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HOW THE PRESENCE OF FEEDERS AFFECTS THE USE OF LOCAL FLORAL RESOURCES BY HUMMINGBIRDS: A CASE STUDY FROM SOUTHERN ARIZONA

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Abstract. For hummingbirds, artificial feeders can serve as an alternative food source to nectar from flowering plants. The presence of feeders may lead to increases in local hummingbird populations and decreases in the use of native plants. We examined how the presence of feeders influenced the rate of hummingbird visits to a changing array of flowering plants in southeastern Arizona. Feeder visits represented approximately 59% of all visits during our yearlong study, but were less common in times of high floral abundance. The ratio of feeder visits to total visits was negatively related to overall floral abundance and to the abundance of the hummingbird-favored plant, *Calliandra californica*. The regular use of feeders by hummingbirds, which increases during periods of low floral availability, may have important implications for pollinator-plant relationships by reducing plant reproductive output. Additionally, this inverse relationship may affect estimates of hummingbird abundance and must be considered when analyzing data from studies that use feeders to attract hummingbirds.

Key words: banding, *Calliandra californica*, feeder, floral abundance, hummingbirds, population estimate, southern Arizona.

Efectos de la Presencia de Alimentadores en el Uso de Recursos Florales Locales por Colibríes: Un Estudio de Caso en el Sur de Arizona

Resumen. Los alimentadores artificiales pueden actuar como una fuente de alimento para los colibríes alternativa al néctar de las plantas con flores. La presencia de alimentadores puede conducir a incrementos en las poblaciones locales de colibríes y a disminuciones en el uso de las plantas nativas. Examinamos cómo la presencia de alimentadores afectó la tasa de visita de los colibríes a un conjunto cambiante de plantas con flores en el sur de Arizona. Las visitas a los alimentadores representaron aproximadamente el 59% de todas las visitas durante nuestro estudio de un año de duración, pero fueron menos comunes en momentos en que la abundancia de flores era alta. El cociente entre las visitas a los alimentadores y las visitas totales estuvo negativamente correlacionado con la abundancia floral total y con la

abundancia de la planta *Calliandra californica*, que es una de las favoritas de los colibríes. El uso regular de alimentadores por los colibríes, el cual aumenta durante períodos de baja disponibilidad de flores, podría tener importantes implicaciones para las relaciones entre polinizadores y plantas, reduciendo el éxito reproductivo de éstas. Además, esta relación inversa podría afectar las estimaciones de abundancia de los colibríes y debe ser considerada al analizar los datos de estudios que usan alimentadores para atraerlos.

The relationship between hummingbirds and the plant species they pollinate has been fine-tuned over time by the process of natural selection (Grant 1966, Heinrich and Raven 1972, Temeles and Kress 2003, Gegear and Burns 2007). Hummingbirds are the principal avian pollinators in the Americas (Schuchmann 1999), and have developed specific behavioral and morphological traits that enable them to best use plant resources (Temeles and Kress 2003). These traits also enable them to utilize artificial feeders. The availability of hummingbird feeders may represent a significant anthropogenic effect on the relationship between hummingbirds and the plants on which they feed. In areas where feeders are available, hummingbird populations can be larger than in areas where they depend solely on flowers to meet their nectar requirements (Wethington and Russell 2003, French et al. 2005). However, the presence of feeders can result in fewer visits by hummingbirds to some native hummingbird-pollinated plants, thus decreasing plant reproductive output by lowering seed production (Arizmendi et al. 2007).

The frequency with which hummingbirds visit feeders versus flowers varies inversely with the abundance of flowering hummingbird-visited plants (Inouye et al. 1991), indicating that hummingbirds are less likely to visit feeders and more likely to visit flowers in periods of high floral abundance, and vice versa. In addition to the population-level effects that feeders may have on hummingbirds and hummingbird-pollinated plants, this pattern must also be considered at a practical research level. Banding studies are frequently used to gather information on hummingbird survival, reproduction, and dispersal rates, as well as population composition, species distributions, and movement patterns (Mulvihill et al. 1992, Calder and Calder 1995, Hilton and Miller 2003). Hummingbirds banded in these studies are often captured at traps associated with feeders; thus, the data gathered in banding studies must be interpreted with caution, as capture rates at feeders are likely influenced not only by changes in survival and

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reproduction, but also by local environmental factors, particularly the abundance of flowering hummingbird-visited plants.

