

Hummingbird foraging patterns: visits to clumps of *Ipomopsis aggregata* inflorescences

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(Received 15 May 1990; initial acceptance 19 July 1990;
final acceptance 3 October 1990; MS. number: A5649)

Abstract. Foraging by two species of territorial male hummingbirds was studied at clumps of scarlet gilia, *Ipomopsis aggregata*, inflorescences. The birds visited relatively few clumps per foraging bout, and visit frequency among clumps was not different from random (Poisson) expectations on 30 of 34 days. Birds did not forage randomly on 4 days, usually because certain clumps were revisited more than expected. Visits to inflorescences within clumps also generally were not different from random, suggesting little or no within-clump visit patterning. Randomness of foraging at the scale of clumps from day to day was associated significantly with foraging randomness at the scale of individual inflorescences on the same territories. Visits were significantly more frequent to clumps with more inflorescences. The location of clumps relative to perches used between bouts frequently influenced where bouts started, but where bouts ended had little influence on the subsequent perch. Thus, randomness of foraging at clumps based on visit frequencies was compounded of differences in visits based on clump characteristics and the frequency distribution of those characteristics in the observation area. These results, coupled with studies of within and between inflorescence foraging, suggest that the primary mechanism for foraging at plants that have accumulated the most nectar per flower involves area-restricted search with differential response to low and high rewards encountered during a foraging bout. Some difficulties of testing for non-random foraging in natural situations are discussed.

Foraging in patchy environments has been studied as a series of decisions about where and how long to forage (Gass & Montgomerie 1981; Pyke 1984; Stephens & Krebs 1986). Patch foraging patterns may involve decisions at several spatial scales influenced by information acquired at different times. Most studies have examined a single spatial scale and attempted to control information content of the environment. For example, Cowie (1977) examined patch residence time for great tits, *Parus major*, at small cups containing equal numbers of prey, while Gass & Sutherland (1985) examined choices by foraging rufous hummingbirds, *Selasphorus rufus*, among clusters of plants, some artificially enriched with known quantities of sugar solution.

Animals that feed on nectar in a local plant population face a hierarchy of spatial scales of patches ranging from individual flowers to inflorescences with multiple flowers to clumps of inflorescences. Various studies have examined decisions within a foraging bout on how long to stay at single flowers (Whitham 1977; Hodges & Wolf 1981), how many

flowers to visit on multi-flowered inflorescences (e.g. Pyke 1978a; Hodges 1985a, b; Cibula & Zimmerman 1987), and how to move between inflorescences (Pyke 1978b, 1981; Heinrich 1979; Soltz 1986). Foraging decisions at clumps of inflorescences and over more than one foraging bout have not been studied in detail (but see Gill & Wolf 1977; Gass & Montgomerie 1981), yet decisions at these large scales may interact with decisions at the smaller ones (Plowright & Lavery 1984). Information on nectar availability at the clump scale may be less exact than information about specific flowers or inflorescences. However, avoiding recently visited clumps may produce higher average nectar levels encountered at a visit than random foraging (Gill & Wolf 1977; Kamil 1978; but see Possingham 1989).

The forager could visit patches non-randomly at most scales by remembering the quality of locations from earlier bouts or responding to the current patch rewards. The first type of information requires memory of patch qualities and locations and presumably will be influenced by the number of

locations that need to be remembered and renewal rates (Smith & Sweatman 1974; Wolf & Hainsworth 1983; Gass & Sutherland 1985). Some observations and experiments suggest hummingbirds and bumblebees do use memory of spatial locations to pattern foraging across several bouts (Manning 1956; Miller & Miller 1971; Cole et al. 1982; Gass & Sutherland 1985). The second type of information requires assessing the value of staying in the patch or visiting nearby patches based on current foraging (e.g. Hodges 1985a, b; Dreisig 1989; Pleasants 1989).

To examine the role of temporal and spatial scales in patch foraging decisions, we studied foraging in monospecific stands of scarlet gilia, *Ipomopsis aggregata*, that were defended by rufous or broad-tailed hummingbirds, *Selasphorus platycercus*. Previous studies suggested hummingbirds primarily used the second type of information within and between inflorescences in territories containing from 6000 to 10 000 flowers on 700–1900 inflorescences spread over areas as large as 1050 m² (Wolf & Hainsworth 1986, 1990). Here we investigate possible information use by hummingbirds foraging at scarlet gilia clumps.

