increased drag (Collins and Paton 1989). However, aerodynamic
Figure 2: Wing lengths of adult rufous hummingbirds (n = 78 birds; 34 males, 44 females). Thirty-two birds were measured from the Vertebrate museum at U.B.C. (16 males and 16 females). Forty-six birds were live captive birds from the years 1991–1995 (18 males and 28 females) usually measured during the late winter of their year of captivity. The wing lengths shown here are the wrist-to-tip lengths of the hummingbirds. The bimodal shape of the graph demonstrates the sexual dimorphism in wing length of adult rufous hummingbirds. The mean for males is 4.066 ± 0.015 cm (mean ± S.E.). The mean for females is 4.436 ± 0.027 cm. The very short wings for some of the live captive females are due to wing wear against the walls of their cages as indicated by the ragged edges and general poor condition of the flight feathers of these individuals.
theory may predict the opposite (Pennycuick 1975; Kodric-Brown and Brown 1978; Norberg and Rayner 1987; Webb, et al. 1992). Increases in wing disc loading increase both $P_{am}$ and $V_{mp}$, so that while the most efficient flying speed for short-winged males is high, long-winged females can actually fly with less power at any speed (see Chapter 3) due to the relative flatness of the hummingbird U-shaped power curve. As well, it has been speculated that since long-winged birds have more economical flight, they should have more economical acceleration too, as they have more power left over for acceleration (Norberg and Rayner 1987). Unfortunately, there have been few empirical studies to see whether animals with lower or higher wing disc loading routinely fly faster. A correlation between open-field flight speeds and wing loading was done in bats, confirming the theory (Norberg and Rayner 1987), but to my knowledge has not been performed for birds. In this study, I investigate this theoretical controversy empirically by comparing the flight performance of males and females.

MATERIALS AND METHODS

The Animals

I used eight rufous hummingbirds (*Selasphorus rufus*), four males and four females, selected from a lab population of 25 birds. They were captured as adults at Sumas Mountain and the Sunshine Coast, B.C., in the spring of 1991 and held individually in 60 x 60 x 60 cm wire cages in a large room. They had *ad libitum* access to commercial hummingbird food (Nektar Plus) in commercial hummingbird feeders (Perky Pet) on weekdays and 20% sucrose solution (w/w) on weekends. All observations were made between February and April 1992.

The Experimental Enclosure

I analyzed videotape records of birds flying through a horizontal tunnel 10 m long, 50 x 60 cm in cross section, and mounted on a wall 1 m above the floor (Fig. 3). Since the maximum wingspan of any bird was 4.8 cm and the birds flew in the approximate center of the tunnel, I assumed that the tunnel walls did not interfere with flights. The feeder end of the tunnel (5 m) was covered in transparent colourless plastic. The perch end (5 m) had plastic on the top and
Figure 3: Experimental Enclosure. Shown is top, end and front views of a 5 m tunnel. The tunnel could be extended to 10 m as indicated by the dashed lines. The mirror is hanging below the tunnel at a 45° angle. This figure is not to scale.
clear Plexiglas on the front, back and bottom. A 5 m x 30 cm mirror was mounted at 45 degrees under the Plexiglas section, to provide two viewpoints for filming. To provide reference markers for digitizing positions, the floor of the tunnel had a 10 cm grid of thin black tape (X and Y dimensions) and the front had horizontal lines 10 cm apart (Z dimension). A perch was placed in the tunnel 4 cm from one end and a feeder was hung at the other end. I adjusted the working length of the tunnel (5 or 10 m) with a posterboard divider. Five 150 W incandescent lights in large reflectors were spaced evenly above the Plexiglas portion of the tunnel and ambient room lighting illuminated the whole.

Training

I trained birds gradually over a day or two, allowing them to learn each new procedure before introducing the next one. First, I put the bird into a 2.5 m section of the tunnel with the perch at one end and a hanging feeder at the other. Most birds found the feeder and the perch within a few minutes and flew to the feeder and back about once every 20 min. All birds explored the tunnel cautiously and in stages; if they learned especially slowly I left them in the tunnel overnight before lengthening the tunnel in 2.5 m stages. It usually took 1-2 hours before the bird found and used the new feeder position each time the tunnel was lengthened.

Experimental protocol

I filmed flights by panning a tripod-mounted video camera (Sony CCD-V101 Hi-8 set at the highest shutter speed possible for the lighting to ensure clear freeze frames; shutter speed set automatically by sports mode) placed 2.8 m from the center of the Plexiglas covered portion of the tunnel (Fig. 3). The shape of the room prevented filming entire 10 m flights, so I filmed only the Plexiglas encased 5 m. Even so, panning introduced large errors whose correction I discuss below.

Birds were free to fly and feed at any time. To increase the number of flights in each feeding bout, I provided only 10 μL of 20% (w/w) sucrose on 5 m flights and 20 μL on 10 m flights. Birds typically made 3-5 trips from perch to feeder within ~1 min., consuming 30–100 μL, and
bouts began irregularly every 6-10 min. Hummingbirds normally telegraph their intention to feed by becoming slightly agitated while perching, so it was relatively easy to estimate when to start taping flights. I taped entire 5 m flights (perch to feeder or feeder to perch) and both the accelerating (perch to feeder) and decelerating (feeder to perch) halves of 10 m flights. I noted the direction of 5 m flights (perch to feeder or vice versa) but did not otherwise distinguish between them in taping. Each bird continued until I had filmed 4 or 5 "good" flights of each of the 3 types (entire 5 m, and accelerating and decelerating 10 m). "Good" flights were continuous (no hesitations, stops, or turns), started or ended within ~0.5 m of the end of the tunnel for 5 m flights or ~1 m of the end of the tunnel for 10 m flights, and the direct and reflected bird images and all relevant tape markers were continuously visible in the frame. I adopted different criteria for the total length of flights because of the behaviour of the birds; in the 10 m tunnel, they tended to stop further away from the end wall than in the 5 m tunnel. For most individuals, about 70% of all flights were "good" after training.

*The Digitizing of Bird Positions from Videotapes*

The average duration of 5 m flights was 1.61 s (48 video frames) and the average total duration of 10 m flights was 3.01 s (90 video frames). I repeated the following procedure for each frame of each "good" flight of each bird (118 flights and ~5500 frames). With the camcorder connected to an image digitizing card (Matrox PIP-1024B) in a PC, I digitized one frame at a time with video image processing software (Digital Optics "V"), then digitized 11 points using a mouse: the tape markers on either side of the bird in X, Y, and Z dimensions, the bird's apparent center of mass on the direct and reflected images, and the identity of each tape. Tape identities were digitized by clicking positions on a "ruler" visible on the digitizing screen (Fig. 4). These data were written to a file, the tape was advanced one frame (1/30 s) and the procedure repeated. These data were converted from units of pixels to metres, then corrected to reduce error due to parallax. Errors of 0.25 cm in the middle of flights and 0.5 cm at the ends due to the grain of pixels on the digitizing screen could not be removed.
Figure 4: Example of digitized frame for analysis. The ruler at the top is used for identifying the lines around the position of the bird. The bird can be seen both directly in the tunnel and in the mirror from below (circles). Shown is the perch end of the Plexiglas portion of the tunnel. In general, the monitor image was of much higher quality than shown here.
Error Correction

The most substantial source of error was parallax due to the narrow room and long tunnel. This error in the raw data was 0 cm in the middle of the tunnel and ~30 cm (about 5 hummingbird body lengths) near the ends, where the filming angles were greatest (and where acceleration was likely to be greatest). Three equations with two unknowns were developed to compute the true position in the tunnel from the two "views" present in the video record (see Appendix A). Two of these equations when combined, in conjunction with the virtual positions from the digitizing (X and Y from the mirror, Z from the tunnel), gave equations for the real position of the bird in the tunnel in three dimensions for each frame of the flight. The Y and Z positions were used only to get the real X position of the bird, the only parameter used in the data analysis, which assumed that Y and Z positions were constant. In actuality, they usually varied < 10 cm during the course of a flight. This method reduced parallax error to < 3 cm, or < 10%, at the ends of the tunnel.

Computation of Flight Parameters

The input to analysis for each flight was a time series of X positions in the tunnel each 1/30 s. I twice applied a digital filtering equation (Winter 1990) with a cutoff frequency of 7 Hz. The first application was in the forward direction (frame 0 to max) which smoothed the data slightly and introduced a phase shift of one data point. A second application in the opposite direction (frame max to 0) smoothed the data further and canceled the phase shift. Instantaneous velocity and acceleration were calculated using the distance traveled between three frames and the time step between those frames (Winter 1990).

\[
V_{xi} = \frac{(x_{i+1} - x_{i-1})}{2\Delta t}, \quad [1]
\]

\[
A_{xi} = \frac{(x_{i+1} - 2x_i + x_{i-1})}{\Delta t^2}, \quad [2]
\]

where \(x_i\) is the distance at step \(i\), \(V_{xi}\) is the velocity at time step \(i\), \(A_{xi}\) is the acceleration at time step \(i\) and \(\Delta t\) is the difference in time between \(x_{i-1}\) and \(x_{i+1}\) (1/15 s). To get velocity and
acceleration for the entire flight, it was necessary to augment (i.e. "pad") the data at the beginning and end of the series. The method of padding mattered little for complete flights as long as an entire window of 7 points was added. I reflected the data over both the time and distance-axes as this gave the best estimate (i.e. the fewest spurious data points) of velocity and acceleration for the terminal 5 m of 10 m flights (Table I). This method gave slightly spurious results for the first and last velocity and acceleration estimates so I discarded these points. I averaged maximum velocity, acceleration and deceleration from all "good" flights of each bird and recorded both the distance and the time at which each of these occurred. Distances and times of maximum velocity and acceleration are reported from the beginning of the flight. Distance and time of maximum deceleration are reported from the end of the flight. I performed Bonferroni corrections on each group of t-tests to ensure against Type I errors (Rice 1989).

RESULTS AND DISCUSSION

Patterns of Flight

In these experiments, individual hummingbirds flew consistently and nearly all good flights were smooth and without hesitations. All hummingbirds flew using the same overall patterns of acceleration, flight near maximum velocity, and deceleration. They accelerated for most of the 5 m flights and flew at near constant velocity between the two "acceleration envelopes" during the 10 m flights (Fig. 5). The coefficient of variation within individuals for maximum accelerations (Amax) and decelerations (Dmax) was < 21% and it was < 14% for maximum velocities (Vmax; see Fig. 6 for explanation of acronyms). Variation within individuals in time and distance of maximum velocity (tVmax and dVmax) was also small (CV < 15%). Most variation among flights came from the time and distance of maximum accelerations (tAmax and dAmax) and decelerations (tDmax and dDmax; CV > 32% and > 64% for time and distance, respectively).

Birds reached the same Vmax (4.38 ± 0.21 m/s; n = 8 birds for all measurements; mean ± S.E.; see Table II for statistical tests), Amax (15.29 ± 1.01 m/s²) and Dmax (-19.76 ± 1.51 m/s²) regardless of flight distance or duration. DVmax occurred in the approximate middle of the
Table I: A comparison of padding methods. The minimum method reflects the data over the distance-axis, producing a minimum (or maximum) point in the data. The inflection point method reflects the data over both the time and distance-axes, producing an inflection point. The accuracy of each method after smoothing can not be seen in the distance data but is clear in the first and second derivatives. The raw data were taken from the first decelerating 10 m flight of male Bird #02.

<table>
<thead>
<tr>
<th>Raw Data (m)</th>
<th>Pad</th>
<th>Smoothed Data</th>
<th>Vel. (m/s)</th>
<th>Accel. (m/s^2)</th>
<th>Pad</th>
<th>Smoothed Data</th>
<th>Vel. (m/s)</th>
<th>Accel. (m/s^2)</th>
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<td></td>
<td>5.237</td>
<td>2.663</td>
<td>-8.977</td>
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Figure 5: Comparison of flights of different distances. A 10 m flight (solid) has the same acceleration "envelopes" as a 5 m flight (dotted) with a section of flight near Vmax in the middle. The flights do not end exactly at 5 m and 10 m as the birds flew to a hovering stop some distance from the end of the tunnel. I filmed 10 m flights in 2 parts (i.e. accelerating and decelerating), thus there is a gap in the middle of the 10 m flight where these two parts were joined together. These flights were from male Bird #02.
Figure 6: Explanation of acronyms used in this paper. Panel A shows a stylistic example of a velocity curve. Panel B shows a stylistic example of an acceleration curve. The x-axis may be time or distance depending on the application.
Table II: Results of paired two-sample one-tailed t-tests for 5 m vs. 10 m flights where * is individually significant at the $\alpha = 0.05$ level and ** is significant at the table-wide level (Bonferroni correction). Acronyms are defined in Fig. 6.