To achieve more accurate estimates of hummingbird population parameters, banding studies that use feeders must take into account the effects of local floral abundance on the use of those feeders by hummingbirds. While the correlation between total floral abundance and feeder use has been demonstrated (Inouye et al. 1991), the relative influence of different plant species has not. Given the wide variety of habitats that hummingbirds occupy throughout their ranges (Grant and Grant 1968), there is great local variation in the plant species they use and pollinate. Therefore, the interaction between the abundance of local flowering plants and feeder visitation rates must be considered within the specific site of each banding study. To examine this interaction in southeastern Arizona, an area with several hummingbird banding sites (Wethington et al. 2005), we investigated how the proportion of hummingbird visits to feeders vs. flowers changed as both the species composition and abundance of flowers varied over a one-year period in a local botanical park.

METHODS

We conducted our study in Tohono Chul Park (hereafter, "Tohono"), Tucson, Arizona, at an elevation of approximately 840 m. Tohono contains numerous gardens with a wide variety of hummingbird-visited plants that vary in flower production throughout the year. Previous banding efforts (Hummingbird Monitoring Network 2005) found that three species of hummingbird, Anna's (*Calypte anna*), Costa's (*C. costae*), and Black-chinned (*Archilochus alexandri*), occur at Tohono in varying numbers throughout the year.

We designated seven contiguous garden patches at Tohono, ranging in size from 0.10 to 0.41 ha, as observation sites. The seven patches were chosen to: (1) represent a wide variety of natural and ornamental plant species, and (2) be sized and arranged so that a single observer could monitor all hummingbird activity within a patch. A hummingbird feeder (Best-1 0.95 l hummingbird feeder, Best-1, Poteet, Texas) was placed in each patch approximately one month before the initiation of the study, and a 1:4 sugar to water solution was maintained in feeders throughout the study (Kodric-Brown and Brown 1978, Hilton and Miller 2003).

From October 2003 to October 2004, observers monitored hummingbird activity in each patch for 3 hr beginning at sunrise approximately once every three weeks ($n = 18$; Stiles 1975). Observers recorded the time of day of all feeding visits to feeders and flowers, and the species of flower visited. We did not determine hummingbird species because of the difficulty of correctly identifying juvenile and female hummingbirds and because the three hummingbird species present at the study site have similar morphology and visit the same plant species (Kodric-Brown and Brown 1978, Brown and Kodric-Brown 1979). Feeder visits were measured from when a hummingbird arrived at a feeder to the time it left the feeder (Sandlin 2000). We considered flower visits to begin when a hummingbird visited a flower within the patch under observation and to end when the bird left the patch, perched, or visited another species of flower or a feeder. We measured ambient temperature at sunrise on each morning of observation.

FLORAL ABUNDANCE MEASURES

Within each patch, the abundance of open flowers of each plant species was scored on a scale of zero to ten (zero representing no flowers present, ten representing full bloom of each plant of

that species within the patch) on the afternoon prior to hummingbird observations. For each date, an overall floral abundance score (also on a zero to ten scale) for each patch was also estimated based on the abundance of open flowers of all plant species. While the longevity of the flowers of each species present at the site is unknown and there may be daily turnover in individual flowers (Dobkin 1987), we are confident that the overall abundance of flowers for each species was similar between the two observation periods. Due to the difficulty of distinguishing three red sage species, *Salvia coccinea*, *S. microphylla*, and *S. greggii*, these species were grouped together as the "red *Salvia* complex" and given a single abundance score for each patch. Plants in the *Hesperaloe* and *Aloe* complexes were noted by genus (e.g., *Hesperaloe* spp.). For each date, we calculated an average abundance score for each species in all patches using the equation $\bar{A}_i = (A_{1i} + A_{2i} + \dots + A_{7i})/7$, where i signifies the plant species and A_{1-7i} represents the abundance score of the species within each of the seven patches on that day. An overall floral abundance score (encompassing all species) for the entire study area on each date was computed using the equation $\bar{A}_o = (A_{1o} + A_{2o} + \dots + A_{7o})/7$, where o denotes overall floral abundance and A_{1-7o} signifies the overall floral abundance score within each of the seven patches on that day.

