WHY HUMMINGBIRDS HOVER

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ABSTRACT.—Hummingbirds are noted for their hovering flight, and it has been shown that a bird that hovers can move more quickly between flowers than one that perches. Because the relative importance of energetic costs vs. speed increases with body size, it has been assumed that if birds forage in ways that maximize their net energy gain, small birds, such as hummingbirds, should hover and large birds should perch. This study shows that hovering is not necessarily the preferred mode of feeding in hummingbirds, and that floral architecture, rather than energetics, dictates whether a bird hovers or perches. *Received 6 December 1984, accepted 7 June 1985.*

HUMMINGBIRDS (Trochilidae), sunbirds (Nectariniidae), honeyeaters (Meliphagidae), and honeycreepers (Drepanidinae) have evolved independently to occupy similar ecological niches in geographically distinct regions. Members of all four families, with few exceptions, are primarily nectar feeders that have evolved in morphologically similar ways to exploit the flowers they pollinate (Brown et al. 1978). However, many hummingbirds forage by hovering at flowers, while most species in the other families perch while probing for nectar.

Pyke (1981) compared the foraging strategies of hummingbirds and honeyeaters, and presented evidence that a bird that hovers while feeding can move more quickly between flowers than one that perches, although the advantage of hovering may be offset by its cost (Hainsworth and Wolf 1972). He evaluated two situations, one for hovering hummingbirds and the other for perching honeyeaters, and developed a model that led him to conclude that each type of flower visitor uses the foraging mode that maximizes its net rate of energy gain (Pyke 1981). The basic premise of Pyke's argument was that the relative importance of energetic costs vs. speed increases with increasing body size. Therefore, if the birds forage in ways that maximize their net energy gain, small birds should hover and large birds should perch.

Many flowers visited by hummingbirds do not provide an opportunity to perch (Grant and Grant 1968). If suitable perches were available, would hummingbirds perch when it is more profitable for them to do so, rather than hover? In other words, in the coevolved system of plants and hummingbird pollinators, is hovering the preferred mode of feeding, or does floral architecture (e.g. corolla form and placement) constrain hummingbird feeding behavior and the ability to express a preference? This study was designed to examine this question.

METHODS

The research was conducted with 2 female Ruby-throated Hummingbirds (*Archilochus colubris*) at the Queen's University Biology Research Station at Lake Opinicon, Ontario in May 1983 and 1 female Antillean Crested Hummingbird (*Orthorhyncus cristatus*) at St. John in the U.S. Virgin Islands in June 1983.

Ruby-throated Hummingbird.—At Lake Opinicon, artificial feeders were placed in the center of a 40 × 40 m mowed grass field. The feeders were of two types. One, an "infinite" supply feeder (Gass 1978), was an inverted laboratory water bottle (capacity 600 ml); the other, a supply-limited feeder (Gass 1978), consisted of an 18-gauge needle and syringe tip (capacity 100 μl), with the reservoir of the syringe tip sealed with a drop of epoxy glue.

The feeders were mounted on green, 17-mm diameter poles at a height of 1.5 m. The perch was a horizontal wire triangle (6 × 6 × 6 cm) taped to the pole in a position that allowed the birds to perch and feed by stretching slightly forward but that did not prevent them from hovering.

Experimental design.—The experiments began with an infinite-supply feeder filled with a 25% (w/w) sucrose solution. A red cardboard disk (5 cm diameter) was placed over the glass sipper tube of the laboratory bottle to act as an "attracting corolla."

The syringe tips of the supply-limited feeders were painted red and were filled with measured amounts of 25% (w/w) sucrose solution. The feeders were positioned by inserting the needle of the syringe tip into the wooden pole at an angle that allowed the birds to feed comfortably when a perch was provided.

TABLE 1. Feeding mode (hover or perch) at a single supply-limited feeder with perch.