<table>
<thead>
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<th>Parameter</th>
<th>t-stat</th>
<th>P</th>
<th>Bonferroni Corrected alpha</th>
</tr>
</thead>
<tbody>
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<td>dVmax</td>
<td>-19.04</td>
<td>$1.37 \times 10^{-7}$**</td>
<td>0.006</td>
</tr>
<tr>
<td>dDmax</td>
<td>-2.69</td>
<td>0.01*</td>
<td>0.006</td>
</tr>
<tr>
<td>tDmax</td>
<td>-2.42</td>
<td>0.02*</td>
<td>0.007</td>
</tr>
<tr>
<td>tVmax</td>
<td>-2.04</td>
<td>0.04*</td>
<td>0.008</td>
</tr>
<tr>
<td>Vmax</td>
<td>-1.99</td>
<td>0.04*</td>
<td>0.01</td>
</tr>
<tr>
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<td>0.01</td>
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<tr>
<td>dAmax</td>
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<td>0.19</td>
<td>0.02</td>
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<td>tAmax</td>
<td>-0.67</td>
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<tr>
<td>Dmax</td>
<td>0.05</td>
<td>0.48</td>
<td>0.05</td>
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</table>

For all tests: $df = 7$, $n = 8$ birds.
total flight distance for both kinds of flights (2.25 ± 0.12 m from the start of 5 m flights and 5.04 ± 0.20 m from the start of 10 m flights; Table II). Hummingbirds decelerate faster than they accelerate and do so closer to the end of the flight. They reached Amax within 0.40 ± 0.08 s of the beginning and Dmax within 0.23 ± 0.04 s of the end of the flight (Table II).

**Accelerating vs. Decelerating Portions of 10 m Flights**

To justify considering the accelerating and decelerating halves of the long flights as complete 10 m flights, I compared the two halves to each other and did corresponding comparisons for short (5 m) flights, using the absolute value of the parameters. In this way, the magnitude of Amax and Dmax could be related even though one was positive and one was negative. Vmax occurred in the middle of the flight for both 5 m and 10 m flights. Since Vmax is as likely to occur in the first or second half of a flight where and when it occurs are meaningless when measured in either half alone. As mentioned earlier, in 5 m flights Dmax occurred closer to the ends of flights (0.17 ± 0.03 s) than Amax occurred from the beginning (0.35 ± 0.03 s). This was also true for 10 m flights but was not significant at the table-wide level (Table III). The result of these comparisons is that I will consider the two sections of the 10 m flights one complete flight from now on.

An important result is that the acceleration and deceleration "envelopes" were independent of flight distance because it suggests that acceleration can be considered stereotypic of individuals (or of their morphology). It also suggests that hummingbirds do not require foreknowledge about the distance of their flights to govern acceleration (Gass 1974; Gass and Sutherland 1985) as the execution of the accelerating portion of flights is related to bird morphology and not to flight distance.

Since birds reach an average Amax of 15.29 m/s² in about 0.4 s and the acceleration "envelopes" are roughly symmetrical on either side of Amax (e.g. Fig. 7), then it is reasonable to
Table III: Results of paired two-sample one-tailed t-tests for the accelerating part of a flight vs. the decelerating part of a flight where * is individually significant at the $\alpha = 0.05$ level and ** is significant at the table-wide level (Bonferroni correction). Acronyms are defined in Figure 6.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>t-stat</th>
<th>P</th>
<th>Bonferroni Corrected alpha</th>
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</thead>
<tbody>
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<td>Amax vs Dmax in all flights</td>
<td>-9.35</td>
<td>0.000017**</td>
<td>0.005</td>
</tr>
<tr>
<td>tAmax vs tDmax in 5 m flights</td>
<td>7.10</td>
<td>0.000097**</td>
<td>0.006</td>
</tr>
<tr>
<td>Amax vs. Dmax in 10 m flights</td>
<td>-5.83</td>
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<td>0.006</td>
</tr>
<tr>
<td>Amax vs. Dmax in 5 m flights</td>
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<td>dAmax vs. dDmax in 5 m flights</td>
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<td>0.004**</td>
<td>0.008</td>
</tr>
<tr>
<td>tAmax vs. tDmax in all flights</td>
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<td>0.02*</td>
<td>0.01</td>
</tr>
<tr>
<td>Vmax in accelerating half vs decelerating half of 10 m flights</td>
<td>1.79</td>
<td>0.06</td>
<td>0.01</td>
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<tr>
<td>dAmax vs dDmax in all flights</td>
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<td>0.02</td>
</tr>
<tr>
<td>tAmax vs tDmax in 10 m flights</td>
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<td>0.16</td>
<td>0.03</td>
</tr>
<tr>
<td>dAmax vs. dDmax in 10 m flights</td>
<td>0.47</td>
<td>0.33</td>
<td>0.05</td>
</tr>
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</table>

For all tests: df = 7, n = 8 birds
Figure 7: Examples of average velocity (closed circles, solid line) and acceleration (open squares, dotted line) data taken from Bird #03 (male). Curves are best fitted polynomials. Notice that the acceleration data is almost symmetrical around Amax.
assume that the accelerating portion of a flight lasts 0.8 s and covers approximately 2.44 m.
Following the same reasoning for deceleration, birds reaching an average Dmax of -19.76 m/s² in
0.23 s decelerate for 0.46 s at the end of a flight and travel 1.04 m. Therefore, if I assume a
maximum velocity of 4.38 m/s, this average bird accelerates and decelerates for 100% of flights
less than 3.48 m and less than 50% of flights longer than 9 m.

If flights less than 3.48 m involve 100% acceleration, how much of their time do wild
hummingbirds spend in steady-state flight? In other words, how much of the time does
aerodynamic theory describe natural hummingbird flight? In densely flowered meadows, 90-95% of
foraging flights are between flowers within patches and are less than 2 m long (Perkins 1977;
Montgomerie 1979; Gass and Montgomerie 1981; Gass and Sutherland 1985). Assuming that
they fly in nature as they do in the laboratory, territorial hummingbirds spend most of their
foraging time on short flights on which they only accelerate and decelerate. Since hummingbirds
actually spend very little time flying at V_{mp}, aerodynamic theory describes very few of their
actual flights.

There is evidence, however, that the cost of deceleration for hummingbirds is relatively
inexpensive. Hummingbirds seem to be passively using drag to decelerate. Since drag (in Watts)
varies with V³ (Norberg 1990), and power equals the product of mass, acceleration and velocity,
then the deceleration resulting from drag should vary with V². I tested this by generating a V²
curve for each flight of each bird and comparing it with the deceleration curve (e.g. Fig. 8).
Although some areas exceeded the predicted curve, the general trend of the V² curve is followed
by the deceleration curve. The behaviour of the birds also indicates that they use drag to slow
down. During the deceleration phase of flights, birds change the posture of their body and fan out
their tails. This greatly increases drag and effectively makes the bird act like a parachute.
Deceleration cannot be entirely free as birds continue to flap their wings and effort must be
exerted to change their posture while fanning their tail. However, it seems clear that most of
deceleration is passive, relatively inexpensive and thus does not contribute much to the overall
cost of an accelerating (and decelerating) flight.
Figure 8: Comparison of deceleration curve (solid line) with $V^2$ curve (dotted line). This example is flight 4 of bird #02 (male) in the 5 m tunnel. Although the deceleration curve fluctuates, the general trend follows $V^2$. The seeming periodicity of the deceleration curve is an artifact due to the cutoff frequency chosen in the digital filtering of the raw data.
Hayes (1929) and Allard (1934) reported flight speeds for automobile-chased ruby-throated hummingbirds (*Archilochus colubris* Linnaeus) as 21 m/s and 25-28 m/s, respectively. These are considerably higher than all subsequent observations, suggesting that they are erroneous, especially in view of the fact that Greenewalt (1960) reported that a ruby-throated hummingbird could not progress against a 12 m/s headwind in a wind tunnel. Gill (1985) measured average flight speeds for long-tailed hermit hummingbirds (*Phaethornis superciliosus* Linné) of $11.57 \pm 0.71$ m/s. These speeds were averaged by stopwatch over a distance of 40 m and were probably fairly close to the maximum velocity attainable. Pearson (1960) released Allen's hummingbirds (*Selasphorus sasin* Lesson) in a culvert (~ 90 m) and measured velocities of 8 and 11 m/s. All of these measurements are considerably higher than the $V_{mp}$ of 5.5 m/s, calculated for all hummingbirds (Gill 1985), suggesting that these values may be top speeds for hummingbirds and not normal cruising speeds. I calculated the average $V_{mp}$ for my rufous hummingbirds as 5.08 m/s (using equations from Pennycuick 1989). Although most of the birds flew at about 80% of this speed (average 4.38 m/s; Fig. 9a), there was no significant difference in the power output at this speed vs. the power output at $V_{mp}$ (df = 7; $t = -2.24$; 2-tailed $P = 0.06$; Fig. 9b). Thus I can consider that my hummingbirds were flying in the centre of their flights using the same power as that required for $V_{mp}$.

*Males vs. Females*

Females reached a higher $V_{max}$ ($4.78 \pm 0.23$ m/s) than males ($3.98 \pm 0.22$ m/s) but the difference was not significant at the table-wide level (Table IV). Females accelerated ($17.60 \pm 0.75$ m/s$^2$) and decelerated ($-23.08 \pm 1.30$ m/s$^2$) significantly faster than males ($12.93 \pm 0.42$ m/s$^2$ and $-16.51 \pm 0.58$ m/s$^2$) (Table IV; Fig. 10). The placement of these parameters (in time and distance) were the same for both sexes (Table IV; Fig. 10).
Figure 9: A) Relating calculated $V_{mp}$ with actual cruising speed of birds in the tunnel. Most birds flew at about 80% of $V_{mp}$. B) Relating power output at $V_{mp}$ and power output at $V_{max}$. The lines represent 1:1 relationships.
Table IV: Results of two-sample one-tailed t-tests assuming equal variance for males vs. females on all flight types where * is individually significant at the $\alpha = 0.05$ level and ** is significant at the table-wide level (Bonferroni correction).

<table>
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For all tests: df = 6, n = 8 birds (4 males, 4 females)
Figure 10: Comparison of averaged 5 m flights of males (solid) and females (dashed). The triangles, circles and squares denote Vmax, Amax and Dmax, respectively. Error bars for Vmax are ± S.E. Standard errors for Amax and Dmax are given in the text. The Vmax values in this figure are lower than that reported in the text due to the effects of averaging whole flights.
The results of the gender comparisons support the prediction of aerodynamic theory that long wings (low wing disc loading) allows for higher acceleration and velocity. Females accelerate significantly faster than males (Fig. 11; slope = 0.69; ANOVA: df = 1 and 6; F = 20.64; P = 0.004) in routine foraging flights and their cruising speed is higher, although not significantly so (Fig. 11; slope = 0.098; ANOVA: df = 1 and 6; F = 2.96; P = 0.14). Therefore, the low wing disc loading of females not only imparts a lower power requirement for hovering (Epting and Casey 1973; Epting 1980) but also allows higher forward flight and acceleration performance. It could be that males have traded off efficient flight economics for increased aggression ability (Feinsinger and Chaplin 1975; Kodric-Brown and Brown 1978). Rufous hummingbirds are among the most aggressive and territorial of the hummingbirds studied. Therefore, female wing length may be a compromise between efficient flight during the breeding season and aggressive ability during the non-breeding season and migration when they set up territories. Males, as they do not care for the young, are not subject to this trade-off and may therefore be selected for greater aggressive ability all year round (Kodric-Brown and Brown 1978).

