TRAPLINE FORAGING BY HERMIT HUMMINGBIRDS: COMPETITION FOR AN UNDEFENDED, RENEWABLE RESOURCE[1]

FRANK B. GILL
Academy of Natural Sciences, Philadelphia, Pennsylvania 19103 USA

Abstract. Traplining hummingbirds face a conflict between waiting for undefended floral nectar to accumulate to higher levels of profit and losing accumulated nectar to competitors. The goal of this research was to learn the rules and temporal patterns of flower visitation by Long-tailed Hermit Hummingbirds (*Phaethornis superciliosus*). Monitors of visits by color-marked individuals, particularly lek males, to natural flowers established patterns of feeding in space and time. Monitors of visits to nectar feeders that were refilled at fixed intervals established patterns of adjustment to nectar availability and competitive losses. Competing hummingbirds tended to segregate among undefended feeding sites, with one individual becoming the primary user of each site. Competition caused hummingbirds to visit a feeder frequently, often before a scheduled refill. In this way one individual could harvest most of the provided nectar. Under conditions of nearly exclusive use of a feeder with artificial nectar, the hummingbirds adjusted their visits to operant (fixed-interval) schedules of food presentation. The scheduled harvesting of floral nectar by traplining hermit hummingbirds thus entails the adaptive use of short, elapsed time intervals.

Key words: exploitative competition; fixed-interval experiments; foraging behavior; hummingbird; operant behavior; Phaethornis; trapline.

INTRODUCTION

Foraging circuits, or traplines, enable animals to harvest renewing food from isolated sites in a regular fashion (Janzen 1971, 1974, Prins et al. 1980, Thomson and Plowright 1980, Davies and Houston 1981). The rate of food renewal in depleted patches influences the foraging patterns of such animals because the rate of renewal determines the profitability of return visits, and the costs of sharing foraging space with other individuals (Waser 1981). In turn, social systems often relate directly to spatial and temporal predictability of renewable food resources, such as ripening fruit or accumulating nectar (Ricklefs 1980, Bradbury 1981). Some hummingbirds, particularly the lek species of hermit hummingbirds (Trochilidae, Phaethornithinae), are specialized trapliners that visit isolated and undefended flowers containing large amounts of sugar-rich nectar (Feinsinger and Colwell 1978, Stiles and Wolf 1979, Snow and Snow 1980). Exploitative competition rather than interference competition prevails at these sites. In addition to remembering the locations of dependable foraging sites, a hermit hummingbird must decide when to visit them profitably. It can delay revisitation to increase accumulation, and hence potential profit, or it can return frequently to reduce competitive losses, called defense by depletion (Charnov et al. 1976, Davies and Houston 1981, Waser 1981, Paton and Carpenter 1984). Because hermit hummingbirds obtain most of their daily energy from such

undefended flowers, they would benefit from harvest schedules that accommodate both the rates of nectar renewal and the intensity of competition.

Hummingbirds are sensitive to short-term changes in net energy gains and adjust their behavior to increase reward size and profitability (Wolf and Hainsworth 1983). Shifting to unvisited flowers is beneficial over short time intervals, given the slow rates of natural nectar renewal (Gill and Wolf 1977, Kamil 1978, Cole et al. 1982, Gass and Sutherland 1985, Wunderle and Martinez 1987), but returns to previously visited flowers will be beneficial over longer time intervals. The amount of nectar available in a flower increases predictably and monotonically as a function of time elapsed since the flower was last visited. A hummingbird's flower visits, therefore, are subject to operant conditioning, in which the hummingbird's own behavior determines reinforcement (Staddon 1983:274). Some laboratory studies of learned instrumental behavior explicitly complement field studies of natural foraging behavior and tests of optimal foraging theory (Lea 1979, Collier and Rovee-Collier 1981, Baum 1982, Abarca et al. 1985). Few studies from nature, however, complement the wealth of laboratory studies of operant behavior (Staddon 1983, Schwartz 1984). The scheduled harvesting of renewable food, such as floral nectar, entails the adaptive use of elapsed time in a natural setting (Pulliam 1981, Kamil and Yoerg 1982).

In this paper I report field studies on the use of time by Long-tailed Hermits (*Phaethornis superciliosus*), a widespread hummingbird species of lowland rainforests in Central and South America. I monitored feeding

visits of color-marked individuals, particularly lek males, to natural flowers. I also tested short-term adjustments of feeding behavior to different schedules of food presentation in artificial flower feeders to answer the following questions. What are the patterns and results of competition for nectar in undefended feeding sites? How do traplining hermit hummingbirds respond to losses of nectar to competitors? Do they learn to return to sources of nectar at designated intervals of reinforcement? Will they wait longer to get more nectar?

METHODS

I conducted the field study from May to July 1982–1983 in Corcovado National Park in southwestern Costa Rica, where Long-tailed Hermit Hummingbirds are abundant. The study area, which included a lek occupied by 12–15 males, was in seasonally flooded lowland rainforests on the north side of the Rio Pavo, 10 km northeast of Sirena. Lek males and nonlek individuals of both sexes visited monitored flowers and experimental feeders. I marked individual hummingbirds with a color-coded plastic tag attached to one leg, and paint spots on the back (Stiles and Wolf 1973). Identity codes, such as W/R, refer to unique color combinations, in this case white-red. The hummingbirds fed mainly at flowers of *Costus pulverulentus* Presl (Zingiberaceae) (= *C. ruber* of Stiles 1975) and those of *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae). At some sites, they also visited flowers of *Costus laevis* R. & P., *Heliconia irrasa* Lane, and *Aphelandra golfodulcensis* McDade. The flowers available daily at *Costus* sites in the Pavo forests typically included 5–15 *C. pulverulentus* flowers and 2–5 *C. laevis* flowers. Lightgap sites with *H. imbricata* contained 3–8 flowers in May and June. I assume that floral nectar is the primary source of energy for these hummingbirds; spiders are an important source of nutrition (Stiles and Wolf 1979).

To study natural foraging patterns, my assistants and I mapped all flowering *Costus* and *Heliconia* plants within 500 m of the lek in 1982 and monitored visits to feeding sites by nine lek males and other, nonlek individuals. Our vigils at natural flowers totalled 171 h in 1982, mostly in the morning from 0700–1200. Revisit intervals to specific flowers define a hummingbird's nectar consumption in terms of nectar accumulation minutes (weighted for changing production rates in the course of a morning) (Gill and Wolf 1977, 1979). A hummingbird's realized nectar consumption is estimated as the total of nectar accumulation minutes elapsed since a previous visit less those credited to intervening visitors.