Nectar (μl)	Feeding bouts		Total	Percent perch
	Hover	Perch		
80	8	20	28	71.4
60	8	21	29	72.4
40	4	23	27	85.2
20	4	23	27	85.2
10	0	42	42	100.0
5	4	28	32	87.5
3	2	23	25	92.0

To determine the effect of nectar reward on whether birds perched or hovered to feed, the nectar reward was reduced in stages from an unlimited supply to limited supplies of 80, 60, 40, 20, 10, 5, and 3 μl of sucrose solution/feeding bout. The effect of interplant distance on feeding behavior was measured by (1) placing 3 syringe-tip feeders with perches 1 m apart in a row and reducing the total nectar reward from 20 to 10 to 5 μl and (2) placing 3 feeders with perches at the same height 7 cm apart in a horizontal "inflorescence" on a single pole. Each feeder was filled with 10 μl of sucrose solution. Tests with micropipettes showed that the feeders were always entirely emptied at each feeding. The distance between flowers was varied to see if the birds would hover, rather than perch, when the flowers were close together.

Antillean Crested Hummingbird.—Antillean Crested Hummingbirds were observed while feeding on nectar from pink and red cultivated *Hibiscus* (*Hibiscus rosa-sinensis* and var. *H. sinensis* × *schisopetaly*) flowers, and at yellow syringe-tip feeders with the needle inserted into the main stem of *Hibiscus* plants with the feeder above and parallel to a lateral branch on which the birds could perch to feed. The feeders were filled with 20 μl of 25% sucrose (w/w) solution. There were 4 *Hibiscus* plants (2 red, 2 pink) located in a square ca. 3 m apart on an open perch.

RESULTS

Ruby-throated Hummingbird.—The 2 females in this study were individually recognizable by plumage. Female #1, which flew to the feeders from perches in trees at the south end of the field, was clearly dominant over female #2, which flew to the field from an active nest, approximately 80 m west of the field. The subordinate female frequently was chased when she approached a feeder and was more tentative than the dominant female in her feeding behavior.

Infinite-supply feeder.—When a wire perch was provided at the infinite-supply feeder, female #1 perched on her second visit and all (36) subsequent visits. Female #2 hovered during her first 3 feeding bouts, and perched on 22 of 31 subsequent bouts. Although bouts were not scored if interrupted by a chase, the more tentative feeding behavior of female #2 due to repeated chases by #1 probably accounts for the bouts during which she hovered to feed. The combined feeding mode for the 2 birds was 86.6% perching/bout.

Supply-limited feeder.—The feeding mode adopted by the 2 birds at a single supply-limited feeder changed when the nectar reward (sucrose solution) was reduced in stages from 80 to 3 μl (Table 1). Again, female #2 was responsible for almost all of the hovering recorded in this experiment.

The fact that the birds tended to perch more frequently as the experiment progressed, even though the nectar reward was being reduced, suggests that there may have been a learning component in adjusting to the conditions of a novel feeder arrangement. A test (FUNCAT) with a linear model of categorical response (Helwig and Council 1982) showed that the chance of a significant response was 34.5%. It is clear, however, that reductions in nectar reward did not decrease the tendency to perch, and perching was the preferred mode of feeding.

When the feeders were separated by 1 m, there was no effect as nectar reward was reduced from 20 to 10 to 5 μl (Table 2). When the feeders and perches were arranged at the same height on a single pole in an "inflorescence" with a horizontal distance of 7 cm between the syringe tips, the ratio of perching to hovering was not significantly affected. In fact, with an interflower distance of 7 cm, the birds did not even hover to fly between perches, but hopped, with only a few wingbeats for balance, from one perch to the next.

There were no significant differences (FUNCAT, Helwig and Council 1982) between the overall hovering frequencies at the different feeder types and arrangements.

Antillean Crested Hummingbirds.—Before the feeders were installed, I observed the feeding behavior of 2 female Antillean Crested Hummingbirds and 1 female Green-throated Carib (*Eulampis holosericeus*) feeding at pink and red *Hibiscus* flowers. The pink *Hibiscus* flowers were mostly upright, with the staminal column in a vertical position and the large petals spread horizontally; the red flowers were mostly horizontal or slightly pendant.