This study has shown that acceleration is an important part of the daily time budget of rufous hummingbirds and the predominant component of the foraging time budget. Most of their flights are less than 2 m long and thus are composed entirely of acceleration and deceleration. Very short flights (between flowers on an inflorescence) probably consist of hovering metabolism at low velocities (pers. obs.; J. Thompson, unpubl. obs.) What happens to the predicted energy budget of the birds if acceleration is more energetically expensive than forward flight at a constant velocity? Chapter 3 will investigate this possibility theoretically.
Figure 11: Average Vmax (open squares and circles = males and females, respectively) and Amax (closed squares and circles = males and females, respectively) of each bird vs. its wing length. The slope of the Vmax regression (dotted line) is 0.098 and is not significantly different from a slope of zero (see text). The slope of the Amax regression (solid line) is 0.69 and is significant (see text). It may be that more data are required to demonstrate a significance in the Vmax regression. The wing lengths measured here are full shoulder to tip wing lengths.
Chapter 3: Acceleration Should Have a Separate Energetic Cost from Steady State Flight

Although all motion to or from zero velocity involves acceleration, the flight of most birds is at constant velocities (e.g. foragers like swallows, soarers like eagles and migrants like geese; Norberg 1990). Consequently, they approximately satisfy the steady-state assumptions of current aerodynamic theory (Pennycuick 1975; Greenewalt 1975; Tucker 1975). This is not true for the foraging flights of hummingbirds, which account for most of their non-migratory flight and up to half of their diurnal time during migratory stopovers (Pearson 1954; Wolf and Hainsworth 1971; Gass and Montgomerie 1981; Sutherland, et al. 1982). Hummingbirds do fly at a constant velocity for the middle portion of flights longer than 3.5 m (Chapter 2). But Perkins (1977) showed that most foraging flights are 1 m or less in one foraging situation, and I showed (Chapter 2) that hummingbirds actively accelerate for 100% of flights less than 3.5 metres in length.

Current theories used to estimate the cost of flight and current applications of the theories make assumptions about those flights. The biggest assumption is that there is no acceleration. Birds fly at a constant velocity between two points. This assumption allows a good estimate of the power required for flapping flight, a considerably difficult concept.

However, acceleration must require more power than steady-state (constant non-zero velocity) flight. For example, according to Newton's first law, there can be no acceleration if there is no net force acting on an object. Therefore, for steady-state flights no net forward force is involved and the power required for these flights can be calculated using equations already developed from three current theories as these theories take into account drag and lift costs (Pennycuick 1989; Norberg 1990). For acceleration, though, a net forward force is required to change velocity, and that force requires power. Therefore, acceleration should cost more than steady-state flight; at least as much as it takes to accelerate the mass. If so, the current equations underestimate the power requirements for hummingbirds by at least that amount, since hummingbirds accelerate and decelerate for a large portion of their flight time. They may also
underestimate the power requirements of small forest-dwelling birds that also spend a lot of time flying short distances. It would follow that the relatively short flights of these types of birds (including hummingbirds) are more expensive than calculated from steady-state assumptions and thus foraging is less profitable.

If acceleration is an expensive activity relative to steady-state flight, there are implications for energetics studies. Many studies have been done on the daily energetics (intake and expenditures) of hummingbirds (Wolf and Hainsworth 1971; Wolf, et al. 1975; Wolf and Hainsworth 1977; Beuchat, et al. 1979; Gass and Sutherland 1985; Bartholomew and Lighton 1986; Wells 1993a). Energy expenditures for flights in these studies assumed either hovering metabolism or a steady-state average velocity (or some combination of the two). If hummingbird flight is more expensive than estimated, then conclusions about energy balance during the day would be inaccurate.

This chapter will be mainly a thought exercise exploring some possibilities that follow from the above assumptions. I will look at the problem from two different perspectives, making appropriate assumptions and following each to its conclusion. I will then discuss these conclusions and how they relate to the wild hummingbird in the field.

THEORETICAL BACKGROUND

Three theories are currently in use for estimating energy budgets and power curves for flight: the blade element theory, the momentum jet theory and the vortex theory (Norberg 1990). The blade element theory is used to describe the static, immobile conditions of an airplane wing, when steady-state or quasi-steady-state conditions can be assumed. This theory is good for describing gliding flight. The momentum jet theory describes the helicopter-like motion of an actuator disk, in which air is driven downwards throughout the area of the disk. This theory also assumes steady-state conditions and is used to describe hovering. The vortex theory relates the lift of a moving wing with the pattern and velocity of the induced flow of the wake behind it and the power needed to generate that flow. This theory is more useful in describing the at least partially
non-steady-state conditions of flapping flight. Various combinations of these theories go into the calculation of the power needed for flight.

The power required for flight incorporates several components. Parasite power is the power required to overcome the body drag and it is proportional to $V^3$. Profile power is that required to overcome the drag associated with the wings. Pennycuick (1989) stated that profile power is nearly constant around $V_{mp}$ due to decreases in wing beat frequency and amplitude as velocity increases. It could thus be calculated as a constant multiple of absolute minimum power ($P_{am}$). Tucker (1973) proposed, however, that profile power is proportional to forward velocity due to increases in the angle of attack of the wings. Induced power is the power required to overcome drag due to lift. This drag is inversely proportional to velocity and is due to the production of vortices at the wing tips. Inertial power is that required to accelerate and decelerate the wings as they flap.

The power required for hovering is the sum of the induced, profile and inertial powers. Profile and inertial powers can be calculated using the blade element theory if a steady-state is assumed, but sometimes a combination of the blade element and momentum jet theories is used. Induced power, however, is calculated more accurately by the vortex theory which accounts for the unsteadiness of air motion (Norberg 1990). The momentum jet theory can be used simply but gives only a minimum value for induced power and should be used when only the morphology of the animal is known and not its kinetics.

The power output required for forward flight at a constant velocity is the sum of all four powers (induced, profile, inertial, and parasite). At medium and fast speeds, inertial power is negligible and can be ignored. Induced power is also small at these speeds and thus can be calculated using the momentum jet theory. Profile and parasite powers are calculated using the blade element theory as before. To calculate power input by the bird, the power output is multiplied by the energy conversion efficiency of the muscles (the efficiency at which chemical energy is converted into mechanical energy). The efficiency of vertebrate muscle seems to be somewhere in the range of 10-25% (Bernstein, et al. 1973; Tucker 1973; Wells 1993b; Chal and
Dudley 1995) depending on the activity of the bird (e.g. hovering) and perhaps on velocity (R.W. Blake, pers. comm.). For this experiment, I assumed efficiency to be constant at 20% (Tucker 1973). The validity of this assumption will be discussed later.

All of these theories are limited, though. They must assume a steady-state (constant velocity; zero for hovering and non-zero for forward flight). This may be accurate for long flights but is problematic for estimating the power required for forward flapping flights over a short distance or for hovering. It is uncertain whether steady-state assumptions can be applied to hovering. Weis-Fogh (1972, 1973) demonstrated that the normal hovering of hummingbirds is consistent with steady-state assumptions, but Ellington (1984e-f), who repeated Weis-Fogh's work with more accurate data, concluded that hovering may not be consistent with steady-state assumptions. The problem is that the fluid conditions around constantly flapping wings are constantly modified by the wing. Therefore, at best, only an approximation of the actions can be achieved. These theories also make no attempt to describe the power required to accelerate a self-propelled flying mass. It is not even known if quasi-steady assumptions can be applied to large wing beat amplitudes and high flapping frequencies (Norberg 1990) like those found in a hummingbird. Yet aerodynamic theory is frequently used to describe the flight and energetics of hummingbirds (Montgomerie 1979; Hainsworth 1981; Gill 1985; Collins and Paton 1989; Tamm 1989).

THOUGHT EXPERIMENT

The cost of acceleration can be divided into two components: the cost of flying at varying (steady-state) velocities and the cost of accelerating the mass. In the absence of a generalized theory for acceleration, a way to estimate the former would be to divide an accelerating flight into small time segments and accumulate the costs for each segment using the power curve estimated from steady-state theories (e.g. Fig. 12). This is equivalent to assuming that hummingbirds fly according to steady state assumptions for very short periods of time and shift between velocities at no cost. The cumulative power (energy) estimated by this method could be compared with that estimated for the same flight assuming a constant average velocity (e.g. the mean velocity of
Figure 12: Power curve for hypothetical 3.5 g rufous hummingbird, calculated using Pennycuick's (1989) equations and assuming energy conversion efficiency of muscles to be 20%. Vmp is 4.86 m/s. Vmr is ~ 8.15 m/s. The output cost of hovering is assumed to be 0.152 W (Suarez, et al. 1990).
the flight as estimated in the field by stopwatch; Gill 1985). This method does not estimate the cost of accelerating, per se; it mainly integrates the variable steady-state costs of flying at variable velocities.

For ease in modeling, in this experiment I synthesized an "average" flight using the data from Chapter 2 and assuming symmetry in acceleration and deceleration phases. In a typical flight, a bird accelerates from a perch to a maximum velocity of 4.61 m/s, then decelerates to hover at a feeder in a flight distance of 3.5 m (Fig. 13). The average velocity of this flight would be 3.5 m / 1.37 s or 2.55 m/s (Fig. 13). Since the acceleration and deceleration "envelopes" are independent of flight distance (Chapter 2), I could synthesize longer or shorter flights by inserting or deleting a segment of constant maximum velocity between them (Fig. 13). In this way, I could reasonably compare horizontal flights of any distance.

The parameters used in all calculations are in Table V. The bird measurements are typical of an average unisex rufous hummingbird. The equations used in calculations of flight cost (Pennycuick 1975; 1989) and the resulting power output curve for this hypothetical bird are shown in Table VI and Figure 12, respectively.

Although other equations could be used to calculate power required for flight (Tucker 1975; Greenewalt 1975; Montgomerie 1979), Welham (1994) concluded that the Pennycuick equations most realistically estimate the cost of steady-state flight. Welham (1994) compared the predicted maximum range velocities from three aerodynamic equations (Pennycuick 1975; 1989; Tucker 1975; Greenewalt 1975) with the actual flight speeds of migrating birds. He found that the Pennycuick equations gave the best estimate of $V_{mr}$ for a wide range of birds and velocities. I assumed that these equations gave the best estimates for $V_{mp}$ as well. I modified some of the equations to reflect the differences between hummingbirds and other birds. For example, King and Farner (1961) reported an equation for basal metabolism that correlates well with that recorded for hummingbirds (Lasiewski 1963) and I have used this equation for basal metabolic calculations ($P_{met}$). I also chose to use Pennycuick's (1989) equations for profile power as the
Figure 13: Velocity curves used in analysis. Curve A is a hypothetical velocity curve with a Vmax of 4.61 m/s. Curve B is the same flight at a constant average velocity of 2.55 m/s. The discontinuities indicate where a section was inserted/taken out to lengthen/shorten the distance of the flight.
Table V: Physical characteristics of *Selasphorus Rufus* and other parameters used in energetic cost equations.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>VALUE</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass (W)</td>
<td>0.0035 kg</td>
<td>this study</td>
</tr>
<tr>
<td>Wing Span (b)</td>
<td>0.0975 m</td>
<td>this study</td>
</tr>
<tr>
<td>Air Density (ρ) (sea level)</td>
<td>1.23 kg/m³</td>
<td>Pennycuick 1989</td>
</tr>
<tr>
<td>Kinematic Viscosity (v)</td>
<td>0.0000145 m³/s</td>
<td>Pennycuick 1989</td>
</tr>
<tr>
<td>Induced Drag Factor (k)</td>
<td>1.2</td>
<td>Pennycuick 1989</td>
</tr>
<tr>
<td>Profile Power Ratio (X₁)</td>
<td>1.2</td>
<td>Pennycuick 1989</td>
</tr>
<tr>
<td>Acceleration due to gravity (g)</td>
<td>9.81 m/s²</td>
<td>Tucker 1973</td>
</tr>
<tr>
<td>Energy Conversion Efficiency (c)</td>
<td>0.20</td>
<td>Pennycuick 1989</td>
</tr>
<tr>
<td>Circulation/Respiration Factor (R)</td>
<td>1.1</td>
<td>Pennycuick 1989</td>
</tr>
</tbody>
</table>
Table VI: Equations* used in energetic cost analysis (Pennycuick, 1989)

<table>
<thead>
<tr>
<th>Equation</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b = 2*WL + BD$</td>
<td>metres</td>
</tr>
<tr>
<td>$S_b = BD^2 \times \pi / 4$</td>
<td>metres$^2$</td>
</tr>
<tr>
<td>$S_d = b^2 \times \pi / 4$</td>
<td>metres$^2$</td>
</tr>
<tr>
<td>$S_p = S_b \times C_d$</td>
<td>metres$^2$</td>
</tr>
<tr>
<td>$r_b = 125000 \times \sqrt{m}$</td>
<td>dimensionless</td>
</tr>
<tr>
<td>$C_d = 1.57 - (0.108*\ln(r_b))$</td>
<td>dimensionless</td>
</tr>
<tr>
<td>$P_{par} = 0.5\rho V^3 S_b C_d$</td>
<td>Watts</td>
</tr>
<tr>
<td>$P_{ind} = km^2 g^2 / 2 S_d V\rho$</td>
<td>Watts</td>
</tr>
<tr>
<td>$P_{pro} = X_1 \times P_{am}$</td>
<td>Watts</td>
</tr>
<tr>
<td>$P_{am} = 0.877k 0.75 (mg)^{1.5} S_p 0.25 / (\sqrt{\rho} \times S_d 0.75)$</td>
<td>Watts</td>
</tr>
<tr>
<td>$P_{met} = 3.6m 0.744$ (King and Farner 1961)</td>
<td>Watts</td>
</tr>
<tr>
<td>$P_{out} = R * (P_{par} + P_{ind} + P_{pro} + P_{met})$</td>
<td>Watts</td>
</tr>
</tbody>
</table>

* see Appendix B for explanation of symbols
profile power calculations from Pennycuick (1968) for the ruby-throated hummingbird 
(*Archilochus colubris*) follow this assumption closely.