Manipulated artificial reward schedules were required to test directly the responses of hermit hummingbirds to patterns of nectar availability, including competitive losses. In 1983, therefore, I studied the return times of four color-marked individuals (R/G,

B/Y, Y/Y, Y/R) to artificial flowers with plastic-tube nectar reservoirs. Up to three widely separated feeders were operated simultaneously on some days, all within 200 m of the lek. Molded of hard plastic, the feeders resembled the inflorescences of *Heliconia imbricata* and *H. wagneriana,* two plants that flowered naturally in the study area. I placed sugar-water in the bottom 10 mm of 55 mm long plastic tubes of 6 mm inside diameter. Hummingbirds with short bills could not reach the artificial nectar, which consisted of a 30% sucrose equivalent mixture of the three sugars (fructose, glucose, and sucrose) present in floral nectars. The hummingbirds removed all nectar in 1–3 s. The amounts of nectar (10–200 μL) available at the feeder were within the range available in natural flowers (Gill 1987, 1988). The individuals tested had several days prior experience with a feeder. Two (R/G, B/Y) were lek males. The age and sex of the other two individuals were uncertain. Following some segregation of individuals among three feeder sites available initially, the two lek males (R/G and B/Y) competed daily for nectar at feeder site number 3, which became the focus of study. I expanded the options available to these two males to include three feeders (numbers 2, 3, and 4) 100 m apart on 28 April, and two feeders (numbers 3 and 4) on 2 May.

The study employed operant reinforcement protocols, primarily fixed-interval (FI) schedules, in which I refilled a feeder at 10- or 15-minute intervals (designated FI 10 min and FI 15 min) following the last successful visit by a particular hummingbird. Unlike real flowers, which accumulate nectar continuously, the feeder remained empty until a scheduled refill. Use of the feeder by two or more individuals disrupted a refill schedule set to the visits of one particular individual. In most cases I quickly replaced the nectar to maintain the schedule. In the case of sustained use by both B/Y and R/G, I refilled the feeder at fixed intervals following the last successful visit, whether by B/Y or by R/G. In this case, intervening visits by different individuals effectively converted a fixed-interval (FI) schedule to a variable-interval (VI) schedule. In FI schedules, the hummingbird could learn that food was available after a minimum amount of time has elapsed, and could adjust the periodicity of its returns accordingly. In VI schedules, there is no reliable relationship between waiting interval and reward for any given individual. Under this reward regime, laboratory pigeons peck at constant rates until food is delivered (Staddon 1983: 132).

To simulate an increase in the nectar contents of real flowers and to provide an incentive to wait longer, I doubled the amount of nectar available in the reservoirs as a step function of elapsed time, or FI 10 + 5 min in the case of 5-min supplement to a FI 10-min schedule. To simulate loss of nectar to a competitor, I emptied the feeder when the hummingbird failed to return 20 min after the FI (e.g., FI 10 + 20 min).
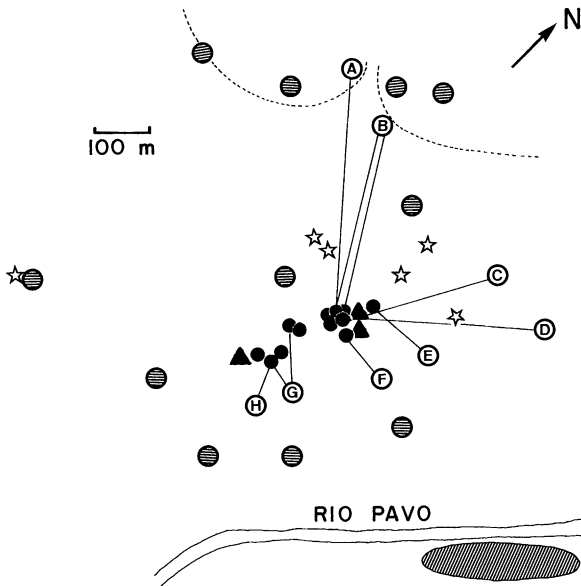
FIG. 1. Feeding sites of color-marked lek male Long-tailed Hermits in the Pavo study area in 1982. Solid lines connect lek territories of nine males to their feeding sites (circles with letters). Three color-marked males were not seen away from the lek; three lek males (▲) remained unmarked. Hatched areas indicate sites with flowers not used by lek males. ☆ nest sites. Dotted lines indicate edge of second-growth vegetation.

RESULTS

Natural foraging behavior

My data from vigils at natural flowers corroborated the observations of Stiles and Wolf (1979), and provided some additional, quantitative detail. Lek male Long-tailed Hermits in our study area commuted to undefended flowers from their territories (Fig. 1). Some fed at flowers near the lek; others flew at least 500 m to feed and never were seen at flowers close to the lek. Lek males were not seen at 11 sites that were visited by other individuals. Individual home ranges overlapped broadly, but the actual feeding sites of lek neighbors were segregated. Normally two males did not feed in the same place, except for infrequent checks of each other's site. When two lek males fed at the same site, they tended to visit different specific flowers, e.g., *Costus laevis* vs. *C. pulverulentus*. Although lek males tended not to overlap with each other, each lek male shared its feeding sites with other, nonlek individuals. Visits by lek males to far sites constituted 17–50% of all visits recorded at each site. Lek male B/B visited two sites (G and H) near the lek on a more exclusive basis (87–100% of all visits). The identities of most covisitors were not known, except at site A, where two color-marked individuals were an adult female and a nonlek male.

Lek males revisited particular feeding sites 3–7 times per morning, at intervals that varied from a few minutes to 2 h. Revisit intervals at far sites (A, B, C) averaged longer ($n = 54$, median = 47 min) than those

at near sites (G, H; $n = 46$, median = 12.5 min) (Kolmogorov-Smirnov two-sample test, $P < .001$). The revisit intervals were not significantly correlated with time of day either at far sites (Fig. 2), or at near sites (one male, $n = 46$, Spearman rank correlation coefficient (r_S) = -0.024). Variations in specific flower visits increased the median intervals from 47 min at far sites to 70 min at specific flowers at those same sites (Median test, $P < .01$). Such regular revisitation by the lek males prevented substantial nectar losses to other individuals that visited the same sites. Only 16% of 127 flower visits by lek males Y/G and B/G were preceded by a competitive visit, resulting in an estimated 10% loss of accumulating nectar.

