

ECOLOGICAL CORRELATES OF HOVERING FLIGHT OF HUMMINGBIRDS

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Summary

Simultaneous recordings of oxygen consumption and wing kinematics were collected from hummingbirds hovering at artificial flowers of different dimensions or when loaded by the addition of small weights to simulate increased fat stores. Hovering at wide-diameter flowers required increased wingbeat frequencies to compensate for decreased wingbeat amplitude, and it was 5% more metabolically expensive than at narrow flowers. Loaded birds increased their wingbeat amplitude to support the extra load whilst maintaining a nearly constant wingbeat frequency. A 10% increase in load required a 5.7% increase in mass-specific oxygen consumption. Although the variation in wing kinematics was associated with an increased metabolic cost, there was very little effect on flight efficiency. This ability to vary wing kinematics allows hummingbirds to exploit a wide range of flower types and to accommodate increased energy stores for seasonal migration.

Introduction

Despite the large number of studies investigating aspects of hummingbird ecology, very little work has focused on the mechanical, and, hence, energetic, interactions between flying hummingbirds and their environment. An example of such an interaction would be the cost of flight whilst foraging from different flowers. Flowers of different designs might be expected to change the costs of foraging if they alter the normal wing kinematics. Furthermore, the seasonal variation in flower abundance in northern North America forces the hummingbirds to migrate to areas of greater flower availability. To fuel this migration, the birds need to carry fuel reserves in the form of fat and this added mass might also be expected to influence flight energetics significantly.

When hummingbirds forage for nectar they generally do so whilst hovering in front of the flower, although they will perch if the opportunity arises (Miller, 1985). Many flowers, particularly those that are adapted for hummingbird pollination, are narrow and tubular and so do not inhibit the normal wing kinematics of a foraging hummingbird.

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Relationships between hummingbirds and specific flower species have been frequently documented (Grant and Grant, 1968, 1979; Feinsinger, 1978; Brown and Kodric-Brown, 1979; Tyrrell and Tyrrell, 1985). However, hummingbirds have also been recorded foraging from flowers of other designs, some of which provide obvious constraints on wing kinematics (for example, see pages 185 and 197 in Tyrrell and Tyrrell, 1985). Two questions stem from these observations. First, is it more expensive to forage from a flower whose shape dictates changes in normal wing kinematics? Second, could this increased cost, if present, have been a driving force in the co-evolution of hummingbirds and the flowers from which they forage?

To test these hypotheses, oxygen consumption and aerodynamic power output of individual hummingbirds were assessed using an open-flow glass respirometry mask attached to the front of a hummingbird feeder together with simultaneous videorecording of wing kinematics, as described in Wells (1993). Three different masks were used to simulate the effects of different flower sizes; these masks are referred to as 'flowers' in this report. If foraging costs are increased with increasing flower size this will affect assessments of daily energy budgets and foraging strategies. Hummingbirds are regarded as excellent models to test these types of ecological questions (e.g. Hainsworth and Wolf, 1983; Hixon *et al.* 1983; Hixon and Carpenter, 1988).

Hummingbirds show significant seasonal changes in body mass. This is particularly marked during the late summer pre-migrational fattening, when birds may increase their body mass by up to 60% with fat stores (Odum and Connell, 1956; Norris *et al.* 1957). Carpenter *et al.* (1983) and Carpenter and Hixon (1988) show that, during the period before migration, rufous hummingbirds gain an average of 0.23–0.30g per day (approximately 8–10% of lean body mass). The largest load that a hummingbird has been recorded lifting was close to 80% of its body mass (rufous-tailed hummingbird, *Amazilia tzacatl*, Marden, 1987) but it is unclear whether the bird was able to fly for any significant period. One of the birds kept captive during the present study showed a 67.5% increase in body mass (from mass at capture) with only a slight decrease in apparent rate of climb. Hummingbirds also tend to increase their body mass during the daily cycle, when mass can increase by up to 16.4% of the early morning body mass (*Calypte anna* at 7°C, Beuchat *et al.* 1979). Furthermore, during the breeding season, females must carry eggs prior to laying that can weigh up to 17% of their body mass (Lack, 1976).

