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ORIGINAL ARTICLE

Traplining by purple-throated carib hummingbirds: behavioral responses to competition and nectar availability

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Abstract We examined the effects of nectar availability and competition on foraging preferences and revisit intervals of traplining female purple-throated caribs hummingbirds (*Eulampis jugularis*) to *Heliconia* patches shared by two individuals or visited solely by one individual. Birds at both shared and solitary patches preferred multiflowered to single-flowered inflorescences, but the magnitude of this preference depended on food availability and competition. During a year of low flower availability, females visited multiflowered inflorescences more frequently than single-flowered inflorescences only when nectar availability was experimentally enhanced; similarly, females at shared patches exhibited a significant preference for multiflowered inflorescences only after experimental increases in nectar availability. Experimental manipulations of nectar availability also had different effects on revisit intervals of birds at shared vs solitary patches. Birds at shared patches responded to patch-wide increases in nectar rewards by increasing the duration of their visit intervals, whereas birds at solitary patches did not. In contrast, birds at solitary patches responded to abrupt losses of nectar at flowers (simulating competition) by decreasing the duration of their visit intervals, whereas a bird at a shared patch did not alter its return interval. The contrasting results between shared vs solitary patches suggest that future studies of traplining behavior should incorporate levels of competition into their design.

Keywords Hummingbird · *Eulampis jugularis* · Foraging · Trapline · Intraspecific competition

Introduction

Traplining is a behavior by which nonterritorial animals harvest renewable food resources from isolated patches by following regular routes, or traplines (Janzen 1971; Thomson and Plowright 1980; Davies and Houston 1981; Gill 1988). The rate of food renewal and the presence or absence of competitors influence the timing and profitability of return visits to a patch (Gill 1988). By delaying revisits, a trapliner can increase food accumulation and hence the profit obtained from a patch, but by revisiting the same patches frequently, a trapliner can reduce losses to competitors through defense by depletion (Charnov et al. 1976; Stiles and Wolf 1979; Davies and Houston 1981; Paton and Carpenter 1984).

Traplining behavior has been described for many species of nectar-feeding invertebrates and vertebrates (e.g., Janzen 1971; Feinsinger 1976; Lemke 1984; Thomson et al. 1987; Gill 1988), and both observational and experimental studies of nectar-feeders have sought to determine how trapliners maximize foraging benefits while minimizing losses to competitors. Thomson (1981, 1988) and Wolf and Hainsworth (1986, 1991) observed that bees and hummingbirds preferentially visited dense "hotspots" of inflorescences over sparser areas. Traplining birds and insects also preferred the most rewarding food plants and visited multiflowered inflorescences more frequently than single-flowered inflorescences (Gill and Wolf 1977; Hudson and Sugden 1984; Ohashi and Yahara 1998). Similar behavior was observed for hummingbirds at artificial food sources; when nectar output was doubled at

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one feeder, birds preferentially visited that feeder over others (Garrison and Gass 1999). By increasing visit frequency to profitable patches and plants, traplining animals presumably reduced their energetic costs of foraging.

Besides adding and removing plants from their foraging circuit, another way traplining animals can maximize their ratio of foraging benefits to foraging costs is by minimizing their losses to competitors through alterations of patch use and revisit intervals. Traplining bumblebees (*Bombus* spp.), for example, expanded their traplines to include flowers normally visited by competitors after their removal (Thomson et al. 1987; Makino and Sakai 2005). When competitors were released, traplining bees returned to their premanipulation foraging circuits. Similarly, when nectar rewards from artificial food sources were abruptly reduced to simulate removal by a competitor, traplining male hermit hummingbirds (*Phaethornis longirostris*) shortened their return intervals in an attempt at defense by depletion (Gill 1988; Garrison and Gass 1999).

To date, experimental studies of traplining behavior in hummingbirds have involved manipulations of artificial food sources in the wild and in captivity (Gill 1988; Tiebout 1992, 1993; Garrison and Gass 1999). Such artificial food sources and environments differ from natural food plants by centralizing the location of food sources for the trapliner, thereby reducing its foraging costs. The purpose of our study was to examine traplining behavior of the purple-throated carib hummingbird, *Eulampis jugularis*, through manipulation of its natural food plants (*Heliconia bihai*).

In previous studies, *E. jugularis* have been observed both defending territories and foraging along traplines (Wolf and Hainsworth 1971; Wolf and Wolf 1971; Temeles et al. 2004, 2005). Males, which are larger than females, aggressively defend dense patches of *Heliconia* (Wolf and Hainsworth 1971; Wolf 1975; Temeles et al. 2004, 2005). Females trapline smaller, undefended patches of *Heliconia*, although they also have been observed intruding onto male territories and infrequently defending small territories (Wolf 1975; Temeles et al. 2005). Whereas the territorial behavior of purple-throated caribs has been well-studied (Wolf and Hainsworth 1971; Wolf 1975; Temeles et al. 2004, 2005), their traplining behavior has received little attention.

