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ABSTRACT

Niche partitioning is an important form of ecological differentiation that allows two or more species to co-exist. It has also been shown to be responsible for maintaining the vast diversity of bat species found in the tropics (Aguirre et al. 2002). A community of frugivorous bats in the San Luis Valley, Costa Rica, was sampled to determine the parameters of niche differentiation used by the bats. The study took place at the San Luis Ecolodge at 1100 meters in elevation in premontane wet secondary forest. Bats were mist netted using two 12-meter mist nets over seven nights in the month of April, 2005. Time of capture, forearm measurements and weights were recorded and fecal samples were collected. Seeds present in the samples were identified to species to determine if the bats were differentiating niches based on species of plant consumed. There was no niche partitioning due to plant species, but statistical significance was found when time of foraging and the size of the bat compared to the species of fruit eaten were analyzed. It was determined that the species were differentiating niches based on fruit size and time of foraging.

RESUMEN

La división de los nichos es una forma importante de diferenciación ecológica que permite a dos o más especies coexistir. Se ha demostrado que también es responsable de mantener la amplia diversidad de especies de murciélagos que se encuentran en los trópicos (Aguirre et al. 2002). Una comunidad de murciélagos frugívoros en el Valle de San Luis, Costa Rica fue usada para determinar los parámetros de la diferenciación del nicho utilizados. El estudio se llevó a cabo en el San Luis Ecolodge de San Luis, a 1100 metros de elevación, en un bosque húmedo premontano secundario. Los murciélagos fueron atrapados, con dos redes de 12 metros de largo cada una, durante siete noches en el mes de abril del 2005. El tiempo de la captura, la longitud del antebrazo y el peso fueron registrados; también se recolectaron muestras fecales. Las semillas presentes en las muestras fueron identificadas para determinar si los murciélagos repartían los nichos de acuerdo con las especies de plantas que consumían. No hubo una división significativa de nichos en las especies de plantas, pero se encontraron diferencias significativas cuando se comparó el tiempo de forrajeo y el tamaño de los murciélagos con el tamaño de la fruta comsumida. Por lo tanto, se determinó que las especies repartían sus nichos de acuerdo con el tamaño de la fruta y el tiempo de forrajeo.

INTRODUCTION

The tropics are famous for the incredible diversity of organisms that they house. According to Fleming (1973), there are twice as many species of mammals in tropical forests than in temperate forests. Many studies have attempted to explain the abiotic and biotic factors that allow this dense and diverse array of flora and fauna to co-exist.

Orians (1966) found that tropical forests contain 2-2.5 times as many resident birds than temperate forests and attributed the increase in species to greater stability of food sources in the tropics. In fact, it was determined that 25-50% of the increase in species was due to the addition of a new food source (Orians 1966). Yet, the Competitive Exclusion Principle states that organisms that compete for the same resources cannot co-exist (Hutchinson 1959). In order to coexist, two species must differ in the ecological resources they utilize by evolving specialized roles or niches within the community (McNab 1971). Many of these parameters of differentiation are associated with the partitioning of food resources (McNab 1971). Most importantly, niche partitioning has been shown to produce and sustain a greater diversity in bat species for the tropics (Aguirre et al. 2002). Niche partitioning can occur for any resource that a species utilizes including food, space, time and microhabitat (Petren 2001). By understanding the niche parameters of an organism, species interactions and community structure can be better understood (Macarthur 1958).

Frugivorous bats rely on a large variety of fruiting plants throughout the year because at any one time of the year, only a certain subset of the plants is fruiting. Thus, one would expect that resource partitioning is occurring among these communities. For example, there are13 species of frugivorous bats that utilize 41 species of fruiting plants in the Monteverde region of Costa Rica (Dinerstein 1983). The 41 species were located in four life zones; of these only ten fruited in April of 1981 and more specifically, of the eight that were located in zone one at 1300 meters, only four fruited during the month of April (Dinerstein 1983). This reduction in variety of resources in one month during the dry season raises the question of how niche partitioning is occurring in this community and along which parameters. The purpose of this study was to determine how a frugivorous bat community in the San Luis Valley, Costa Rica divided resources during this time of lower food availability.