These observations lead to questions about the effect of these mass changes on flight performance. How do hummingbirds respond to mass changes in terms of oxygen consumption and wing kinematics? How much more muscle power output is required and what are the effects of increased body mass on flight efficiency? These questions were examined using the system described in Wells (1993) and artificially loading the hummingbirds with small fishing weights.

Materials and methods

Experimental animals

The two studies examined the flight energetics of broad-tailed hummingbirds (*Selasphorus platycercus* Swainson) and a single rufous hummingbird (*Selasphorus rufus*

Gmelin). The birds used and the conditions under which they were captured and maintained at the Red Buttes Environmental Biology Laboratory near Laramie are described in Wells (1990, 1993). A large free-flight aviary allowed regular exercise, with a separate experimental area. In nearly all cases the complete set of manipulations for one experiment was performed on one same day.

Experimental equipment

The open-flow feeder-mask respirometry system used in these experiments has been described previously (Wells, 1993). The only change in design was the size of the mask attached to the feeder used in the experiments investigating the influence of flower size. Three glass masks were used; the standard small mask used in all the other experiments (outer diameter 14mm), a medium-sized mask with an outer diameter of 29mm and a large-sized mask with an outer diameter of 38mm. The internal dimensions of all of the masks were identical (8mm). The different masks had no detectable effect on the characteristics of the respirometry system, which retained a full response time of 3–3.5s.

For the loading study, a small harness was constructed from elastic cord in the form of two loops joined with Velcro to form a figure of eight. One loop was placed over the head and the other over the tail. The Velcro junction then lay on the dorsal surface of the bird approximately between the shoulders. This did not interfere with the motion of the wings. Small lead split shot fishing weights could then be crimped to the harness junction, thus placing the weights close to the centre of mass of the bird.

Wing kinematics were recorded using standard CCTV video cameras. Careful attention was given to the stroke plane angle, as it was thought likely that this would be affected by the experimental manipulations. Metabolic power input is presented as the product of mass-specific oxygen consumption and the energetic yield assuming carbohydrate metabolism (21.1 joules per millilitre of oxygen).

Post mortem morphometric and aerodynamic analyses were performed as described by Ellington (1984a–f) and Wells (1993). The aerodynamic analyses are presented for the two opposing conditions of perfect and zero elastic storage of inertial energy. For the former, it is assumed that the kinetic energy is stored as elastic potential energy, during deceleration of the wing, and then released to accelerate the wing on the next stroke. If no energy is lost during storage, then the net inertial power requirement over the cycle is zero. In the absence of elastic storage, the muscles must actively decelerate the wing in the second half of the stroke and then provide additional energy to accelerate the wing on the next stroke. This will require a substantially increased muscle power output as the inertial power requirement far outweighs the aerodynamic power requirement (by a factor of 4, Wells, 1993). Muscle power output was calculated from the total body mass-specific power output divided by the fraction of the body mass attributable to the flight muscles. Flight efficiency was calculated from power output divided by power input.

Data were analysed using a one-way analysis of variance (ANOVA); differences due to experimental manipulations were considered significant at the $P < 0.05$ level. On all the graphs mean values of 5–14 flights per bird for each experimental condition are displayed \pm one standard error.

Results

Artificial flowers

During these experiments it was often noted that, on initial introduction to the test situation, the birds approached the feeder with a high wingbeat frequency and small wingbeat amplitude, presumably protecting their wings from damage. Within a couple of visits a consistent pattern of wing kinematics was established. With increases in 'flower' size, metabolic power input increased significantly in all individuals (Fig. 1), wingbeat amplitude decreased, and wingbeat frequency and stroke plane angle increased (Figs 2 and 3). In the large 'flower' test, R5 appeared to be resting on the rim of the mask and possibly saving some energy expenditure in this manner.