Competition for nectar at feeder sites

Several individuals competed for nectar at a newly established feeder, but one of them usually became the primary visitor that harvested most of the nectar. Hummingbird Y/Y emerged as the primary visitor at feeder number 1, which initially was visited by at least six individuals. Its visits increased in number and also in predominance over a 3-d period, to 90% of all visits (Fig. 3A). One of the other individuals (Y/R) switched to feeder number 2, 200 m away. At first, it competed there with lek males R/G and B/Y, but its visits increased daily to 90% of all visits (Fig. 3B) and yielded nectar 88% of the time, as R/G shifted to feeder number 3, 100 m away (Fig. 4).

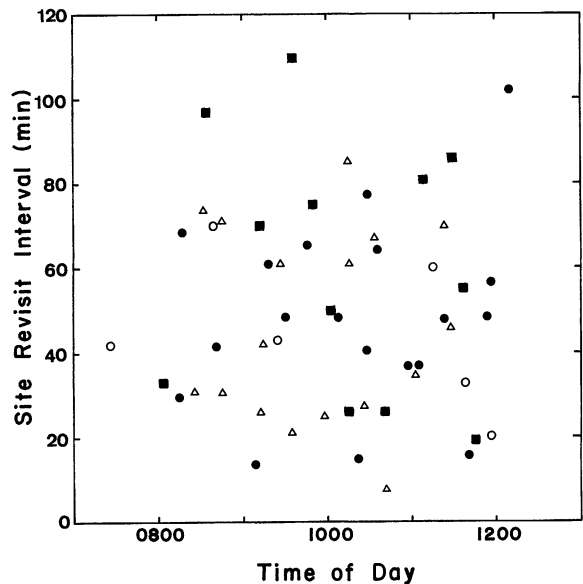Competitive interactions between R/G and B/Y at feeder number 3 continued for over a week, with res-

FIG. 2. Revisit intervals to far visits as a function of the time of day. Intervals between visits to far sites ranged widely without significant temporal trend for all data combined ($n = 54$, $r_S = -0.139$) or for the individual (B/G) with the largest sample size ($n = 17$, $r_S = -0.080$). Symbols indicate data for particular lek males: ○ G/R and Y/B; ● B/G; ■ Y/W; △ Y/G.
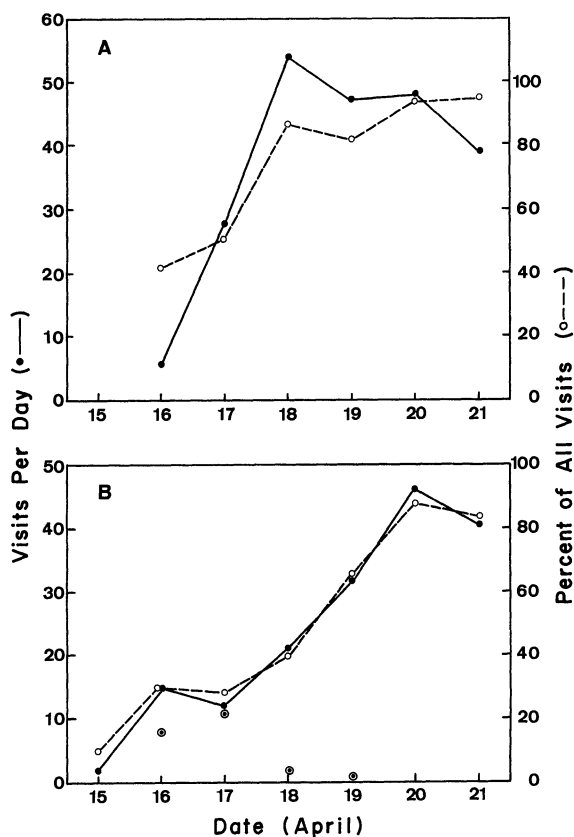
FIG. 3. Visits by one individual (the primary user) of a feeder increased in number, whereas visits by competing individuals decreased. (A) hummingbird Y/Y at feeder number 1; (B) hummingbird Y/R at feeder number 2. ⊙ visits by Y/R to feeder number 1 as it shifted to feeder number 2.

olution on some days but not on others. On the 1st d (21 April), both lek males fed ad libitum; visits by one had no effect on the amount of nectar obtained by the other (Fig. 5A). The constraints of FI schedules then resulted in frequent unrewarded visits on 22–27 April. The two males competed with alternating success on 22 April, when 200-μL rewards were offered. One individual or the other became the primary visitor on each of the next 4 d, when nectar rewards were lower (Fig. 5B–E). B/Y obtained most of the nectar on 23 and 24 April, but then R/G did so on 25 and 26 April. A return to 200 μL nectar rewards on 27 April repeated the results of 22 April.

The results of competition between these two individuals varied among concurrent feeders. When three feeders were in operation on 28 April (Fig. 6), R/G controlled feeder number 2 whereas B/Y controlled feeder number 4. B/Y visited feeder number 2 sporadically with poor results; R/G visited feeder number 4 sporadically with poor results. An unmarked individual returned to feeder number 4 at short intervals after obtaining nectar on two visits, but left after four unrewarded visits. Feeder number 3 offered less nectar at a longer FI interval than the other two feeders. Hum-

mingbirds R/G and B/Y visited it regularly throughout the day, but obtained little nectar.

