

## Good to the last drop: feeding behavior of the nectar bat *Leptonycteris yerbabuena* (Chiroptera, Phyllostomidae) at hummingbird feeders in Tucson, Arizona

THEODORE H. FLEMING<sup>1,2</sup>

<sup>1</sup>Department of Biology, University of Miami, Coral Gables, FL 33142, USA

<sup>2</sup>Corresponding author: E-mail: tedfleming@dakotacom.net

Many individuals of the nectar-feeding phyllostomid bat, *Leptonycteris yerbabuena*, visit hummingbird feeders in southern Arizona for nearly three months each year prior to migrating back to Mexico. We monitored bat activity at four feeders with trail cameras or security cameras all night for 19–57 nights during the 2021 ‘nectar bat season’. As in previous years, peak visits occurred in mid-September. Detailed analysis of data from one feeder on 22 nights indicated that non-adults (juveniles and yearlings) were visiting it and that visitation patterns were highly variable from night to night. Statistical analysis of these patterns revealed that clusters of bats were visiting this feeder more often than expected by chance, suggesting that bats are foraging in groups. Surprisingly, bats did not leave feeders once they were drained but continued to visit them for up to five hours each night. Energetic calculations suggest that some bats are potentially expending half of their foraging energy visiting empty feeders. Studies of individually tagged bats are needed to begin to understand this behavior.

**Key words:** Arizona, energetics, group foraging, hummingbird feeders, *Leptonycteris yerbabuena*, trail camera sampling

### INTRODUCTION

Before migrating back to Mexico, the nectar-feeding bat *Leptonycteris yerbabuena* (Chiroptera, Phyllostomidae) is a common visitor to hummingbird feeders in southern Arizona between late August and late October each year (Fleming *et al.*, 2021). During this time, a handful to dozens of bats can be seen visiting feeders each night in September, the peak month of the ‘nectar bat season’. Since 2011, most of these bats have been juvenile or yearling females. Relatively few are adult females, and fewer still are adult males although adult bats were apparently common visitors to feeders prior to 2011 (Lowery *et al.*, 2009).

Fleming *et al.* (2021) was based on an ongoing community science project in which data were collected by 50 to > 100 households each year, beginning in 2007. While providing important data on bat numbers and duration of the ‘nectar bat season’, most participants in this project get only fleeting glimpses of bats visiting their feeders, and no effort has been made to systematically record visitation patterns using trail cameras or other recording devices. As a result, we currently do not know how long and how many bats continue to visit particular

feeders each night. We also do not know whether these patterns are consistent or highly variable from night to night. Nor do we know how quickly bats drain particular feeders and what happens after feeders are drained. Do bats continue to visit feeders after they have been drained or do they leave them? Finally, do bats consistently visit feeders in groups or as single individuals? Answers to these questions are important for understanding the foraging behavior of this nectar bat, which is an important pollinator of columnar cacti and paniculate agaves in southern Arizona and northwestern Mexico (e.g., Fleming *et al.*, 1996; Ober *et al.*, 2005).

My goal here was to provide preliminary answers to these questions by systematically recording bat visitations to several feeders all night throughout one season in Tucson, Arizona. None of the bats in this study were tagged, so we cannot easily infer individual behaviors from these data. But they do allow us to begin to answer most of the questions posed above. And these observations produced a surprising result. Many bats did not abandon feeders once they had been drained. Instead, they often continued to visit them for several hours, apparently lapping up the remaining few molecules of sugar water in them before returning to their day roosts.

## MATERIALS AND METHODS

### *The Study Area and Bat Netting*

This study was conducted in five backyards in and around Tucson, Arizona (latitude 32.3°N, longitude 110.9°W), from 16 August to 5 November 2021. I collected most of the detailed data in this paper at one of two saucer style feeders with transparent nectar wells in my yard; these feeders contained a total of 0.47 L of 22% (wt/wt) sugar water. Depth of the feeder well from the top of an opening to the bottom was 40 mm, which indicates the minimum tongue length bats need to touch the feeder's bottom. For comparison, the operational tongue length (i.e., the length of a bat's extended tongue when its snout is inserted into a 9–15 mm diameter feeding tube) of *L. yerbabuena* is 53–70 mm (Winter and von Helversen, 2003), suggesting that bats should be able to empty these feeders completely. These feeders were located about 12 m apart and hung from shepherd crooks about 1.8 m above ground. Many years of observation indicated that one feeder was always visited more often and was drained faster than the other one, so this is the one that was monitored during this study.

My colleagues and I have mist-netted bats in this yard on six occasions between 2009 and 2021. All captures were *L. yerbabuena*, and 67 of 68 (98.5%) were non-adult bats (juveniles and yearlings). Mean mass ( $\pm$  SE) of 19 bats captured in two 6-m mist nets between 19:10–21:00 h on 23 September 2021 was  $22.5 \pm 0.6$  g; captures included 13 females and 6 males (all non-adults). Therefore I assume that all of the bats visiting these feeders in 2021 were non-adult *L. yerbabuena*, and video clips confirmed this based on size and fur color (light in non-adults vs. darker in adults). When handling bats, we followed the guidelines of the American Society of Mammalogists (Sikes *et al.*, 2016).