I divided my synthetic flights into 1/30 sec intervals and then summed the costs over all 
intervals to estimate the energetic cost of the whole flight in Joules. I assumed that any interval 
cost that was greater than the cost of hovering was actually the cost of hovering (0.76 W; Suarez, 
et al. 1990). By this analysis, which still ignores Newtonian acceleration, the cost of an 
accelerating flight is 150 % more than that of a steady-state flight. A 3.5 m flight at a constant 
velocity of 2.55 m/s requires an energy output of 0.10 J (or 21 W/kg – mean mass specific power 
output), but the same flight accelerating from 0 to 4.61 m/s and decelerating back to 0 costs 0.25 
J (52 W/kg). This method incorporates the steady-state costs of flying at a sequence of velocities 
but assumes that there is no extra cost of accelerating the mass.

The other component of the cost of acceleration is the cost of accelerating the mass of the 
bird. Newton's law states that accelerating a mass costs energy. The rate of energy expenditure 
for an accelerating mass is:

\[ P = FV = maV \]  

[3]

where P is the power required to accelerate the mass, F is the force required to accelerate the 
mass, m is the mass, a is the acceleration and V is the velocity (Halliday and Resnik 1986; May 
1991). I could have calculated this cost as the kinetic energy over the metabolic conversion 
efficiency (Welham and Ydenberg 1993) but this assumes a constant acceleration which clearly 
doesn't match the data.

I calculated the cost of accelerating the bird at each time interval of the synthetic flight, 
summed over all time intervals and then added this result to the cost of an accelerating flight. The 
final result was a cost for the accelerating flight (3.5 m) of 0.33 J (69 W/kg); a 230 % increase 
over the original steady-state assumptions. This analysis was performed for various distances 
(Fig. 14). Since longer flights are composed of the same acceleration and deceleration patterns 
with a section of steady-state flight in the middle, as flight distance increases, the
Figure 14: Mean mass specific power output during flight for a rufous hummingbird over various distances. Mean mass specific power output was calculated as the total energy output (J) during the flight divided by the duration of the flight in seconds and the mass of the bird. A) steady-state flight  B) accelerating flight  C) accelerating the mass added to accelerating flight  D) accelerating the mass. Notice that power output during a steady-state flight is constant over all distances because the velocity doesn't change. The greatest difference in power output between a steady-state flight and an accelerating flight occurs during short flights of < 3.5 m. The power output during the two types of flights converges for long distance flights indicating that acceleration does not influence the cost of long distance flights (e.g. migration). Note that the cost of accelerating the mass is the greatest for flights < 3.5 m. For comparison, the cost of hovering in these units is about 45 W/kg (Suarez, et al. 1990).
contribution of the cost of accelerating the mass to the total cost of the flight decreases. The influence of the cost of accelerating the mass is greatest for flights of less than 3.5 m.

I also did a sensitivity analysis of the effect of the bird's mass and wing length and the distance flown on the cost of steady-state flights (Fig. 15). I did this by plotting the change in energetic cost across a standardized range for each variable while the other variables were held at their original value. The original bird weighed 3.5 g and had a wing length of 4.25 cm. This is typical of a unisex rufous hummingbird. As hummingbird wings are sexually dimorphic in length, the perturbations of the analysis extend from male wings to the long female wings. The original flight distance was 3.5 m. Increasing mass or distance increases the energetic cost of a flight, but the same flight costs less if the wings are longer. Distance has a relatively small effect on the energetic cost of a flight with a slope of 0.56. The effect of mass is almost 3 times that of distance with a slope of 1.39. Wing length is negatively correlated with energetic cost with a slope of -1.03.

DISCUSSION

The mean power outputs for a steady-state flight and an accelerating flight converge for flights of great distances (Fig. 14), indicating that acceleration does not influence the cost of long distance flights (e.g. migration). Therefore, estimation of the cost of hummingbird migration would be unaffected by these results since most of a migration flight is flown at a steady-state velocity (presumably maximum range velocity; Pennycuick 1969; Welham 1994). Therefore, steady-state assumptions would apply to migratory flights and the current theories are sufficient.

The mean power output required to accelerate the mass of the bird decreases with distance because the acceleration "envelopes" are stereotypical for flights greater than 3.5 m. The bird spends more time at a constant maximum velocity on longer flights and so decreases the proportion of total cost due to accelerating the mass. Using the current assumptions, it seems that most of the cost of the accelerating phase of a flight is due to flying at low velocities and not to accelerating the mass.
Figure 15: Sensitivity analysis of aerodynamic theory. Distance has a range of 0.5–12 m, an original value of 3.5 m and a slope of 0.56. Mass has a range of 2.45–5.25 g, an original value of 3.5 g and a slope of 1.39. Wing length has a range of 3.613–5.100 cm, an original value of 4.25 cm and a slope of -1.03. The ranges of mass and wing length were kept within realistic limits for the characteristics of rufous hummingbirds.
Notice the extremely high estimates for the power output required for acceleration. Suarez et al. (1990) reported a mass specific power input for hovering of 226 W/kg for rufous hummingbirds, a figure that is less than that reported here for acceleration (power output/metabolic conversion efficiency = 345 W/kg power input). This means that acceleration may cost even more than hovering. However, there are some sources of error in these results. Since accelerating flight occurs most often at low to medium velocities, inertial power may become significant but was not taken into account in this study. As well, profile power may be overestimated at these low velocities (Pennycuick 1968). This method also doesn't take into account the possibility of almost entirely passive deceleration. This just confirms that current aerodynamic theory is insufficient for estimating the cost of acceleration.

The choice of 20% as the metabolic conversion efficiency was a somewhat arbitrary assignment. Wells (1993b) and Chal and Dudley (1995) have indicated that a hovering hummingbird's muscles operate at an efficiency of approximately 10% assuming perfect elastic storage. However, vertebrate muscle efficiencies are dependent on the rate of muscle shortening and thus would be dependent on the velocity of movement. The range of muscle efficiencies is 10–25%. Hovering was not included in this analysis and there is evidence that smaller animals operate muscles less efficiently than larger animals (Heglund and Cavagna 1985; Casey and Ellington 1989). I thus chose an efficiency that had been used before (Tucker 1973) and facilitated calculations.

Wells (1993b) measured the maximum power output of the flight muscles during hovering as 250–300 W/kg of muscle if zero elastic storage was assumed. The mass specific muscle power output of my accelerating birds (assuming flight muscles are 23.4% of body mass; Wells 1993b) was 295 W/kg muscle. This shows that accelerating hummingbirds may be performing at near maximum power output. However, this estimate may be overestimated due to passive deceleration due to drag.

The contribution of wing length to the cost of steady-state flight is such that the total cost of a flight of any distance is less for longer winged birds. If two birds have equal mass and fly the
same speed, but one is a short-winged male and the other a long-winged female, the female's flight will be less costly because her wing disc loading would be lower. Epting (1980) demonstrated that the cost of hovering decreases with lower wing disc loading. This study shows that this is also true for the range of wing lengths for hummingbirds during forward flight at near \( V_{mp} \).

Wolf and Hainsworth (1977) estimated the time course of accumulation of energy over the day for 2 species of hummingbird (\textit{Lampornis clemenciae} Lesson and \textit{Archilochus alexandri} Bourcier and Mulsant) under \textit{ad libitum} conditions in the laboratory. In one day, birds accumulated some 3.2 kcal (13.4 kJ) to sustain it through the night, an accumulation of 36\% and 105\% (\textit{L. clemenciae} and \textit{A. alexandri}, respectively) more than they needed. In this case, they expected a weight gain of 0.08 g and 0.15 g, respectively. Unfortunately, these values were within the measurement error of their balance and could not be detected. Therefore, because they did not report weight changes, it is unknown whether birds gained weight, excreted the excess energy (Wolf and Hainsworth 1977) or perhaps used it to power acceleration. The birds were housed in 2.5 x 2.5 x 2 m flight rooms so acceleration probably formed the greater portion of the birds' flight.

An extra cost for acceleration would have implications for hummingbirds as they spend most of their time flying short flights between patches and flowers. Wolf and Hainsworth (1971) estimated that territorial hummingbirds (\textit{Eulampis jugularis} Linné and \textit{Calypte anna} Lesson) average 15\% of time foraging. This small amount of time, however, accounts for an average of 40\% of the energy budget. Pearson (1954) reported similar results for \textit{Calypte anna}. In one field study (Perkins 1977; Gass and Montgomerie 1981), most foraging flights were less than 2 m long within individual clumps of flowers. This means that almost all flights are less than 2 metres long and consist entirely of acceleration and deceleration (with a considerable addition in cost if acceleration costs more than steady-state flight). However, steady-state aerodynamic theory gives poor estimates of the cost of the accelerating portion of a flight (Fig. 14; Pennycuick 1989). But even without this added cost, acceleration should play an important role in the daily time and energy budgets of territorial hummingbirds like the rufous.
The results of this exercise could have many implications for energetics studies of hummingbirds. Hummingbirds accelerate and decelerate throughout most of their foraging flights. Accelerating flights theoretically cost more than a same distance flight at a constant velocity for at least two reasons (the cost of steady-state flight at various velocities and the cost of accelerating the mass). This means that current assumptions in the literature underestimate the energetic cost of flight in hummingbirds. This study estimated acceleration costs using steady-state assumptions. However, Pennycuick's (1989) aerodynamic equations are accurate for only a small range of velocities around $V_{mp}$. They do not accurately describe the power required for very low or very high velocity flights. As well, the slow speeds and high wing beat frequencies of an accelerating hummingbird may introduce non-steady-state conditions (Norberg 1990). However, this may be compensated by an overestimate in the profile power. Additional costs could be imposed if switching between velocities or switching between modes of flight (e.g. hovering and forward flight) is expensive. Empirical lab studies might be able to shed more light on this subject (see chapters 4 and 5). On the other hand, a totally different method of thought may be required for estimating the cost of accelerating flight. These are relevant directions for further study.
Chapter 4: Velocity and Acceleration of Rufous Hummingbirds in Inclined Flight

Chapter 2 showed experimentally that rufous hummingbirds accelerate at a high rate and accelerate and decelerate consistently regardless of the length of the flight. Chapter 3 argued theoretically that accelerating flights should be more expensive energetically than steady-state flights of the same average velocity and estimated that cost as close to maximum muscle power output. It also demonstrated, however, that current aerodynamic theory is insufficient to predict this cost. This chapter will investigate the power required for accelerating flight by evaluating the velocity and acceleration of flights at various inclinations.

There is a maximum amount of sustainable power output ($P_{\text{max}}$) that can be developed by flight muscles (Weis-Fogh and Alexander 1977). The ability of birds to perform a range of actions in flight (e.g. to fly at a high speed, to accelerate at a high rate, to hover, to climb steeply or to carry loads) essentially depends on the residual power available; i.e. difference between $P_{\text{max}}$ and the power to fly unloaded at $V_{\text{mp}}$ (Hedenstrom and Alerstam 1992; 1994). If a hummingbird were flying horizontally at $P_{\text{max}}$ for a long flight (e.g. migratory flight) then it would achieve very high velocities with this residual power. It would achieve high acceleration if it flew horizontally at $P_{\text{max}}$ for a short distance. I can assume that birds fly at $P_{\text{max}}$ during climbing flight (Hedenstrom and Alerstam 1992), and can consider this value to have horizontal and vertical components. The vertical component of power output is:

$$P_{\text{vert}} = m(g+a)V_{\text{vert}}.$$  \[4\]

where $m$ is the mass, $g$ is the acceleration due to gravity, $a$ is the acceleration of the bird, and $V_{\text{vert}}$ is the vertical velocity. I can estimate $P_{\text{max}}$ by extrapolating a function relating acceleration to inclination to 90°, where there is no horizontal component and all energy output will power climbing.
If the acceleration vs. inclination curve is linear, this demonstrates that power is a limiting factor. Because the birds only have a limited amount of power to apply to flight, they achieve lower accelerations at high inclinations and vice versa. I can thus assume that the power required to accelerate and decelerate in a horizontal tunnel will be equal to $P_{\text{max}}$ as there is no vertical component to the power output.