When more than one individual used a feeder, the principal user visited frequently, often prematurely before a scheduled FI refill. The behavior of B/Y on 2 May at two feeders 100 m apart, one visited also by R/G, the other uncontested, illustrates this response. Both feeders provided 100 μL at FI 15 min. The median return time at the contested feeder was 12 min,
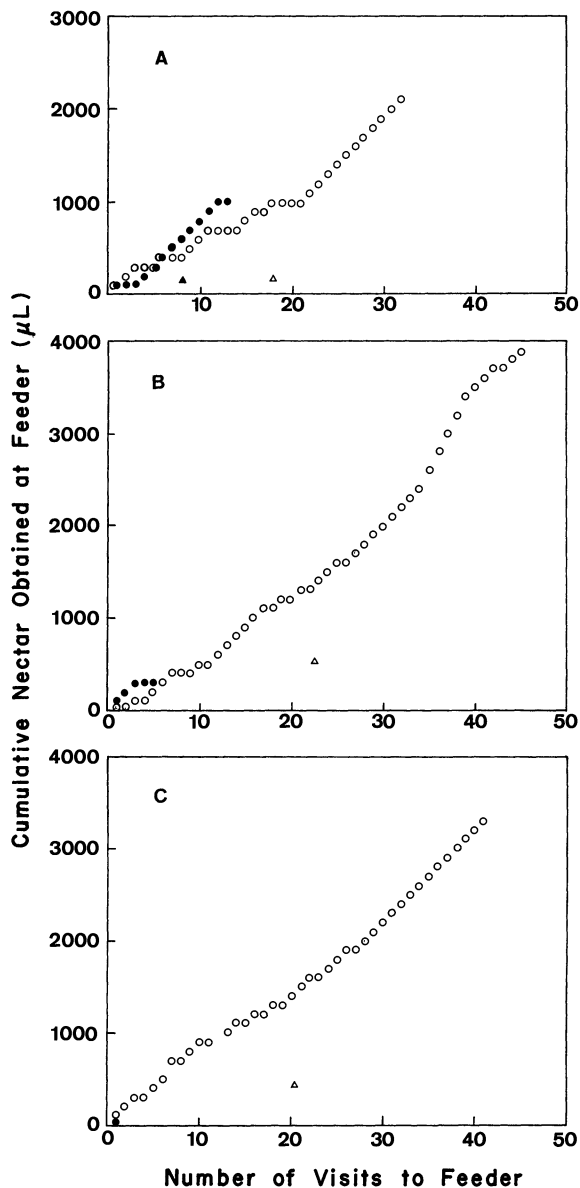

FIG. 4. Cumulative nectar obtained by hummingbird Y/R (O) on three successive days (19–21 April 1983; A, B, C) with decreasing competitive interference from hummingbird R/G (●). Longer return times within each day reduced unrewarded visits. Observations started at 0600 and stopped at 1400; triangles are time markers indicating 1000. 200-μL nectar volumes were available for 2+ h during the afternoon of 20 April (B; visit numbers 32–39).
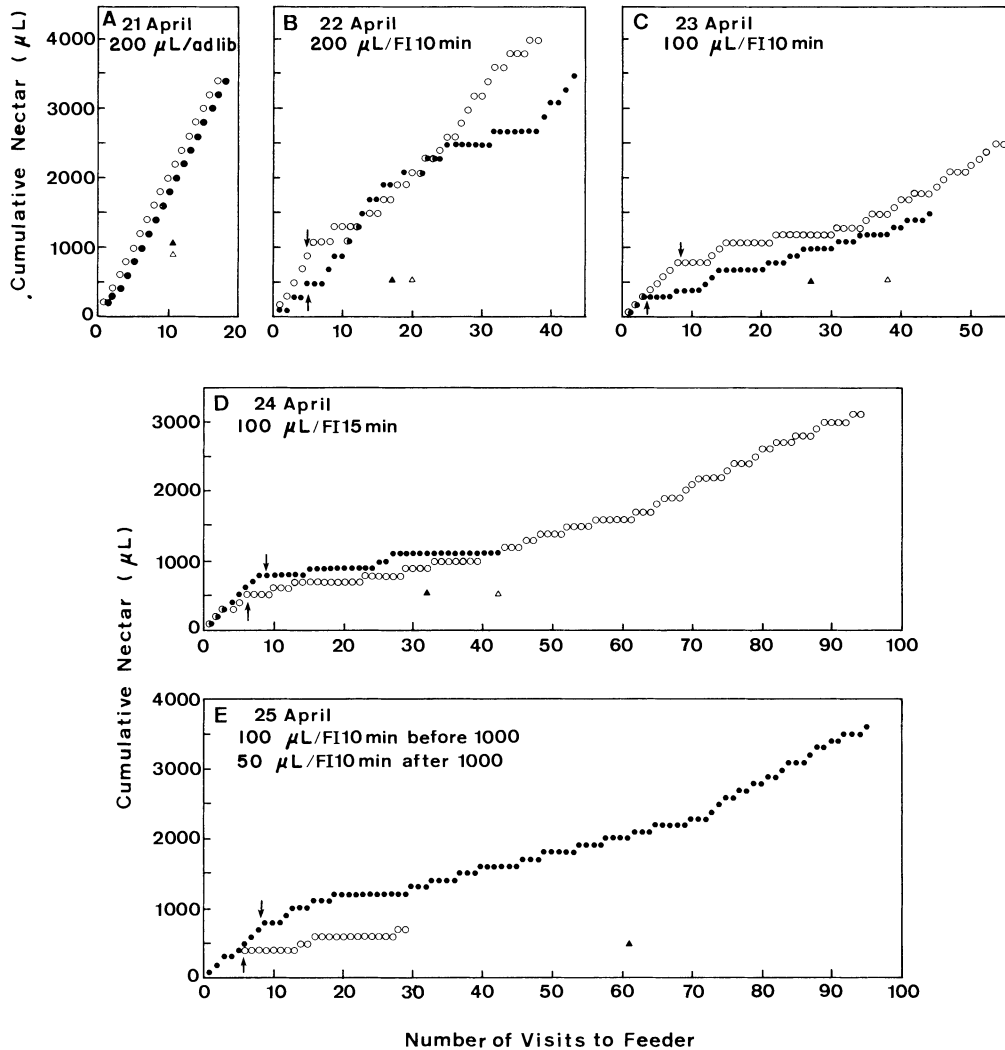
FIG. 5.   Competition by two lek males (● R/G , ○ B/Y) for nectar in feeder number 3. Arrows = onset of fixed-interval (FI) nectar replenishment schedules beginning with most recent successful visit; nectar was available ad libitum prior to this time each day. Triangles are time markers indicating 1000. Data for 26 April (not shown) are essentially the same as those illustrated for 25 April.

compared with 20 min at the uncontested feeder (Median test, $P < .05$). B/Y visited the contested feeder 21 times by 1000, compared with 13 times at the uncontested feeder. It failed to obtain nectar on 9 of the 21 visits to the contested feeder as a result of premature returns (6) and competitive losses (3). When it found the feeder empty after a 22-min absence, because of a prior visit by R/G, it returned 2 min later. Alternating rewarded and premature visits produced a stepped pattern of cumulative rewards with time unlike the linear increase at the uncontested feeder.