MATERIALS AND METHODS

Study Site

The study was conducted at 1100 meters in premontane wet secondary forest at the San Luis Ecolodge in the San Luis Valley, Costa Rica. The study site was located on a system of trails directly behind the Ecolodge, some of which were lined with cuadrado patches and casitas, while the rest were lined by secondary undergrowth (Figure 1).

Field Work

Bats were mist netted seven nights at the end of April and beginning of May 2005 (see Table 1 for weather data). Two 12-meter nets were used each night, except for one night in which only one net was used, and they were opened at 6:30 PM and closed at 10:00 PM. The nets were placed lengthwise on the trails and were never within visual distance of each other. They were moved every two days to prevent avoidance by the bats; however, several sites were used more than once after seven or more days without use.

Each night, the nets were each baited with two cuadrados and were checked every 15 to 30 minutes.

Upon capture, bats were carefully taken from the nets and if a fecal sample was available at that time, they were processed and released immediately. If a fecal sample could not be obtained directly after capture, the bats were placed in cloth holding bags for 30 to 45 minutes to allow defecation. The bats were never held for more than an hour. They were then removed and identified to species using the book "Murciélagos de Costa Rica" (LaVal R. K. and B. Rodíguez-H 2002) and the field guide "A Field Key to the Bats of Costa Rica" (Timm R. M. and R. K. LaVal 1998). Digital pictures were taken when identification could not be made in the field, and Richard LaVal was consulted at a later date for accurate species identification. The reproductive states were assessed after identification and weights and forearm measurements were taken and recorded (Appendix B, Figures 3 and 4, respectively). The forearm was defined as the length of the wing when folded. Bats were marked with paint pens prior to release either on the wing or tail membrane to ensure that recaptures were not counted as different individuals. Samples were collected from the holding bag and placed in a marked glass vial, and the holding bag was cleaned of all feces and seeds before being reused (Figures 3 and 4).

Lab Work

Seeds from the fecal samples were cleaned using a tweezers and alcohol in a petri dish and placed in clean alcohol for preservation. They were examined under a dissecting microscope and identified using fruit samples from the field and Richard LaVal's seed collection. Individual species found were preserved and labeled for future reference.

RESULTS

A total of 56 bats were caught, 14 species in seven genera, 12 of which were frugivorous (Figure 2, Appendix B). Fecal samples were obtained from 37 bats, 22 of which contained *Cecropia obtusofolia*, 12 samples contained *Piper bisasperatum*, one sample contained *Piper auritum*, one sample contained *Piper cuspidispicum* and one sample contained both *C. obtusofolia* and *P. bisasperatum* seeds (Appendix A). Both the weight and forearm measurements differed significantly between species that yielded samples containing *Cecropia* seeds versus those measurements of the species that yielded samples containing *Piper* seeds (t-test for weights $p = 0.018$, t-test for forearm lengths $p = 0.001$) (Figures 3 and 4). Statistical significance was also found when the difference in the time of capture was analyzed for all species (Kruskal-Wallis $p = 0.009$), for species that ate *Cecropia* fruit (Kruskal-Wallis $p = 0.006$) and the difference in time of capture for the large species that ate *Cecropia* fruit (Kruskal-Wallis $p = 0.014$) (Appendix B). Statistical significance was not found when the difference in time of capture was analyzed for species that ate *Piper* (Kruskal-Wallis $p = 0.176$) nor was it significant for the small species that ate *Piper* (Kruskal-Wallis $p = 0.156$).

DISCUSSION

Since each of the twelve species of frugivorous bats ate either *C. obtusofolia* or *P. bisasperatum* with little or no overlap, niche partitioning was not occurring according to the species of plant consumed (Appendix A). However, niche partitioning was occurring according to the size of the bat and the size of the fruit (Figures 3 and 4). The species that ate *C. obtusofolia* were significantly larger than those that ate *P. bisasperatum*, and although the dry mass of these fruits was never measured, according to Richard LaVal and personal observations, *C. obtusofolia* is the larger of the two fruits (LaVal pers. comm.).

