HUMMINGBIRD FLIGHT SPEEDS

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Abstract.—Long-tailed Hermits (*Phaethornis superciliosus*) normally fly faster than the velocity predicted to minimize their cost of transport. The average speed we measured for individuals flying a known 40-m course was 11.5 m/s. Rapid flower visitation yields rewards that could compensate for the extra costs of fast flight. *Received 2 March 1984, accepted 30 July 1984.*

How fast should a bird fly? Intermediate flight speeds that minimize instantaneous power costs (V_{mp}), or more realistically that minimize the cost of flying a certain distance (V_{mr}), can be predicted from aerodynamic theory that is devoid of ecological context. The potential for minimization of power costs at intermediate speeds emerges from the U-shaped form of the relationship between power costs and flight speed (Fig. 1; Pennycuick 1969, 1975; Greenewalt 1975).

When can birds justify the extra energetic investment required for flight at speeds slower or faster than V_{mr}? The advantages of power dives, top-speed chases, and escape flights clearly outweigh the energetic sacrifices of brief high-speed flights. Stationary flight, such as hovering at flowers, also may yield net rewards (Pyke 1981). However, the natural flight speeds of birds in routine contexts rarely are compared to aerodynamic models. In one exceptional study Schnell and Hellack (1979) found that gulls and terns (Laridae) cruise near their colonies at velocities between V_{mp} and V_{mr}, i.e. at intermediate speeds at the bottom of the power curve.

The need for more such information is heightened by the recognition that time gained by flying fast may be used profitably in ways that compensate for the extra energy expended (Norberg 1981). Hummingbirds should be of particular interest in this context because of their sensitivity to the energetic consequences of alternative behaviors (DeBenedictis et al. 1978).

Previous analyses of the ecological correlates of hummingbird wing lengths have stressed the costs of hovering flight, a hummingbird specialty. The cost of hovering is a direct function of body weight and wing span (Greenewalt 1960a, 1975; Pennycuick 1969, 1975). Slight variations in wing lengths relative to body mass

relate to differences in flight ecology (Feinsinger and Chaplin 1975, Feinsinger et al. 1979). Theoretically, forward flight speeds also should influence a hummingbird's flight costs and optimal wing lengths (Pennycuick 1969, Greenewalt 1975); however, these speeds have not been determined in an ecological context.

Here I consider the flight speeds of a 6-g hermit hummingbird, the Long-tailed Hermit (*Phaethornis superciliosus*). Hermit hummingbirds relate directly to the questions posed above because forward flight is the dominant component of their routine flight ecology. They fly considerable distances between dispersed flowers (Stiles 1979). Some species of hermit hummingbirds, including the species featured here, also commute frequently from lek display grounds to distant flowers. The estimates of flight speeds I present are the first for a hermit hummingbird and among the few natural flight speeds recorded for any hummingbird.

Methods

This study was carried out in the lowland rain forest on the Osa Peninsula of Costa Rica. In June 1982 a single observer with a stopwatch timed flights of Long-tailed Hermits as they flew 40 m directly from one artificial flower to another along a broad trail. These hummingbirds visited the flowers regularly as a part of normal, daily trapline foraging. The observer sat near one flower, started the stopwatch when the hermit left, and stopped the stopwatch as the bird pulled up to the distant flower. Arrivals were studied at the distant flower through 10× binoculars. Some slight error in judgment, reaction time, and parallax was inherent in these measurements. Minor acceleration and deceleration of unknown duration near the beginning and end of a flight make these measurements slight underestimates of true flight speed. We excluded times of flights during which the hummingbird veered off the trail and out of sight.