In this chapter, I will infer an energetic cost for acceleration by documenting the influence of inclined flight on acceleration and velocity. I will test the validity of the above assumptions using knowledge about the consistency of the velocity and acceleration curves (Chapter 2) and the shape of the acceleration vs. inclination curve.

**METHODS AND MATERIALS**

*The Animals*

I used eight Rufous hummingbirds (*Selasphorus rufus*), four males and four females selected randomly from a laboratory population of 20 birds. They were captured as adults at Sumas Mountain and the Sunshine Coast, BC, in May/June 1994 and held individually in 60 x 60 x 60 cm wire cages in a large room. They had *ad libitum* access to commercial hummingbird food (Nektar Plus) in commercial hummingbird feeders (Perky Pet) on weekdays and 20% sucrose solution (w/w) on weekends. All observations were made between June and August 1994.

*The Experimental Enclosure*

I analyzed videotape records of birds flying through an inclined tunnel 2.5 m long, 50 x 60 cm in cross section, and mounted from the ceiling by pulleys (see Figure 3, Chapter 2). A 2.5 m x 30 cm mirror was mounted at 45 degrees under the tunnel to provide two viewpoints for filming. I could adjust the inclination of the tunnel (from 0 to 45° in either direction) simply by raising and/or lowering the ends of the tunnel. Two 150 W incandescent lights in large reflectors were placed at either end of the tunnel and ambient room lighting illuminated the whole.
Training

I trained birds gradually over a day or two, allowing them to learn each new procedure before confronting the next. First, I put each bird into a horizontal tunnel with the perch at one end and a hanging feeder at the other. Most birds found the feeder and the perch within a few minutes and flew to the feeder and back about once every 20 min. All birds explored the tunnel cautiously at first and in stages; if they learned especially slowly I left them in the tunnel overnight.

Experimental protocol

After birds flew consistently, strongly and without hesitating, I filmed them in horizontal (0 degrees) flight. Two or three flights were filmed in each direction (perch to feeder and feeder to perch). I chose 4 other angles for filming (+45 °, +22.5 °, -22.5 ° and -45 °) and randomized the order to discount the possibility that the birds were learning a protocol. An adjustment period (usually 1-3 hours, sometimes overnight) was required before birds settled down each time the tunnel was inclined at a new angle. Some birds could be filmed at all 5 angles within a day, while others took up to three days.

I filmed flights from behind a blind by panning a tripod-mounted video camera (Sony CCD-V101 Hi-8 with variable shutter speed) 2.8 m from the center of the tunnel. The camera was tilted at the same angle as the tunnel so that each frame contained a "horizontal tunnel" regardless of the inclination. This simplified the parallax adjustments and the calculation of the real position of the bird in three dimensions (see Appendix A, Chapter 2). Birds were free to fly and feed at any time. I provided only 10 µL of 20% (w/w) sucrose each time the bird went to the feeder and birds typically made 3-5 trips from perch to feeder within ~1 min. consuming 30–50 µL in total. These bouts began irregularly every 6-10 min.

Hummingbirds telegraph their intention to feed by becoming slightly agitated while perching, so it was relatively easy to film flights. For each inclination, I distinguished flights as "to feeder" or "to perch". Each bird continued until I had filmed 2 or 3 "good" flights of each of the 4 types. Since flights to the feeder began from a perching start and flights to the perch began from a
hovering start, I wanted to know if their acceleration patterns differed. I assumed that these flights were equivalent but distinguished the two types to test this assumption. "Good" flights were continuous (no hesitations, stops, or turns), started or ended within ~0.5 m of the end of the tunnel, and the direct and reflected bird images and all relevant tape markers were continuously visible in the frame. For most individuals, about 60% of all flights were "good" after training. Hesitations and early stops were more frequent in downward than in climbing flights.

*The Digitizing of Bird Positions from Videotapes*

Flights averaged 1.25 s, or 40 video frames. I repeated the following procedure for each frame of each "good" flight of each bird (238 flights and ~9600 frames, total). With the camcorder connected to a Silicon Graphics workstation (SGI Indy), I grabbed one frame at a time as a digital image using the Silicon Graphics image processing utility ("capture"). These images were stored on 8mm backup tape to be analyzed at my convenience. I analyzed one frame at a time on a PC with video image processing software (Digital Optics "V"). I digitized 11 points per frame using a mouse: the tape markers on either side of the bird in X, Y, and Z dimensions, the bird's apparent center of mass on the direct and reflected images, and the identity of each tape. Tape identities were digitized by clicking positions on a "ruler" visible on the digitizing screen (see Figure 4, Chapter 2). These data were written to a file, the tape was advanced one frame (1/30 s) and the procedure repeated. Later, I converted the data from units of pixels to metres and then corrected to reduce error due to parallax. Errors of 0.25 cm in the middle of flights and 0.5 cm at the ends due to the grain of pixels on the monitor could not be removed.

*Parallax Correction*

The shape of the room forced me to pan the camera during filming, introducing parallax errors (0 cm in the middle of records; ~15 cm near the ends, where filming angles were greatest). I transformed the data using the equations from Appendix A (Chapter 2) to adjust for parallax and transform the data to metres. The result was the real position of the bird in the tunnel in three dimensions for each frame of the flight. The Y and Z positions were used only to get the real X
position of the bird; the only parameter used in the data analysis. This method reduced the error to < 3 cm at the ends.

*Computation of Flight Parameters*

The input to analysis for each flight was a vector of X positions in the tunnel each 0.033 s. I applied Winter's (1990) digital filtering equation twice to smooth the data. I calculated velocity and acceleration using the equations from Winter (1990) (see Chapter 2). I padded the data at the beginning and the end using a reflection method (Table I, Chapter 2). This method gave spurious results for the first and last velocity and acceleration estimates and I discarded these points as a result. I averaged maximum velocity, acceleration and deceleration from all "good" flights of each bird and recorded both the distance and the time at which each of these occurred. Distances and times of maximum velocity and acceleration are reported from the beginning of the flight. Distance and time of maximum deceleration are reported from the end of the flight. I performed Bonferroni corrections on each group of t-tests to ensure against Type I errors (Rice 1989).

**RESULTS AND DISCUSSION**

**General Results**

Birds flew in a pattern similar to that in Chapter 2, although the steady-state velocity section in the middle of the flight was very short or non-existent due to the distance restrictions. Females flew at a slightly higher rate of acceleration and deceleration than males, with a corresponding difference in maximum velocity, but not significantly so. All birds generally flew at a higher velocity toward the feeder but again the difference was not significant at any angle. The only significant differences (at the table-wide level) between "to feeder" flights and "to perch" flights were tDmax and Amax in the 45° tunnel (df = 7; t = -6.49; P = 0.0002, and df = 7; t = -5.18; P = 0.0006, respectively; values were higher for flights to the feeder) and tVmax in the -45° tunnel (df = 7, t = 4.69, P = 0.001; values higher for flights to the perch). I thus concluded that the hummingbirds flew in the same manner regardless of the goal (perch or feeder) and combined the two types for all other comparisons. Each bird, therefore, had 5 or 6 flights at each of 5 angles.
Together, these flights at all inclinations had an average duration of $1.35 \pm 0.02$ s with no significant difference between the angles (ANOVA: df = 4 and 35; F = 1.00; P = 0.42).

_Inclination Results_

Birds reached the same $V_{\text{max}}$ ($3.07 \pm 0.06$ m/s) regardless of the inclination of flight. However, $A_{\text{max}}$ decreased with positive and decreased with negative inclination (df = 4 and 35, F = 7.41, P = 0.0002; Fig. 16 and 17). This resulted in differences in the time and distance of maximum velocity at different inclinations ($t_{V_{\text{max}}}$ – df = 4 and 35, F = 3.30, P = 0.02; $d_{V_{\text{max}}}$ – df = 4 and 35, F = 5.88, P = 0.001). Birds generally reached maximum velocity sooner in the downward inclinations (Fig. 17).

Notice that in Figure 16, the maximum acceleration for -45° is much less than would be predicted using the other four values. I think that this is an artifact of the bird's behaviour. The hummingbirds did not seem to like going downward at an angle of 45°, and were therefore more cautious. They decreased their maximum acceleration, although they reached the same $V_{\text{max}}$ as in flights of other inclinations. The birds were using the force of gravity to power their flight, rather than putting out the same power as at other inclinations. Therefore, the birds were not using maximum power output at an inclination of -45°. As a result, I did not use this data point in estimating maximum power output.

_Predictions_

Since the average maximum accelerations of individuals are negatively and linearly correlated with inclination (Fig. 16), I can assume that energy is at least partially limiting in the rufous hummingbird and that they are flying at close to $P_{\text{max}}$. If they had kept their maximum accelerations consistent regardless of the inclination, then this would have indicated that the available sustainable power of the muscles was not limiting the performance of the birds. Since the tunnel is only 2.5 m long, I can assume that the flight consists of 100% acceleration and deceleration and that all available power for flight will go into paying for the cost of accelerating and decelerating (Chapter 2). If I assume that hummingbirds would perform the same way in a
Figure 16: Correlation between maximum acceleration and inclination of flight. Line A (dotted) shows the slope of the regression (-0.03; $r^2 = 0.37$) through all available data points (squares and circle). Line B (solid) shows the slope of the regression (-0.06; $r^2 = 0.98$) through 4 of the data points (squares only; excluding the outlier at -45°) and the extrapolations to ± 90° (X's). Explanation of the outlier is given in the text. For maximum power output estimations, I used regression line B.
<table>
<thead>
<tr>
<th></th>
<th>Amax (m/s²)</th>
<th>dVmax (m)</th>
<th>tVmax (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>45°</td>
<td>10.58</td>
<td>1.06</td>
<td>0.638</td>
</tr>
<tr>
<td>22°</td>
<td>11.86</td>
<td>1.07</td>
<td>0.697</td>
</tr>
<tr>
<td>-45°</td>
<td>12.23</td>
<td>1.15</td>
<td>0.701</td>
</tr>
<tr>
<td>0°</td>
<td>13.68</td>
<td>1.20</td>
<td>0.710</td>
</tr>
<tr>
<td>-22°</td>
<td>14.44</td>
<td>1.26</td>
<td>0.792</td>
</tr>
</tbody>
</table>

Figure 17: Tukey test results for maximum acceleration (Amax), time and distance at maximum velocity (tVmax and dVmax, respectively). Generally, maximum acceleration increased with decreasing angle of flight. The exception was for -45° where birds tended to hesitate more than at other angles. Vmax occurred earliest in the horizontal tunnel (0°) and latest in the +45° tunnel where acceleration was slowest.
vertical tunnel (where the horizontal component is negligible; see extrapolation Fig. 16B), then
$P_{\text{max}}$ was 54.5 W/kg and the mean maximum sustainable muscle power output (assuming flight
muscle mass is 23.4% of total mass; Wells 1993b) was 224 W/kg. This is close to the maxima
reported for vertebrate muscles of 250-300 W/kg by Wells (1993b) and Chal and Dudley (1995).
According to Pennycuick's (1989) equations, the power output for a corresponding steady-state
flight at $V_{\text{mp}}$ (4.1 g bird flying at 5.31 m/s in horizontal tunnel) is 19 W/kg (mass specific muscle
power output—81 W/kg). The accelerating portion of a flight, therefore, costs $2.76 \times$ as much as
flying the same distance at $V_{\text{mp}}$ if deceleration is nearly passive. This is comparable to the results
from Chapter 3. In that chapter, using steady-state assumptions during small time intervals,
aerodynamic theory predicted that an accelerating flight should cost between 2.5 and 3.3 $\times$ as
much as a flight at a constant velocity.