The bats were also partitioning according to the time of foraging, as proven by the statistical significance found when the times of capture were analyzed (Appendix B). More specifically, temporal niche partitioning was shown in the *Cecropia* eating subset of bats with significance found not only when the time of capture for all species was compared, but also when the time of capture for the large species of bats were analyzed. However, this was not the case when the times of capture were analyzed for all *Piper* eating bats or for the small species found eating *Piper*. This could be due to the fewer number of individuals that ate *Piper* compared to the number that ate *Cecropia* (Figures 3 and 4). It could also be that there is greater competition between the larger bats for the *Cecropia* fruits in order to minimize foraging efforts and maximize nutrient intake. The Optimal Foraging Theory states that the fitness of a foraging animal is a function of the efficiency of foraging as assessed in terms of some currency, usually energy (Pyke et al. 1977). Of the many factors that influence energy expenditure in mammals, the most important one is body size (McNab 1979). Mass-specific measurements show decreasing energy use with increasing body mass meaning that larger bats would have a lower rate of energy use when proportionally compared to smaller bats (Masters K. and A. Masters 2005). Even though small bats have higher energy requirements than large bats, it is still beneficial to the fitness of both to be as efficient as possible when foraging. Because of this, it would be more efficient for both sizes to minimize activity spent foraging by eating large fruits. However, there is a larger base of fruits that small bats can efficiently use if both *Cecropia* and *Piper* are considered to be available resources. Conversely, if by the Optimal Foraging Theory, *Cecropia* is considered the only fruit present in the samples that large bats could efficiently exploit, then there is a smaller base of fruits available to them. In order for the species of large bats to coexist with these restricted parameters and increased competition, finer niche partitioning is occurs. This is one of the possible explanations for the more specialized time niche partitioning seen not only in the guild of *Cecropia* eating bats, but in the large bat species that ate *Cecropia* as compared to the *Piper* eating guild which had no significance regarding time of foraging.

In summary, the community of bats studied differentiated along fruit size and temporal parameters and did not differentiate based on species of fruiting plants exploited. Unfortunately, a list of species and their fruiting peaks and patterns in the San Luis Valley does not exist; therefore, it is not possible to know if these four species were the only fruiting plants available at that time, or if there were others fruiting which were neglected by the bats. However, it is clear that the individual species in this community exploited resources during this dry season month through niche partitioning based on temporal and fruit size parameters.

Future studies could add to the knowledge of this topic by assessing the fruiting peaks and patterns of the San Luis Valley and comparing these trends to the manner of niche partitioning utilized by the bat populations during that time of year. In addition, a comprehensive list of bat species for the San Luis Valley does not exist and would be very helpful for future studies conducted there.

ACKNOWLEDGEMENTS

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TABLE 1. Weather data during April and May of 2005 for the nights when the mist nets were set up. The full moon occurred on April 24, 2005.

Date	Min Temp (C)	Max Temp (C)	Precip (mm)	Cloud Cover (%)
22-Apr	17	31	1	25
24-Apr	17	31	2	5
26-Apr	18	32	3	30
27-Apr	17	32	2	45
28-Apr	19	34	0	50
2-May	17	30	0	70
3-May	17	32	4	65