Additional data were provided by four volunteers from the community science project (Fleming *et al.*, 2021). At the beginning of the 2021 'nectar bat season', an email announcement was sent to the volunteer community asking for people to monitor bat activity at their feeders with trail cameras or other recording devices. A data sheet requesting the following information was included: type of recording device, number and type of feeders being monitored, and a table with the following columns: date, time of first and last visits, time feeder(s) was drained, approximate number of bats visiting feeders following the ordinal scale used by Fleming *et al.* (2021), and general observations. Three people responded and provided a complete record for the nectar bat season; a fourth person submitted data from only the months of October and November.

### *The Recording and Data Summary Protocol*

To record bat visits for detailed analysis, I used a Browning Strike Force Max HD Trailcamera® (model BTC-5HD-MAX) powered by six Energizer Lithium® batteries (as recommended by the manufacturer) and mounted on a light stand 1.5 m above ground and placed about 2.8 m from the feeder. The motion-activated camera recorded 21 sec clips on a 32 GB SD card with a 5 sec delay between clips. I obtained most of the data for this report by surveying video clips on 22 nights between 28 August and 25 October after which neither feeder was completely drained. I usually viewed and scored only one clip every two minutes to avoid data redundancy and scored a mean ( $\pm$  SE) of

$49.7\% \pm 2.9\%$  ( $n = 21$  nights; an incomplete recording occurred on one night) of the clips each night. For each clip I recorded the number of feeding visits, being careful not to score approaches to the feeder but with no feeding as a visit, and the minimum number of bats seen in it. With practice I could usually identify new visits vs. revisits by bats in the same clip based on the timing of visits. I also scored the level of sugar water as percent remaining in the feeder throughout each night and noted when a group of bats was visiting the feeder. Bat behavior as well as the apparent absence of liquid in the feeder indicated when it was drained. After the feeder was drained, many bats continued to visit the feeder and attempted to acquire some liquid. During these visits it was often possible to see a bat's tongue 'searching' for droplets from the bottom of the feeder when it was empty. Finally, to document the intensity of use of the two feeders by bats throughout the season, I recorded the total percent liquid remaining in them early each morning before refilling them.

The four volunteers used either a trail camera ( $n = 2$ ) or security camera ( $n = 2$ ) to monitor their feeders. Recording devices were located within 3 m of a feeder. Methods used to determine time the feeder(s) was drained included visual inspection ( $n = 1$ ) or video images ( $n = 3$ ).

### *Data Summary*

For each of 22 nights between 16 August and 5 November 2021, I recorded the total number of video clips recorded; number of video clips scored; and number of feeding visits and minimum number of bats seen in each clip. For each of these nights, I also determined the total time in min between first and last visits; the time between first visit and peak visits (see below) and when the feeder was drained; and the time between when the feeder was empty and last visits. For the volunteers' datasets, I determined the time between when the feeder was drained and last visits each night and calculated an average for each observer's data. Their other data regarding time of first and last visits each night and length of the 'nectar bat season' were very similar to mine.

### *Statistical Analysis*

I used PSI-Plot v. 8 software ([www.polysoftware.com](http://www.polysoftware.com)) to summarize and analyze my nightly video data. I first calculated the overall mean  $\pm$  SE number of feeding visits and minimum number of bats per clip on 22 nights. On the 19 nights when the feeder was drained, I divided these data into two sets — one before the feeder was drained and one after it was drained — and recalculated mean number of visits and minimum number of bats for each set. I used a *t*-test to determine the probability that the means before and after the feeder was drained were the same each night. I also used this software to generate smooth curves based on 4th-order polynomial regression for data on feeding visits and minimum number of bats per clip for 22 nights. In these curves the independent variable was clip sequence number as a proxy for time and the dependent variables were numbers of feeder visits and bats per clip. The greatest number of bats per clip in the regression data was used to identify the time of peak bat visitation each night. I also used polynomial regression to summarize data on the mean number of bats per clip on 22 nights and the amount of liquid remaining in the two feeders combined each morning for the entire 'nectar bat season'.

From reviewing the clips and the temporal pattern of visits, it appeared that groups of bats were visiting the feeder. I used two methods to document this using data from 21 nights (19 in which the feeder was drained and two in which the feeder wasn't completely drained) between 28 August and 25 October. In the first method, I compared the number of bats recorded during successive time blocks of 10, 20, or 30 minutes to the number that would be expected based on a Poisson (random) distribution using the same mean value as that of the real observations. All 21 nights were combined in this analysis. I then compared the observed and expected distributions using  $\chi^2$  after pooling the data into six blocks: 0, 1–5, 6–10, 11–15, 16–20, and > 20 bats per 20 min period. Results using time blocks of 10 or 30 mins were similar.

In the second method, I examined each of the 21 complete night's data file to identify clusters of clips containing a higher than average number of bats for that night. For example, on 29 August between 01:00–01:08 h a series of consecutive clips contained the following number of bats: 2, 2, 5, 4, 4, 2, 2. I considered this string to represent the presence of a group of bats at the feeder between 01:04 h and 01:05 h. Using this method, it was relatively easy to identify most putative group visits each night. Comments in the 'Observations' column of these files that explicitly identified group activity usually supported this conclusion. Nonetheless, on a few occasions when more than one cluster of bats occurred close together in time, I had to decide whether these clusters represented the same or a different group. For example, on 12 September between 22:12 h and 23:10 h, the string of consecutive clips was 5, 5, 5, 6, 5, 5, 2, 4, 7, 3, 2, 4, 7, 6, and 7 bats. I scored this as two group visits: one at the feeder from 22:12 h to 22:46 h (the first nine clips) and another from 23:04 h to 23:10 h (the last three clips). I was generally conservative when this occurred and scored clusters of bats that occurred close in time as a single group rather than as separate groups. Because no individuals were tagged or otherwise recognizable, these data do not tell us whether the same or different group of individuals was visiting the feeder each night. In addition to tentatively identifying group visits each night, I also used the survey data to determine the length of time putative groups stayed at the feeder. I tallied each group visit on 21 nights as lasting  $\leq 10$  min (a short visit) or  $> 10$  min (a longer visit).