Failures to obtain nectar as a result of losses to competitors and losses as a result of premature returns were negatively correlated in the data for R/G and B/Y at feeder number 3 (Fig. 7). Other features of the relation between nectar obtained and visit patterns include the following. R/G lost significantly less nectar directly to

B/Y because it visited more frequently ($r_S = -0.67$, $n = 10$, $P < .05$). A similar relationship for B/Y was not significant ($r_S = -0.52$, $n = 10$, $P > .05$). The proportion of unrewarded visits was directly correlated with the number of premature returns (R/G: $r_S = 0.78$, $n = 10$, $P < .01$; B/Y: $r_S = 0.78$, $n = 10$, $P < .01$). B/Y's competitive losses were inversely correlated with R/G's competitive losses ($r_S = -0.86$, $n = 10$, $P < .01$).

Adjustments to FI schedules

Hermit hummingbirds typically explore and test new nectar sources. They periodically try natural flowers at which they are not the primary visitor. At first, they also visited my feeders irregularly at long intervals. Then with regular rewards they returned more frequently to feeders, often before a scheduled refill. Un-
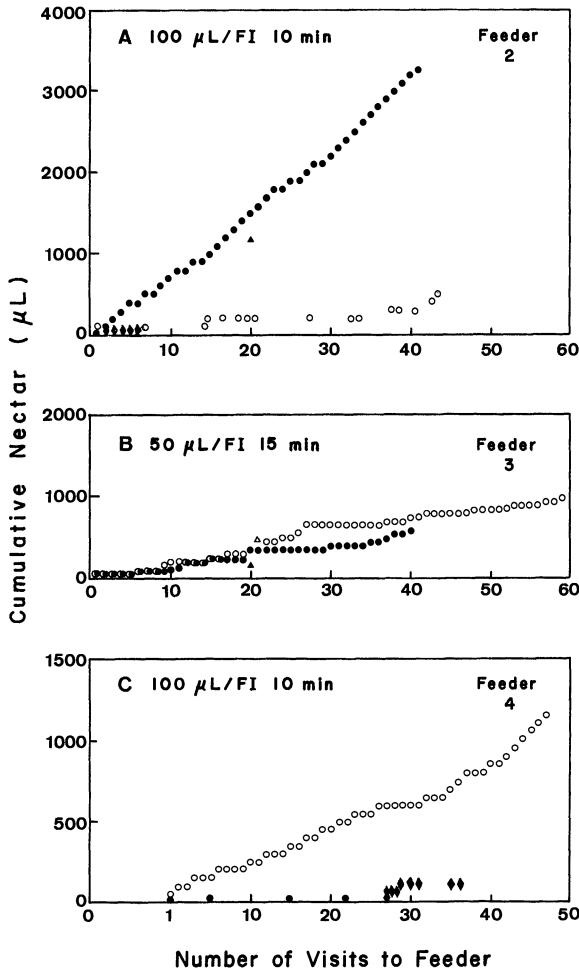
FIG. 6. Competition by two lek males (● R/G, ○ B/Y) at three feeders 100 m apart on 28 April. The indicated volume of nectar was available at the specified fixed nectar replenishment interval (FI). ◆ visits by an unmarked individual. Visits by unmarked individuals, by B/Y at feeder number 2, (A, ○), and by R/G at feeder number 4 are positioned in temporal relation to visits of the primary user. Observations started at 0600 at feeders number 2 and number 3, and stopped at 1600 at all three sites; feeder number 4 was not filled until 0958. Triangles are time markers indicating 1000.

der conditions of nearly exclusive use of a feeder, return intervals increased to longer than the FI refill schedule, thereby increasing the probability of obtaining nectar. Such adjustments were evident in the behavior of hummingbirds Y/R (Fig. 4), B/Y (see Competition for Nectar at Feeder Sites, above), and Y/Y at feeder number 1 (Table 1). Hummingbird Y/Y increased its median return times significantly from early morning to mid-morning on 19 April and 20 April to correspond to a FI 10-min schedule. This hummingbird's median return times also increased significantly among early morning periods of the 3 d ($\chi^2 = 7.40$, df = 2; $P <$ .05). Increased return times during the day could be a natural trend of declining foraging effort unrelated to operant reinforcement (though see Discussion); in-

creased return times between successive days, however, indicate adjustments to the FI schedule controlled for time of day. Adjustments to the FI schedule significantly increased the frequency of obtaining nectar (Table 1).

Under conditions of exclusive use of a feeder, a hummingbird would benefit by waiting longer to get more nectar. Return times of hummingbird Y/Y increased when the amount of nectar available in the feeder doubled at FI 10 + N min in late morning (1030 to 1230) on 19 April (Fig. 8) and after 0830 on 21 April (Table 1). Its median return time (25 min) under this regime on 21 April was 10 min longer than it was during the same hours the preceding day, when no larger rewards were available (Median test, $P < .01$). An issue, however, is whether a hummingbird waits longer to get more, or whether it reduces feeding activity as a result of satiation. Effects of satiation were sometimes evident. Comparison of the visits of hummingbirds Y/R and Y/Y to separate feeders 200 m apart during the afternoon of 20 June 1983, for example, suggests a direct effect of meal size (Table 2). In this case I reversed the meal sizes (100 µL vs. 200 µL) at the two feeders after eight visits by each individual. The larger reward (200 µL) prompted longer return times than a smaller reward (100 µL). The differences in median return times were significant for Y/R, and for the pooled data, but not for Y/Y.