We examined three aspects of females' traplining behavior: preferential visitation, patch utilization, and return intervals. In contrast to earlier studies of traplining behavior of hummingbirds in which the effects of a competitor were weakly assessed or simulated by human manipulation of nectar sources, we specifically observed patches utilized by either single individuals ("solitary") or shared by two individuals ("shared").

Because previous research has indicated that trapliners preferred inflorescences bearing the most flowers (Thomson 1981; Ohashi and Yahara 1998), we hypothesized that birds on both shared and solitary patches would preferentially visit inflorescences with multiple flowers as opposed to single flowers. Because Thomson et al. (1987) as well as Makino and Sakai (2005) found that bees expanded their traplines to include competitors' flowers after their removal, we expected that solitary birds would visit most, if not all, the inflorescences in their patch, whereas birds at shared patches would partition the patch, with each concentrating on a subset of the available inflorescences. Like Gill (1988) and Garrison and Gass (1999), we hypothesized that birds would respond to nectar addition by increasing return intervals. In response to nectar removal to simulate competition, we expected return intervals to decrease as birds utilized a strategy of defense by depletion.

Materials and methods

We conducted our study in the Des Cartiers forest reserve (13°50′12″N, 60°58′34″W) on the island of St. Lucia, West Indies, from approximately May 10 to July 1 2003 and 2004. In both years, we spent the first 2 weeks of our study capturing purple-throated caribs with mist nets to mark them for identification. After capture, each bird was banded with a numbered aluminum band and a celluloid colored band. To further facilitate identification, in 2003, we color-marked individuals by painting small dots or lines of nontoxic, acrylic paint on their heads, whereas in 2004, we glued a single circle (3 mm diameter) of colored flagging tape to the crown or back of each captured bird. Each bird also was given a unique code referring to color combinations (e.g., PD = "pink dot").

During the months of May and June on St. Lucia, heliconias comprise the chief understory food plants of purple-throated caribs (Temeles et al. 2000; Temeles and Kress 2003). At Des Cartiers reserve, the primary heliconias utilized by purple-throats were the red–green-bracted and green-bracted morphs of *H. bihai* (Temeles et al. 2000; Temeles and Kress 2003). The two *Heliconia* morphs at this reserve differ in the number of bracts per inflorescence, with the red–green morph averaging 5.0±0.2 (mean±SE) bracts per inflorescence and the green morph averaging 4.3±0.1 bracts per inflorescence (Temeles and Kress 2003). On average, each bract of *H. bihai* contains 12 flowers, except for the terminal bract which may contain 10 flowers (Temeles et al. 2005). During the 2 years of our study, the average number of inflorescences per plant (1.57±0.09, range=0–13, n=201 plants) did not differ between *Heliconia* morphs or between years (red–green, 2003 vs 2004: t=0.32, P=0.75; green, 2003 vs 2004: t=0.10, P=0.92;

between morphs: t=0.44, P=0.66). The number of open flowers per plant, however, was significantly less for the green morph in 2003 (0.56±0.09, range=0–3, n=72 plants) than in 2004 (1.31±0.15, range=0–8, n=81 plants; t=4.24, P<0.0001). By contrast, no significance difference in the number of open flowers per plant was observed between years for the red–green morph, which averaged 0.94±0.18 flowers per plant for the 2 years combined (range=0–4, n=48 plants, t=0.12, P=0.9).

Within *Heliconia* bracts, each flower opens sequentially and lasts for a single day (Temeles and Kress 2003). Nectar production decreases and eventually ceases by early afternoon, at which time purple-throated caribs shift their foraging activity to the rainforest canopy (Temeles et al. 2005). Accordingly, we conducted observations for 4-h periods between 0630 to 1100 h. From 1999 to 2002, males had been observed defending territories of *H. bihai* at Des Cartiers, but during the years of our study, males were virtually absent from patches of *Heliconia*. By contrast, females were commonly observed traplining at green, red–green, and mixed patches of *H. bihai*. In 2003, we studied five patches, three of which were visited by a single female (“solitary” patches) and two of which were visited by two females (“shared” patches). In 2003, one of the females at a shared patch stopped visiting the patch in the middle of the third day of the experiment; thus our analysis in 2003 included three females at shared patches and three females at solitary patches. In 2004, we studied four patches, three visited by a single female (n=3 females) and one visited by two (n=2 females). In each year and for each experimental replicate described below, we measured the size (area) of the patch utilized by the bird(s) using a 50-m tape measure to define a polygon around the outermost plants at the patch. Patches were separated by distances of 50 to 1,000 m. Each individual female was observed traplining at only one patch of *Heliconia*; whether these females traplined at other patches of heliconias is unknown due to the inaccessibility of many areas of the mountain rainforests and our inability to track individuals. Females foraged on flowers of *Hibiscus elata* in the rainforest canopy, however, and also were observed hawking for insects (Temeles et al. 2004, 2005).