## RESULTS

### Nectar Bat Season

In 2021, nectar bats visited one or both of the two feeders from 16 August to 5 November (80 days). As in previous years, this curve was unimodal with a peak on 12 September in 2021 (Fig. 1). Both feeders were totally drained every night from 24 August

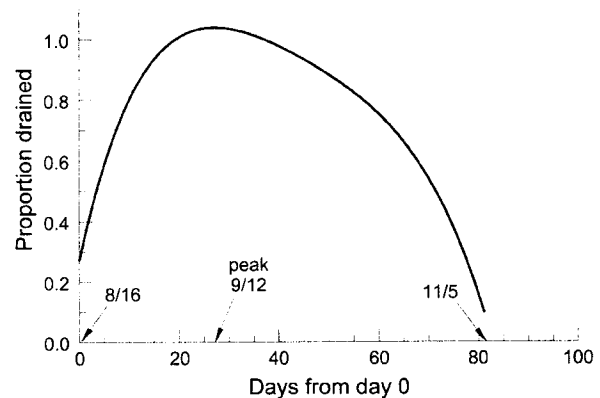


FIG. 1. Smoothed polynomial curve showing the proportion of liquid removed by *L. yerbabuena* from two feeders containing a total of 0.47 L each night during the 2021 nectar bat season. Correlation coefficient for this curve and the raw data is  $r = 0.74$ ,  $d.f. = 64$ ,  $P \ll 0.01$

to 6 October. The feeder I monitored was last drained completely on 24 October and was only partially drained each night from then until 5 November. Three of the four volunteers reported a similar length of the nectar bat season.

### Nightly Visitation Patterns

On many nights, particularly from early September on, bats began visiting this feeder shortly after sunset, which varied from 19:08 h MST on 15 August to 17:35 h MST on 31 October. Time of first visits each night varied from 20:33 h (about 1.5 h after sunset on 28 August) to 18:44 h (about 1 h after sunset on 21 October); time of last visits to the feeder ranged from 24:20 h (on 6 September) to 05:10 h (on 26 October). Data on mean length of time bats visited this feeder each night, the time between first visits to peak visits and when the feeder was drained, and the time from when the feeder was empty until bats left for the night are summarized in Table 1. Bats visited the feeder for about 7.2 h each night; peak visits occurred about 2.4 h after first visits; the feeder was drained about 3.7 h after first visits; and bats left the yard about 3.1 h after the feeder was drained. Three volunteers reported that

TABLE 1. Drain and duration statistics (in mins) for data recorded at one feeder on 22 nights between 28 August and 25 October 2021. Non-adults of *L. yerbabuena* were visiting this feeder.  $n$  = number of nights

Statistic	$n$	$\bar{x} \pm SE$	Median	Range
Time between first and last visits (mins)	22	429.3 $\pm$ 26.6	387	259–667
Time from first visits to peak visits (mins)	21	141.6 $\pm$ 30.4	130	0–572
Time from first visits to feeder drained (mins)	18	222.0 $\pm$ 20.5	232	82–462
Time from feeder drained to last visits (mins)	19	188.9 $\pm$ 24.3	171	18–351

the average time elapsed from when their feeders were drained to the last bat visit each night ranged from 3.5 h to 5.5 h (Table 2).

Data on average number of feeding visits and minimum number of bats per 21 sec video clip on 22 nights between 28 August and 25 October are summarized in Supplementary Table S1. Number of feeder visits and number of bats per clip were highly correlated, so I report only number of bats here. The greatest number of bats per clip ( $4.35 \pm 0.31$ ,  $n = 62$ ) occurred on 18–19 September (near the middle of the season), and the lowest number ( $1.76 \pm 0.12$ ,  $n = 74$ ) occurred on 21–22 October (near the end of the season). After a peak in the first half of September, average number of bats visiting this feeder each night remained more or less constant for a month until they gradually declined from 18 October on (Fig. 2).

The overall pattern of feeder visits and number of bats per clip was highly variable from night to night (see three examples of this variation in Fig. 3). Peak numbers of bats occurred before 22:30 h (about midway between periods of major bat visitations each night) on 13 of 21 nights (62%), but the feeder was drained before 22:30 h on only five of 18 nights (28%). Therefore, peak bat visits usually occurred well before the feeder was drained; but, notably, peak visits and when the feeder was drained both occurred after 22:30 h on eight of 18 nights (44%).