The wing lengths and masses of Long-tailed Hermits netted and marked on the Osa Peninsula in 1979–
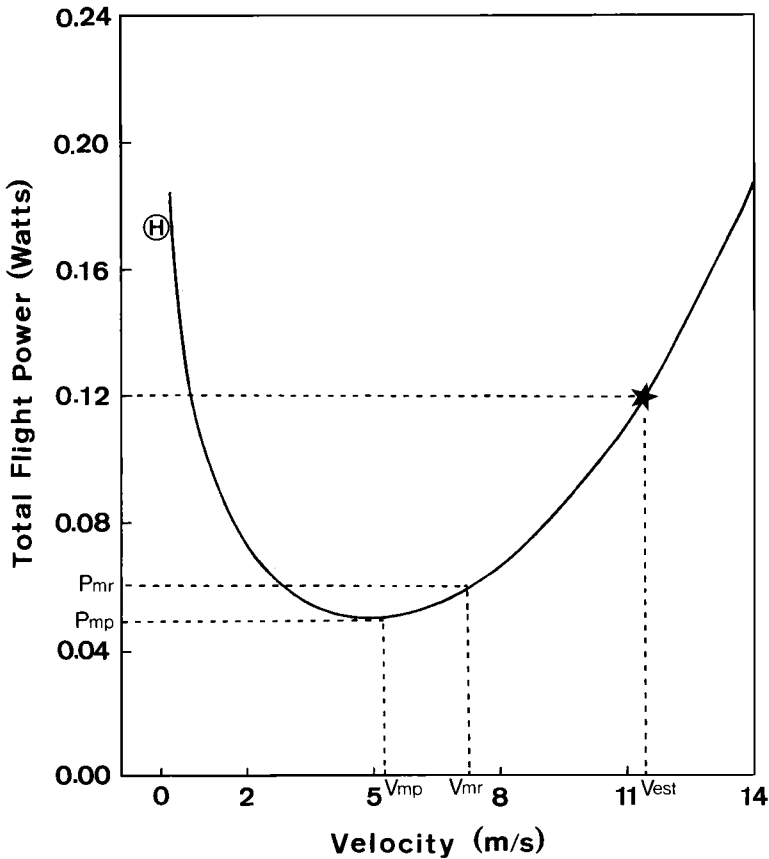
Fig. 1. Theoretical flight power curve for the Long-tailed Hermit calculated from Eq. 44 in Greenewalt (1975: 39). Minimum power velocity (V_{mp}) and maximum range velocity (V_{mr}) and associated power requirements for this species are indicated by dashed lines. *H* is the cost of hovering projected from Eq. 38 in Greenewalt (1975: 38). The position of the average flight speed (V_{est}) presented in this paper for the Long-tailed Hermit is indicated by a star.

1982 were 61.8 ± 0.2 mm and 6.3 ± 0.4 g (*n* = 271). These values fall close to the fitted regression for hummingbirds as a group (Fig. 2).

RESULTS

V_{mp} is about 5.5 m/s (20 kph) for all hummingbirds; the range of hummingbird body masses and wing spans is not sufficient to affect this greatly (Greenewalt 1975: 39). V_{mr} is higher [7.5 m/s (27 kph)] for hummingbirds. Using Greenewalt's Eq. 45 (1975: 39) for the Long-tailed Hermits studied, we projected V_{mp} to be 5.4 m/s and V_{mr} to be 7.3 m/s. The power requirements of this species flying at 1.4 m/s and 12.5 m/s should be about 3 times those at V_{mp} and only slightly less than the cost of hovering (Fig. 1).

The flight times we recorded averaged 3.47 s (*n* = 10, SD = 0.216, range 3.2–3.8 s), which calculates to an estimated average velocity of 11.57 ± 0.71 m/s (41.8 ± 2.56 kph). The Long-tailed Hermits flew 40 m in 5.3 s. These hermit hummingbirds flew not at V_{mp} or V_{mr}, but faster—at speeds of 2.1 × V_{mp} and 1.6 × V_{mr}, costing 72% of the energetic requirements of hovering at flowers (see Fig. 1). Our slowest recorded flight speed (3.8 s = 10.5 m/s) was 3.2 m/s faster than V_{mr} for this species.