Nectar addition experiment

In 2003 and 2004, we conducted nectar addition experiments to examine whether female purple-throated caribs would decrease their visitation rates to patches after a patch-wide increase in nectar reward at *Heliconia* flowers in the same way that hermit hummingbirds decreased their visitation rates when the sucrose solution delivery rate was experimentally increased at all feeders (Gill 1988; Garrison and Gass 1999). At each patch, we spent 3 days observing birds for 4 h periods; the first and third days at each patch involved observations at unmanipulated flowers, whereas the second day at each patch involved observations at flowers to which nectar had been added. On each day, we recorded the identity of the purple-throat visitor, the time of each feeding visit, and the inflorescences visited by the bird during that visit. After the first visit to an inflorescence, we gave it a number in sequence (i.e., 1, 2, 3...) by applying Bic Wite Out® correction fluid to one of its bracts to identify it for future reference. Inflorescences retained the same number across the 3 days of the experiment. We also recorded the number of bracts and the number of flowers for every inflorescence, visited or unvisited, within the patch on each day of the experiment. On the second day of the experiment, we manipulated the patch by adding 25 μl of 25% sucrose solution (weight:weight) to every flower within the patch (25% sucrose approximates the sucrose concentration of *H. bihai* flowers, whereas 25 μl per flower is at least double the standing crop of nectar of undefended *H. bihai* flowers; see Temeles et al. 2005). Flowers were refilled with sucrose solution after each hummingbird visit. On the third day of each experiment, we repeated observations at unmanipulated flowers; the third day thus served as a control to assess whether our nectar additions had any lingering effects on birds’ behavior.

Nectar removal experiment

In 2004, we conducted a nectar removal experiment to examine whether female purple-throated caribs would increase their visits to flowers which had their nectar experimentally removed (simulating competition) in the same way that hermit hummingbirds reacted to nectar reductions at artificial feeders (Gill 1988; Garrison and Gass 1999). Each experiment lasted 2 days with the first day consisting of observations at unmanipulated flowers and the second day consisting of observations at experimentally manipulated flowers on the same inflorescences. On the second day of the experiment, we simulated the presence of a competitor by removing nectar from five *Heliconia* inflorescences (seven to nine flowers) using a pipetter fitted with a gel-loading pipet tip. To enhance the likelihood that birds would associate our nectar removals with visits by competitors, we deliberately removed nectar from flowers that birds had visited that morning, and from which they had obtained nectar as deduced from observations of licking and swallowing behaviors. We repeated our nectar removals at 20-min intervals, and measured the volume of nectar removed by transferring the nectar from the pipetter to calibrated capillary pipets. We removed 254 and 222 μl of nectar from the two solitary patches, and 201 μl of nectar from the shared patch. Birds did not revisit some of the manipulated flowers, and thus our sample sizes consisted of three and four manipulated inflorescences (six flowers per patch) at two solitary patches (two birds), and four manipulated inflorescences (seven flowers) at the shared patch (only one of the two birds at this patch was observed due to time constraints). Our observational methods and data recorded follow those described above for the nectar addition experiment.

Statistical analyses

We used paired *t* tests with Bonferroni corrections (Rice 1989) to examine whether the number of flowers on each patch (flowers per square meter) changed over the course of our experiments, and *t* tests to compare floral characteristics between shared and solitary patches and between years (we used the average number of flowers across the 3 days of experiments for comparisons between shared and solitary patches and between years). To determine whether traplining females preferred multiflowered to single-flowered inflorescences and whether such preferences were affected by our nectar additions or the presence of competitors, we employed a multivariate repeated measures analysis of variance (MANOVA) from the GLM procedure in SAS (SAS Institute 1999) with day (i.e., before, addition, after) and inflorescence (multi- or single-flowered) as the repeated measures and patch (solitary or shared) and year (2003 or 2004) as the subject variables. We used the average number of visits to multi- and single-flowered inflorescences for each day for each bird as the response variable in this analysis. Repeated measures MANOVAs avoid violations of the assumption that orthogonal components are uncorrelated and have equal variance, which occur when a traditional univariate mixed-model ANOVA is used to analyze repeated measures data (O'Brien and Kaiser 1985).

We also used repeated measures MANOVAs to determine whether birds at solitary and shared patches differed in their use of patches over the 3 days of the addition experiment, and whether they altered their return intervals to patches after our nectar additions. For the both analyses, day was the repeated measure and patch and year were the subject variables. The proportion of the patch visited (arcsine-transformed) and the average return interval on each day for each bird were the response variables. Lastly, we used paired *t* tests with Bonferroni corrections to determine whether birds preferred multiflowered inflorescences to single-flowered inflorescences, whether birds at solitary and shared patches differed in the proportions of flowers visited within their patch, and whether birds' return intervals changed between experimental and control days in the nectar addition and removal experiments. With the exception of the MANOVAs, all statistical analyses were performed with Minitab software (Minitab Inc. 1997) and data are presented as means±SE.