Muscle power output fell with increasing 'flower' size in the zero elastic storage analysis for Bt12 and R5 but did not change significantly in the case of the other two birds (Fig. 4). In the perfect elastic storage analysis, muscle power output increased significantly with increasing 'flower' size for all birds (Fig. 4). As metabolic power input increased with increasing 'flower' size, the flight efficiency and, by extrapolation, the muscle efficiency, decreased significantly in the zero elastic storage analysis but remained almost constant in the perfect elastic storage analysis with increasing 'flower' size (Fig. 5).

Loading

The birds did not appear to be unduly distressed by the presence of the harness and after several flights showed no apparent attention to it. In some cases the handling associated with fitting the harness or the addition of weights upset the bird and several had to be

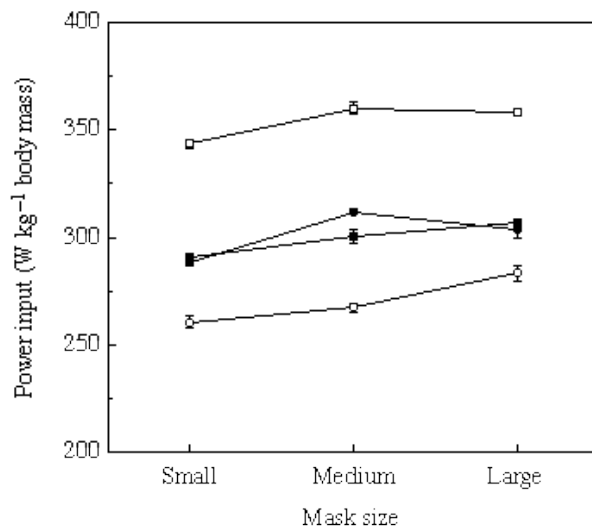


Fig. 1. Hummingbird metabolic power input whilst hovering at artificial flowers of different sizes. Open squares, Bt4; filled squares, Bt10; open circles, Bt12; filled circles, R5. In all the figures, values are mean \pm s.e.m. Error bars are often smaller than the size of the symbol.

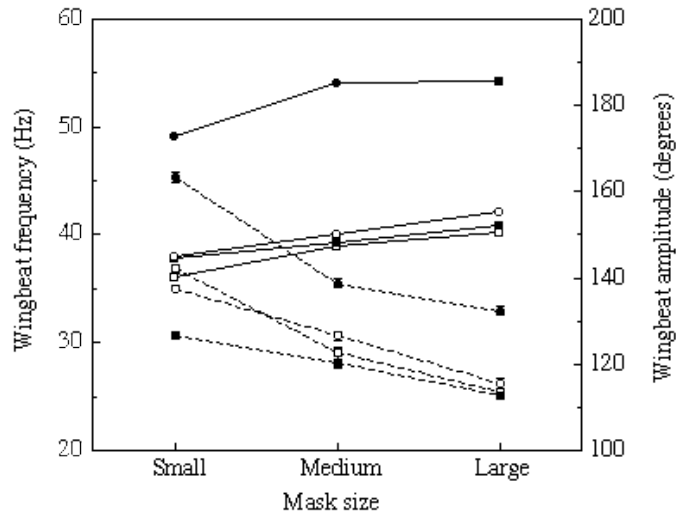


Fig. 2. The wingbeat frequency (solid lines) and wingbeat amplitude (broken lines) of hummingbirds hovering at artificial flowers of different sizes. Symbols as in Fig. 1.

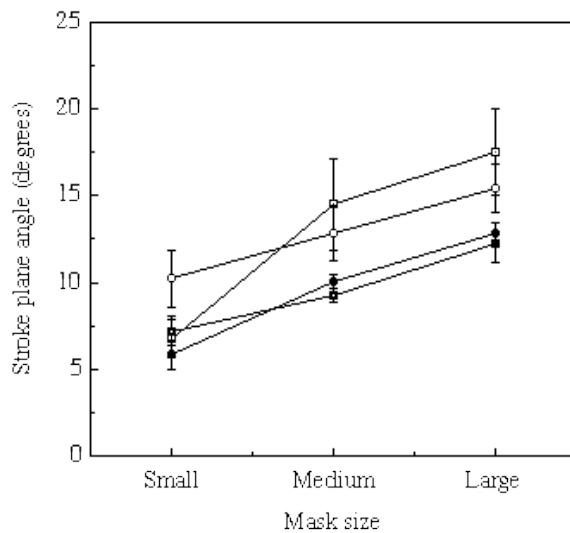


Fig. 3. The stroke plane angle of hummingbirds hovering at artificial flowers of different sizes. Symbols as in Fig. 1.

excluded from the study as a result of prolonged periods of fasting. None of the birds would use the feeder reliably for longer than 3s at a time if loaded by more than 20–30% of their body mass.