Long-tailed Hermits also fly fast when they commute through relatively clear midstrata of the rain forest between lek territories and feeding areas up to 500 m away. The two flight speeds of commuting hummingbirds that we were able to measure were 10 and 11 m/s.
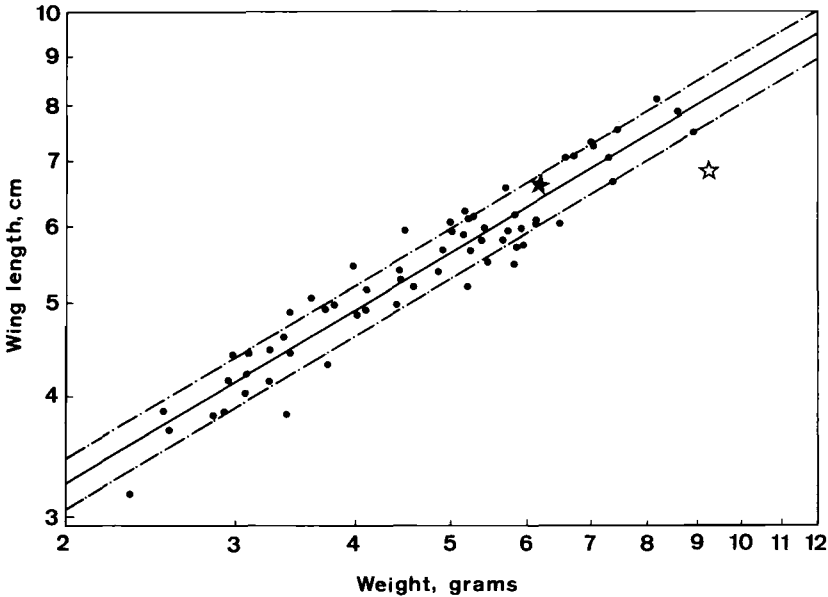
Field measurements of flight speeds with a

Fig. 2. Dimensions of hummingbirds for which sample sizes of more than 15 specimens were available (from Greenewalt unpubl.). Broken lines indicate 1 SD of the least squares regression, the equation for which is $\log L = 0.5973 \log M + 3.315$, and the standard deviation of the intercept = 0.0264. The average dimensions of the Long-tailed Hermit are indicated by a black star, while those of *Eutoxeres* are indicated by a white star.

stopwatch are estimates subject to several sources of error. Individual errors of reaction time or parallax, however, were at the level of 0.1–0.2 s or less, an order of magnitude less than the difference between estimated flight speed and V_{mr}. More detailed studies and larger sample sizes are needed to establish the flight speeds of Long-tailed Hermits precisely, but these data leave little doubt that they fly faster than V_{mr}.

DISCUSSION

It remains to be established that any hummingbird routinely flies at speeds that minimize its power costs. The few published records of hummingbird flight speeds vary greatly but do not suggest usual flight speeds at V_{mp} or V_{mr}.

Pearson (1961) released Allen's Hummingbirds (*Selasphorus sasin*) inside a highway drainage pipe and timed their escape speeds at 8 m/s (30 kph) and 11 m/s (40 kph). He concluded that normal cruising speeds of small hummingbirds were approximately 11 m/s (40 kph). Early reports of 21 m/s (75 kph) and 25–28 m/s (90–100 kph) (Hayes 1929, Allard 1934) by au-

tomobile-paced Ruby-throated Hummingbirds (*Archilochus colubris*) are not consistent with subsequent observations. Ruby-throated Hummingbirds, for example, could not progress against a 12 m/s (45 kph) headwind in wind tunnel experiments, suggesting that their maximum air speed was in this range (Greenewalt 1960b).