Results

Patch characteristics

Solitary patches averaged 984±219 m^2 in 2003 (n=3) and 551±47 m^2 in 2004 (n=3), whereas shared patches averaged 648±48 m^2 in 2003 (n=2) and 708 m^2 in 2004 (n=1). Differences in size between shared and solitary patches within (shared vs solitary, 2003: t=1.5, P=0.27; 2004: t=3.37, P=0.08) or between years (solitary 2003 vs 2004: t=1.93, P=0.19; shared 2003 vs 2004: t=1.25, P=0.43) were not significant. The average daily number of flowers on solitary patches (28.0±3.2) was higher than that on shared patches (20.8±1.3) in 2003, but not significantly so (t=2.1, P=0.17), whereas in 2004, the daily number of flowers (81) on the one shared patch was significantly higher than the average daily number of flowers (49.3±4.9) on solitary patches (t=6.45, P=0.023). Because of differences in size between shared and solitary patches, however, the average density of flowers did not differ between shared vs solitary patches in either 2003 (solitary: 0.031±0.005 flowers per square meter; shared: 0.032±0.005 flowers per square meter; t=0.27, P=0.81) or in 2004 (solitary: 0.091±0.016 flowers per square meter; shared: 0.114 flowers per square meter; t=1.44, P=0.29). Both the average daily number of flowers and flower densities on shared and solitary patches were significantly higher in 2004 than in 2003 (solitary 2003 vs 2004: t=4.58, P=0.02; shared 2003 vs 2004: t=18.11, P=0.04).

During 2003 and 2004, the average density of flowers at each patch did not differ over the 3 days of the addition experiments or the 2 days of the nectar removal experiments (ts<0.8, Ps>0.4, paired t tests with Bonferroni corrections). As a result, any changes in the return intervals of birds over the course of the experiments presumably resulted from our nectar manipulations, rather than from changes in the densities of available flowers.

Inflorescence and micropatch preferences

Traplining female purple-throats visited multi- as opposed to single-flowered *Heliconia* inflorescences significantly more often when data were analyzed across years, patches, and days of the addition experiment, averaging 3.63±0.24 visits to each multiflowered inflorescence and only 2.61±0.19 visits to each single-flowered inflorescence (Table 1; MANOVA, inflorescence effect P=0.001). On both shared and solitary patches in 2003 and on shared patches in 2004, females visited multiflowered inflorescences more often

Table 1 Repeated measures MANOVA of the number of visits by traplining purple-throated caribs at shared and solitary patches (patch) to multi- and single-flowered inflorescences (inflorescence) over the 3 days of the addition experiment (day) in 2003 and 2004 (year)

Source	*df*	*F*	*P*
Year	1, 7	7.01	0.033
Patch	1, 7	17.53	0.004
Day	2, 6	1.80	0.244
Inflorescence	1, 7	27.2	0.001
Year × patch	1, 7	5.92	0.045
Year × day	2, 6	0.26	0.782
Year × inflorescence	1, 7	0.50	0.502
Patch × day	2, 6	0.11	0.900
Patch × inflorescence	1, 7	0.33	0.586
Day × inflorescence	2, 6	4.15	0.074
Year × patch × day	2, 6	3.40	0.103
Year × patch × inflorescence	1, 7	0.07	0.803
Year × day × inflorescence	2, 6	3.05	0.122
Patch × day × inflorescence	2, 6	1.78	0.247
Year × patch × day × inflorescence	2, 6	0.03	0.975

than single-flowered inflorescences on each of the 3 days of the addition experiment, but their preference for multi-flowered inflorescences was significant only on the addition day of our experiments ($P<0.05$, paired *t* tests with Bonferroni corrections; Fig. 1). By contrast, females on solitary patches in 2004 made significantly more visits to multi- as opposed to single-flowered inflorescences on all 3 days of the experiment ($P<0.05$, paired *t* tests with Bonferroni corrections, Fig. 1). Females visited multi-flowered inflorescences more often than single-flowered inflorescences even though the former was rarer on both shared and solitary patches in 2003 and 2004. Multi-flowered inflorescences comprised 24% of all *Heliconia* inflorescences on shared and solitary patches in 2003 ($n=264$ inflorescences) and 35% of all *Heliconia* inflorescences on shared and solitary patches in 2004 ($n=308$ inflorescences).

Patch use

In both years of the nectar addition experiment, females traplining at shared patches visited a lower proportion of flowers than females traplining at solitary patches ($P<0.001$, repeated measures MANOVA, patch effect, data arcsine-transformed, Table 2). Across the 3 days of the nectar addition experiment, females at solitary patches visited on average 96.4±0.1 and 93.7±0.1% of the flowers in their patches in 2003 and 2004, respectively. By contrast, females at shared patches visited only 62.7±0.1% of the flowers in their patches in 2003, and 66.7±0.1% of the flowers in their patches in 2004. Females at shared patches shared 33.2±13.2% of the flowers in their patches in 2003 and 25.3±3.2% of the flowers in their patches in 2004 over the 3 days of the experiment. In 2003, females at both shared and solitary patches responded to nectar additions by visiting a lower proportion of flowers in their patches, whereas in 2004, our nectar additions had very little effect on the proportion of flowers visited by females on shared and solitary patches ($P=0.008$, repeated measures MANOVA year × day effect, Table 2, Fig. 2). The proportions of flowers shared by birds at shared patches did not differ significantly across the 3 days of the experiment in either 2003 (before: 52.7±11.1; addition: 8.0±8.0; after: 38.5± 5.5) or in 2004 (before: 20.0±2.1; addition: 25.0±5.0; after: 31.0± 3.0; paired *t* tests with Bonferroni corrections, $P>0.05$ overall).