Additional evidence for this variation can be seen by dividing each night into two ‘halves’: early evening  $\leq 22:30$  h and late evening  $> 22:30$  h. Similarly, the entire season can be divided into two ‘halves’: early = before 21 September (near the midpoint of the season) and late = 21 September and later. Of the 12 nights with early peak bat numbers (i.e., those occurring at or before 2230 h), five (42%) occurred in the first half of the season and seven (58%) occurred in the second half (Table 3). Of nine nights with late peaks (i.e., those occurring after 22:30 h), three (33%) occurred in the first half of the season and six (67%) occurred in the second half. A similar tally of the occurrence of the time of feeder draining revealed that four of five early

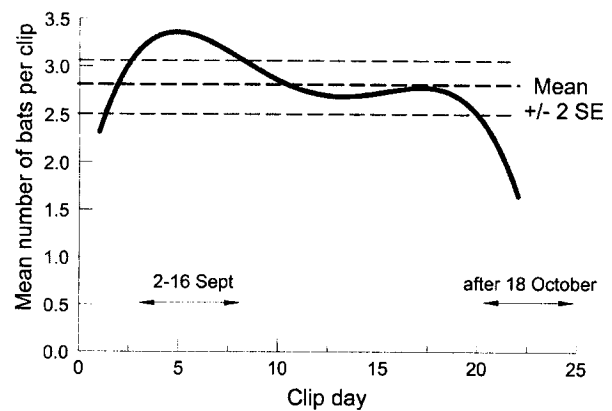


FIG. 2. Smoothed polynomial curve showing the mean  $\pm 2$  SE number of *L. yerbabuena* per video clip visiting one of feeder on 22 nights between 28 August and 25 October 2021. The figure indicates days in which the number of bats is significantly greater or less than the overall mean. Correlation coefficient for this curve and the raw data is  $r = 0.57$ ,  $d.f. = 20$ ,  $P = 0.01$

evening drains (80%) occurred in the first half of the season whereas nine of 13 late evening drains (69%) occurred in the second half of the season (Table 2). These data indicate that peak bat numbers sometimes occurred early in the evening throughout season whereas late evening peak numbers occurred mostly in the second half of the season. Bats were visiting the feeder later at night as the season progressed. Similarly, feeder drains in the early evening occurred mostly early in the season whereas late evening feeder drains were more common in the second half of the season, again indicating that bats were visiting this feeder later at night in the latter half of the season.

#### Response to Drained Feeders

Bats did not stop visiting the feeder once it was drained. Data summarizing the number of feeder visits and number of bats per clip before and after the feeder was drained are in Supplementary Table S2. On seven of 13 nights (54%), both number of feeder visits and number of bats per clip were significantly greater ( $P \leq 0.01$ ) before rather than after the feeder was drained. On one night visits

TABLE 2. Times of occurrence of peak visitation by non-adults of *L. yerbabuena* and when one feeder was drained on up to 21 nights between 28 August and 25 October, 2021

Time of visitation peaks and feeder drained	Dates of visitation peaks and feeder drained		Totals
	At or before 20 September	After 20 September	
Peaks at or before 22:30 h	5	7	12
Peaks after 22:30 h	3	6	9
Drained occurs at or before 22:30 h	4	1	5
Drained occurs after 22:30 h	4	9	13

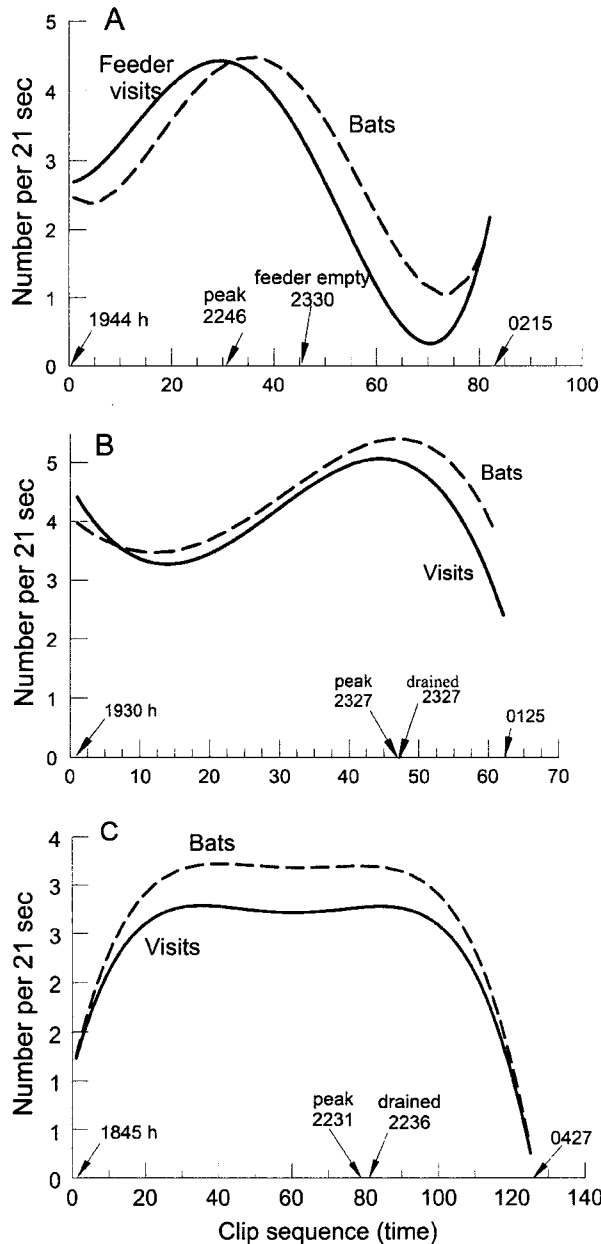


FIG. 3. Smoothed polynomial curves showing three examples of variation in the number of feeder visits by *L. yerbabuenae* and number of bats in 21 sec video clips at one feeder. The figure shows times of first and last visits and times of peak number of bats and when the feeder was drained. A — 12 September; B — 18 September; C — 10 October. Correlation coefficients for these data range from  $r = 0.27$  to  $0.57$  with  $d.f.$  of 60–134; all correlations are significant at  $P$  of  $0.05 > P > 0.01$  to  $P << 0.01$

were significantly greater after the feeder was drained, and on three nights number of bats per clip was significantly greater after the feeder was drained. On five and three nights, respectively, differences between number of visits and number of bats before and after the feeder was drained were not

significant. On no nights did bats stop visiting the feeder shortly after it was drained. As indicated above, some bats continued to visit feeders for up to 5.5 h or more after they were drained each night.