Both species of hummingbird used the petals of the horizontal pink flowers as a landing platform and probed the nectaries, with their wings fluttering slightly for balance, although the smaller Antillean Crested Hummingbirds seemed more adept and more successful at this mode of feeding. At the pendant, red *Hibiscus* flowers, the Green-throated Carib always fed by hovering, but the Antillean Crested Hummingbirds frequently grasped the staminal column and clung to it while probing the nectaries.

When two syringe-tip feeders were installed above lateral branches on a single *Hibiscus* plant, territorial conflict ensued immediately after the feeders were discovered. The Green-throated Carib quickly was excluded from the area, and the Antillean Crested Hummingbirds ceased feeding at flowers and concentrated their activities on the more rewarding feeders. After several vigorous fights, one female established dominance and the entire area became her territory. She then perched at every visit during a total of 20 h of observations (4 h/day for 5 days) and seldom visited the flowers while the feeders contained food.

DISCUSSION

It is assumed in optimal foraging that if the decision rules that would maximize an animal's foraging efficiency are known, we can predict foraging behavior (Pyke et al. 1977, Krebs 1978). While recent applications of the idea of decision rules have provided a powerful approach to problems in behavioral ecology (Gass and Montgomerie 1981, McCleery 1978), it is necessary, as Pyke et al. (1977) point out, to recognize constraints on a system that may restrict the expression of alternative behaviors.

Size and feeding mode.—While Pyke (1980) has shown that hovering birds can move more quickly between flowers than those that perch, it does not necessarily follow that hovering is the consequence of a decision rule used to choose among alternative behaviors. Moreover, there is little evidence to show that whether a bird hovers or perches is a function of body size. My results show that the small Ruby-throated Hummingbird (3.5 g) and Antillean Crested Hummingbird (3.0 g) will, in fact, perch preferentially if given the opportunity.

TABLE 2. Feeding mode (hover or perch) at 3 supply-limited feeders separated by 1 m and by 7 cm.

Distance between feeders	Nectar (μl)	Feeding mode		Total	Percent perch
		Hover	Perch		
1 m	20	6	34	40	85.0
1 m	10	12	59	71	83.1
1 m	5	6	31	37	83.8
7 cm	10	11	51	62	82.2

Whether a hummingbird perches or hovers to feed is not a function of body size but is, instead, a question of plant architecture, and whether a perch is available. The White-tipped Sicklebill (*Eutoxeres aquila*) is primarily a percher on *Heliconia* (Ridgely 1976, L. L. Wolf pers. comm.), Scintillant Hummingbirds (*Selasphorus scintilla*) perch beside the flowers they probe, and the relatively large (average weight of males 8.8 g, females 8.0 g) Andean Hillstars (*Oreotrochilus estella*) perch to feed at the cactus *Chuguiraga spinosa* but hover at *Eucalyptus*, where no perch is available (Carpenter 1976). The Violet Sabrewing (*Campylopterus hemileucurus*) of Costa Rica weighs up to 12.8 g (males), but usually hovers to feed because its flowers lack perch opportunities (P. Feinsinger pers. comm.). The small (2.7 g) Bumblebee Hummingbird (*Atthis heloisa*) hovers at blossoms of *Erythrina americana*, but perches on a stem to feed when the position of the flower makes this possible (Wagner 1946). At the extreme of body weights for hummingbirds, the Bee Hummingbird (*Mellisuga helenae*, <2 g) of Cuba frequently perches by grasping the staminal columns of *Hibiscus* flowers or perches on upright flowers (R. Woodbury pers. comm.). Similarly, both the Antillean Crested Hummingbird (this study) and the Giant Hummingbird (*Patagona gigas*, 20 g) hover to feed if necessary (R. W. Ridgely pers. comm., C. G. Sibley pers. comm.), in spite of their relatively slow wingbeats of 8–10/s (Greenewalt 1960). Ruby-throated Hummingbirds have even been observed to perch by clinging to the bark of trees to feed on sap from sapsucker drills (Bolles 1892, Wright and Wright 1918, Southwick and Southwick 1980).