Metabolic power input increased significantly with increasing load in all four of the birds studied (Fig. 6). Mass-specific metabolic power input was calculated using the bird's body mass determined for the unloaded trials. Wingbeat amplitude increased but

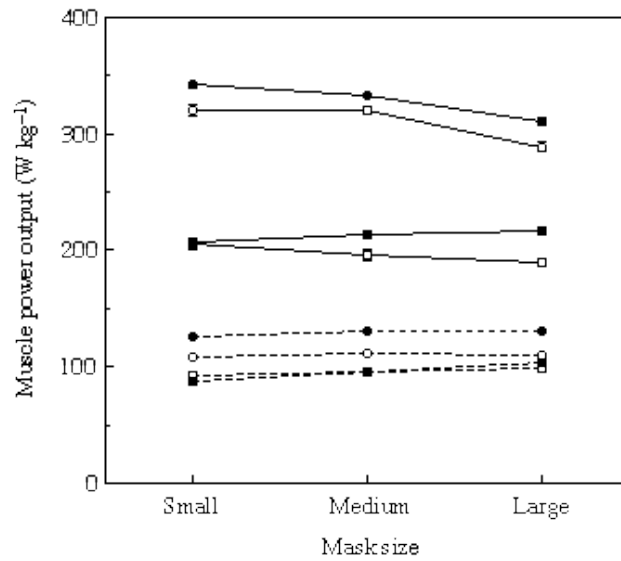


Fig. 4. Muscle power output of hummingbirds hovering at artificial flowers of different sizes. Symbols as in Fig. 1. The solid lines are the results for the zero elastic storage analysis and the broken lines are those for the perfect elastic storage analysis.

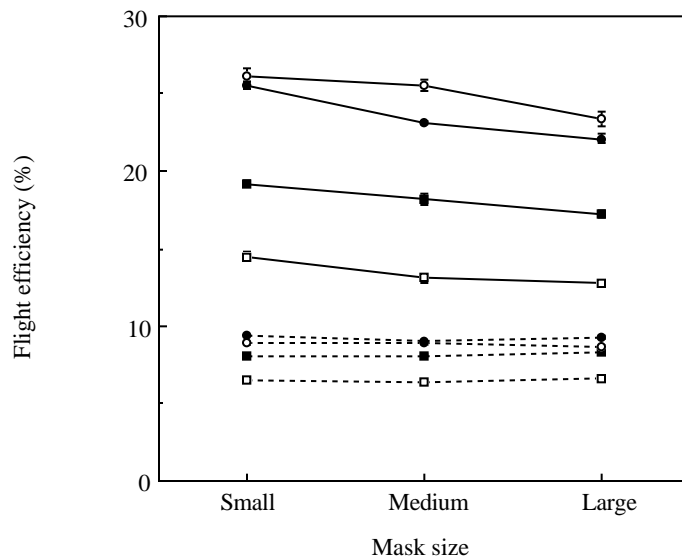


Fig. 5. Flight mechanochemical efficiency of hummingbirds hovering at artificial flowers of different sizes. Symbols as in Fig. 1. The solid lines are the results for the zero elastic storage analysis and the broken lines are those for the perfect elastic storage analysis.