Return intervals

Nectar addition experiment Based on earlier studies of traplining by hummingbirds (Gill 1988; Garrison and Gass 1999), we expected that female purple-throated caribs would increase the duration of their return intervals to patches after a patch-wide increase in nectar owing to either satiation or a perceived decrease in competition. We observed such an increase, but only by females traplining at shared patches in 2003 (Fig. 3; Table 3). Return intervals (44.3±4.0 min, $n=3$ females) were significantly longer on the addition day of our experiment than on either the days before (30.4±6.3 min) or after (28.9±4.1 min) the experiments ($P<0.05$, paired *t* tests with Bonferroni corrections) on shared patches in 2003. In contrast, we observed no significant effect of nectar additions on return intervals of traplining females at solitary patches in either 2003 or 2004. In fact, in both years, return intervals were shorter on the addition day of the experiment (2003: 16.6±0.7 min; 2004: 9.1±1.5 min; $n=3$ different females in each year) than on the day before the experiment (2003: 17.4±1.7 min; 2004: 12.0±2.1 min; Fig. 3). We also observed no significant effect of nectar additions on return intervals of females at shared patches in 2004, although in contrast to birds at solitary patches, return intervals were slightly longer on the addition day than on either the days before or after the experiment (Fig. 3).

Nectar removal experiment Based on earlier studies of traplining by hummingbirds (Gill 1988; Garrison and Gass 1999), we expected that female purple-throated caribs would decrease the duration of their return intervals to inflorescences which had nectar experimentally removed from their flowers (simulating competition) as an attempt at defense by depletion. Females on solitary patches did, in fact, decrease their return intervals to manipulated inflorescences. Return intervals of solitary females to