Although hovering flight is highly developed in hummingbirds, this ability is not exclusive to the Trochilidae and does not necessarily support the idea that this is their primary or predominant mode of feeding. This notion probably originated because their hovering flight is particularly spectacular (Greenewalt 1960), and most observations of hummingbird foraging have centered on temperate species associated with "hummingbird flowers" (Grant 1951, Grant and Grant 1968); these flowers are characteristically tubular and pendant and do not provide an opportunity for birds to perch.

For example, the members of the following 9 genera (40 species), which occur at upper elevations in the Andes, typically cling or perch while feeding (R. W. Ridgely pers. comm.): *Adelomyia, Aglaeactis, Pterophanes, Boissonneaua, Heliangelus, Eriocnemis, Metallura, Chalcostigma,* and *Oxypogon. Chalcostigma olivacea* often walks or hops on the ground in puna, and *Oxypogon guerinii* forages in the same manner, feeding at low, matted plants in páramo grassland. *Oreotrochilus estella* walks on the ground to feed on insects, as well as hovering and perching at flowers (Carpenter 1976).

In the classic pollination syndrome of hummingbirds and their flowers described by Grant and Grant (1968), some plants have evolved flowers that tend to exclude bees and attract hummingbirds (Heinrich and Raven 1972). In this coevolved system the floral characteristics force the hummingbirds to hover to probe the nectaries for the relatively large nectar rewards these flowers offer (Grant and Grant 1968). This suggests that the plants rather than the pollinators drive this aspect of the coevolved system. In other words, floral architecture dictates the feeding mode of the hummingbird, forcing it to adapt to a particular set of foraging conditions that precludes perching and forces the hovering mode of feeding. The fact that hummingbirds that hover to feed move more quickly between flowers than birds that perch (Pyke 1980, 1981) may be more advantageous to the plants than to their pollinators, forcing a cost on the birds that is less than optimal. Gill (1985) measured the flight speeds of Long-tailed Hermits (*Phaethornis superciliosus*) traplining between dispersed nectar sources and found that they normally fly faster than the speed predicted to minimize their transport cost. Gill concluded that the advantages of rapid flower visitation could yield nectar rewards that compensate for the extra costs of fast flight. This also could be translated into an advantage to the plants.

The energetics of pollination systems have been studied intensively in recent years, especially since the publication of the seminal paper on energetics and pollen ecology by Heinrich and Raven (1972), but the details of how this system operates remain unclear (cf. Waser 1982, Carpenter 1983), in spite of the emergence of several hypotheses that seemed attractive initially but could not be supported by subsequent tests (cf. Carpenter 1983). Bird pollination may be advantageous to plants because hummingbirds are more dependable pollinators than insects over a wider range of seasonal and altitudinal climatic changes (Cruden 1972, Stiles 1978, Carpenter 1983). Hummingbirds also may carry larger pollen loads over greater distances and increase the probability of out-crossing (Heinrich and Raven 1972). Whatever the details of pollination energetics that contribute to the fitness of both members of this coevolved system, it seems apparent that foraging by hummingbirds often is constrained by boundary conditions set by the plants. The optimality question should perhaps be approached from the point of view of the plants, rather than exclusively from that of the hummingbirds.

The most obvious explanation of why hummingbirds hover is that the flowers of some plants give them no alternative choice, and the decision rules available to them are, in this respect, restricted. Four of the species in the nectar-feeding community studied by Feinsinger and Colwell (1978) perched whenever possible while feeding, but they noted that many long-tubed flowers are presented in such a way that perching is precluded. In other words, hovering is not necessarily a preferred mode of feeding, but one that cannot be avoided.

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