Remember that these values are power outputs. In order for birds to actually perform at these
levels, they must supply more power to their muscles due to limited muscle efficiency; i.e. they
must be concerned with power input. Power input equals power output divided by the muscle
conversion efficiency (Pennycuick 1968; Lasiewski and Dawson 1967). In this case, assuming an
efficiency of 20%, the power input for flight at $V_{\text{mp}}$ is 95 W/kg and the power input for an
accelerating flight of the same duration is 272.5 W/kg. This is 21% higher than the Suarez et al.

However, this conclusion may be slightly underestimated. The birds did not actually keep
output power strictly constant because birds reached the same maximum velocity at all
inclinations. Therefore, they must have been putting out slightly more power at higher
inclinations and less power at lower inclinations than during horizontal flights. This is particularly
shown in the maximum acceleration at -45°. The angle was steep enough that the birds did not
have to use the same power output as the other inclinations to achieve the same maximum
velocity. Therefore, I conclude that they conserved energy and let gravity do much of the work
for downhill inclinations. In this case, if they had produced maximum power at all inclinations, I
would estimate a higher power output during accelerating flight than I observed.
This experiment also provided more behavioural evidence that rufous hummingbirds decelerate passively using drag. In the horizontal tunnel, deceleration involved a posture change and tail fanning. As inclination increased, however, the birds were able to rely on gravity to help slow them down. During the deceleration phase of the 45° inclination flights, birds no longer changed posture or used their tail. The posture stayed approximately parallel to the tunnel and birds simply slowed down.

What effect does this increased cost have for the daily energy budget of the hummingbird? I will assume that a 4.1 g hummingbird spends 20% of a 14 hour day foraging (reasonable average from the following: Pearson 1954; Wolf and Hainsworth 1971; Gass 1974; Montgomerie 1979) and that 95% of foraging flights are less than 2 m long (Perkins 1977; Montgomerie 1979; Gass and Montgomerie 1981; Gass and Sutherland 1985). If I assume that all forward flight is at V_{mp}, then the energy expenditure is 3.73 kJ. This is approximately 14% of the total energy expenditure of a bird during this time period (27.3 kJ/day; Montgomerie and Gass 1981). If I assume that all forward flight is acceleration and deceleration, that acceleration takes up 63% of flight duration and that deceleration is nearly passive, then the energy expenditure is almost 2 x greater; 6.95 kJ, or 25% of the total daily energy expenditure. Pearson (1954) reported that Anna hummingbirds (Calyptra anna) spend 36% of a 13 hour energy budget in foraging for food. Wolf and Hainsworth (1971) reported that at times during the day, *Eulampis jugularis* spends 46% of its energy budget in foraging. Both of these papers assumed that all flight was hovering, and used rather high estimates of the metabolic cost of hovering (379 W/kg and 242 W/kg; Pearson (1954) and Wolf and Hainsworth (1971), respectively).

In concurrence with the results of Chapter 3, this chapter reports a cost for acceleration near maximum sustainable power output, assuming zero elastic storage. The result of this high energy output during foraging is close to reported foraging energy expenditures when all flight is assumed to be at hovering metabolism.
Chapter 5: The Energetic Cost of Acceleration

Ecology, the study of plants and animals and their relationships to each other and their environment, includes the study of time and energy budgets. Time budgets are important for defining the niche of an animal (i.e. the sum of interactions between a species and its specific biotic and abiotic environment; Bock and von Wahlert 1965). They are also important for determining energy budgets. Energy budgets are one basis for studies of reproduction, competition, foraging, migration and many other aspects of an animal's daily life. It may even be argued that time and energy are the foundation of all ecology (Lindeman 1942).

Unfortunately, time and energy budgets are difficult to calculate for many species, especially in the wild. For example, it is difficult to divide the day into discrete categories of activities, even if the energetic cost of each is known (Pearson 1954), and usually it is not. As well, many activities are complex and involve more than just a simple description of the actions. Nevertheless, birds have long been used for time and energy calculations (Kendeigh 1949, 1969; LeFebvre 1964; Verbeek 1964; Verner 1965; Kontogiannis 1968; Kendeigh et al. 1969; Schartz and Zimmerman 1971; King 1974; Collins and Clow 1978; Blake 1985). In spite of the many difficulties, birds display relatively discrete activities and their high visibility makes them easy to observe.

Nectar-feeding birds are ideally suited for cost/benefit analyses (Wolf and Hainsworth 1978) and they have been used extensively as subjects (Pearson 1954; Stiles 1971; Wolf and Hainsworth 1971, 1977; Wolf 1975; Wolf et al. 1975; DeBenedictis et al. 1978; Beuchat et al. 1979; Hainsworth et al. 1981; Montgomerie and Gass 1981; Carpenter et al. 1983; Hainsworth and Wolf 1983; Hixon et al. 1983; Montgomerie et al. 1984; Hixon and Carpenter 1988, among many others). Food intake for hummingbirds (flower nectar or sucrose solution) is easily measured in volume units and converted to energy equivalents. As well, much is known about the energetic cost of activities, such as sleeping, torpor, perching, and hovering, and these activities represent
more discrete metabolic states than for many other animals (Gass and Montgomerie 1981). Even so, studies in the wild necessitate many assumptions and some laboratory studies have incorporated some of these assumptions as well.

For example, birds are often out of sight of observers (Wolf and Hainsworth 1971; Schemske 1975; Hixon et al. 1983; Hixon and Carpenter 1988). This proportion of the time budget could be as little as 5% of the time budget (Hixon et al. 1983; Hixon and Carpenter 1988) or as great as 22% (Schemske 1975). Even for territorial birds, the amount of time a bird spends on its territory is a function of the quality of that territory. A bird can spend as little as 20% of its time on its territory if conditions are poor (Gass and Montegomerie, 1981). In either case, this is a substantial amount of time for which the investigators have no information. Assumptions about activity during this time may substantially affect the calculations of energy budgets. Another problem is that flight is usually divided into categories based what birds do during flights (foraging, chasing, hawking, etc.; Wolf and Hainsworth 1971; Hixon et al. 1983; Hixon and Carpenter 1988). This is beneficial for time budget analyses but is confusing for energy budget calculations. For these, flight should be divided using cost considerations (e.g. hovering, steady-state forward flight, accelerating flight, manoeuvering flight, etc.), but both the relative duration and the specific energetic cost of some of these activities are unknown (i.e. acceleration). This necessitates the use of assumptions and the lumping together of activities. For example, some studies assume that all flight is at hovering metabolic rate (Pearson 1954; Beuchat et al. 1979) while others assume that all forward flight occurs at the minimum power velocity (Wolf et al. 1975). Even those who incorporate a combination of the two (Gass and Sutherland 1985), still make no allowance for transitions between states. Despite the number of problems, field studies are necessary for a true understanding of the ecology of organisms.

Laboratory studies are better for energy budget calculations as it is possible to account for many factors that are unpredictable in field studies. Temperature, light cycles, flight distances and, in some instances, the activity of the bird can all be controlled. In laboratory studies, the energetic costs of perching (Lasiewski 1962; Epting 1980; Suarez et al. 1990), sleeping and
torpor (Hainsworth and Wolf 1970, 1978a, b; Hainsworth et al. 1977; Hiebert 1990; 1991; 1992; 1993), and hovering (Lasiewski 1962; Suarez et al. 1990) have been measured. Although it is predicted from theory (Pennycuick 1969; 1975; 1989; Tucker 1975; Greenewalt 1975), the cost of forward flight is difficult to measure as it requires large areas of space. Many laboratory studies involving energy budgets have eliminated the cost of forward flight by using a small space and assuming correctly that all flight was hovering (Beuchat et al. 1979; Hainsworth et al. 1981).

The cost of forward flight could be estimated by elimination if total energy expenditure and the cost of all other activities were known (Fig. 18). In many energy studies, it is assumed that hummingbirds balance their energy budgets (input = output) over long periods of time (i.e. 24 hours; Pearson 1954; Hainsworth 1978). However, this is not necessarily the case as hummingbirds gain and lose mass quickly (Carpenter et al. 1983). However, even if energy is not balanced, the difference between energy input and energy output must equal the product of the change in mass and a fat-energy conversion factor, k, as long as water balance remains constant (see Calder and Hiebert 1983).

\[ k \times \Delta m = I - O \]  \[5\]

Or if this is looked at in another way, if the change in mass is known then net energy intake can be calculated due to conservation of energy. If I measure energy input at the same time as mass change for a hummingbird during the day, then its energy output is easily calculated.

Energy output consists of many components, however. All activities of the bird, including basal metabolism, carry metabolic costs and total energy output is their sum (Fig. 18). Fortunately, as mentioned before, for hummingbirds, these activities are few and the metabolic costs of most are known. The only cost shown in Figure 18 that is not known is the cost of acceleration, and this list is both exhaustive and mutually exclusive (Gass and Montgomerie 1981). By measuring intake, mass changes, and the duration of all activities, I can calculate the cost of acceleration.
Figure 18: Model of energy balance in hummingbirds. Intake equals sum of all output and changes in fat reserve. Basal metabolic output is incorporated into all activity outputs. The metabolic cost of all activities except acceleration are known.
Useful comparisons leading to more accurate estimates follow from controlling the proportion of time spent in acceleration in a flight. Since acceleration patterns in straight flight are stereotypical (Chapter 2), I can control the proportion of acceleration in a flight by controlling the flight distance; the longer the flight, the more time spent in steady-state flight and the lower the proportion of the flight spent accelerating. Here, I estimate the cost of acceleration by comparing the overall energy balance of birds flying in a short tunnel (2.5 m; ~100% acceleration) and in a long tunnel (7.5 m; ~50% acceleration) but both flying the same proportion of time during the day. To the extent that acceleration is energetically expensive, birds in short tunnels should expend more energy for the same flight time under these conditions. Over several days, they should eat more, lose more mass (or gain less mass), and/or spend more time in nocturnal torpor than those in the long tunnel. Due to the inter-relationship of these parameters, it is uncertain whether some or all of them will reflect this difference.

MATERIALS AND METHODS

The 5 adult male Rufous hummingbirds I used in this experiment were captured as adults at Sumas Mountain and the Sunshine Coast, B.C., in May 1995 and held individually in 60 x 60 x 60 cm wire cages in a large room. They had ad libitum access to commercial hummingbird food (Nektar Plus) in commercial hummingbird feeders (Perky Pet) on weekdays and 20% sucrose solution (w/w) on weekends. All observations were made between July and September 1995. During the experiment, I fed the birds 20% sucrose solution (w/w). The experimental enclosures for this experiment were two tunnels (50 x 60 cm) of different lengths (2.5 m and 7.5 m) similar to those described in other experiments (Chapters 2 and 4). The photo-period during the experiment was 14:10 hours light:dark.

At the beginning of training, I placed one bird in the short tunnel and another in a 2.5 m section of the long tunnel. Each tunnel had a perch at one end and an ad libitum feeder at the other. Both birds found the perch within 15 min. I then lengthened the long tunnel in 2.5 m stages over 1-2 days until each bird routinely flew the full length of its tunnel from the perch to
the feeder and back again. Birds learned quickly to use the wall feeder, because they had been feeding from similar feeders in their individual cages for a few days before the trials.

I controlled as many of the birds' activities as I could, and recorded their duration. Since acceleration was the key activity, it was imperative to keep the amount of time spent flying in short and long tunnels approximately equal. In this way, the proportions of time spent in steady-state flight and in acceleration would differ, yet the overall activity budgets would be similar (Table VII). I controlled the time spent flying by controlling the amount of food available per foraging bout. During preliminary trials, I calculated the activity budget of each bird over a 14 hour day. If it flew too much, I increased the amount of food delivered per foraging bout. If a bird flew too little, I decreased the amount of food delivered to make the bird fly to the feeder more often. This pattern continued until the amount of time spent flying by each bird was similar for a 14 hour day. My target was about 20–25% time flying forward in both tunnels. Birds could feed whenever they wanted during experiments, as long as they returned to the perch after each visit to the feeder.

Activity Budgets

Each tunnel contained a perch at one end and a feeder at the other. I attached a photodarlington to each perch and feeder and the computer recorded to the nearest millisecond when each beam was broken or joined. From this information, I calculated the duration of each bout of perching, hovering at the feeder and forward flying (including both steady-state and acceleration). Together, these yielded activity budgets.