STATISTICAL ANALYSES

Data from each observation period were summed across all patches to produce the total number of feeder visits and total number of visits to each flower species for each period. The ratio of feeder visits to total number of visits (feeder and all flower visits combined) was calculated for each morning. For all analyses, only flower species actually visited by hummingbirds (Table 1) were included. For each of these species, a relative preference score (Stiles 1976), which is a measure of hummingbird use of each species relative to its abundance, was calculated using the equation $RP_i = \text{visits}_i / \bar{A}_{\text{all}i}$, where i signifies the plant species, visits_i are the total number of visits to that species over the entire study period, and $\bar{A}_{\text{all}i}$ is the average abundance score of the species over the entire study period and is calculated as $\bar{A}_{\text{all}i} = (\bar{A}_{1i} + \bar{A}_{2i} + \dots + \bar{A}_{7i})/7$, where \bar{A}_{a-r} denotes the average abundance score for each date.

To determine which variables explained a significant proportion of the variation in feeder or flower use, we used multiple logistic regression to model the proportion of feeder visits as a function of the average abundance scores of the eight plant species for which hummingbirds showed the greatest preference (relative preference score >25.0; Table 1), overall floral abundance, and ambient temperature at sunrise. The number of visits to feeders was specified as the response variable and the total number of visits (feeder and flower combined) as the binomial denominator (specifying a binomial error structure and logit link function; Ramsey and Schafer 2002). A Spearman's rank correlation test was used to determine if flower size was related to the percentage of hummingbird visits to each species. For the "red *Salvia* complex," the percentage of visits to the group was divided by three, and the species ranked identically according to the average flower size of the group. Values are reported as means \pm SE.

RESULTS

The number of feeder and flower visits by hummingbirds varied throughout the study, with an average of 48.6 ± 5.9 visits to flowers ($n = 916$) and 96.7 ± 15.1 visits to feeders ($n = 1741$) recorded

TABLE 1. Relationships between floral abundance of hummingbird-visited plants at Tohono Chul Park, Arizona, and number of hummingbird visits. Average floral abundance is the average of the floral abundance of that species for the study's duration, across all seven studied garden patches, measured on a zero to ten scale (with zero representing no flowers present and ten representing full bloom of each plant in each patch). Relative preference scores were calculated by dividing the total number of hummingbird visits to each plant species by the average flower abundance rank for that species. The number of times that hummingbirds visited each species relative to all of their visits to flowers is shown in the "percentage of visits" column. Flower size (as measured by corolla and petal length) was determined by a literature review, and species were then ranked from smallest to largest (plants that were only grouped to genus were not ranked, as flower size varies within genus).

Species	Family	Average floral abundance (0–10) ± SE	Relative preference score	Percentage of visits	Flower size rank
Mexican bush sage (<i>Salvia leucantha</i>) ^{a,b,c}	Lamiaceae	0.4 ± 0.1	285.4	13.3%	11 ^d
Baja fairy duster (<i>Calliandra californica</i>) ^{a,b,c}	Fabaceae	1.4 ± 0.2	167.4	24.9%	17 ^d
Hummingbird bush (<i>Anisacanthus quadrifidus</i>) ^b	Acanthaceae	0.2 ± 0.1	123.8	2.6%	18 ^d
Penstemon (<i>Penstemon</i> spp.) ^{a,b,c}	Plantaginaceae	0.6 ± 0.3	106.8	7.2%	—
Red <i>Salvia</i> complex (<i>Salvia</i> spp. [red]) ^{a,b}	Lamiaceae	4.5 ± 0.4	86.4	42.3%	13 ^{d,c}
Hesperaloe (<i>Hesperaloe</i> spp.) ^{a,b,c}	Agavaceae	0.4 ± 0.1	80.9	3.1%	—
Aloe (<i>Aloe</i> spp.)	Asphodelaceae	0.6 ± 0.2	49.4	3.0%	—
Mexican honeysuckle (<i>Justicia spicigera</i>) ^{a,b,c}	Acanthaceae	0.1 ± 0.1	26.4	0.2%	16 ^d
Texas mountain laurel (<i>Sophora secundiflora</i>) ^b	Fabaceae	0.1 ± 0.1	24.0	0.3%	10 ^f
Hummingbird carpet (<i>Zauschneria californica</i>) ^{a,b,c}	Onagraceae	0.2 ± 0.1	17.4	0.4%	15 ^d
Sweet acacia (<i>Acacia smallii</i>) ^{a,b,c}	Fabaceae	0.1 ± 0.1	11.2	0.1%	1 ^d
Baja ruellia (<i>Ruellia peninsularis</i>) ^{a,b,c}	Acanthaceae	1.0 ± 0.2	7.7	0.9%	3 ^g
Olive (<i>Olea europaea</i>)	Oleaceae	0.2 ± 0.1	6.7	0.1%	2 ^f
Butterfly bush (<i>Buddleia marrubifolia</i>) ^{a,b,c}	Loganiaceae	0.8 ± 0.2	6.6	0.6%	4 ^f
Creosote (<i>Larrea tridentate</i>) ^{a,b,c}	Zygophyllaceae	0.2 ± 0.1	5.6	0.1%	7.5 ^g
Yellow bells (<i>Tecoma stans</i>) ^{a,b,c}	Bignoniaceae	0.4 ± 0.1	5.1	0.2%	19 ^d
Mealy cup sage (<i>Salvia farinacea</i>) ^b	Lamiaceae	1.0 ± 0.2	3.0	0.2%	5 ^d
Brittlebush (<i>Encelia farinosa</i>) ^{a,b,c}	Asteraceae	0.8 ± 0.2	2.5	0.2%	3 ^g
Blue palo verde (<i>Parkinsonia florida</i>) ^{a,b,c}	Fabaceae	0.5 ± 0.3	2.0	0.1%	9 ^g
Goodding verbena (<i>Verbena gooddingii</i>) ^{a,b,c}	Verbenaceae	1.2 ± 0.4	0.8	0.1%	7.5 ^d