In conclusion, I return to the issue of premature returns in response to loss of nectar to a competitor.
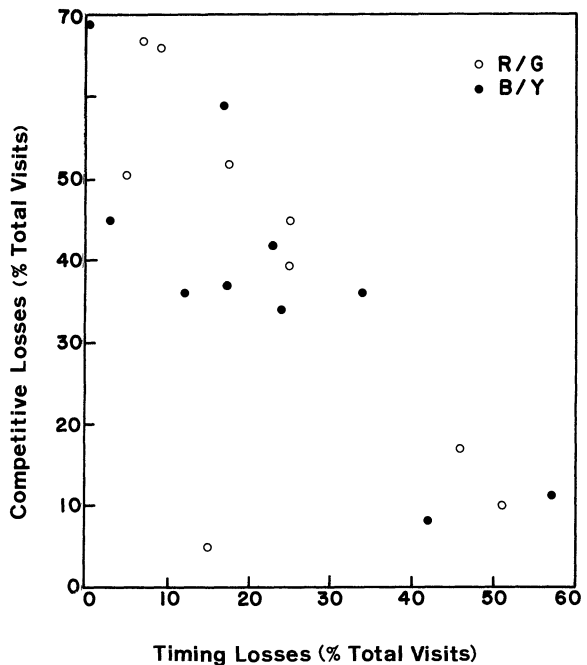

FIG. 7. Competitive losses are negatively correlated with (timing) losses due to returns before the feeder was refilled on a fixed-interval schedule. Spearman rank correlation coefficients (r_s) were -0.73 ($P < .02$) for R/G (●) and -0.82 ($P < .01$) for B/Y (○).

TABLE 1.   Responses of hummingbird Y/Y to fixed-interval (FI) 10-min nectar replenishment schedules in early (0630–0830) vs. mid-morning (0830–1030) on three successive days.* Number of visits in parentheses.

	Median return times (min)			Rewards (% of visits)		
Day	Early morning	Mid-morning	P†	Early morning	Mid-morning	P†
19 April	7.5 (15)	14 (9)	.002	43	88	.032
20 April	8.5 (16)	12 (9)	.030	62	89	.150
21 April	11.0 (11)	16 (8)	.050	91	100	.570

* The significant difference between early and mid-morning periods on 21 April reflects the response to doubled rewards (see last paragraph of Methods). Adjustments to the FI schedule significantly increased median return time within mornings of 19 and 20 April and among early mornings of the 3 d ($\chi^2 = 7.40$, df = 2, $P < .02$).

† Comparisons of early vs. mid-morning on each date. Level of significance estimated with Fisher's exact test because some expected values in 2×2 contingency tables were ≤ 5.

Following regular rewards and increasingly longer return intervals, individuals reacted to an empty feeder by returning quickly and repeatedly at short intervals. Lek male B/Y did so on 2 May after a 22-min absence and intervening loss of nectar to R/G. Lek male R/G reacted similarly to experimental decrease (from 200 µL to 25 µL) in the reward available at feeder number 3 on 9 May. To directly simulate competitive nectar losses by an individual with exclusive use of a feeder and adjusted to the FI schedule, I deliberately emptied feeder number 1 on 19 April when hummingbird Y/Y failed to return at FI 10 + 20 min (Fig. 8). It responded to the empty feeder by returning at short intervals until nectar was obtained. Return times then increased progressively in duration. The response was repeated a second time that afternoon.

DISCUSSION

Responses to competition

Optimal foraging patterns in a patchy environment depend on local rates of food renewal and depletion, including the intensity of exploitative competition (Miller 1967, McNair 1979, Waser 1981, Stephens and Charnov 1982, Yamamura and Tsuji 1987). The intensity of competition experienced by traplining hermit hummingbirds varies from site to site and from day to day. How a hummingbird responds to competition should depend on whether it controls the harvest schedule or whether it only visits a site sporadically to check its status and potential for regular visits. When the hummingbird is the primary visitor that controls the harvest schedule, empty flowers signal prior visits by a competitor and trigger more frequent visits. Frequent visits reduce loss of nectar and discourage competitors that find the flower empty (Paton and Carpenter 1984). Unharvested nectar that accumulates in flowers, however, invites regular visits and possibly takeover of the primary harvest schedule by a competitor.

Among hummingbirds, trapline foraging is one alternative to feeding territoriality (Stiles 1975, Feinsinger and Colwell 1978). Defense of food by depletion incurs measurable costs, as does defense by territorial aggression (Paton and Carpenter 1984). Instead of chasing intruders, traplining hummingbirds invest time and energy into repeated, sometimes unproductive, returns to flowers. Returns to my feeders often preceded the FI schedule and hence yielded no nectar. In cases of competition for nectar in natural flowers, most visits (except immediate returns) would yield small amounts of nectar that might not pay for the costs of a return flight. Possibly this is the reason why one of the two hummingbirds B/Y and R/G sometimes gave up in the competition for feeders with little nectar, but continued to compete at feeders with much nectar.
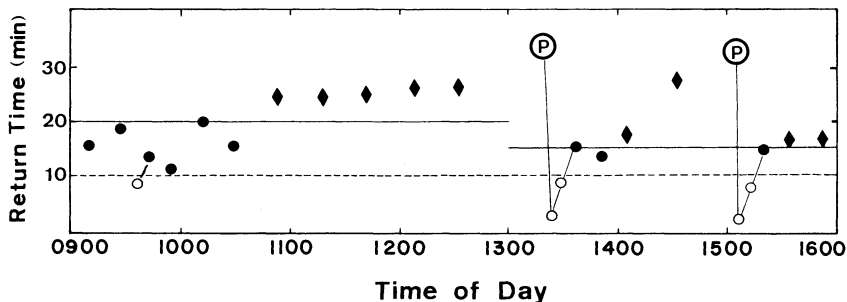

FIG. 8.   Hummingbird Y/Y's response to an empty feeder (P) on 19 April 1983 after adjustment to a fixed replenishment interval (FI) 10-min schedule (– – – at 10-min return time) by 1030, and to a FI 10 + 10 min schedule (x µL nectar supplied 10 min after a successful visit, plus the same volume added 10 min later) yielding 200 µL (——— at 20 min) from 0900 to 1300. After 1300, 200 µL of nectar were available on a FI 10 + 5 min schedule (——— at 15 min), and the feeder was emptied at 30 min if the hummingbird failed to return. Return times are plotted in cumulative fashion (lines connect successive visits) until nectar was obtained. ● 100 µL nectar; ◆ 200 µL; ○ no nectar.