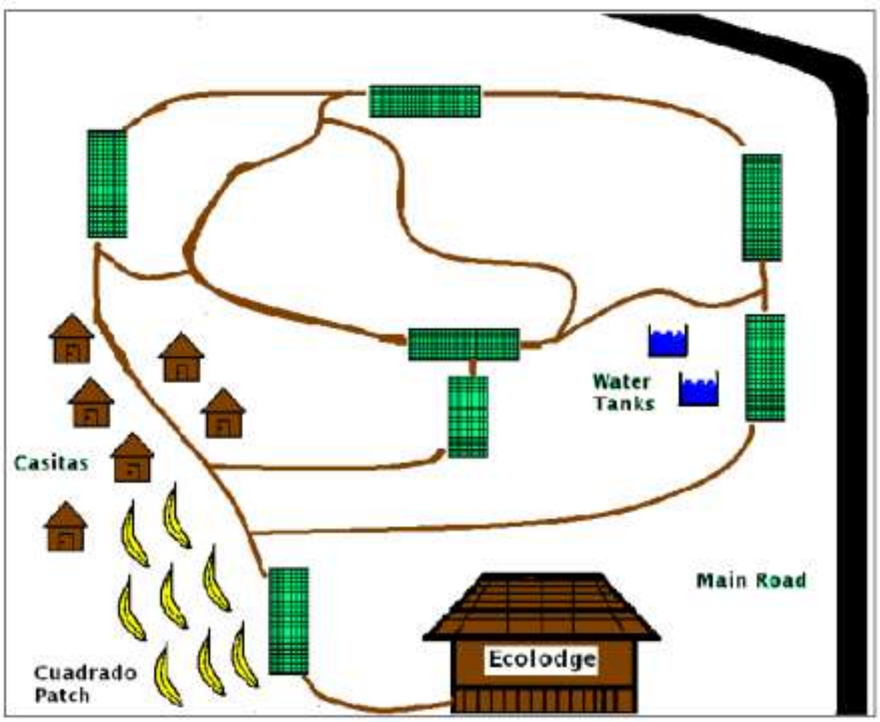

FIGURE 1. Diagram of the San Luis Ecolodge in the San Luis Valley, Costa Rica. All of the mist net sites used are marked by a net on the trail. Nets were always placed lengthwise along the trails and were only left in the same place for two days but may have been used again with a week in between.

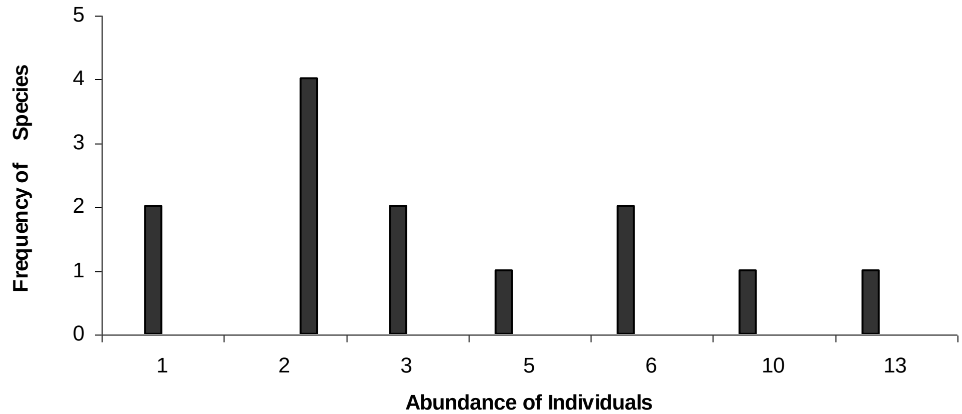

FIGURE 2. Frequency distributions of the bat species caught at the San Luis Ecolodge in the San Luis Valley, Costa Rica. There was an uneven distribution of individuals caught for each species. Also see Appendix B.