^aSpecies is native to the range of the Anna's Hummingbird (*Calypte anna*).

^bSpecies is native to the range of the Black-chinned Hummingbird (*Archilochus alexandri*).

^cSpecies is native to the range of the Costa's Hummingbird (*Calypte costae*).

^dCalderón de Rzedowski and Rzedowski (2001).

^eNote: the rank of the "red *Salvia* complex" is based on the average flower size for the group.

^fAbrams and Ferris (1923).

^gShreve and Wiggins (1964).

each morning. The highest number of feeder visits ($n = 242$) and the lowest number of flower visits ($n = 10$) were recorded on the same morning, when the average floral abundance of the eight most preferred plant species was lowest. The mean ratio of feeder visits to total visits was 0.59 ± 0.05 , i.e., feeder visits represented approximately 59% of all visits.

Floral abundance across all species averaged 2.7 ± 0.4 on the 0 to 10 scale. The red *Salvia* complex had the highest average floral abundance (4.5 ± 0.4), and was visited most frequently by hummingbirds, representing 42% of the flower visits recorded. Relative preference scores (Table 1) ranged from 0.8 for Goodding verbena (*Verbena gooddingii*; relatively abundant, not frequently visited) to 285.4 for Mexican bush sage (*Salvia leucantha*; relatively scarce, but frequently visited).

The ratio of feeder visits to total visits was negatively related to overall floral abundance ($\chi^2_1 = 150.2$, $P < 0.001$) and the floral abundance of Baja fairy duster (*Calliandra californica*) ($\chi^2_1 = 33.3$, $P < 0.001$). When feeder visits were high relative to flower visits, overall floral abundance (and the abundance of Baja fairy duster) was low ($r^2 = 0.68$; Fig. 1). For each one unit increase in

overall floral abundance, the odds of a hummingbird visiting a feeder decreased by 0.63, and for each one unit increase in Baja fairy duster the odds decreased by 0.74. The total number of feeder visits each morning (independent of flower visits) was also negatively related to overall floral abundance ($r^2 = 0.58$; Fig. 2) Ambient temperature at sunrise and the average abundance scores for the seven other plant species examined were not related to the ratio of feeder visits to total visits. Flower size also was not related to visit frequency ($r_s = 0.36$, $P = 0.13$).