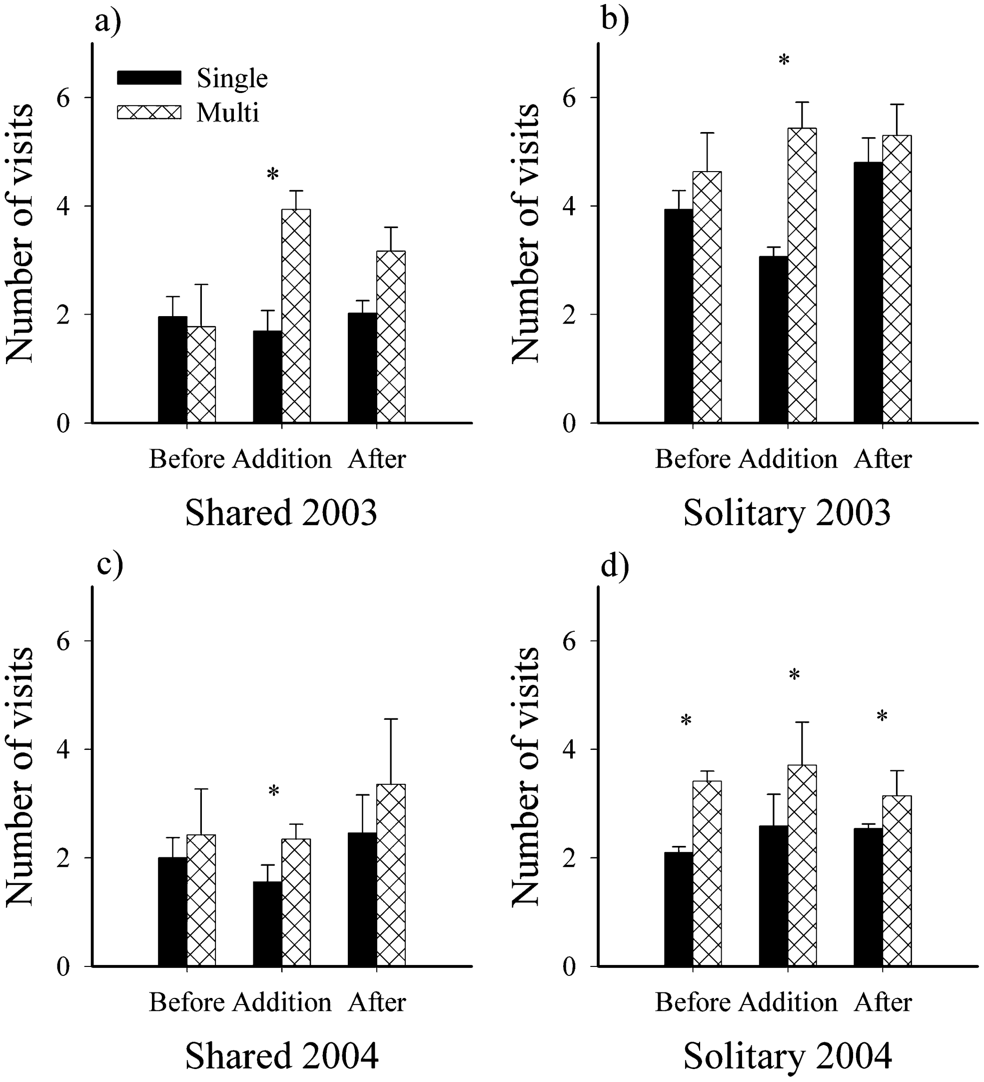

Fig. 1 Number of visits (mean± SE) to multi- and single-flowered *Heliconia* inflorescences by female purple-throated caribs traplining at shared and solitary patches in 2003 and 2004 across the 3 days (before, addition, and after) of the addition experiment. **a** Number of visits by females at shared patches, 2003 (*n*=3 females); **b** number of visits by females at solitary patches, 2003 (*n*=3females); **c** number of visits by females at shared patches, 2004 (*n*=2 females); **d** number of visits by females at solitary patches, 2004 (*n*=3 females). Significant differences in the number of visits to multi- vs single flowered inflorescences on each day are noted by *asterisks* (*P*<0.05 overall, paired *t* tests with Bonferroni corrections)

inflorescences which had nectar removed from their flowers were significantly shorter (PD female 34.7± 5.0 min, *n*=3 inflorescences; YD female 79.5±16.6 min, *n*=4 inflorescences) than on the day before the manipulation (PD female 61.7±11.3 min, *n*=3 inflorescences; YD female 94.8±19.5 min, *n*=4 inflorescences; paired *t* tests, *t*s>3.3, *P*s<0.04; note that the longer intervals here relative to those reported in the addition experiment are a consequence of our examining intervals per inflorescence, as opposed to intervals per patch). Return intervals of these females to unmanipulated inflorescences did not differ significantly between the 2 days of the experiment (PD female, day 1: 59.0±6.0 min; day 2: 52.1±8.7 min, *n*=8 inflorescences; YD female, day 1: 36.8±10.3 min; day 2: 43.2±4.1 min, *n*=12 inflorescences; paired *t* tests, *t*s<0.7, *P*s>0.2). By contrast, return intervals of a female on a shared patch to inflorescences which had nectar removed from their flowers (PB female: 42.0±7.0 min, *n*=4 inflorescences) did not differ significantly from return intervals on the day before the manipulation (36.5±7.4 min; paired *t* test, *t*=0.56, *P*=0.6), nor were there any differences between return intervals to unmanipulated flowers on the same inflorescences between the first and second days of the experiment (day 1: 42.3±8.0 min; day 2: 63.4±10.9 min; *n*=6 inflorescences, *t*=1.94, *P*=0.94).

Discussion

Foraging preferences

Female purple-throated caribs visited inflorescences with multiple flowers more often than those with single flowers,

Table 2 Repeated measures MANOVA of the proportion of flowers visited by traplining purple-throated caribs at shared and solitary patches (patch) over the 3 days of the addition experiment (day) in 2003 and 2004 (year)

Source	*df*	*F*	*P*
Year	1, 7	0.20	0.670
Patch	1, 7	37.37	<0.001
Day	2, 6	12.00	0.008
Year × patch	1, 7	0.04	0.857
Year × day	2, 6	12.14	0.008
Patch × day	2, 6	0.51	0.627
Year × patch × day	2, 6	1.96	0.221

Proportions were arcsine-transformed.

even though single-flowered inflorescences were at least three times more abundant than multiflowered inflorescences. Such a preference makes sense: by visiting the most profitable inflorescences, females maximized their nectar reward while minimizing foraging time and energy costs spent traveling between plants. Only on solitary patches in 2004, however, was females' preference for multiflowered inflorescences significant on all 3 days of our addition experiment (Fig. 1). The absence of significant preferences for multiflowered inflorescences by females on shared patches and on solitary patches in 2003 may be a consequence of resource availability and competition. Optimal foraging theory predicts that a forager should become more selective as the overall abundance of food items in the environment increases (e.g., Werner and Hall 1974; Krebs et al. 1977). Flower densities were three times higher on solitary patches in 2004 than in 2003, which may have allowed birds in 2004 to be more selective, focusing on multiflowered inflorescences. Flower densities were three times higher on shared patches in 2004 than in 2003, yet females on shared patches did not visit multiflowered inflorescences significantly more often than single-flowered inflorescences on the before and after days of our addition experiment. We suggest that the absence of significant preferences for multiflowered inflorescences on these days was the result of competition between females for inflorescences at these patches, which forced females to be less selective in their choice of inflorescences (MacArthur and Pianka 1966; Schoener 1974). One prediction stemming from these interpretations is that females on shared and solitary patches should become more selective and choose multiflowered as opposed to single-flowered inflorescences as the availability of energy increases on patches. Consistent with this prediction, females on both shared and solitary patches in both 2003 and 2004 exhibited statistically significant preferences for multiflowered inflorescences on the nectar addition day of our experiment.