Wolf et al. (1976) reported that Green Violet-ears (*Colibri thalassinus*) flew 0.2–1.2 m/s (0.7–4.3 kph) between flowers less than 1 m apart. The linear relation of flight speed to distance in these data suggests that acceleration and deceleration constrained flight speed over such short distances. Montgomerie (1979) recorded speeds of 0.3–1.2 m/s by Cinnamon Hummingbirds (*Amazilia rutila*) flying short distances (less than 1 m) between flowers. Thus, slow flight speeds may characterize hummingbirds flying between adjacent flowers on a bush or hedgerow.

Norberg's (1981) ecological model of optimal flight speeds suggests that birds should increase their speed above V_{mr} when foraging, if the travel time saved compensates for the increased travel costs. The foraging ecology of Long-tailed Hermits provides this opportunity.

The 1.9 s saved by flying 40 m at 11.6 m/s instead of 7.5 m/s is close to the time a Long-tailed Hermit takes to extract nectar from one flower (Gill pers. obs.). The extra cost of flying 40 m between flowers at 11.6 m/s is roughly 0.144 J, whereas 1 μl of nectar in flowers the hermits typically visit (e.g. *Costus* and *Helico-nia*) contains roughly 5 J. Extended to hundreds of flowers visited daily, the accumulated gain could be substantial.

There are two other features of the natural history of Long-tailed Hermits that potentially may be more important than simple energetic compensation. First, nectar rewards in the un-defended, dispersed flowers these birds visit depend on which bird gets to a flower first. Individuals rarely have exclusive use of a par-ticular flower (Gill pers. obs.). Even slight re-visitation delay can result in loss of nectar to a competing individual. Second, male Long-tailed Hermits potentially sacrifice reproductive per-formance when they leave their lek territory (Stiles and Wolf 1979). Minimization of forag-ing time by means of fast flight and rapid flow-er visits should be advantageous if the time saved is used instead for lek activities.

Our evidence of fast flight in hermit hum-mingbirds also bears on the issue of adaptive wing-length variations in hummingbirds. Traplining hummingbirds that visit dispersed or low-yield flowers have longer wings and lower hovering costs than do territorial hum-mingbirds (Feinsinger and Chaplin 1975, Feinsinger et al. 1979). Paradoxically, some specialized trapliners, such as the hermit hummingbirds (Phaethorninae), do not have long wings and may even have shorter-than-average wings (Feinsinger et al. 1979).

There is no aerodynamic reason to expect high-speed trapliners, such as the Long-tailed Hermit, to evolve longer-than-average wings. Selection should favor longer-than-average wings in hummingbirds that fly slowly or that hover at low-yield flowers for much of their foraging time (Feinsinger et al. 1979). How-ever, selection could favor shorter-than-aver-age wings in hummingbirds that fly fast be-cause shorter wings reduce power costs of profile drag, which increase with the cube of velocity (Pennycuick 1969, Rayner 1979).

Hermit hummingbirds as a group do not have shorter-than-average wing lengths. The rela-tion between wing length (L, mm) and body mass (M, g) in a large sample ($n = 244$) of 130

hummingbird species spanning the family's size range (Greenewalt MS) is

$$\log L = 0.5186 \log M + 0.3891. \qquad (1)$$

The relatively longer wings of large humming-birds compensate for their weight in such a way that their specific per-gram hovering costs are the same as those of small hummingbirds (Hainsworth and Wolf 1972, Greenewalt 1975). Hermit hummingbirds do not have atypical wing lengths, despite their various body sizes. The regression for hermits of the genera *Phae-thornis*, *Glaucis*, *Threnetes*, and *Eutoxeres* is

$$\log L = 0.4724 \log M + 0.3966. \qquad (2)$$

The lower slope of this equation does not differ significantly ($d = 1.6110, P > 0.10$) from that of the equation for all hummingbirds excluding these hermit genera, namely,

$$\log L = 0.5647 \log M + 0.3735. \qquad (3)$$

Hermits of the genus *Eutoxeres* are aberrant, big (9–12 g) hummingbirds with short wings that correspond in length to those of hum-mingbirds about 7 g in mass. Instead of hov-ering, they usually cling to *Heliconia* bracts while feeding. Their wing lengths certainly do not relate to efficient hovering. The regression of wing length vs. mass for hermits excluding *Eutoxeres* is even more similar to Eq. 3:

$$\log L = 0.5092 \log M + 0.3760. \qquad (4)$$

The high average wing disc loading of hermit hummingbirds mentioned by Feinsinger et al. (1979) apparently was the result of including *Eutoxeres* in their sample of "hermits"; the av-erage value of their data set excluding *Eutoxeres* (by my calculations) was not significantly dif-ferent from other groups of hummingbirds.

