## Response to F. R. Hainsworth

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Hainsworth's (1986) calculations for the relative rates of net energy gain for hummingbirds perching or hovering at a food source in relation to distance from a central-place foraging perch suggest an interesting experiment that might more directly validate or falsify the optimal foraging model based on energetics. However, the values for these calculations are based on measurements of the metabolism of hummingbirds in a constant, laboratory environment (Hainsworth and Wolf 1978, Wolf and Hainsworth 1983). This raises the question of how closely the values represent the rates of net energy gain of hummingbirds that forage in natural environments, where birds experience diurnal temperature fluctuations, where daily changes in body mass occur in relation to food intake and activity, and where flight distances from perch to food source can be highly variable (cf. Carpenter et al. 1983, Gass and Sutherland 1985, Paton and Carpenter 1985). These and other possible environmental variables are not included in Hainsworth's calculations.

When the round-trip distance from perch to food source is reduced from 20 m, at which there is no significant advantage to either mode of feeding, to a distance of 4 m (2 m from perch to food source), the advantage of hovering over perching in rate of net energy gain is only 0.47 J, or 2.3%. Can a hummingbird subject to the variables of a natural environment detect a 2.3% difference in rate of net energy gain during its daily foraging activities?

Indirect evidence (Miller 1985) suggests that hummingbirds would not change their feeding mode from perching at long round-trip distances to hovering at short distances from perch to food source. Hainsworth stated correctly that the minimum flight distance of the *Archilochus colubris* I worked with was 20 m from perch to feeder, or a round-trip distance of 40 m, which would favor perching; but when birds were presented with an array of 3 feeders at the same position only 7 cm apart, they hopped from one perch to the next and perched to feed (see Miller 1985). Also, the *Orthorhynchus cristatus* at St. John, U.S. Virgin Islands, often perched within about 3 m of the feeders, and perched to feed during each visit. She hovered in flight from one feeder to the next but invariably perched at each feeder, even though feeders were only 10-20 cm apart. More importantly, I provided (Miller 1985) ample documentation that hummingbirds, throughout the size range from 2 to 20 g, will perch to feed if a perch is available, but will hover to feed otherwise.

The important point of my article (Miller 1985) was that the floral architecture of the plant, by not providing a perch, forces the hummingbird to hover, regardless of the relative costs or benefits of the two feeding modes. To investigate and understand the forces of natural selection that produce co-evolved systems, such as the mutual interactions between hummingbirds and the "hummingbird flowers" they pollinate (Grant and Grant 1968), it might be instructive to consider the question from the perspective of the plants, not just the hummingbirds, and to understand the extent to which the plants might dictate hummingbird foraging strategies. In this sense, optimal foraging theory can be a useful guide in the development of testable hypotheses. However, the fact that environmental constraints, such as floral architecture, might force the animal to use a foraging mode that is not necessarily optimal in terms of rate of net energy gain should not be ignored.

### LITERATURE CITED

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*Received 14 May 1986, accepted 16 May 1986.*

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