METHODS

Study Area and Organisms

Observations were made near Crested Butte, Colorado, U.S.A. (elevation ca 3100 m) on individual hummingbirds that controlled territories of *I. aggregata*. Three territories were observed in 1978 and two in 1979 for a total of 30 days. Data on number of inflorescences visited per foraging bout were from other studies of territorial birds in the same area in 1980 and 1981.

Territorial residents were male broad-tailed and rufous hummingbirds with some turnover of individuals between days. Birds were not individually marked, but residents perched in easily observed locations, and their movements during a daily observation period could be followed. The sex and species of intruders were identified, although this paper considers only foraging by residents.

Plant and Bird Observations

We defined natural clumps of inflorescences by shorter distances between inflorescences within than between clumps. The area between clumps was usually empty of flowers, but in a few cases we

removed some inflorescences to make boundaries more discrete. Clumps differed considerably in area because of natural variation in plant dispersion. We mapped the position of all clumps and determined the numbers and density of inflorescences in clumps. We estimated nectar standing crop on the territory at the beginning and end of daily observations by randomly picking about 50 flowers, each from a different inflorescence. We measured nectar volume in each flower with calibrated microcapillary tubes.

Observations of territories for whole days provided data on clump use by all hummingbird foragers. Observations normally started at about 0700 hours and continued until foraging activity slowed in the late afternoon. For each foraging bout, we recorded time of day, sequential clumps visited and, for some days, the perch from which a bout was started and that to which the bird flew at the end of a bout.

Details of foraging within selected clumps were obtained from films taken each time a bird visited the clumps. Visits were filmed for entire days and films were viewed with a stop-frame projector to identify the inflorescences and the number of flowers visited. Time of day and bird identity were recorded for each visit. Open flowers on each inflorescence were counted at the end of each day.

To document foraging patterns at the inflorescence level, we monitored visits to randomly selected inflorescences scattered throughout the territory. Each inflorescence on a territory was marked with a small piece of coloured surveyor's tape and the same plants were monitored on subsequent days. We recorded the times of visits and the identities of each visitor.

Analysis

The null hypothesis for clump foraging patterns was that each clump had an equal probability of being visited. The frequency distribution of observed visits per clump was therefore compared with a Poisson distribution based on the mean number of visits per clump (Gill & Wolf 1977). The birds could produce unequal probabilities of visiting clumps by selecting clumps based on apparent quality cues, such as number or density of inflorescences. The expected frequency distribution of visits would then depend on the quality cues that produced the unequal probabilities and the underlying frequency distribution of clump quality. For

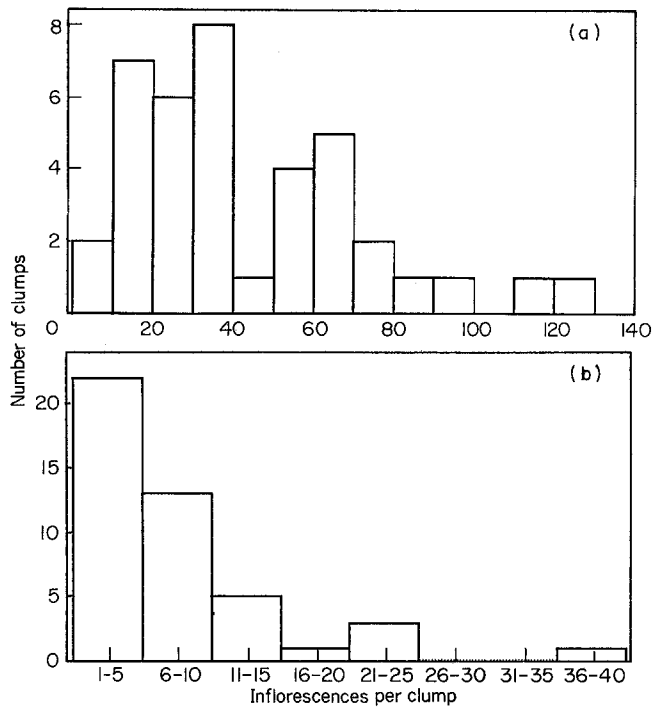


Figure 1. Examples of the frequency distribution of inflorescences per clump on 21 July 1978 in territory 3 (a) and on 6 July 1979 in section B of territory 1 (b). Note differences in axis scaling.