Response to nectar additions

We expected that females at both solitary and shared patches would lengthen their return intervals to patches in response to a 25 μl addition to every available flower at a patch, as in earlier experimental studies of hummingbirds (Gill 1988; Garrison and Gass 1999). Females at shared patches did, in fact, lengthen their return intervals as expected, and in 2003, this lengthening was statistically significant. Gill (1988) offered two hypotheses for why traplining hummingbirds might lengthen their return intervals to patches after nectar additions based on (1) satiation or (2) the perception of a reduction in competition. We cannot rule out either explanation. Why females at solitary patches did not exhibit a similar response is unclear, but may depend on both the number and size of patches included in their traplines, and the degree of exclusive use, which in turn may be a function of individual variation in exploitative and interference competitive abilities. The exclusive nectar rewards on solitary patches may have encouraged females to specialize on them and include

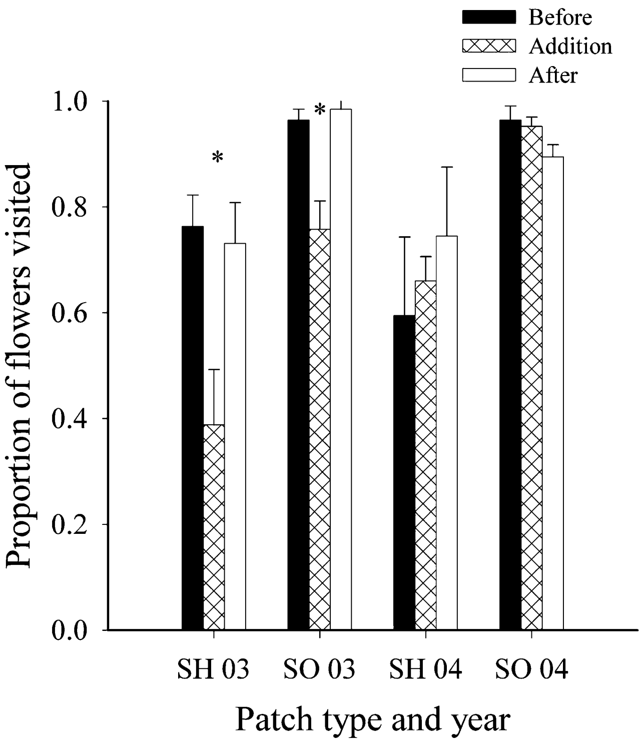

Fig. 2 Proportion of *Heliconia* flowers (mean±SE) visited by female purple-throated caribs traplining at shared and solitary patches in 2003 and 2004 (SH 03, SO 03, SH 04, and SO 04, respectively) across the 3 days (before, addition, and after) of the addition experiment. Within each year and patch combination, *asterisks* indicate that a lower proportion of flowers was visited on the addition day of the experiment than on the days before and after the manipulation ($P<0.05$, paired *t* tests with Bonferroni corrections, data arcsine-transformed)

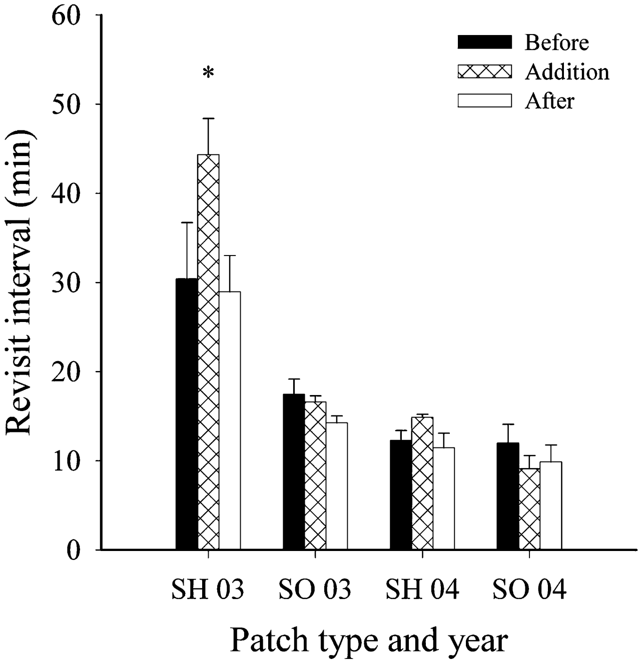

Fig. 3 Revisit intervals (mean±SE) of female purple-throated caribs traplining at shared and solitary patches in 2003 and 2004 (SH 03, SO 03, SH 04, and SO 04, respectively) across the 3 days (before, addition, and after) of the addition experiment. Within each year and patch combination, *asterisks* indicate that revisit intervals were significantly longer on the addition day than on the days before and after the manipulation ($P<0.05$ overall, paired *t* tests with Bonferroni corrections)

fewer patches in their traplines as a result (Cartar 2004). In contrast, females at shared patches may have been unable to specialize on a single patch if such patch-sharing lowered their energy intake relative to females on solitary patches and required them to visit more patches as a result, which may explain why birds at shared patches responded significantly to the nectar additions in 2003 in contrast to 2004. Higher nectar rewards due to higher flower densities might explain why females in 2004 did not visit a smaller proportion of flowers after nectar additions, in contrast to females in 2003, if such higher rewards resulted in specialization on fewer patches in 2004 relative to 2003. Extending addition experiments over several days might provide insights on the degree to which increases or decreases in the nectar reward from a given patch result in increases or decreases in the number of patches in an animal's trapline.