Variations in wing disc loading and hover-ing power requirements discussed by Feinsing-er and Chaplin (1975), Feinsinger et al. (1979), and others are departures from the average trend, the variance about the regression rather than the slope of the regression itself. How-ever, this variance (Eq. 1) is not great; the stan-dard deviation of the intercept is 0.0393. Con-ceivably, some traplining hermit hummingbirds have higher wing disc loadings than other species with which they coexist, a result per-haps of local sorting of species with different foraging strategies and corresponding wing

lengths (Feinsinger et al. 1979). If this proves to be the case, details on flight speeds would be needed to determine whether flight power considerations were involved in any way. The short wings of territorial hummingbirds (see Feinsinger and Chaplin 1975), for example, probably relate to the ability to accelerate and maneuver in chases and displays rather than to energetic considerations.

LITERATURE CITED

ALLARD, H. A. 1934. Speed of the Ruby-throated Hummingbird's flight. Auk 51: 84.

DeBENEDICTIS, P. A., F. B. GILL, F. R. HAINSWORTH, G. H. PYKE, & L. L. WOLF. 1978. Optimal meal size in hummingbirds. Amer. Natur. 112: 301–316.

FEINSINGER, P., & S. M. CHAPLIN. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. Amer. Natur. 109: 217–224.

———, R. K. COLWELL, J. TERBORGH, & S. M. CHAPLIN. 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. Amer. Natur. 113: 481–497.

GREENEWALT, C. H. 1960a. Hummingbirds. Garden City, New York, Doubleday & Co.

———. 1960b. The hummingbirds. National Geographic 118: 658–679.

———. 1975. The flight of birds. Trans. Amer. Phil. Soc. (New Series) 65(4): 1–67.

HAINSWORTH, F. R., & L. L. WOLF. 1972. Power for hovering flight in relation to body size in hummingbirds. Amer. Natur. 106: 589–596.

HAYES, S. P., JR. 1929. Speed of flying hummingbirds. Auk 46: 116.

MONTGOMERIE, R. 1979. The energetics of foraging and competition in some Mexican hummingbirds. Unpublished Ph.D. dissertation, Montreal, Quebec, McGill Univ.

NORBERG, R. A. 1981. Optimal flight speed in birds when feeding young. J. Anim. Ecol. 50: 473–477.

PEARSON, O. P. 1961. Flight speeds of some small birds. Condor 63: 506–507.

PENNYCUICK, C. J. 1969. The mechanics of bird migration. Ibis 111: 525–556.

———. 1975. Mechanics of flight. Pp. 1–75 in Avian biology, vol. 5 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

PYKE, G. H. 1981. Why hummingbirds hover and honeyeaters perch. Anim. Behav. 29: 861–867.

RAYNER, J. M. V. 1979. A new approach to animal flight mechanics. J. Exp. Biol. 80: 17–54.

SCHNELL, G. D., & J. J. HELLACK. 1979. Bird flight speeds in nature: optimized or a compromise? Amer. Natur. 113: 53–66.

STILES, F. G. 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. Brenesia 15(suppl.): 151–180.

———, & L. L. WOLF. 1979. Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird. Ornithol. Monogr. 27: 1–78.

WOLF, L. L., F. G. STILES, & F. R. HAINSWORTH. 1976. Ecological organization of a tropical, highland hummingbird community. J. Anim. Ecol. 45: 349–379.