DISCUSSION

The rate at which hummingbirds visited feeders was negatively related to the relative abundance of flowering plant species at Tohono Chul Park. Hummingbirds were less likely to visit feeders when hummingbird-visited plants had many flowers, with the presence of blooming Baja fairy duster, in particular, decreasing visits to feeders. Members of the *Calliandra* genus are known to be relatively rich nectar sources for hummingbirds (Hernández-Conrique et al. 2007) and this is likely the reason for the high

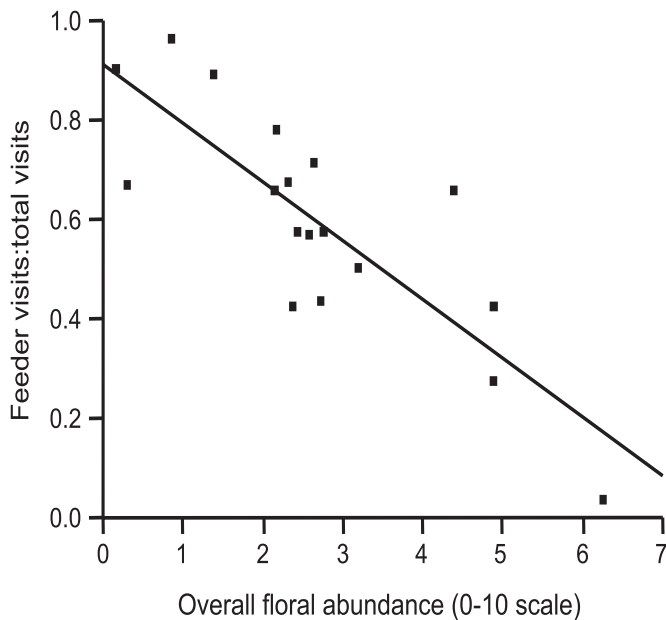


FIGURE 1. Hummingbirds' use of feeders versus flowers at Tohono Chul Park, Tucson, Arizona, was inversely related to overall floral abundance. Each data point represents one morning of observations, with feeder use shown as the ratio of visits to feeders vs. total visits to feeders and flowers on that morning. Overall floral abundance is an average of the total floral abundance per patch from seven garden patches, measured on a zero to ten scale, with zero representing no flowers present and ten representing full bloom of each plant in each patch.

visitation rates to these flowers. Hummingbird-pollinated plants typically have sucrose-dominant nectar, with a 22% to 26% sugar concentration (Stiles and Freeman 1993), and, in preference tests, hummingbirds prefer higher sugar concentrations and larger volumes of nectar (Pimm et al. 1985, Sandlin 2000).

In addition to Baja fairy duster, hummingbirds showed a marked preference for hummingbird bush (*Anisacanthus quadrifidus*), *Hesperaloe* spp., *Penstemon* spp., the red *Salvia* complex, and Mexican bush sage. All of these species are known to attract hummingbirds (Stiles 1976, Baltosser and Russell 2000, Livingston 2004), but the strong preference of hummingbirds for Mexican bush sage relative to the others was unexpected. While flower size has been shown to be a proxy for the amount of nectar available in flowers from different plant species (Dobkin 1984, Arizmendi and Ornelas 1990), it did not correlate significantly with the relative preference of hummingbirds for the plant species in this study. Mexican bush sage, which has tall spikes of fuzzy, purple flowers (Irish 2002) that are smaller than the flowers in the other above-mentioned species, was only present in a single patch at Tohono, and was not in bloom for the majority of the year. However, on mornings when Mexican bush sage was in bloom, the majority of hummingbird visits were concentrated there, and on many occasions several hummingbirds were observed feeding concurrently on individual plants of this species.

While Mexican bush sage is a hummingbird-pollinated plant (Classen-Bockhoff et al. 2004), and many guides to gardening for hummingbirds recognize this species as a "hummingbird plant" (Nielsen and Newfield 1996, Kress 2000, Roth 2001), hummingbird use of Mexican bush sage has rarely been documented in

the scientific literature. This is likely due to the fact that this species is native to Central America, and is therefore found only in cultivated sites in North America and not in the natural areas where many hummingbird studies have been conducted (Grant and Grant 1968, Kodric-Brown and Brown 1978).

