

Temporal resource partitioning by bats at water holes

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Abstract

The temporal axis of niche (temporally based resource partitioning) is an understudied mechanism for resource partitioning in mammals even though it provides a potential means for species coexistence. Herein we evaluate species-specific use curves based upon capture times during the overlapping activity of bat species at two water holes in an arid environment where bats likely suffer high levels of evaporative water loss during roosting. During the first 75 min after sunset, intense bat activity at each water hole ensued and, although visitation times overlapped, there was a significant difference among species use curves. In addition, pairwise comparisons showed high similarity in temporal visitation patterns across sites for species in which capture numbers were comparable, whereas other species shifted to significantly earlier arrival times when their capture numbers were higher. There were no significant differences in mean roost site emergence times among species, nor in distance of roost sites from water holes. Our data provide one of the few statistically verified examples of fine-grain temporal partitioning by mammals simultaneously using the same resource. We conclude that temporal partitioning helps facilitate bat species coexistence in water-stressed environments.

Introduction

In mammals, niche differences that facilitate species coexistence have been most intensely studied for sympatric species of Carnivora, and many of these investigations have elucidated coarse-grain (large-scale) differences associated with prey size preferences related to predator body sizes (Greene & Jaksic, 1983; Dayan *et al.*, 1990; Carbone & Gittleman, 2002), habitat partitioning (Lavin *et al.*, 2003; Chamberlain & Leopold, 2005) and temporal partitioning (i.e. dusk to night vs. morning activity peaks; Jácomo, Silveira & Diniz-Filho, 2004). Other studies have documented microhabitat differences among sympatric carnivore species (Johnson & Franklin, 1994; Kruuk *et al.*, 1994), and thus the use of fine-grained analysis can uncover resource partitioning that is missed by more coarse-grain analysis.

Similarly, some coexisting bat species have been shown to demonstrate coarse-grain differences in time and space with respect to food resources and habitat use (Jones, 1965; Kunz, 1973; La Val *et al.*, 1977; Reith, 1980; Thomas, 1985; Aldridge & Rautenbach, 1987; Willig, Camilo & Noble, 1993; Arlettaz, 1996). Although these studies have added significantly to our understanding of bat species coexistence, investigations into more fine-grained temporal partitioning of resource use may reveal refinements that are subtle, but nonetheless important for species coexistence.

In the present study, we use a fine-grain analysis of overlapping visitation times at water holes to test the

hypothesis that bat species will temporally partition the use of water holes that are too small to accommodate spatial separation and thus simultaneous use. This approach not only provides insight into fine-grain resource partitioning and species coexistence, but also offers a model for investigations of the temporal axis of niches.

Our rationale for investigating how bats use water resources in water-limited environments is prompted by previous laboratory studies on bat ecophysiology, behavior and ecology. Small-bodied, temperate bats experience high levels of evaporative water (15–31% body mass) loss during diurnal roosting when placed in a high-temperature (≥ 26.8 °C), low-humidity environment ($\leq 20\%$) (e.g. Studier, Proctor & Howell, 1970; O'Farrell, Studier & Ewing, 1971; Studier & O'Farrell, 1976; Webb, 1995; Webb, Speakman & Racey, 1995) and replenishment of at least 20% of daily water reserves is achieved through drinking at water sources (Kurta *et al.*, 1989a,b; Kurta, Kunz & Nagy, 1990; McLean & Speakman, 1999). Naturally occurring calm water sources in xeric habitats are scarce and small point sources, because of their limited size and availability, typically concentrate high levels of bat activity (Szewczak *et al.*, 1998; Adams & Simmons, 2002), which may limit physical access to the resource (Findley, 1993). Thus, xeric regions provide an opportunity to test whether water holes can exert a structuring force on sympatric bat populations.

Despite the potentially significant constraints imposed by limited water availability in xeric environments, few studies have addressed the potential for resource partitioning by bat

species. Commissaris (1961) gathered data on visitation times for most of 16 bat species at two water holes in Arizona. Cockrum & Cross's (1964) analysis of Commissaris's data showed temporal displacement, but they could not account for observed patterns because of a lack of data for potential causative factors (i.e. roost site emergence times and distances between roost sites and water holes). Jones (1965) pooled data on bats captured at water tanks, mines and caves in Arizona to test for species differences in general activity, but data on specific arrival times at water holes were not presented. O'Farrell & Bradley (1970) presented compelling evidence that greatest differences in arrival times between *Pipistrellus hesperus* and *Myotis californicus* at a desert spring in Nevada occurred from May to September, presumably when water demands for bats are highest.