Food Consumption

Feeders were the cups of disposable plastic syringe needles mounted behind 3 mm diameter holes in flat metal plates. The plates were painted green and the holes were surrounded by circular bright orange stickers. Sucrose solution (20% w/w) was supplied by a solenoid valve (hereafter, "pump") located behind the wall. I calibrated the pump to deliver $0.2 \pm 0.04 \mu L$ of
Table VII: Comparison of time budgets of birds in the long tunnel vs. birds in the short tunnel. If I control the time spent flying in both tunnels, I can control the proportion of acceleration that each bird performs. By monitoring the rest of the activities of the birds, I can compare energy budgets and calculate a cost for acceleration.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Long</th>
<th>Short</th>
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<tbody>
<tr>
<td>% Time Perching</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>% Time Hovering</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>% Time Flying</td>
<td>≈</td>
<td></td>
</tr>
<tr>
<td>% Time Steady-state Flying</td>
<td>&gt;</td>
<td></td>
</tr>
<tr>
<td>% Time Acceleration</td>
<td>&lt;</td>
<td></td>
</tr>
<tr>
<td>Time Sleeping</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>Time Torpor</td>
<td>open</td>
<td></td>
</tr>
<tr>
<td>Mass Changes</td>
<td>open</td>
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</table>
sucrose per squirt. The fine calibration allowed me to minutely adjust the amount of food each bird received by varying the number of squirts per visit. A bird would receive approximately 2 - 2.5 µL (short tunnel) or 6 - 7 µL (long tunnel) of solution during one feeding bout depending on its performance in the preliminary trials. A bout was defined as one trip to the feeder and the bird was required to perch again before more food was delivered. I imposed this rule by delivering food only when birds probed the feeder (within 10 ms, during the first lick; Roberts 1995) after perching. The feeders are emptied on each visit (pers. obs.) and thus by keeping track of the number of squirts given to each bird, I could calculate food consumption on the scale of single bouts and over entire days.

**Mass Changes**

The perches sat on electronic balances (one Mettler PM-series and one PE-series) and the computer recorded the mass of the bird every time it perched. Unfortunately, the tare mark of the balances had a tendency to wander over long periods of time. I considered a tare reading to be any mass recorded when the bird was off the perch. To correct for this, only those masses immediately following tare readings were used. The difference between these records was the true mass of the bird. Since birds never left the perches at night, there could be no tare readings then. Therefore, for mass changes overnight, I used the difference between the last reading of the day and the first reading of the next morning. Although the first reading of the day followed the first feeding, the ~0.45 mg weight of the meal was far below the 10 mg sensitivity of the balance and so I ignored meal loads in all calculations (see Pennycuick 1989).

**Temperature Changes**

I attached two thermisters to each perch—one on the cross bar and one on the upright bar below it—to measure bird body surface and ambient temperatures, respectively. The thermisters were accurate to ± 1 °C with a sensitivity of approximately 0.1 °C. I used the ambient temperatures to calculate the cost of each stage of torpor (Hiebert 1990). Upon entering torpor,
the body temperature of hummingbirds decreases (Hiebert 1990). Thus, by recording the surface body temperature of the birds, I could estimate the timing of entry into and exit from torpor.

Integration

A Silicon Graphics Indy computer monitored the photodarlingtonons, balances, and thermisters and controlled the pumps. It recorded the times of arrival and departure from the feeder and perch, time of food delivery and number of squirts delivered, mass of the bird each time it perched and a tare reading when it left the perch, and ambient and bird body surface temperature each hour during the day and each minute during the night for each tunnel for 72 hours (Fig. 19). I calibrated the feeder pumps each morning before the lights came on.

Analysis of Data

For each hour during the day, I tabulated the total food intake (μL), the average mass of the bird (g), and the total amount of time (in seconds to the millisecond) spent perching, hovering and forward flying. The mass of the bird at the beginning of each hour was also tabulated using the mean of the first 10 reading. For each night, I tabulated the total amount of time (in seconds to the nearest minute) spent sleeping (perching in the dark, not in torpor), entering torpor, in steady-state torpor and leaving torpor. I differentiated between these states by the changes in surface body temperature and estimated the duration by counting the number of data points (one per minute) in each stage. I defined each of these separately as each carries a different metabolic cost (Hiebert, 1990).

I then converted each of the above terms to an energy value. For sucrose intake, a 20% w/w sucrose solution contains 20 g of sucrose / L of solution and 1 g of sucrose contains 16.5 kJ of metabolizable energy (Weast 1969). I assumed the assimilation efficiency for sucrose to be 100% (Hainsworth 1974). The costs of sleeping and hovering were taken from Suarez et al. (1990). In that paper, Suarez et al. measured the oxygen consumption of rufous hummingbirds while hovering at a feeder (225.9 W/kg) and while restrained in the dark (which I have called sleeping; 55.3 W/kg). This value is comparable to Hiebert's (1990) and Lasiewski's (1963)
Figure 19: Flow chart of program monitoring of activity, mass and temperatures. The program actually waits for the input from the bird (AP, AF, etc.) and then acts accordingly; storing information in the data file, delivering food, etc. Temperatures were requested from the thermisters every hour during the day and every minute during the night. The main program ran 2 subprograms like this; one for each tunnel.
measurements (59 W/kg and ~50 W/kg, respectively) but is high compared to other measurements (Hainsworth and Wolf 1970; 35 W/kg) Although they also measured a perching cost (158 W/kg), I considered this cost too high for my purposes as the birds in their experiment were feeding while perching. Instead, I used an average cost of perching derived from Lasiewski (1963) and Wolf and Hainsworth (1971) of 61.4 W/kg (20.1 J/cc O₂; Calder 1974). I calculated these costs for each hour of the day using the average mass and average ambient temperature during that hour.

I assumed that birds stored energy as fat at 39.4 kJ/g, with a 14% conversion loss (Kleiber, 1961). I used the same conversion rate (without the conversion loss; King 1974) for the use of fat for energy. Since hummingbirds are known to have a high water flux (3 x their body weight per day; Beuchat et al. 1990; Weathers and Stiles 1989), I must take changes in weight due to water gain and loss into account. Beuchat et al. (1979) found that rufous hummingbirds in the laboratory showed rapid increases in body mass during the first and last hours of daylight, presumably due to water gain and rapid decreases in body mass (about 50% of the total overnight mass change) during the first hour after lights out, due to water loss. I thus assumed that the mass changes over the first and last hours of the day were due mostly to water gain and discounted them in energetic considerations. I assumed that otherwise during the day the hummingbirds maintained water balance through intake from the sucrose solution and output from respiration and urination. I also assumed that 50% of the overnight mass change was due to water loss overnight.

Since estimated changes in mass are proportional to changes in net energy intake over time periods longer that 3-4 hours (Tooze and Gass 1985), I estimated the energy contributions from mass changes over 4-hour periods (except for the last one of each day) using the initial masses in the first and last hour of each period, not the average mass in each hour.

Hiebert (1990) measured oxygen consumption by rufous hummingbirds during each stage of torpor (entry, steady-state and arousal) and derived equations for the calculation of these costs in relation to ambient temperature. Since ambient temperature varied less than 3°C over 24 hours, I
used the average ambient temperature for the night to calculate the cost of each stage of torpor. As oxygen consumption during entry into torpor is independent of ambient temperature, I avoided underestimating this cost by choosing a value for the cost of entry that was higher than average.

Using the above calculations and equation 5, I was able to calculate a net energy intake for each bird in 4-hour time periods during the day and in 1 time block overnight. This energy would have to be used for forward flight as all other energy expenditures are accounted for.

I calculated the costs of steady-state forward flight using the same equations as in Chapter 3. Using data from Chapter 2 (for 7.5 m flights) and Chapter 4 (for 2.5 m flights), I calculated the proportion of flying time that was spent in steady-state flight for each bird. For long tunnel birds, 45% of the flying time was spent in steady-state flight; for the short tunnel birds, 0%. I could then estimate a cost for acceleration by subtracting the cost of steady-state flight from the net energy intake.

RESULTS

Activity Budgets

Overall, birds spent 23.78 ± 0.02% (mean ± S.E.) of the 14 hour days flying back and forth between the perch and the feeder (i.e. not perching or hovering). Birds in the short and long tunnels spent the same proportion of time flying (long: 24.9 ± 2.9%; short: 22.67 ± 1.7%; df = 4; t = 0.64; 1-tailed P = 0.28), satisfying the fundamental requirement of the experiment. On average, the difference between each individual's flying time in the long tunnel and in the short tunnel was 3.58 ± 1.1% (range 0.65 - 6.84%). The time course of flying times is shown in Figure 20. Birds also spent similar amounts of time perching and hovering (68.90 ± 2.8% and 5.47 ± 0.97%, respectively) and I assumed the time budgets to be equivalent at this course scale.

Food Consumption

The average energy intake over 14 hour days for all birds in both tunnels was 24.6 ± 1.7 kJ with a range of 17.4 - 32.1 kJ. The energy intake of individuals in the long tunnel was not
different from their intake in the short tunnel (df = 4; t = 1.20; 1-tailed P = 0.15) and the time course of energy intake in the two cases is very similar (Fig. 20). Similarly, the average rates of energy intake during the day for birds in both tunnels is similar (short – 1.60 kJ/hr; long – 1.91 kJ/hr; Fig. 21). Notice that the rate of energy intake tapers off during the last 9 hours of the day and then increases in the last 2 hours. Most investigations of net energy intake under ad libitum conditions in the laboratory, report that net energy intake rates are constant during the whole day (Wolf and Hainsworth 1977; Hainsworth et al. 1981; Hainsworth 1978). However, there are reports of decreases in activity during the afternoon (Garrison 1995) and increases in food consumption during the last hour of the day (Calder et al. 1990) for wild hummingbirds in the field.

**Mass Changes**

Birds in the long tunnel lost an average of 0.13 ± 0.04 g during the day and birds in the short tunnel lost 0.13 ± 0.02 g (df = 4; t = 0.12; 1-tailed P = 0.46). These correspond to an average rate of weight change of 0.01 g/hr. The time course of the mass changes is similar for birds in both tunnels (Fig. 20) and follows the time course of flight times and energy intake on a courser scale. The average mass change overnight was -0.09 ± 0.01 g for the birds in the long tunnel and -0.08 ± 0.01 g for the birds in the short tunnel (df = 4, t = -1.59; 1-tailed P = 0.09). The average rate of weight change overnight for these birds was -0.01 g/hr for both long and short tunnel birds. These mass changes are true mass changes due to fat deposition and consumption and do not include temporary mass changes due to water gain and loss.

**Temperature Changes and Torpor**

Ambient temperatures varied cyclically during the experiment, reaching a maximum of 20 – 21 °C in mid-afternoon and a minimum of 17 – 18 °C just before morning. The tunnels were near each other in the same room and their ambient temperatures differed by < 1 °C at all times (Fig. 22). The birds' surface body temperature during the day could not be compared as birds were not continuously in contact with the thermister and the extent of that contact varied due to the
Figure 20: Time courses of flying times, energy intake, mass changes and net energy available for flight. Notice the similarity in all graphs although mass changes and net energy available for flight are on a courser time scale. Closed circles are for long tunnel birds and open squares are for short tunnel birds.
Figure 21: Cumulative energy intake during a 14 hour day. Average intake rates for the day were 0.53 W for birds in the long tunnel (closed circles) and 0.44 kJ/hr for birds in the short tunnel (open squares). Note that intake rates are higher during the first 9 hours of the day and then taper off.
Figure 22: Time course of ambient and surface body temperatures (SBT) for day 2 of Bird #13 in the short tunnel (Panel A: ambient – diamonds; SBT – circles) and in the long tunnel (Panel B: ambient – diamonds; SBT – circles). These data were taken on August 19 and 25, 1995, respectively. Notice that ambient temperatures differed over the two days by less than a degree. In the short tunnel, the bird started entry into torpor before lights out (vertical line). In the long tunnel, the bird did not enter torpor until approximately 12:30 am. The variation in the SBT during the day is due to the fact that the bird is not in constant and close contact with the thermister.
birds' position on the perch. Birds differed significantly in the patterning of their nocturnal surface body temperature (Fig. 22). The lowering of the surface body temperature at night indicates entry into torpor. Birds in the long tunnel spent an average of $6.93 \pm 0.72$ hours in torpor (including entry, steady-state and arousal) and $3.09 \pm 0.65$ hours sleeping at normothermy. Birds in the short tunnel spent an average of $9.82 \pm 0.41$ hours in torpor ($df = 4; t = -3.72; 1$-tailed $P = 0.01$) and $0.87 \pm 0.18$ hours sleeping ($df = 4; t = 3.08; 1$-tailed $P = 0.02$). Notice that for the short tunnel birds, the sum of the average time spent sleeping and in torpor is approximately 10 hours and 41 minutes. The short tunnel birds typically went into torpor before the lights went out (see Fig. 22).