days when the number of visits was significantly correlated to the number of inflorescences per clump, the null hypothesis was changed to incorporate the bias, and the expected frequency distribution of visits per clump was recalculated based on the apparent bias. The biased number of visits to the i th clump, V_i , was calculated from:

$$V_i = \bar{X} \left(\frac{X_i - a}{(Z_i)(b)} \right)$$

where \bar{X} is the average number of visits per clump for the day, X_i is the observed visits to the i th clump containing Z_i inflorescences, and a is the intercept and b the slope of the equation relating observed visits to number of inflorescences per clump. V_i indicates the equivalent number of visits based on the quality biases represented by the observed mean number of visits to all clumps.

RESULTS

Characteristics of Resource Distribution

Sizes, densities and total number of clumps varied within and among territories (Fig. 1; Table

I). Most clumps had relatively few inflorescences (Fig. 1). The characteristics of individual clumps also changed through the blooming season (Table I). The average nectar content of flowers was much less than the 8–9 μ l that would accumulate over 2 days (Table I; Pleasants 1983). The variance in nectar volumes ranged from 3.6 to 0.09 (Table I), indicating that flowers often were available with considerably higher than average rewards.

Clump Visit Pattern

Resident birds visited an average of 1.3–3.3 clumps per foraging bout in 1978. On different days, this average was correlated negatively with average nectar volumes in flowers on the territory ($r^2 = 0.40$, $P < 0.02$, $N = 14$ for morning volumes; $r^2 = 0.33$, $P < 0.05$, $N = 14$ for average of morning and afternoon volumes), but was not correlated to the average number of inflorescences per clump ($r^2 = 0.23$, $P > 0.25$, $N = 5$). Clumps were visited from zero to eight times per day (0 to < 1 per h) and averaged 0.60–3.66 times per day, depending on total observation time and foraging intensity of the resident.

Table 1. Summary of clump quality characteristics and sampled nectar volumes (μl) on territories observed in 1978 and 1979

Date	Territory	Nectar volumes $\bar{X} \pm \text{SE} (N)$		Inflorescences per clump $\bar{X} \pm \text{SE} (N)$
		a.m.	p.m.	

1978				
8 July	1	1.30 ± 0.18 (55)	1.63 ± 0.23 (58)	14.9 ± 1.8 (49)
17 July	2	0.32 ± 0.08 (55)	0.58 ± 0.14 (55)	38.0 ± 3.6 (47)
22 July	2			40.8 ± 4.1 (47)
26 July	3	0.17 ± 0.12 (59)	0.04 ± 0.02 (59)	18.9 ± 1.8 (46)
29 July	3	0.24 ± 0.07 (58)	0.21 ± 0.05 (58)	20.0 ± 2.0 (46)
1979				
3 July	1A	0.85 ± 0.12 (55)	1.40 ± 0.19 (55)	4.5 ± 0.7 (38)
3 July	1B	0.51 ± 0.09 (55)	0.60 ± 0.11 (55)	5.4 ± 0.8 (51)
6 July	1A	0.39 ± 0.09 (55)	0.53 ± 0.08 (55)	5.6 ± 0.7 (40)
6 July	1B	0.41 ± 0.11 (55)	0.50 ± 0.10 (55)	7.3 ± 1.0 (51)
10 July	1A	0.14 ± 0.04 (55)	0.35 ± 0.09 (55)	6.6 ± 0.8 (40)
10 July	1B	0.48 ± 0.16 (55)	0.20 ± 0.05 (55)	8.8 ± 1.1 (52)
13 July	2	0.14 ± 0.09 (55)	0.24 ± 0.09 (55)	9.2 ± 1.1 (54)
16 July	2	0.60 ± 0.12 (55)	0.60 ± 0.11 (55)	10.0 ± 1.1 (54)

The number of visits to clumps over whole days or over half-days rarely differed significantly from a Poisson distribution. Residents significantly avoided revisiting recently visited clumps on only one of 34 days and visited some clumps significantly more than expected on 3 days. They significantly avoided revisits for only 5 of 52 half-day periods and preferentially visited particular clumps for only 2 half-day periods. Visit frequencies could not be distinguished from random during the other 45 half-day periods. The few departures from randomness on either full- or half-day scales would be expected by chance in these data. These results suggest that the birds either foraged randomly among clumps or that any inequalities in visit probabilities were masked by an underlying frequency distribution of clump characteristics.