These rules that apparently govern site visitation derive primarily from single (feeder) sites. Lek male Long-tailed Hermits must regularly visit 10 or more sites with *Costus* or *Heliconia* flowers to satisfy their daily energy requirements, but the sequence or pattern of visits to the sites on a trapline remains unknown. They probably visit subsets of sites on different foraging bouts (F. Gill, *personal observation*). Extension of the rules for a single site to the management of multiple sites will require solutions to complex algorithms similar to those applied to the classic travelling salesman problem, in which optimal solutions to minimizing travel distances and repeat visits depend on the two-dimensional geometric relationships of the cities in the salesman's working district (Lawler 1985).

Adaptive operant behavior in hermit hummingbirds

My results indicate that free-living hummingbirds adaptively use temporal information, namely short, elapsed time intervals. When not challenged by competitors, four color-marked individuals responded predictably to fixed-interval schedules. Adjustments of median return times within and between days increased the frequency of obtaining nectar. Such behavior is to be expected because floral nectar accumulates at predictable rates after a hummingbird visit (Stiles 1975, Gill 1988), causing the reward value of a flower to approximate a fixed-interval schedule (Staddon 1983:274). Not all natural patterns of food renewal approximate fixed-interval schedules. Food renewal often involves random or stochastic interval processes that prescribe a constant return time that maximizes net energy gain (Davies and Houston 1981, Staddon 1983:279). Such was the case for territorial Pied Wagtails (*Motacilla alba*) that harvested accumulating, dead insects at the river's edge (Davies and Houston 1981). Competitors (= intruders) depressed the density of insects and the owner's feeding rate, but the effect of competition on return times of owner wagtails was obscured by complex interactions among food abundance, defense time, and intruder tolerance. In the case of floral nectar consumed by traplining hermit hummingbirds, intervening visits by competitors converted fixed-interval schedules to variable-interval schedules, which promoted frequent, but often unrewarded visits.

I conducted this study with free-living Long-tailed Hermits with substantial travel costs to determine whether some basic rules guided schedules of visits to undefended flowers, and whether simple expectations of operant behavior were manifest in a natural, adaptive context. I conclude that there are scheduling rules and that traplining hummingbirds practice adaptive operant behavior. Each primary result, e.g., adjustments to FI schedules, responses to competitive losses, etc., was manifest in the behavior of more than one individual on several occasions. These conclusions, however, are based on the behavior of only a few in-

TABLE 2. Effect of larger meal sizes on return times of two hermit hummingbirds (Y/R and Y/Y) to different feeders 200 m apart on 20 April 1983.* Number of returns in parentheses.

| | Median return time (min) | | |
Hummingbird	100 μL	200 μL	P†
Y/Y	15 (9)	20 (5)	.36
Y/R	13 (6)	18 (8)	.05
Pooled	14.5 (15)	18 (13)	<.05

* Both individuals adjusted to a 10-min FI schedule during the morning. Nectar rewards at Y/R's feeder were doubled to 200 μL for eight visits from 1215 to 1430. Nectar rewards at Y/Y's feeder were doubled for eight visits from 1400 to 1600.

† Fishers exact probability calculated for Y/Y and Y/R data sets; for pooled data, $\chi^2 = 5.17$, df = 1.

dividuals. Also, circumstances in the rainforest varied unpredictably and uncontrollably from day to day and from hour to hour. What many of the hummingbirds did away from the feeder usually was unknown. They did not linger near the feeder awaiting a refill. Certainly, they fed elsewhere. Better controlled experiments than I was able to conduct are now needed to refine these results and to understand the limits of temporal learning by traplining hummingbirds.

Preprogrammed changes in natural foraging schedules with time of day potentially confound the interpretation of fixed-interval experiments with free-living hummingbirds. Some hummingbirds return to flowers less often as the day proceeds and as the rate of natural nectar production declines (Stiles 1975, Feinsinger 1978). My results were not simply due to such an artifact. Return times by marked individuals to natural flowers in the study area varied without significant temporal trend; these hummingbirds visit feeders and flowers frequently throughout the day if it is profitable to do so. Comparisons of performances during the same time periods on different days helped control for this potential problem, assuming no differences in hunger levels. Also, the fact that these hummingbirds responded to the feeders with reward schedules that were substantially different from the declining values of natural flowers at other, *concurrent,* feeding sites suggests the hummingbirds can flexibly adjust their revisitation rules to site-specific conditions.

Delayed harvest vs. satiation

When the risk of competitive loss is low, that is, when future uncertainty does not devalue delayed food (Staddon 1983, Kagel et al. 1986), hummingbirds should postpone visits to obtain more accumulating nectar and thereby reap greater profit in return for the travel costs they invest to visit a site. In general, it appears that foragers discount the future and prefer immediate rewards over delayed rewards (Grosch and Neuringer 1981, Kagel et al. 1986). My results suggest that free-living hummingbirds will wait to get more, but still unclear is the role of meal size, which affects

a hummingbird's feeding intervals (Wolf and Hainsworth 1977, 1983). Large amounts of nectar, such as the 200 μL-rewards I used at times, could fill a Hermit Hummingbird's crop to levels that reduce feeding effort (Hainsworth and Wolf 1972, DeBenedictis et al. 1978). In the laboratory, hummingbirds control rate of accumulation of stored energy reserves through adjustments of meal size and meal frequency (Wolf and Hainsworth 1977, Hainsworth 1978, Wolf and Hainsworth 1983, Tooze and Gass 1985). Level of satiation also effects whether Great Tits (*Parus major*) are likely to choose small, immediate rewards over large, delayed rewards (Rechten et al. 1983). Future experiments with trapline foragers may profitably address the interaction between external factors, such as competition and resource renewal, and internal and physiological factors that influence the operant behavior of higher animals (Staddon 1983:162).

LITERATURE CITED

Abarca, N., E. Fantino, and M. Ito. 1985. Percentage reward in an operant analogue to foraging. Animal Behaviour 33: 1096–1101.

Baum, W. M. 1982. Choice, changeover, and travel. Journal of the Experimental Analysis of Behavior 38:117–132.

Bradbury, J. W. 1981. The evolution of leks. Pages 138–169 in R. D. Alexander and D. W. Tinkle, editors. Natural selection and social behavior: recent research and new theory. Chiron, New York, New York, USA.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. American Naturalist 110:247–259.