Over the course of this study, hummingbirds at Tohono showed marked differences in their visitation rates to feeders depending on the available floral resources. This choice between feeders and flowers represents a kind of cost-benefit analysis for hummingbirds (Gass and Roberts 1992). Depending on the types and numbers of flowers available, feeders may or may not represent a rewarding alternative. Hummingbirds can generally extract a given quantity of nectar more quickly from high-volume feeders than from flowers, as hummingbirds must insert and withdraw their bills from the corolla of each flower regardless of the amount of nectar withdrawn, resulting in an increased handling time relative to feeders, which present no such variation (Gass and Roberts 1992). In times of low floral abundance, when hummingbirds must expend more time and energy to locate blooms containing nectar, feeders are a more concentrated resource. Additionally, while our study only monitored hummingbirds during the morning, with the nectar productivity of most hummingbird-visited plants peaking early in the day (Stiles 1975), the value of feeders may increase throughout the day as floral resources decline. However, while feeders may represent a quicker and easier way to obtain nectar, the nectar available from flowers may be more nutritionally rewarding. The typical 1:4 sugar solution used in hummingbird feeders represents a 20% sugar concentration and most hummingbird-pollinated plants contain

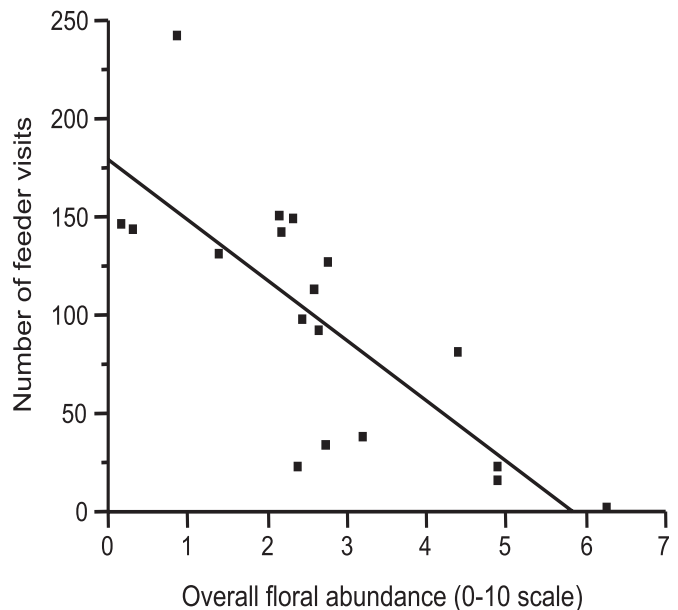


FIGURE 2. Hummingbirds at Tohono Chul Park, Tucson, Arizona, visited feeders more when overall floral abundance was low, and less when overall floral abundance was high. Each data point represents one morning of observations, and the number of feeder visits represents the total number of visits to feeders by hummingbirds in all patches during a 3 hr observation period. Overall floral abundance is an average of the total floral abundance per patch from seven garden patches, measured on a zero to ten scale, with zero representing no flowers present and ten representing full bloom of each plant in each patch.

nectar with equal or higher average sugar concentration (Stiles and Freeman 1993, Roberts 1996). Thus, at times when their preferred flowers are sufficiently abundant, hummingbirds may compensate for the additional search and handling time associated with feeding at flowers by obtaining more sugar.

The inverse relationship between feeder visitation rates and floral abundance first reported by Inouye et al. (1991), and supported by this study, shows that the presence of local flowering plants can affect the use of feeders by hummingbirds and vice versa (Arizmendi et al. 2007). The results of this study also suggest that identifying key nectar resources in an area and monitoring their abundance and flowering phenology are important factors in determining the influence of nearby nectar resources on estimates of hummingbird population sizes.

When flowers were scarcer, hummingbirds primarily visited feeders, largely leaving the remaining flowers unvisited. The option of obtaining nectar from feeders may therefore result in hummingbirds failing to fully pollinate plants at times when few flowers are present or in areas where flowers are not clustered. For the hummingbird-pollinated plant ocotillo (*Fouquieria splendens*), increased seed set occurred when peak bloom time corresponded with peak numbers of migrating hummingbirds (Waser 1979). Flower phenology is closely related to climate; even minor changes in climate can produce changes in blooming dates that may decouple the mutualism between hummingbirds and the plants that they pollinate (Bazzaz 1998). Likewise, timing and occurrence of hummingbird abundance patterns can vary from year to year (Wethington and Russell 2003) and are important to the success of this mutualism. On a more practical level, researchers must be aware that the frequency with which hummingbirds visit feeders (and therefore are captured and banded) is not independent of local floral abundance; estimates of population parameters that take this into consideration will be more representative of actual changes and differences.

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