A bird's memory of specific locations visited may be compromised by large numbers of locations or increasing time between visits. Thus, randomness of foraging based on memory of visited sites may be sensitive to both variables. We examined possible changes in randomness of foraging over time by calculating chi-squared values within days as total visits accumulated (null is a Poisson frequency distribution of visits per clump; $df=1$; Fig. 2). Increasing chi-squared values denote that over the incremental clump visits considered, the bird generally avoided or revisited previously visited clumps,

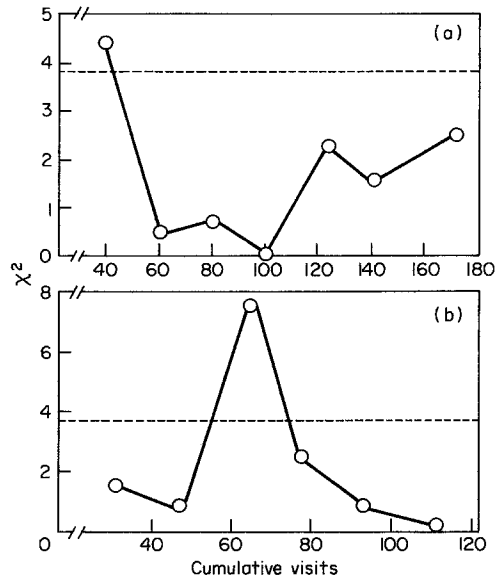


Figure 2. Change in chi-squared values measuring goodness-of-fit to a Poisson distribution as the number of clump visits accumulates throughout the day. Data from 20 July 1978 (a) and 6 July 1979 (b). All chi-squared values were calculated with $df=1$. The critical value for rejecting the null hypothesis of randomness is 3.84 and is indicated by a broken line.

while decreasing chi-squared values suggest the opposite.

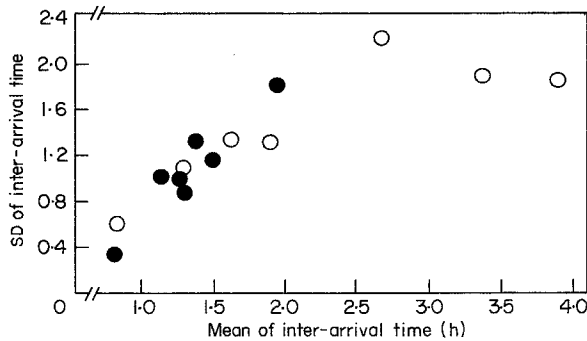


Figure 3. Relation between standard deviation and means of inter-arrival times for high- (●) and low-quality clumps (○).

Some evidence supported changes in degree of visit randomness as visits accumulated, although most of the data suggested little temporal change. For combined data from both years ($N=38$ area-days) birds on 3 days significantly avoided revisits while on 19 days they were not different from random throughout the day. On 5 days a bird initially foraged at clumps in a pattern not different from random expectations ($\chi^2 < 3.84$) and later became non-random ($\chi^2 \geq 3.84$) while on 9 days the bird showed the reverse pattern (Fig. 2a). On the other 2 days the pattern fluctuated between non-random and random through the day (Fig. 2b).

We examined the relationship of the coefficient of variation of inter-arrival times for high- and low-quality clumps for 7 days in 1978 to see if birds differentially patterned visits based on clump quality (Possingham 1989). High- and low-quality clumps were those in the upper and lower third of the distribution of inflorescence number, respectively. The coefficients of variation of high- and low-quality clumps were not significantly different (paired t -test; $df=6$; $P=0.42$). The similarity of the coefficients of variation was not due to the similarity of mean inter-arrival times (paired t -test on mean inter-arrival times at high- and low-quality clumps across the 7 days; $df=6$; $P=0.03$), but to the general trend for the standard deviation of inter-arrival times to increase with the mean time, although perhaps only to an asymptotic level (Fig. 3).