**Energy Budgets**

For the ambient temperatures in this experiment, the cost of torpor was 15.48 W/kg for entry, 7.74 W/kg for steady-state, and 27.1 W/kg for arousal (Hiebert 1990). Using Fig. 18 and equation 5, I can calculate the energy budgets of the birds. Since the only unknown is the cost of forward flight, any energy inequalities that result from the equation can be attributed to forward flight cost. Birds in the long tunnel spent an average of $19.44 \pm 3.61$ kJ for flight over 24 hours and those in the short tunnel spent insignificantly less ($17.99 \pm 1.67$ kJ; $df = 4; t = 0.30; 1$-tailed $P = 0.39$; Fig. 20). Therefore, the average power input (according to this method) during flying was $360 \pm 49$ W/kg and $446 \pm 58$ W/kg ($df = 4; t = -1.12; 1$-tailed $P = 0.15$), respectively.

However, approximately 45% of the flight of the birds in the long tunnel was spent in steady-state flight at Vmp while all of the flight of the short tunnel birds was spent accelerating and decelerating and the cost of flight at Vmp is known from theory (Pennycuick 1989). Assuming this estimate is accurate, applying it to the flight time budget and subtracting the result from the total, the birds in the long tunnel spent an average of $589 \pm 90$ W/kg during the accelerating portions of flight ($df = 4; t = 1.34; 1$-tailed $P = 0.11$; assuming that deceleration is nearly passive).

The average daily energy expenditure (DEE) of all the birds was $32.8 \pm 2.2$ kJ. There was no significant difference between the average DEE of birds in the long tunnel and those in the short
tunnel (df = 4; t = 1.21; 1-tailed P = 0.15). It is higher than the DEE predictions of King (1974; 27.7 ± 1.1 kJ/day; df = 9; t = 2.56; 1-tailed P = 0.01) but is similar to that measured by Powers and Nagy (1988) using a doubly labeled water technique (32 kJ/day).

DISCUSSION

Pearson (1954) was the first to report an activity budget for hummingbirds. He reported that an Anna hummingbird (*Calypte anna*) spends 82% of its day perching and 15% foraging for nectar. The other 3% is spent in maintaining a territory, in hawking insects and in other activities. Other measurements for Anna hummingbirds were taken by Stiles (1971) and Beuchat *et al.* (1979) and they generally concur with Pearson's (1954) results. Activity budgets reported for tropical hummingbirds (Wolf and Hainsworth 1971: *Eulampis jugularis*; Schemske 1974: *Amazilia rutila* DeLattre) showed that they generally spend about the same amount of time perching but slightly less time foraging (*Eulampis*: 11%; *Amazilia*: 9.3%) and more time in other activities like hawking insects. Schemske's (1974) results are inconclusive as the birds spent a lot of time out of sight of the observer (17.2%). The reports on rufous hummingbirds (Gass 1978; Beuchat *et al.* 1979; Sutherland *et al.* 1982; Hixon *et al.* 1983; Gass and Sutherland 1985; Hixon and Carpenter 1988) indicate that they spend 12-30% of their time foraging. The activity budgets of the birds in this experiment are well within the range of those observed in the wild.

Torpor in hummingbirds has been said to be used for fat conservation during migration (Carpenter and Hixon 1988) and for energy conservation during times of thermal regulation stress (Hainsworth and Wolf 1970) or food deprivation (Hainsworth *et al.* 1977). Since birds actually lost weight in my experiment and they are not obliged to enter torpor at these ambient temperature ranges (Hiebert 1990), I can assume that birds went into torpor at night due to energy deficits during the day. Since mass changes and energy intake were similar in both tunnels, the significant difference in time spent in torpor is the only indication that short tunnel birds were more energetically stressed than long tunnel birds. Because each individual experienced both tunnels and the pattern held both within and among individuals, I consider this result a strong one.
I further conclude that the high energetic cost of acceleration accounts for this difference in energy balance.

The estimates of the power input for acceleration in this experiment (~528 W/kg) are higher than can be expected. Wells (1993b) reported maximum sustainable muscle power output for hovering hummingbirds (assuming zero elastic storage) of 360 W/kg. Chal and Dudley (1995) reported about 355 W/kg using the same assumptions by measuring oxygen consumption of hummingbirds hovering in a heliox mixture. Converted from mean power input (assuming that flight muscle mass is 23.4% of total mass; Wells 1993b; and that muscle conversion efficiency is 20%), the mass-specific muscle power output in this experiment is 451 W/kg. This is 25% higher than the predicted maximum and is clearly not possible. Given these considerations, I conclude that the cost of acceleration is near the maximum sustainable power output for hummingbird flight muscles and there is some dominating error in my assumptions which accounts for the overestimate of this cost.

My guess as to the most likely source of error is my assumption about the muscle conversion efficiency. Efficiency varies with velocity and has a range of ~7–25% (Beuchat et al. 1990). Since the highest accelerations occur at relatively low velocities, it might be more correct to assume a lower efficiency for the muscles. As well, there is the possibility of near-perfect elastic storage of inertial energy in the flight muscles (Wells 1993b). The constancy of wing beat frequency and its relationship to wing length suggest that hummingbird wings act like tuned oscillators (Greenewalt 1960). Wells (1993b) calculated efficiency during hovering as 9–11% assuming perfect elastic storage. The birds in this experiment spent more time at low velocities than at hovering, so if I assume an efficiency of ~15% and perfect elastic storage, the muscle power output of these birds is 338 W/kg; a figure that is well within the range of possibility.

Why is it then, if acceleration is so expensive, and it has rarely been taken into account, that energy budgets of hummingbirds reported in the past (Pearson 1954; Wolf and Hainsworth 1971) have balanced? Beuchat et al. (1990) noticed that rufous hummingbirds consume far more energy than they apparently need in moderate temperatures, but he assumed that this excess was just
excreted. Pearson (1954) assumed in his experiment that all hummingbird flight is at hovering metabolism. It is conceivable that the costs of hovering and flying at $V_{mp}$ averaged out in Pearson's analysis. Pearson (1954) also did not measure mass changes in his birds. In this experiment, mass changes, both during the day and overnight, contributed greatly to the overall energy balance. And Pearson (1954) did not measure energy intake; he only inferred it from the number of flowers on the bush that the bird was principally feeding on. Nor did Wolf and Hainsworth's (1971) measure mass changes and energy intake in the field (only intake rate in the laboratory). Gass and Sutherland (1985) distinguished between hovering and forward flight, but their estimates of energy expenditure may have been underestimated as they assumed that all forward flight occurred at $V_{mp}$. It seems then that most studies have simply assumed that energy budgets were balanced based on the studies of Pearson (1954) and Hainsworth (1978) and then, after calculating energy expenditures (with various assumptions), showed that these deficits could be met by the food sources in the area.

The results of this experiment, in conjunction with the previous three, shows that hummingbirds fly at high accelerations with an energetic cost of near maximum sustainable muscle power output. It also provides some indirect corroborating evidence for the theory of perfect elastic storage in hummingbird flight muscles.
In Chapter 2, I demonstrated the importance of acceleration and its potential cost to activity and energy based considerations for rufous hummingbirds. These birds actively accelerate at high rates and do so stereotypically. The magnitude and timing of acceleration and deceleration are independent of flight duration, at least for flights longer than 3.5 m. For flights shorter than that, the magnitudes of acceleration and deceleration decrease due to distance restrictions. The consistency of the acceleration and deceleration curves allows one to easily estimate the proportion of time spent accelerating in the activity budget of the bird and leads the way for energetic considerations. The results of this experiment also seem to indicate that hummingbirds use drag to decelerate passively. I also empirically demonstrated in this experiment that aerodynamic theory is correct in predicting that longer winged females with low wing disc loadings should routinely fly faster and accelerate faster than short winged males.

In the absence of a unified theory for predicting the aerodynamic cost of acceleration, in Chapter 3, I used steady-state aerodynamic theory to predict an average mass-specific power output (for an accelerating flight with a maximum velocity of ~ 4.5 m/s) of 52–69 W/kg. This is equivalent to a power input of 260–345 W/kg, assuming zero elastic storage and a metabolic conversion efficiency of 20%. The power input required for sustained hovering is 226 W/kg according to Suarez et al. (1990). If this is correct, it appears then that hovering is not the most energetically expensive activity—acceleration is. However, the validity of this estimate is questionable as there are problems with using steady-state aerodynamic theory to predict acceleration costs such as overestimation of profile power and underestimation of inertial power.

In Chapter 4, I loaded the hummingbirds with a component of acceleration due to gravity, by flying them in inclined tunnels. I estimated a power output for acceleration of 54.5 W/kg (power input = 272.5 W/kg). This may be underestimated as the assumption that the birds were flying at $P_{\text{max}}$ may not be correct. But the power input is still greater than that of hovering.
In Chapter 5, by measuring energy intake and mass changes, and by estimating energy expenditures, I predicted a power output for acceleration of 106 W/kg (power input = 528 W/kg) assuming no elastic storage and a muscle conversion efficiency of 20%. If I assume perfect elastic storage and an efficiency of 15%, then power output for acceleration is 79 W/kg. Once again, this is greater than the cost of hovering and is close to the maximum sustainable power output taken from the literature.

The results of this thesis are strengthened by the fact that the same power output was predicted by three widely different methods. A word of caution, though; since acceleration is not constant in these flights, the power output required for it cannot be constant either. The power outputs predicted here are probably the maximum that occur at Amax.

Due to the importance of acceleration in the time and energy budgets of hummingbirds, a comprehensive theory of the power required for acceleration in flight is the next logical step. I know of one current attempt at the University of Washington using bats as subjects (E. Stockwell, pers. comm.). I hope that the empirical data provided here on hummingbirds will aid in the formation of such a theory.
LITERATURE CITED


APPENDIX A: Vector equations for correction of parallax error. Not to scale.

The equation of the line through point \( v \) in direction \( p \) is: \( w = v + pt \)
where \( t = \) any real number

The equation of the line through point \( v' \) in direction of \( p' \) is: \( w' = v' + p's \),
where \( s = \) any real number

The bird is located at the intersection of these two lines: \( w = w' = v + pt = v' + p's \)
Since there are 2 variables (\( s \) and \( t \)) 3 equations are required:

1. \( xt = x's \)
2. \( A + (D-A)t = y's \)
3. \( zt = A - A \)

Combining #2 and #3 results in equations for the variables:

\[ s = \frac{(A + (D-A)t)}{y'} \]
\[ t = \frac{(A - A)}{z} \]

These can be incorporated into one equation that can be substituted into the intersection equation:

\[ s = \frac{(A^2 + Az - DA)}{(zy' + A^2 - DA)} \]

to obtain equations for the 3-dimensional co-ordinates of the bird:

\[ x(\text{real}) = x's \quad \quad y(\text{real}) = y's \quad \quad z(\text{real}) = A*(s - 1) \]

Therefore, using these equations, the real position of the bird can be obtained if the \( x \) and \( y \) positions from the mirror and the \( z \) position from the tunnel are known.
APPENDIX B: Symbols Used In This Exercise

\( \rho \) = Air Density (kg/m\(^3\))
\( \nu \) = Kinematic Viscosity (m\(^2\)/s)
\( b \) = Wing Span (m)
\( BD \) = Body Diameter (m)
\( c \) = Energy Conversion Factor
\( C_d \) = Coefficient of Drag
\( g \) = Acceleration due to Gravity (m/s\(^2\))
\( k \) = Induced Drag Factor
\( m \) = Mass (kg)
\( P_{am} \) = Absolute Minimum Power (W)
\( P_{ind} \) = Induced Power (W)
\( P_{met} \) = Metabolic Power (W)
\( P_{par} \) = Parasite Power (W)
\( P_{pro} \) = Profile Power (W)
\( r_B \) = Body Reynold's Number
\( S_B \) = Body Frontal Area (m\(^2\))
\( S_d \) = Disc Area (m\(^2\))
\( S_p \) = Equivalent Flat Plate Area (m\(^2\))
\( V \) = Velocity (m/s)
\( V_{mp} \) = Minimum Power Velocity (m/s)
\( V_{mr} \) = Maximum Range Velocity (m/s)
\( WL \) = Wing Length (m)
\( X_1 \) = Profile Power Ratio