Response to nectar removals

Studies by Lemke (1984), Gill (1988), and Garrison and Gass (1999) suggest that experimental removal of nectar simulates the presence of competitors, and that traplining bats and hummingbirds will attempt to deter this "competition" by shortening their visit intervals to keep nectar levels low as a form of defense by depletion. We therefore expected traplining female purple-throated caribs to respond to our nectar removals from a few selected inflorescences by decreasing their return intervals to those inflorescences. Birds at solitary patches behaved as predicted by decreasing their return intervals to manipulated inflorescences, but not to unmanipulated inflorescences. Such behavior is consistent with defense by depletion (Paton and Carpenter 1984; Gill 1988). In contrast, the bird at our shared patch did not decrease its return intervals in response to nectar removals. Garrison and Gass (1999) noted that *P. longirostris* in the wild did not respond to competitive visits by decreasing their visit intervals, and hypothesized that the relationship between competitive visits and the amount of nectar lost to competitors was weak. Possibly, the effect of our removal was too small a cost to elicit a behavioral change in this female, although the behavior of birds on solitary patches contradicts this hypothesis. Alternatively, perhaps this female had already shortened her return intervals to flowers to the extent permitted by her energy needs and costs in response to competition at this shared patch.

Patch sharing vs exclusive use

Females at shared patches visited a significantly smaller percentage of total flowers (Table 2; Fig. 2) and made fewer visits to multiflowered inflorescences than females at solitary patches (Table 1; Fig. 1). The presence of competitors thus may have limited females' total use of all the flowers in shared patches, although removal of putative competitors is necessary to verify this explanation. Thomson et al. (1987) and Makino and Sakai (2005) observed that bees' traplines were noticeably different when foraging among competitors than when foraging alone, and that in the presence of competitors, bees partitioned resources with each bee visiting a subset of available flowers. Gill (1988) noted that traplining hermit humming-

Table 3 Repeated measures MANOVA of revisit intervals of traplining purple-throated caribs at shared and solitary patches (patch) over the 3 days of the nectar addition experiment (day) in 2003 and 2004 (year)

Source	*df*	*F*	*P*
Year	1, 7	28.05	0.001
Patch	1, 7	16.34	0.005
Day	2, 6	11.85	0.008
Year × patch	1, 7	10.10	0.016
Year × day	2, 6	10.06	0.012
Patch × day	2, 6	17.66	0.003
Year × patch × day	2, 6	3.59	0.095

birds reacted similarly to competitors, and that they divided patches and visited subsets of available flowers. Nonetheless, although several individuals initially competed for nectar at newly established feeders in Gill's experiments, one usually became the primary visitor over time. Concentrating a food source in the form of a feeder may have facilitated a bird's ability to control access to nectar rewards. In our study, however, pairs of females shared patches for several weeks, whereas other females had nearly exclusive access to different patches. Why some patches were shared whereas others were not requires additional study, but depends on the number, energy reward, and size of patches relative to the number of birds, which affects both competition and exclusive access to patches, as well as individual differences in competitive abilities. A critical question is the extent to which exclusive patch use by a traplining hummingbird results from differences in exploitative or interference competitive abilities between individuals, or some combination of the two. Sazima et al. (1995) noted that traplining saw-billed hermit hummingbirds (*Ramphodon naevius*) chased each other if two birds arrived simultaneously at the same patch. We also observed aggressive interactions between traplining females, and as might be expected given the use of shared patches by more than one female, aggressive interactions were more frequent at shared as opposed to solitary patches, albeit infrequent (less than 0.1 chases per hour of observation). Thus, although traplining hummingbirds exhibit less frequent aggression than territorial hummingbirds, interference competition as well as exploitative competition may have a role in establishing and maintaining an individual's trapline.

Future considerations

Our study differed from those of Gill (1988) and Garrison and Gass (1999) by manipulating the behavior of traplining birds at both shared and solitary patches, and as shown in this study, competition between birds at shared patches may affect their use of inflorescences as well as their decisions to increase or decrease revisit intervals in response to increases or decreases in nectar in flowers. Thus, future studies of traplining behavior should attempt to incorporate levels of competition (i.e., patch sharing) into their design. Such designs may help us understand why some patches are shared by trapliners, whereas others are not, as well as the relative importance of exploitative vs interference competition in gaining access to a patch. In addition, Garrison and Gass (1999) noted that although hummingbirds responded readily to nectar manipulations from high-reward feeders in their study as well as Gill's (1988), it was unclear whether they would respond similarly to smaller changes at multiple patches in the field. They hypothesized that changes in nectar availability at patches of flowers in the field would have to be relatively large and represent a big gain or loss in order for birds to respond by altering their traplines. Our study supports their hypothesis and indicates that traplining birds will respond to manipulations of their natural food sources, but we emphasize that we manipulated nectar at single, not multiple, patches used by each traplining subject. Traplining animals are difficult to follow, especially in the rainforest; nonetheless, studies of an animal's entire trapline are necessary to fully understand the effects of competition and resource availability on traplining behavior.

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