Clump Visit Intensity

An important question is how similar visit intensities were to specific clumps over time. To examine variation in visit intensity to particular

clumps on consecutive days, each clump was placed in a low- or high-intensity category for a whole day. The low-intensity category varied from 0 to 0.3 visits per day depending on activity levels. For the five territories combined for 1978 and 1979, a 2×2 test rejected a hypothesis of independence of visits for 15 of 19 consecutive pairs of days ($P < 0.05$). In each case the birds tended to avoid or revisit specific clumps more than expected by chance. For comparisons within days, use intensity for morning and afternoon was classified as low (0 or 0.1 visit) or high (≥ 1 or > 1 visit), and days were analysed separately. Significant dependence of morning and afternoon foraging (2×2 test of independence, $P < 0.05$) occurred on only 4 of 21 days (for four territories). Again, the dependence generally was due to avoiding or revisiting particular clumps more than expected by chance. The frequency distribution of clump visits for the entire day departed significantly from Poisson for only 1 of these 4 days.

Foraging Within Clumps

In territory 1 in 1979, the resident birds foraged at an average ($\pm SE$) of 5.2 ± 0.47 inflorescences ($N=47$, range = 1–14) in clumps with 25–31 inflorescences each time a clump was visited. This is similar to average numbers of inflorescences visited during complete foraging bouts on 2 days each in 1980 and 1981 (averages = 7.14, 5.54, 3.83, 3.25; Wolf & Hainsworth 1990) and suggests the birds rarely visited all inflorescences in clumps with 10 or more in bloom. The number of inflorescences visited might increase as more nectar accumulated since the last visit. For three clumps filmed over 9 days in 1979, number of inflorescences visited was not correlated with time since the last visit,

regardless of whether the last visit was by the resident ($r=0.22$, $N=47$, $P>0.10$) or an intruder ($r=0.14$, $P>0.10$). It was not known if a visit was the last in a bout, which could explain some visits to few inflorescences after a long inter-visit interval.

Resident birds in 1978 generally visited inflorescences in a clump with frequencies not different from a Poisson distribution (21 of 24 days), while in 1979 visits for 6 of 9 days were significantly non-random, with more uniform visit frequencies than expected by chance. No visit frequencies in either year were significantly biased toward particular inflorescences. Within clumps, resident birds also did not favour inflorescences with more flowers. For only 5 of 23 clump-days were visits significantly correlated with flower number, all positively. Days when visits were correlated with flower number also were among those when the visit pattern to inflorescences was not different from random.

Simultaneous Patterns at Clumps and Inflorescences

To compare foraging randomness at two spatial scales, visit frequency distributions to all clumps were compared with data on visits to marked inflorescences scattered throughout the territory without regard to clumps in which they were located. At both scales, visitation patterns were classed as random, 'non-random+' (avoid revisits) or 'non-random-' (preferential revisit). Visit frequencies were biased toward particular inflorescences on 1 day, more uniform across inflorescences than expected on 10 days, and random on 23 days. Six of 10 days with uniform visits to inflorescences had random clump visits, and 4 days had both clump and inflorescence visits more uniform than expected. For all days together, random foraging at both the inflorescence and clump scales during a day tended to co-occur more often than expected by chance as did non-random foraging (Fisher's exact test; $P=0.02$).

Biases in Clump Visits

Visit patterns to clumps could be influenced by several characteristics that might reflect clump quality. We examined number of inflorescences within a clump and clump locations within the territory.

Inflorescence number

The number of visits to a clump was positively correlated with the number of inflorescences for 9

of 16 days in 1978 (three territories) and for all 6 days in both sections of territory 1 in 1979 (Fig. 4; $P_s<0.05$). However, visits were consistently correlated with number of inflorescences in a clump only for territory 2 in 1978 and territory 1 in 1979. Significant correlations were not differentially associated with Poisson or non-Poisson frequency distributions of visits per clump (Fisher's exact test, $P=0.28$).