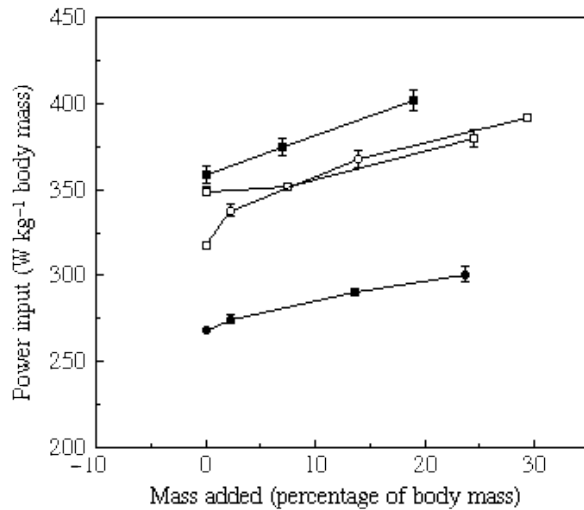


Fig. 6. The metabolic power input of loaded hummingbirds hovering at an artificial feeder. Open squares, Bt4; filled squares, Bt5; open circles, Bt10; filled circles, Bt12.

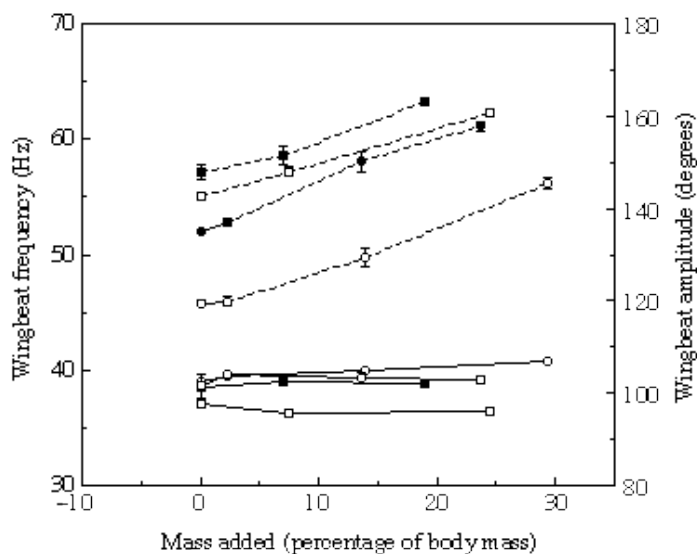


Fig. 7. The wingbeat beat frequency (solid lines) and wing amplitude (broken lines) of loaded hummingbirds. Symbols as in Fig. 6.

wingbeat frequency remained almost constant with increased loading (Fig. 7). Stroke plane angle varied very little with increasing load but tended to approach the horizontal at higher loadings (Fig. 8), although in the cases of Bt10 and Bt12 the records are incomplete. Muscle power output increased significantly with increased loading in both the zero and perfect elastic storage analyses (Fig. 9). Because the metabolic power input

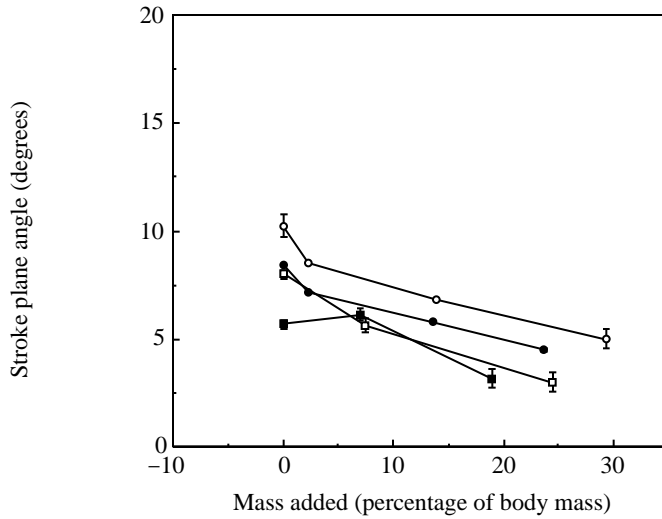


Fig. 8. The stroke plane angle of loaded hovering hummingbirds. Symbols as in Fig. 6.