#### Occurrence of Groups at the Feeder

On most nights it was obvious that groups of nectar bats were visiting the feeder. Reflecting this, video clips would suddenly become filled with several bats flying around and visiting the feeder in rapid succession. Statistical support for the hypothesis that bats forage in groups comes with a comparison with a Poisson distribution which models independent events (visits). The observed number of bats recorded in 20 min time blocks (bins) differed greatly from a Poisson distribution with the same mean number of visits each night ( $\chi^2 = 237.7$ ,  $d.f. = 5$ ,  $P << 0.001$  — Fig. 4). Many more time bins contained either zero or many bats than expected by chance. Results using time bins of 10 or 30 mins were similar. Results also remained the same when the last hour before the feeder was drained was removed, showing that group visits were not solely the result of nectar levels.

On 19 nights in which the feeder was drained, average number of group visits was  $6.37 \pm 0.77$ . Number of group visits before the feeder was drained each night was significantly greater than the number after it was drained (before:  $\bar{x} \pm SE = 4.47 \pm 0.49$ ; after:  $1.89 \pm 0.33$ ;  $t = 4.34$ ,  $d.f. = 36$ ,  $P < 0.001$ ). Again, these results are notable because groups continued to visit the feeder after it was drained, often well into the early morning.

Duration of most group visits was short, and frequency of visits differed by time in the season. For example, out of a total of 131 group visits identified by this method, 92 (70.2%) lasted 10 min or less and 39 (29.7%) lasted more than 10 min. Only 32 (24.4%) of these visits occurred on or before 21 September, and 99 (75.6%) occurred after 21 September. Therefore, while most group visits were short throughout the season, group visits were over twice as common in the second half of the season as in the first half.

TABLE 3. Time between when feeders were drained and final departures of *L. yerbabuenae* each night as reported by three community science volunteers in Tucson, Arizona

Site	<i>n</i> nights	$\bar{x} \pm SE$ (min.)	Range (min.)
1	22	$296.5 \pm 29.7$	12–473
2	19	$208.3 \pm 16.5$	49–314
3	57	$327.4 \pm 13.1$	4–455

## DISCUSSION

This study has revealed that bats visit a particular feeder for up to seven hours a night, including five hours or more after a feeder has been drained; that visitation patterns are variable from night to night; and that groups of bats are likely to be visiting feeders. Results of previous studies of radio- or GPS-tagged individuals of *L. yerbabuena* can help us interpret these data. Studies conducted in southern Arizona and northern Sonora, Mexico, indicate that individuals of this cave- or mine-roosting bat travel substantial distances from their day roosts to their feeding areas (Table 4). For example, Lowery *et al.* (2009) reported that radio-tagged bats visiting hummingbird feeders in Tucson were commuting 2–40 km each night to feed. Average commuting distances reported in several studies ranged from 19 to 54 km (Table 4). Data from these studies indicate that flight speeds of commuting bats ranged from 15.5–32.8 kph (Buecher and Sidner, 2013).

Radio-tracking studies of *L. yerbabuena* (Table 4) also report that the estimated size of their foraging areas are large. In these relatively short-term studies, these areas ranged from 0.4 km<sup>2</sup> to 3.2 km<sup>2</sup>. Although Buechner and Sidner (2013) did not report size of foraging areas of bats visiting feeders in southern Arizona, their foraging maps also suggest that they had large foraging areas. In addition, these short-term tracking studies report that bats return to the same feeding areas on successive nights, that they forage for up to seven hours/night, and that they spend 17–37% of their time while foraging resting and digesting their food. Finally, group foraging in *L. yerbabuena* has been reported in bats visiting *Agave* inflorescences in southeastern Arizona, hummingbird feeders in southern Arizona,

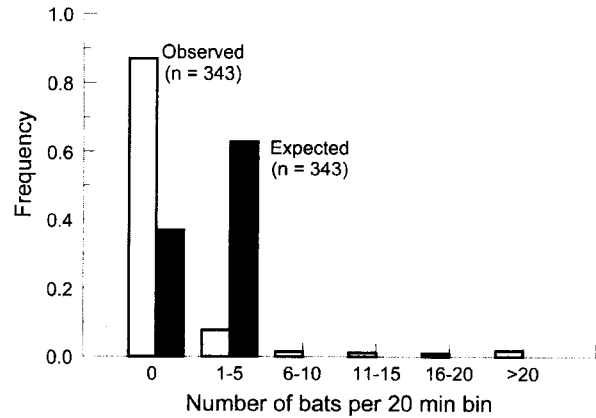


FIG. 4. Frequency distributions of the observed and expected number of *L. yerbabuena* recorded in 21 sec video clips at one feeder in consecutive time periods of 20 mins on 21 nights combined. The expected distribution is based on a Poisson (random) process based on the overall mean number of bats during these time periods. All values > 1–5 bats are observed (not expected) values. The two distributions are significantly different ( $\chi^2 = 237.7$ ,  $d.f. = 5$ ,  $P < 0.001$ )

and flowers of columnar cacti in Sonora, Mexico (Howell, 1979; Horner *et al.*, 1998; Buecher and Sidner, 2013). In contrast, group foraging was not reported to occur in bats feeding at saguaro flowers in northern Sonora (Egert-Berg *et al.*, 2018; Goldshtein *et al.*, 2020).