The apparent importance of clump quality to number of visits could be related to how different inflorescence number was among clumps. The consistent positive correlations between number of visits and number of inflorescences for territory 2 (1978) were associated with higher mean and variance of inflorescences per clump (means ranged from 38 to 41; variances from 620 to 790) than the other two territories in 1978 (means 15–20; variances 150–180). However, the positive correlations in territory 1 in 1979 were associated with an average of 5–10 inflorescences per clump and variances of 23–64. The coefficients of variation of inflorescences per clump were similar in 1978 for territories 2 and 3 (65–69) and slightly higher in territory 1 in both 1978 and 1979 (77–92).

The expected number of visits per clump based on the birds' perception of quality differences always indicated a significant departure from a Poisson distribution with the same mean number of visits per clump. This departure was in the direction of too few clumps visited one or two times and too many visited zero or more than two times. For all days, clumps with many inflorescences, although they tended to receive more total visits, actually received slightly fewer than would be expected from the observed relation between number of visits and clump quality. Approximately equal numbers of low-quality clumps received more or fewer visits than expected from the bias.

Clump location

First clump in a bout. The choice of first clump of a foraging bout might be influenced by several characteristics, including distance and the number of intervening clumps from the starting perch and the number or density of inflorescences. We used multiple regression, using total number of starts in a clump as the dependent variable, to test the contribution of each independent variable for data combined over several days in two territories in 1978 and in two sections of a single territory in

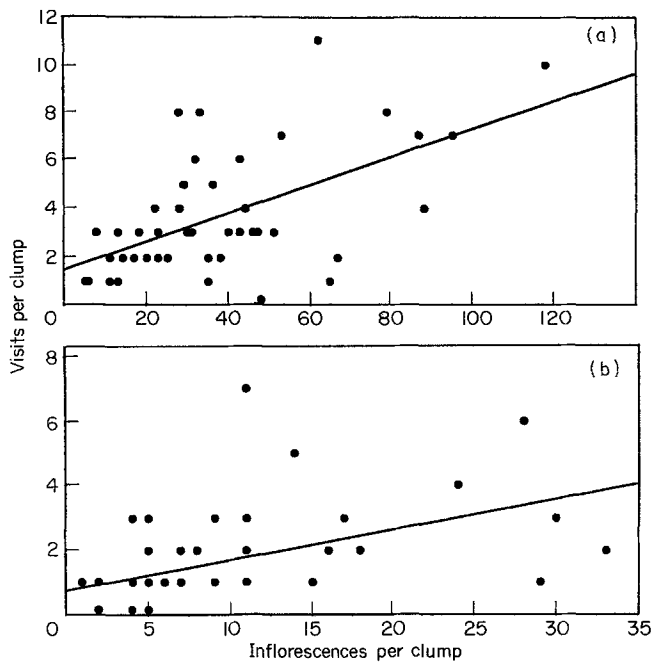


Figure 4. The relation between number of visits to a clump and the number of inflorescences in the clump for 17 July 1978 (a) and 10 July 1979 (b). For the linear regressions, $Y = 0.72 + 0.095X$, $r^2 = 0.23$ (a) and $Y = 1.43 + 0.058X$, $r^2 = 0.33$ (b). Note differences in axis scaling.

1979. In one territory in 1978, none of the factors was significantly correlated with the number of times a clump was visited first. For the other three areas, the resident more frequently started at clumps with more inflorescences and in two cases (one each in 1978 and 1979) at clumps close to the perch. Inflorescence density and the number of intervening clumps did not correlate significantly with number of starts at a clump when the effects of inflorescence number and distance from the perch were held constant.

The influence of perch location also could reflect influences of foraging locations on the perch subsequently used. Perches at the start and end of most foraging bouts were recorded in one territory (divided into two sections) in 1979. A multi-way contingency table analysis incorporated the two sections as well as start and stop locations in two commonly used perches and three combined perches that were rarely used (Table II). The interaction of the three factors was significant ($G = 11.87$, $df = 2$, $P < 0.005$), so two-factor tests of independence were calculated for the separate levels of each factor (Sokal & Rohlf 1981). The perch used at

Table II. Locations of perches used at start and end of foraging bouts in two sections of territory I in 1979