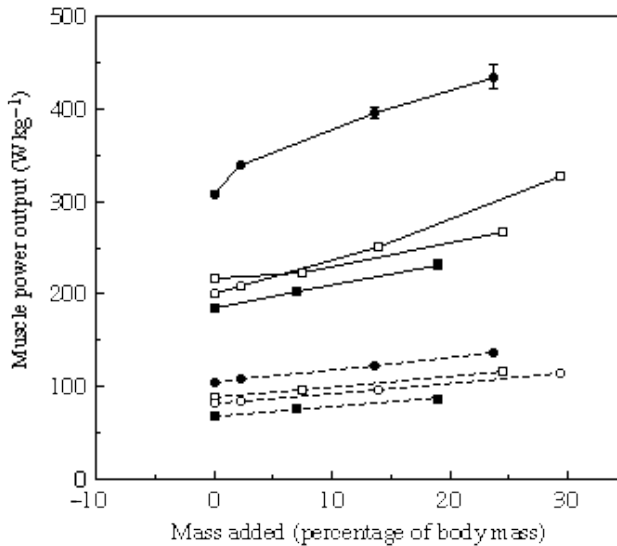


Fig. 9. Muscle power output of loaded hummingbirds. Symbols as in Fig. 6. The solid lines are the results for the zero elastic storage analysis and the broken lines are those for the perfect elastic storage analysis.

also increased with increased loading, the flight efficiency and, by extrapolation, the muscle efficiency, remained almost constant in both the zero and perfect elastic storage analyses (Fig. 10). However, upon a closer examination of the perfect elastic storage analysis, all birds except Bt12 showed a slight but significant decrease in flight efficiency.

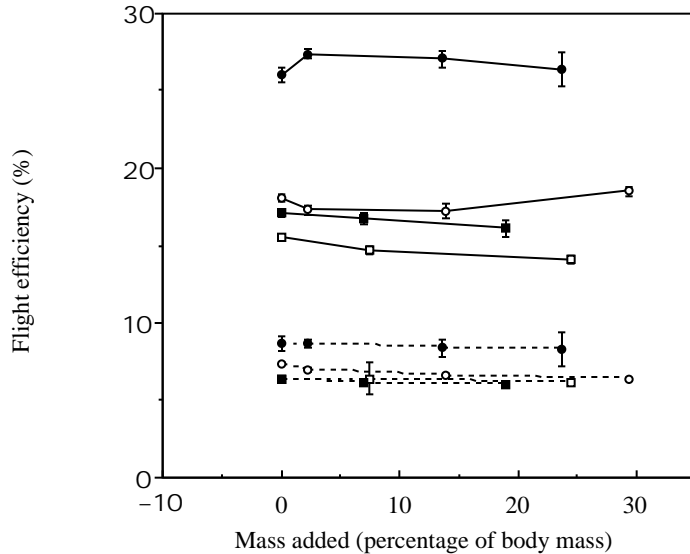


Fig. 10. Flight mechanochemical efficiency of loaded hummingbirds. Symbols as in Fig. 6. The solid lines are the results for the zero elastic storage analysis and the broken lines are those for the perfect elastic storage analysis.

Discussion

Artificial flower study

From the increase in metabolic power input it is clear that larger flowers are a more expensive resource from which to forage but that the increase in cost is not very great. Is the increased metabolic cost of $5.3 \pm 1.4\%$ from the small to the large 'flower' enough to present a sufficient evolutionary driving force for the selection of specific flower types? Other features such as nectar quality and quantity are likely to be of much greater importance to foraging hummingbirds (Stiles, 1976; Hainsworth and Wolf, 1976; Feinsinger, 1978; Pyke and Waser, 1981; Tamm and Gass, 1986). This conclusion is reinforced by the observation that some flowers that would alter wing kinematics appear to depend mainly on hummingbirds for pollination, although other vectors may be important (e.g. the hedgehog cactus, *Echinocereus triglochidiatus*, Grant and Grant, 1979). However, the increased energetic cost associated with the broader flowers may interact significantly with reductions in the rate of energy intake associated with anti-predatory vigilance (Lima, 1991).