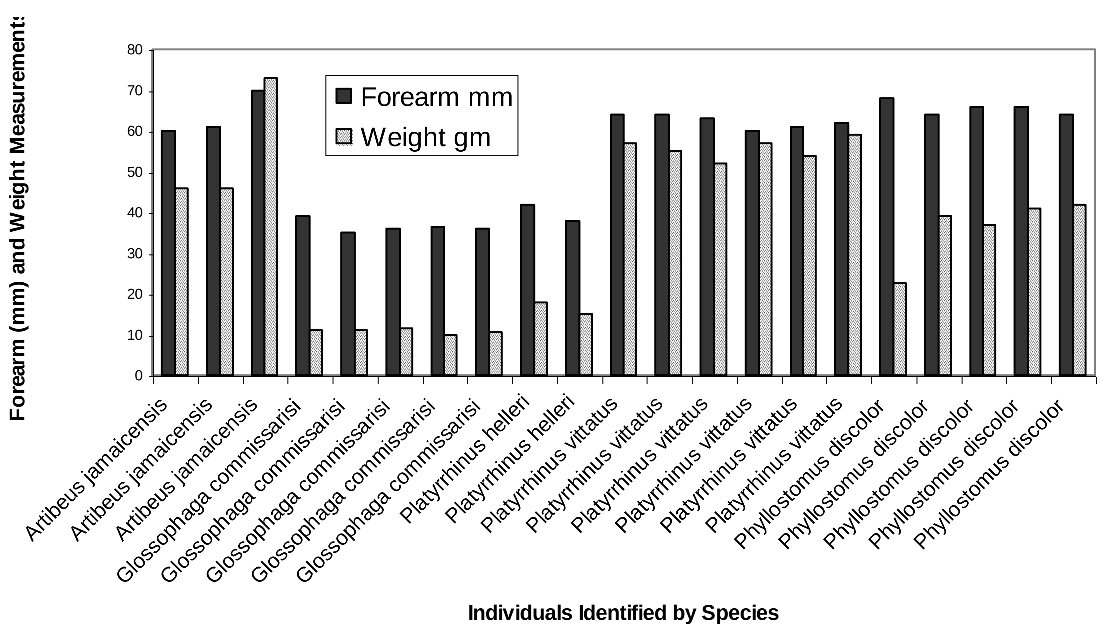

FIGURE 3. Forearm (mm) and weight (g) measurements for all individuals, by species that ate *C. obtusofolia*.