Given the variation in time of arrival of bats to the feeders in my yard each night, it is likely that they were coming from several different roosts. Previous studies of radio-tagged *L. yerbabuena* and other observations indicate that time of arrival at feeding areas is positively correlated with distance from their day roost (studies cited in Table 4 and Fleming *et al.*, 1998). Thus, bats arriving shortly after sunset were coming from a relatively close roost that was likely located  $\leq 10$  km from this yard whereas later arriving bats were possibly

TABLE 4. Examples of commuting distances from day roosts to feeding areas and size of foraging areas of radio- or GPS-tagged *L. yerbabuena*. Modified from Buecher and Sidner (2013)

Study area	Food resource	Average commuting distance (km)	Size of foraging areas (km <sup>2</sup> )	Source
Pima Co., AZ	Sugar water	28.8	0.40–0.50	Lowery <i>et al.</i> (2009)
Pima Co., AZ	Sugar water	35.4	Not reported but large	Buecher and Sidner (2013)
Cochise Co., AZ	Paniculate agaves	19.2	–	Ober and Steidl (2004)
Cochise Co., AZ	Paniculate agaves	27.4	–	Sidner (1996)
Sonora, MX	Columnar cacti	32.5	1.3–3.2 <sup>2</sup>	Horner <i>et al.</i> (1998)
Sonora, MX	Columnar cacti	44.5 <sup>1</sup>	–	Medellin <i>et al.</i> (2018)
Sonora, MX	Columnar cacti	53.5	Ca. 0.50 <sup>3</sup>	Goldshtein <i>et al.</i> (2020)

<sup>1</sup> — Determined using fluorescent dyes

<sup>2</sup> — Composite over three days

<sup>3</sup> — As determined from Fig. 2A

commuting from more distant roosts located in the Santa Catalina and Rincon mountains north and east of Tucson, respectively (Lowery *et al.*, 2009). Also, given that these bats have large foraging areas, the feeders in this yard are likely to be just one stop within their feeding areas. The high degree of variation in the timing and pattern of feeding visits each night suggests that bats were feeding in different parts of their foraging areas on different nights.

Howell (1979) reported that after ingesting about 4 g of nectar when feeding at inflorescences of *Agave palmeri* in southeastern Arizona, individuals of *L. yerbabuenae* rested for about 20 mins before feeding again. We presume bats visiting feeders in this study also took breaks to digest their meals. The occurrence of these breaks probably accounts for much of the ebb and flow of bats at feeders each night.

Contrary to the report by Egert-Berg *et al.* (2018) and Goldshtein *et al.* (2020), which concluded that *L. yerbabuenae* does not forage in groups when it visits flowers of saguaro (*Carnegiea gigantea*) based on acoustic and video evidence, several studies, including this one, report that group foraging occurs in this species (see studies cited in Table 4). Groups of these bats also visit flowers of cardón cactus (*Pachycereus pringlei*) in Baja California Sur (Winifred Frick, pers. comm.). Hence, most studies support the idea that *L. yerbabuenae* often forages in groups at the northern end of its geographic range. Since *L. yerbabuenae* appears to be a group forager that feeds on spatio-temporally predictable resources (i.e., flowering plants and hummingbird feeders), its behavior does not support the conclusion of Egert-Berg *et al.* (2018) that group foraging in bats, including *L. yerbabuenae*, occurs in species feeding on resources that have low spatio-temporal predictability. Whether their food resources are flowers of columnar cacti and agaves, fruits of columnar cacti, or sugar water in hummingbird feeders, groups of these bats are feeding on resources of relatively high nightly spatio-temporal predictability.

An alternate explanation for the temporally clumped arrival patterns of *L. yerbabuenae* at hummingbird feeders in the Tucson area is that bats are attracted to feeders based on detecting the feeding activity of other bats (Y. Yovel, personal communication), as occurs in insect-eating bats and gulls feeding on swarms of prey (Gotmark *et al.*, 1986; Boonman *et al.*, 2019). Based on the results of previous studies and this study, however, this explanation seems less likely than the hypothesis of group foraging. The rapid and usually short-lived

appearance of groups of bats at feeders does not suggest that they are the result of feeding attraction. Nonetheless, a study of the behavior of tagged individuals is needed to determine which of these two hypotheses is correct.

The most novel result from this study is that individuals and groups of *L. yerbabuenae* visit feeders long after they are drained. In my yard, one possible reason for this is that the second, less popular, feeder remained undrained after the first feeder was drained, giving bats a reason to prolong their stays. But when liquid levels in the two feeders were monitored simultaneously on 22 September, although bats drained the monitored feeder faster, both feeders were drained by 23:30 h and yet bats continued to visit the monitored feeder until 04:13 h (Supplementary Table S1 and author's unpublished data). Thus, it is unlikely that the second feeder continued to contain liquid much after the first feeder was drained each night. Bats probably continued to visit both empty feeders for an average of about 3 h after they were drained every night.