The consequences for flight efficiency are dependent on the degree of elastic storage of inertial energy. As a result of the increased power input and the constant or reduced power output, efficiency decreased with increasing 'flower' size for the zero elastic storage analysis. However, it appears likely that hummingbirds show a fairly substantial elastic storage of inertial energy (Wells, 1993). If this is indeed the case, then muscle power output increased significantly with increases in 'flower' size. As a consequence, flight efficiency remained essentially constant. In the perfect elastic storage analysis,

foraging from larger flowers entails only a small increase in energy expenditure and does not affect flight efficiency.

Loading study

Only a limited range of additional loading was tolerated by the birds (to a maximum of 19–29.4% of body mass). There are several possible explanations for this observation. First, the birds may adopt a more rapid foraging pattern with increased loading, thus preventing data collection with our feeder-mask system. Second, many of the birds tested were already carrying some additional mass due to the deposition of fat whilst on an *ad libitum* captive diet. Weight records since capture suggest that this was of the order of 20% of lean body mass. Consequently, the birds may have been approaching their maximum premigratory load-carrying capacity in the loading experiments.

Increases in body mass were not obtained without an increase in total hovering cost, as shown by the significant increase in metabolic power input in all four birds. Regardless of which assumption is made about the degree of elastic storage of inertial energy, as load increased, muscle power output increased to generate the necessary additional lift. There was very little effect on overall flight efficiency within the range of loading tested but, in the perfect elastic storage analysis, efficiency decreased slightly with increased loading. The impressive increases in power output demonstrate a considerable reserve in muscle performance. This reserve is probably in the form of motor units that are not active during unloaded hovering flight. Because the hummingbird flight muscles are homogeneous (Grinyer and George, 1969), the progressive recruitment of new motor units would not be expected to produce major changes in muscle efficiency. The total mass gain possible for the birds may be dictated by the number of these reserve motor units. This could, in turn, play a role in the timing of migration.

The flower size and loading experiments produced almost opposite changes in wing kinematics. When loaded, the birds appeared to prefer to change their wingbeat amplitude rather than their wingbeat frequency, although they could do either. The results seem to support the contention of Greenewalt (1960, 1975) that hummingbirds normally operate with a relatively fixed wingbeat frequency, although this can alter rapidly during lateral changes in direction (Rüppell, 1977). The two experiments also produced opposite changes in stroke plane angle (Figs 3 and 8). In the loading study, the change towards horizontal was probably an artefact caused by the presence of the harness and the position of the weights. In the 'flower' experiment, tilting the wings avoided the broadest aspect of the 'flower' and therefore would have allowed a slightly greater wingbeat amplitude.

These experiments have demonstrated that broader flowers are indeed a more expensive resource from which to forage, but the importance of this small extra cost will depend on the other energetic constraints faced by the bird, for example premigratory fattening or decreased lift from damaged or moulting feathers. The loading studies demonstrated that hummingbirds carry a considerable quantity of muscle that they do not appear to utilise during stationary hovering flight. This may represent a safety reserve that is required for short periods during acrobatic manoeuvres and fast forward flight. A 10% increase in load required a $5.7 \pm 0.9\%$ increase in mass-specific oxygen consumption.

The ability of hummingbirds to vary their wing kinematics with very little effect on

flight efficiency allows them to exploit a wide range of flower types and to accommodate energy stores for seasonal migration.