Section	Perch used		
	1	2	3-5
A Start of bout	5	70	12
End of bout	11	69	3
B Start of bout	60	91	9
End of bout	36	124	11

the end of a bout was independent of the section in the territory where the bout ended ($G = 3.63$, $df = 2$, $P > 0.10$), but the location of a foraging bout depended on the perch from which the bird came ($G = 36.13$, $df = 2$, $P < 0.005$). One commonly used perch regularly led to foraging in one section (60 of 65 starts) while starting from the other four perches led to similar numbers of starts in both sections (82: 100). The bias associated with the starting perch did not lead to non-random use of the two territory

Table III. Frequency distribution of movements to i th nearest-neighbour clumps during foraging bouts by resident hummingbirds on three territories in 1978

Territory	i th nearest neighbour				
	1	2	3-4	5-7	>7
1	85 (79)*	20 (26)	39 (35)	23 (24)	25 (28)
2	195 (192)	73 (63)	91 (86)	54 (58)	54 (68)
3	116 (125)	37 (41)	47 (56)	44 (38)	61 (44)

*Numbers in parentheses are expected values under a null hypothesis of independence of nearest-neighbour visit distributions among territories.

sections. Foraging bouts on 4 of 5 days began randomly in both sections (runs test, $P > 0.10$; Wolf & Hainsworth 1983). On the fifth day the bird alternated start sections more than expected by chance.

Sequential movements within a bout. Many foraging bouts included more than one clump. The majority of moves between clumps in all three territories in 1978 were to the closest or the second closest clump, while from 12 to 20% of all moves were to clumps more distant than the sixth nearest neighbour. Patterns of visits to the n th nearest neighbour were significantly different among the three territories (Table 3; $\chi^2 = 17.06$, $df = 8$, $P < 0.05$). However, two of 15 cells contributed nearly 50% of the chi-squared value, and both were associated with moves beyond the sixth nearest neighbour. Fewer than expected distant clumps were visited in territory 2, while more than expected were visited in territory 3. The difference may have been associated with intruders (nearly 44% of all clump visits for territory 3 were by intruders, 30% in territory 1, and 18% in territory 2). Although chases by a resident were considered to end a foraging bout, flights toward an intruder followed by foraging were recorded as within-bout moves. In spite of the two major departures from independence expectations in the contingency table analysis, most aspects of moves to the n th nearest neighbour were similar across territories.

DISCUSSION

Our conclusions regarding the pattern of foraging by these hummingbirds at clumps depended on the type of analysis. Comparison of frequency distributions of visits per clump to Poisson expectations generally indicated random foraging, either over whole or half days. However, the temporal pattern of statistical departure from Poisson expectations was not consistent within days, suggesting shifting influences on where birds foraged as well as requiring considerable caution in interpreting the results from observation periods that differed in duration and foraging intensity.

The apparent randomness of foraging based on a null model of equal visit probabilities resulted from the combination of variations in clump quality with the preference of the birds for visiting high-quality clumps. The results that were consistent with Poisson expectations often did not meet the assumption of equal probability of visiting each clump; in fact, the birds preferentially visited clumps with more inflorescences. Once the apparent preference for clumps with more inflorescences was incorporated into visit expectations, the observed distribution of visit frequencies was always different from random with an excess of plants receiving too few and others too many visits relative to expectations. High-quality clumps tended to receive fewer visits than expected from the observed preferences suggesting some tendency toward equality of visit probabilities.

The overall foraging pattern at clumps depended primarily on where the foraging bout started and the number and location of additional clumps visited. A foraging bout usually began by visiting clumps that had large numbers of inflorescences and were close to the perch. Thus, clump quality, as defined by number of inflorescences and/or flight costs, appeared to be the predominant variable influencing location of the start of foraging bouts. The birds did not appear to select the perch used at the end of a bout in relation to where they had been feeding. The birds might choose start locations non-randomly at a spatial scale larger than a clump (e.g. Gill & Wolf 1977). However, analysis for a territory in 1979 with two convenient spatial subsections (separated by a large area with no inflorescences) revealed no pattern of consecutive starts in the subsections (Wolf & Hainsworth 1983).