This behavior contrasts strongly with the foraging behavior of this bat at flowers of cardón cacti in Sonora, Mexico, and inflorescences of a paniculate agave (*Agave palmeri*) in southeastern Arizona. In both species, *L. yerbabuenae* did not completely drain individual flowers or inflorescences each night (Howell, 1979; Horner *et al.*, 1998; Slauson, 2000). However, they do drain and visit empty flowers of saguaro cacti in northern Sonora (Y. Yovel, personal communication). Nonetheless, it is striking that individuals and groups of *L. yerbabuenae* attempt to harvest the last dregs long after hummingbird feeders have been drained in Tucson.

A preliminary estimate of the foraging energetics of *L. yerbabuenae* and what visiting empty hummingbird feeders might cost them can be made using data from Sonora found in Fleming *et al.* (1996) and Horner *et al.* (1998). These studies describe nectar production in three species of columnar cacti (see below) and the foraging behavior of this bat while visiting their flowers. In the present study, my hummingbird feeders each contain 0.24 L of 22% w/w sugar solution (a similar nectar concentration as in saguaro flowers) for a total of about 915 kJ/feeder or 1,829 kJ in both feeders each night. Bats remove about 0.1 mL of nectar (= 0.41 kJ) per visit to cardón flowers (Fleming *et al.*, 1996), and I assume this holds for bats visiting hummingbird feeders. Based on a time-energy budget analysis, Horner *et al.* (1998) estimated that a 23 g non-reproductive *L. yerbabuenae* requires about 40.2 kJ/day to meet

its energetic needs. This value is similar to two other estimates (Howell, 1979; Nagy, 1987), and this value was used for my energetic calculations. In Sonora, a total of about 19.3 kJ of this daily budget is spent away from the day roost commuting (6.6 kJ), foraging (11.1 kJ), and night roosting (0.4 kJ).

In 7.2 h of foraging and night roosting each night, about 3.7 h (51%) occurs from first visits until the feeder is drained and an additional 3.1 h (49%) occurs between the time the feeder is drained and bats leave these feeders (Table 1). Of course, these values are global ones that do not necessarily reflect the times that individual bats are foraging; they are maximum values across all bats visiting these feeders. Nonetheless, they suggest that some bats could be expending nearly half of their foraging time (possibly about 5.6 kJ or 14% of their daily energetic needs) visiting feeders without obtaining an appreciable energetic reward.

These calculations suggest that attempting to obtain the last drops at hummingbird feeders can be energetically expensive for *L. yerbabuena*. The question then becomes, Why not leave empty feeders in search of other feeders or return to the day roost? Why do these bats continue to fly around expending energy and visiting feeders long after they are empty, especially at a time of year when they need to increase their fat reserves prior to migrating (Ceballos *et al.*, 1997)? While I cannot give a definitive answer to these questions, I can speculate about a possible reason for this behavior. Hummingbird feeders are obviously new food sources for these bats (especially non-adults) and in visiting them, they bring with them their experience with nectar production in flowers they have encountered in their current and past evolutionary history. When they visit flowers of columnar cacti and paniculate agaves, for example, they encounter relatively small amounts (1–2 mL) of 22–30% nectar per flower. Nectar production in these flowers occurs throughout the night, but it responds slowly to nectar removal by pollinators (Fleming *et al.*, 1996). Flowers can therefore be depleted each night, although bats do not necessarily do this before moving to another flower.

Given these flower characteristics, perhaps *L. yerbabuena* considers feeders to be giant flowers and continues to visit empty feeders with the expectation that they will begin to produce more ‘nectar’ each night. But it seems likely that these bats (even relatively inexperienced non-adults) should learn quickly that once feeders are empty, they will not begin to refill later that night. They should also

learn quickly that feeders usually do refill completely the next day, so perhaps this reinforces their tendency to continue visiting them after they’ve been drained. My data indicate that fewer bats appear to be visiting the feeder after it has been drained on most (but not all) nights, so it is possible that only a subset of the bat population persists in visiting empty feeders. Some bats probably move elsewhere once feeders are drained. Nonetheless, those that stay or arrive at empty feeders are burning a lot of energy with no apparent energetic reward. This implies that these bats must have plenty of energy to burn when feeding at hummingbird feeders. If this weren’t the case, this energetically non-optimal behavior should be strongly selected against.

Answering these questions ultimately depends on a better understanding of the foraging behavior of tagged individuals that visit hummingbird feeders. Do individuals consistently visit particular feeders throughout the season? How many feeders and different locations do they visit each night? Do groups of individuals consistently forage together night after night? Finally, how long do individuals continue to visit empty feeders each night and is this behavior consistent from night to night? Sandy Wolf and David Dalton have been pit-tagging *L. yerbabuena* captured at hummingbird feeders in southern Arizona. Their preliminary results seem to indicate that the behavior of individual bats is highly variable. Some individuals spend long periods each night visiting a feeder whereas others visit it for a short time before leaving and sometimes returning later that night; some individuals return to feeders night after night whereas others do not (S. Wolf, personal communication). These results and data from the present study tell us that we still have much to learn about the foraging behavior of this relatively well-studied nectar bat.

#### SUPPLEMENTARY INFORMATION

Contents: Supplementary Tables: Table S1. Summary of the feeder data at the main feeder that was monitored in Tucson, Arizona, in 2021. Mean number of feeder visits and minimum number of bats seen are for 21 sec video clips. Data from 22–23 September come from the second feeder in this yard; Table S2. Summary of visits by *L. yerbabuena* before and after one feeder was drained on 13 nights in 2021. Data come from 21 sec video clips. Supplementary Information is available exclusively on BioOne.