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References

- BEUCHAT, C. A., CHAPLIN, S. B. AND MORTON, M. L. (1979). Ambient temperature and the daily energetics of two species of hummingbirds, *Calypte anna* and *Selasphorus rufus*. *Physiol. Zool.* **52**, 280–295.
- BROWN, J. H. AND KODRIC-BROWN, A. (1979). Convergence, competition and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology* **60**, 1022–1035.
- CARPENTER, F. L. AND HIXON, M. A. (1988). A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* **90**, 373–378.
- CARPENTER, F. L., PATON, D. C. AND HIXON, M. A. (1983). Weight gain and adjustment of feeding territory size in migrant Rufous Hummingbirds. *Proc. natn Acad. Sci.U.S.A.* **80**, 7259–7263.
- ELLINGTON, C. P. (1984a). The aerodynamics of hovering insect flight. I. The quasi-steady analysis. *Phil. Trans. R. Soc. Lond. B* **305**, 1–15.
- ELLINGTON, C. P. (1984b). The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil. Trans. R. Soc. Lond. B* **305**, 17–40.
- ELLINGTON, C. P. (1984c). The aerodynamics of hovering insect flight. III. Kinematics. *Phil. Trans. R. Soc. Lond. B* **305**, 41–78.
- ELLINGTON, C. P. (1984d). The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Phil. Trans. R. Soc. Lond. B* **305**, 79–113.
- ELLINGTON, C. P. (1984e). The aerodynamics of hovering insect flight. V. A vortex theory. *Phil. Trans. R. Soc. Lond. B* **305**, 115–144.
- ELLINGTON, C. P. (1984f). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. Lond. B* **305**, 145–181.
- FEINSINGER, P. (1978). Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol. Monogr.* **48**, 269–287.
- GRANT, K. A. AND GRANT, V. (1968). *Hummingbirds and Their Flowers*. New York: Columbia University Press.
- GRANT, V. AND GRANT, K. A. (1979). The pollination spectrum in the southwestern American cactus flora. *Pl. Syst. Evol.* **133**, 29–37.
- GREENEWALT, C. H. (1960). *Hummingbirds*. New York: Doubleday and Co.
- GREENEWALT, C. H. (1975). The flight of birds. *Trans. Am. Phil. Soc.* **65**, 1–67.
- GRINYER, I. AND GEORGE, J. C. (1969). Some observations on the structure of the hummingbird pectoral muscles. *Can. J. Zool.* **47**, 771–774.
- HAINSWORTH, F. R. AND WOLF, L. L. (1976). Nectar characteristics and food selection by hummingbirds. *Oecologia (Berlin)* **25**, 101–113.
- HAINSWORTH, F. R. AND WOLF, L. L. (1983). Models and evidence for feeding control of energy. *Am. Zool.* **23**, 261–272.
- HIXON, M. A. AND CARPENTER, F. L. (1988). Distinguishing energy maximizers from time minimizers: A comparative study of two hummingbird species. *Am. Zool.* **28**, 913–925.
- HIXON, M. A., CARPENTER, F. L. AND PATON, D. C. (1983). Territory area, flower density and time budgeting in hummingbirds: an experimental and theoretical analysis. *Am. Nat.* **122**, 366–391.
- LACK, D. (1976). *Island Biology. Illustrated by the Land Birds of Jamaica*. Berkeley: University of California Press.
- LIMA, S. L. (1991). Energy, predators and the behaviour of feeding hummingbirds. *Evol. Ecol.* **5**, 220–230.
- MARDEN, J. H. (1987). Maximum lift production during takeoff in flying animals. *J. exp. Biol.* **130**, 235–258.
- MILLER, R. S. (1985). Why hummingbirds hover. *Auk* **102**, 772–726.
- NORRIS, R. A., CONNELL, C. E. AND JOHNSTON, D. W. (1957). Notes on fall plumages, weights and fat condition in the ruby-throated hummingbird. *Wilson Bull.* **69**, 155–163.

- ODUM, E. P. AND CONNELL, C. E. (1956). Lipid levels in migrating birds. *Science* **123**, 892–894.
- PYKE, G. H. AND WASER, N. M. (1981). The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* **13**, 260–270.
- RÜPPELL, G. (1977). *Bird Flight*. New York: Van Nostrand Reinhold Co.
- STILES, F. G. (1976). Taste preferences, color preferences and flower choice in hummingbirds. *Condor* **78**, 10–26.
- TAMM, S. AND GASS, C. L. (1986). Energy intake rates and nectar concentration preferences by hummingbirds. *Oecologia (Berlin)* **70**, 20–23.
- TYRRELL, E. Q. AND TYRRELL, R. A. (1985). *Hummingbirds. Their Life and Behavior*. New York: Crown.
- WELLS, D. J. (1990). Hummingbird flight physiology: muscle performance and ecological constraints. PhD dissertation, University of Wyoming.
- WELLS, D. J. (1993). Muscle performance in hovering hummingbirds. *J. exp. Biol.* **178**, 39–57.