Cole, S., F. R. Hainsworth, A. C. Kamil, T. Mercier, and L. L. Wolf. 1982. Spatial learning as an adaptation in hummingbirds. Science (NY) 217:655–657.

Collier, G. H., and C. K. Rovee-Collier. 1981. A comparative analysis of optimal foraging behavior: laboratory simulations. Pages 39–76 in A. C. Kamil and T. D. Sargent, editors. Foraging behavior: ecological, ethological, and psychological approaches. Garland, New York, New York, USA.

Davies, N. B., and A. I. Houston. 1981. Owners and satellites: the economics of territory defense in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157–180.

DeBenedictis, P. A., F. B. Gill, F. R. Hainsworth, G. H. Pyke, and L. L. Wolf. 1978. Optimal meal size in hummingbirds. American Naturalist 112:301–316.

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional, tropical community. Ecological Monographs 48:269–287.

Feinsinger, P., and R. K. Colwell. 1978. Community organization among neotropical nectar-feeding birds. American Zoologist 18:779–795.

Gass, C. L., and C. D. Sutherland. 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. Canadian Journal of Zoology 63:2125–2133.

Gill, F. B. 1987. Ecological fitting: use of the nectar in *Heliconia stilesii* flowers by three species of hermit hummingbirds. Condor 89:779–787.

———. 1988. Nectar removal increases rates of nectar accumulation in *Heliconia imbricata* flowers. Biotropica 20: 169–171.

Gill, F. B., and L. L. Wolf. 1977. Nonrandom foraging by sunbirds in a patchy environment. Ecology 58:1284–1296.

Gill, F. B., and L. L. Wolf. 1979. Nectar loss by Golden-winged Sunbirds to competitors. Auk 96:448–461.

Grosch, J., and A. Neuringer. 1981. Self-control in pigeons under the Mischel paradigm. Journal of the Experimental Analysis of Behavior 35:3–21.

Hainsworth, F. R. 1978. Feeding: models of costs and benefits in energy regulation. American Zoologist 18:701–714.

Hainsworth, F. R., and L. L. Wolf. 1972. Crop volume, nectar concentration, and hummingbird energetics. Comparative Biochemistry and Physiology 42:359–366.

Janzen, D. H. 1971. Euglossine bees as long distance pollinators of tropical plants. Science (NY) 171:203–205.

———. 1974. The deflowering of Central America. Natural History 83:48–53.

Kagel, J. H., L. Green, and T. Caraco. 1986. When foragers discount the future: constraint or adaptation? Animal Behaviour 34:271–283.

Kamil, A. C. 1978. Systematic foraging for nectar by amakihi, *Loxops virens*. Journal of Comparative Physiology and Psychology 92:388–396.

Kamil, A. C., and S. I. Yoerg. 1982. Learning and foraging behaviour. Pages 325–364, in P. P. G. Bateson and P. H. Klopfer, editors. Perspectives in ethology. Volume 5. Plenum, New York, New York, USA.

Lawler, E. L., editor. 1985. The travelling salesman problem: a guided tour of combinatorial optimization. John Wiley and Sons, New York, New York, USA.

Lea, S. E. G. 1979. Foraging and reinforcement schedules in the pigeon: optimal and non-optimal aspects of choice. Animal Behaviour 27:875–886.

McNair, J. N. 1979. A generalized model of optimal diets. Theoretical Population Biology 21:269–288.

Miller, R. S. 1967. Pattern and process in competition. Advances in Ecological Research 4:1–74.

Paton, C. C., and F. L. Carpenter. 1984. Peripheral foraging by territorial rufous hummingbirds: defense by exploitation. Ecology 65:1808–1819.

Prins, H. H., R. C. Ydenberg, and R. H. Drent. 1980. The interaction of Brant geese *Branta bernicla* and sea plaintain *Plantago maritima* during spring staging: field observations and experiments. Acta Botanica Neerlandica 29:585–596.

Pulliam, H. R. 1981. Learning to forage optimally. Pages 379–388 in A. C. Kamil and T. D. Sargent, editors. Foraging behavior. Garland, New York, New York, USA.

Rechten, C., M. Avery, and A. Stevens. 1983. Optimal prey selection: why do great tits show partial preferences? Animal Behaviour 31:576–584.

Ricklefs, R. E. 1980. To the editor. Condor 82:476–477.

Schwartz, B. 1984. Psychology of learning and behavior. Norton, New York, New York, USA.

Snow, D. W., and B. K. Snow. 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. Bulletin of the British Museum (Natural History) Zoology 38(2): 105–139.

Staddon, J. E. R. 1983. Adaptive behavior and learning. Cambridge University Press, Cambridge, England.

Stephens, D. W., and E. L. Charnov. 1982. Optimal foraging: some simple stochastic models. Behavior, Ecology, and Sociobiology **10**:251–263.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology **56**:285–301.

Stiles, F. G., and L. L. Wolf. 1973. Techniques for color-marking hummingbirds. Condor **75**:244–245.

Stiles, F. G., and L. L. Wolf. 1979. Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird. Ornithological Monograph Number 27. American Ornithologists' Union, Washington, D.C., USA.

Thomson, J. D., and R. C. Plowright. 1980. Pollen carry-over, nectar rewards, and pollinator behavior with special reference to *Diervilla lonicera*. Oecologia (Berlin) **46**:68–74.

Tooze, Z. J., and C. L. Gass. 1985. Responses of rufous hummingbirds to midday fasts. Canadian Journal of Zoology **63**:2249–2253.

Waser, P. M. 1981. Sociality or territorial defense? The influence of resource renewal. Behavior, Ecology and Sociobiology **8**:231–237.

Wolf, L. L., and F. R. Hainsworth. 1977. Temporal patterning of feeding by hummingbirds. Animal Behaviour **25**: 976–989.

Wolf, L. L., and F. R. Hainsworth. 1983. Economics of foraging strategies in sunbirds and hummingbirds. Pages 223–264 *in* E. P. Aspey and S. L. Lustick, editors. Behavioural energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus, Ohio, USA.

Wunderle, J. M., Jr., and J. S. Martinez. 1987. Spatial learning in the nectarivorous bananaquit: juveniles versus adults. Animal Behaviour **35**:652–658.

Yamamura, N., and N. Tsuji. 1987. Optimal patch time under exploitative competition. American Naturalist **129**: 553–567.