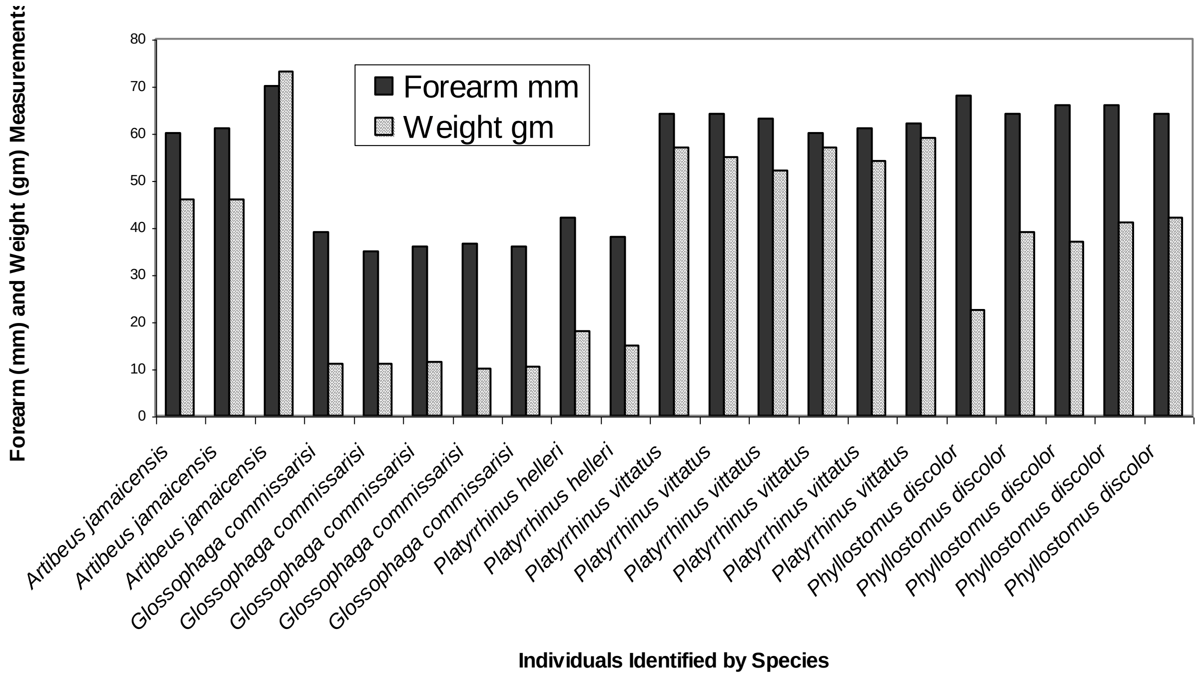

FIGURE 4. Forearm (mm) and weight (g) measurements for all individuals, be species that ate *P. auritum, P. bisasperatum*, and *P. cuspidispicum*.

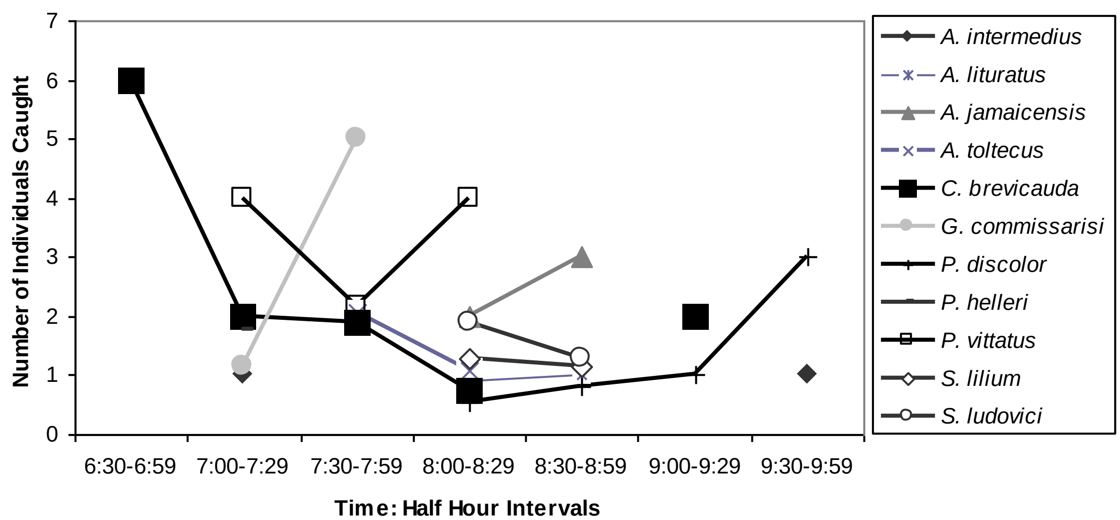

FIGURE 5. Time Niche Partitioning within all species of frugivorous bats caught in the San Luis Valley, Costa Rica. Time scale is every half hour from 6:30 PM to 10:00 PM. Also see Appendix B.

APPENDICES

Appendix A: List of individuals, by species, caught in the San Luis Valley Costa Rica and what was found in their fecal sample.

Species	Seeds Found in Feces Sample
Artibeus intermedius	P. bisosperatum
Artibeus lituratus	C. obtusofolia
Artibeus jamaicensis	C. obtusofolia
Artibeus jamaicensis	C. obtusofolia
Artibeus jamaicensis	C. obtusofolia
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. cuspidispicum
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. bisosperatum
Carollia brevicauda	P. bisosperatum
Glossophaga commissarisi	C. obtusofolia
Glossophaga commissarisi	C. obtusofolia
Glossophaga commissarisi	C. obtusofolia
Glossophaga commissarisi	C. obtusofolia
Glossophaga commissarisi	C. obtusofolia
Glossophaga commissarisi	C. obtusofolia., P. bisosperatum
Phyllostomus discolor	C. obtusofolia
Phyllostomus discolor	P. bisosperatum
Phyllostomus discolor	C. obtusofolia
Phyllostomus discolor	C. obtusofolia
Phyllostomus discolor	C. obtusofolia
Phyllostomus discolor	C. obtusofolia
Platyrrhinus helleri	C. obtusofolia
Platyrrhinus helleri	C. obtusofolia
Platyrrhinus vittatus	C. obtusofolia
Platyrrhinus vittatus	C. obtusofolia
Platyrrhinus vittatus	C. obtusofolia
Platyrrhinus vittatus	C. obtusofolia
Platyrrhinus vittatus	C. obtusofolia
Platyrrhinus vittatus	C. obtusofolia
Sturnira lilium	P. auritum
Sturnira lilium	P. bisosperatum
Sturnira ludovici	P. bisosperatum