The quality of a potential starting clump apparently was not judged by how recently it had been

visited. 'Clever' birds might preferentially return to high-quality clumps that were not depleted on earlier visits. Large clumps usually had less than half their inflorescences visited in a bout, so a short-term memory between bouts for unvisited inflorescences might increase the probability of returning on the next visit. However, the similarity of the coefficients of variation of inter-arrival times at high- and low-quality clumps does not support such preferential return patterns (Possingham 1989). Also, a short-term memory of recently visited, but undepleted clumps would be useful only if the birds tended to visit inflorescences not depleted on the previous bout. Film data for 1978 showed birds foraged randomly among inflorescences within clumps, not avoiding recently visited inflorescences, and only sometimes did they bias visits towards inflorescences with many flowers. In 1979, birds often foraged non-randomly within a clump on sequential bouts. These results leave open the possibility of maintaining within clump information that predicts quality of remaining inflorescences based on current reward.

Birds visited relatively few clumps during a foraging bout. This made start locations and a few subsequent moves critical to any long-term pattern. Most subsequent moves within a bout were to nearby clumps. The actual number of clumps visited during a bout, as expected, tended to vary inversely with average nectar rewards in the flowers. However, the film data suggested that the birds did not bias the number of inflorescences they visited within clumps by the recency of the previous visit. Thus, while the birds did bias visits in relation to the current reward by staying at an inflorescence (Wolf & Hainsworth 1986), we found no evidence of a similar response at the scale of clumps. However, we do not know what led to departures from large clumps before half of the inflorescences were visited. Perhaps an increasing probability of revisits within the clump as the bird visits more inflorescences makes early departures the optimal policy, as Pyke (1978a) suggested for foraging within an inflorescence.

The importance of clump quality is influenced once a bird begins a foraging bout by its movements in response to the quality of individual inflorescences. For each short-term movement decision, the hummingbirds mainly used information from local reward levels acquired once foraging started to adjust subsequent foraging locations (Wolf & Hainsworth 1986, 1990). Responses to local rewards

tended to move birds away from recently visited inflorescences. Thus, the birds appeared to choose locations at which to start a foraging bout using visual cues of patch quality, and then to adjust subsequent foraging locations in relation to local information at the inflorescence level. This area-restricted search within and between inflorescences rather than selection of foraging sites prior to visits may be shared with nectarivorous birds in other families, including sunbirds (Gill & Wolf 1977) and Hawaiian honeycreepers (Kamil 1978) that forage in a systematic pattern.

No data for these hummingbirds clearly implicated a role for memory of reward locations in the foraging patterns chosen. However, other studies with hummingbirds document spatially biased foraging that suggests use of memory (Miller & Miller 1971; Paton & Carpenter 1984; Gass & Sutherland 1985). There may be several reasons why these hummingbirds apparently did not use memory of clump visits. The first possibility is that the value of memory or even of systematic foraging is low. However, the low average nectar volumes in flowers suggest considerable possible benefit in reduced foraging time and energy from being selective (Wolf et al. 1975). Another possibility is that the reliability of the information is low because of the large number of sites that must be remembered (Orians 1981; Wolf & Hainsworth 1983). Finally, the birds may use memory to determine the pattern of their foraging, but we may have investigated the wrong temporal or spatial scale. For example, birds may remember only the last N clumps visited or only some clumps, perhaps ones with many inflorescences, as suggested for Clark's nutcrackers, *Nucifraga columbiana*, recovering cached seeds (Balda et al. 1986).

The number of factors that could influence randomness of choice of foraging locations, other than by area-restricted search, complicates the testing of hypotheses about this use of memory in nature. Such is also the case in laboratory studies of the effects of time constraints on patch use (Shettleworth & Plowright 1989). The results do not mean that the birds do not use memory to determine their pattern of foraging, just that where we hypothesized the use of memory information at a particular spatial scale, we found relatively little evidence for it. Even experiments demonstrating regular use of memory (e.g. Gass & Sutherland 1985) showed only that the hummingbirds had the capacity to use memory at a particular spatial and

temporal scale. To show they do so in a complex natural environment with all its influences is more difficult.

ACKNOWLEDGMENTS

We thank T. Mercier for expert technical assistance in data reduction and analysis. This study was supported by grants from the National Science Foundation. The *Ipomopsis* study group at Rocky Mountain Biological Laboratory provided a stimulating intellectual environment during these studies. W. T. Starmer helped with calculation of expected visits with quality bias.

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