#### ACKNOWLEDGEMENTS

I am especially grateful to four community science volunteers — Wes Bunker, Ralph Monge, Steve Powell, and Melina



Tye — for providing results of their video monitoring efforts. Rhonda James monitored my feeders when I was away. Scott and Kendra Richardson and Marcia Fleming assisted with bat netting. I thank Chuck Claver for help with a preliminary analysis of nightly bat visitation patterns and Sandy Wolf for sharing their pit-tagging observations. Yossi Yovel graciously helped with the Poisson analysis. Brock Fenton, Nathan Muchhala, Yossi Yovel, and Jerry Wilkinson provided useful discussions about these results. Brock Fenton, Nathan Muchhala, and Yossi Yovel commented on previous versions of this paper. I thank two anonymous reviewers for their comments that improved this paper.

#### LITERATURE CITED

- BOONMAN, A., B. FENTON, and Y. YOVEL. 2019. The benefits of insect-swarm hunting to insect-eating bats, and its influence on the evolution of bat echolocation signals. *PLoS Computational Biology*, 15: e1006873.
- BUECHER, D. C., and R. SIDNER. 2013. Long distance commutes by lesser long-nosed bats (*Leptonycteris yerbabuena*) to visit residential hummingbird feeders. Pp. 427–433, in *Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III and 7th Conference on Research and Resource Management in the Southwestern Deserts*; May 1–5, 2012; Tucson, AZ (G. J. GOTTFRIED, P. F. FFOLIOTT, B. S. GEBOW, L. G. ESKEW and L. C. COLLINS, comps.). Proceedings RMRS-P-67. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station, 593 pp.
- CEBALLOS, G., T. H. FLEMING, C. CHAVEZ, and J. NASSAR. 1997. Population dynamics of *Leptonycteris curasoae* (Chiroptera: Phyllostomidae) in Jalisco, Mexico. *Journal of Mammalogy*, 78: 1220–1230.
- EGERT-BERG, K., E. R. HURME, S. GREIF, A. GOLDSHTEIN, L. HARTEN, G. H. M. LUIS, *et al.* 2018. Resource ephemerality drives social foraging in bats. *Current Biology*, 28: 3667–3673.e5.
- FLEMING, T. H., M. D. TUTTLE, and M. A. HORNER. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. *Southwestern Naturalist*, 41: 257–269.
- FLEMING, T. H., S. MAURICE, and J. L. HAMRICK. 1998. Geographic variation in the breeding system and the evolutionary stability of trioecy in *Pachycereus pringlei*. *Evolutionary Ecology*, 12: 279–289.
- FLEMING, T. H., S. RICHARDSON, and E. H. SCOBIE. 2021. 'Free' food: nectar bats at hummingbird feeders in southern Arizona. *Journal of Mammalogy*, 102: 1128–1137.
- GOLDSHTEIN, A., M. HANDEL, O. EITAN, A. BONSTEIN, T. SHALER, *et al.* 2020. Reinforcement learning enables resource partitioning in foraging bats. *Current Biology*, 30: 1–7.
- GOTMARK, F., D. W. WINKLER, and M. ANDERSSON. 1986. Flock feeding on fish schools increases individual feeding success in gulls. *Nature*, 319: 589–591.
- HORNER, M. A., T. H. FLEMING, and C. T. SAHLEY. 1998. Foraging behaviour and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). *Journal of Zoology*, 244: 575–586.
- HOWELL, D. J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and to the host plants. *American Naturalist*, 114: 23–49.
- LOWERY, S. F., S. T. BLACKMAN, and D. ABBATE. 2009. Urban movement patterns of lesser long-nosed bats (*Leptonycteris curasoae*): management implications for the Habitat Conservation Plan within the city of Tucson and town of Marana. Research Branch, Arizona Game and Fish Department, Phoenix, Arizona, 25 pp.
- MEDELLIN, R. A., M. RIVERO, A. I. BARA, J. A. DE LA TORRE, T. P. GONZALEZ-TERRAZAS, T. P. TORRES-KOOP, *et al.* 2018. Follow me: foraging distances of *Leptonycteris yerbabuena* (Chiroptera: Phyllostomidae) in Sonora determined by fluorescent powder. *Journal of Mammalogy*, 99: 306–311.
- NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs*, 57: 111–128.
- OBER, H. K., and R. J. STEIDL. 2004. Foraging rates of *Leptonycteris curasoae* vary with characteristics of *Agave palmeri*. *Southwestern Naturalist*, 49: 68–74.
- OBER, H. K., R. J. STEIDL, and V. M. DALTON. 2005. Resource and spatial-use patterns of an endangered vertebrate pollinator, the lesser long-nosed bat. *Journal of Wildlife Management*, 69: 1615–1622.
- SIDNER, R. 1996. Sixth annual monitoring of potential roostsites of the lesser long-nosed bat (*Leptonycteris curasoae*) and other species of bats on the Fort Huachuca Military Reservation, Cochise County, Arizona, May–December 1995. USAG Commander through Engineering and Environmental Consultants, Inc., 122 pp.
- SIKES, R. S., and THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97: 663–688.
- SLAUSON, L. A. 2000. Pollination biology of two chiropterophilous agaves in Arizona. *American Journal of Botany*, 87: 825–836.
- WINTER, Y., and O. VON HELVERSEN. 2003. Operational tongue length in phyllostomid nectar-feeding bats. *Journal of Mammalogy*, 84: 886–896.

Received 03 July 2022, accepted 27 September 2022

Associate Editor: Wiesław Bogdanowicz