Appendix B: List of all individuals, by species, caught in the San Luis Valley of Costa Rica, the time of capture of each individual, and the reproductive state of the individual. ‘Lactating Female” was a female with mammary glands under the wings, “Reproductive Male” was a male with prominent testes, “Male” was a male that lacked prominent testes and “Term Pregnancy” was a female with an enlarged abdomen and above average weight measurement.

Species	Time of Capture	Reproductive State
Artibeus intermedius	19:00	Lactating Female
Artibeus intermedius	21:30	Reproductive Male
Artibeus jamaicensis	20:00	Reproductive Male
Artibeus jamaicensis	19:20	Lactating Female
Artibeus jamaicensis	20:45	Male
Artibeus jamaicensis	20:45	Male
Artibeus jamaicensis	20:50	
Artibeus lituratus	20:00	Reproductive Male
Artibeus lituratus	20:30	Reproductive Male
Artibeus toltecus	20:15	Lactating Female
Artibeus toltecus	19:30	Male
Artibeus toltecus	19:45	Lactating Female
Carollia brevicauda	18:30	Lactating Female
Carollia brevicauda	18:30	Term Pregnancy
Carollia brevicauda	18:30	Term Pregnancy
Carollia brevicauda	18:45	Male
Carollia brevicauda	19:30	Term Pregnancy
Carollia brevicauda	20:00	Reproductive Male
Carollia brevicauda	18:40	Male
Carollia brevicauda	19:20	Reproductive Male
Carollia brevicauda	19:50	Reproductive Male
Carollia brevicauda	19:11	Term Pregnancy
Carollia brevicauda	18:30	Male
Carollia brevicauda	21:10	Reproductive Male
Carollia brevicauda	21:10	Lactating Female
Carollia perspicallata	20:15	Male
Glossophaga commissarisi	19:30	Reproductive Male
Glossophaga commissarisi	19:30	Male
Glossophaga commissarisi	19:45	Reproductive Male
Glossophaga commissarisi	19:45	Reproductive Male
Glossophaga commissarisi	19:45	Reproductive Male
Glossophaga commissarisi	19:10	Male
Myotis keaysi	21:00	Male
Platyrrhinus helleri	19:00	Lactating Female
Platyrrhinus helleri	19:05	Male
Platyrrhinus vittatus	19:00	Reproductive Male
Platyrrhinus vittatus	19:00	Reproductive Male
Platyrrhinus vittatus	20:15	Reproductive Male
Platyrrhinus vittatus	20:15	Male
Platyrrhinus vittatus	19:30	Reproductive Male

Platyrrhinus vittatus	19:10	Reproductive Male
Platyrrhinus vittatus	20:00	Reproductive Male
Platyrrhinus vittatus	20:20	Reproductive Male
Platyrrhinus vittatus	19:20	Reproductive Male
Platyrrhinus vittatus	19:50	Reproductive Male
Phyllostomus discolor	20:25	Male
Phyllostomus discolor	20:50	Reproductive Male
Phyllostomus discolor	21:00	Male
Phyllostomus discolor	21:30	Male
Phyllostomus discolor	21:40	Male
Phyllostomus discolor	21:40	Male
Sturnira lilium	19:50	Reproductive Male
Sturnira lilium	20:20	Lactating Female
Sturnira ludovici	20:15	Term Pregnancy
Sturnira ludovici	21:30	Term Pregnancy
Sturnira ludovici	20:00	Term Pregnancy