We tested the hypothesis of temporal partitioning of bat species at water holes by quantifying the arrival (capture) times of individuals of five *Myotis* species visiting two active water holes in Colorado. Our hypothesis is that there would be no significant temporal differences among bat species using the same water hole (i.e. complete overlap). In addition, we radio-tagged individuals, located roost sites and collected data on time of emergence as well as calculated the distance of roost sites from the water holes to evaluate their influence on species arrival times.

Materials and methods

Study site and bat species

To test our hypothesis, we chose two water holes that lay in close proximity to the majority of roost sites known for bat species in the area. We reasoned that water holes closest to bat roosting sites would be the most likely to have activity levels necessary to induce resource partitioning. Both were located in mixed coniferous forest, along streams that run ephemerally, but maintain small pools year round. The two water holes were separated by about 2.9 km and ridges ranging from 2170 to 2232 m in elevation and were located in the foothills west of Boulder, Colorado. They were similar in size [Bear Creek Canyon (BCC) = 2.5 m diameter; Shadow Canyon (SC) = 2 m diameter] and occurred at similar elevations (BCC = 1829 m, SC = 1922 m). Along both drainages, dense overhanging vegetation made access by bats difficult, except where gaps in vegetation coincided with pools of water.

Although 12 species (Armstrong, Adams & Taylor, 2006) occur in the area, we concentrated on *Myotis* species because they comprise the majority of captures and represent a closely related group of ecologically similar species (Armstrong, Adams & Freeman, 1994).

Capturing bats

We used mist nets (Avinet Inc., Dryden, NY, USA) to capture bats at the water holes in June, July and August 1996–1998. Because mist netting is invasive and can potentially affect the behavior patterns of bats, we restricted our

netting efforts to 12 nights (six at each water hole) over the 3-year period. To standardize our sampling efforts, we used two 2 × 6 m nets at each site. One net was positioned to bisect the water hole and the other extended perpendicular to the bisecting net along the water's edge. Nets were set *c.* 30 min before sunset and left up for 5.5 h. The times of capture were recorded for each individual and converted to minutes after sunset (MAS) using sunset data provided for Boulder County by the National Oceanic and Atmospheric Administration (NOAA).

For all captures we recorded species, sex, mass and reproductive condition, and marked each with a split-ring, numbered, plastic forearm band (Hughes Ltd, Middlesex, UK) before release. A total of 16 individuals representing the five *Myotis* species were equipped with 0.45 g radio-transmitters (model LB-2, Holohil Systems Inc., Carp, Ontario, Canada) attached to the dorsal fur of the intrascapular region with surgical glue (Barclay & Bell, 1988). We tracked radio-tagged individuals to diurnal roosts using TRX 48S telemetry receivers (Wildlife Materials Inc., Murphysboro, IL, USA). We used a Magellan 4000 XL global positioning system (GPS) to determine coordinates for each roost and topographical software of the study area (Topo Mapping Software; Dehorme, Yarmouth, ME, USA) to map and calculate linear distances between water holes and roost sites. The mean roost emergence times were determined by averaging data from multiple visual observations at each roost and represent the time when approximately one-half of the individuals had emerged. In the case of *Myotis ciliolabrum* and *Myotis evotis*, which roosted either singly or in groups of two or three individuals, emergence time indicates when we observed the radio-tagged individual to leave the roost.

Data analyses

Data on arrival times were categorized into 10-min intervals. We plotted histograms of capture times of individuals to characterize species-specific use curves. We used general overlap adjusted for sample size (GO_{adj}) and specific overlap (SO) statistics (Ludwig & Reynolds, 1988) as derived from χ^2 analysis (Petraitis, 1979) to test for significant differences in use curves. Complete general overlap of use curves among species equals 1 and is computed as a weighted average of species use curves [$GO = e^E$, where $E = \sum_i^s \sum_j^r [n_{ij}(\ln c_j - \ln p_{ij})/T$, where n_{ij} is the total number of cases (time intervals) used by each bat (i), p_{ij} is the proportion of cases in which each resource (time) j was used by each species (i), c_j is the combined portion of cases in which both species used each resource class and $T = \sum_{j=1}^r (t_j)$, where t_j are the tallied totals of resource class] (Petraitis, 1979; Peres, 1992; Adams, 1996). The pairwise specific overlap test of species i onto species k is the probability that the use curve of species i could have been drawn from species k .

We tested for both similar activity patterns by each species between the two water holes, and differences in use by co-occurring species at each water hole. Differences

among species in roost emergence times and distances between roost sites and water holes were assessed using Kruskal–Wallis one-way analysis. Spearman rank correlation analysis was used to assess the relationship between distance of roost sites from water holes and arrival times.

Results

Capture data

Each water hole was netted six times from 1996 to 1998, resulting in a total of 532 captures of *Myotis* bats. An average of 45 individuals was captured per trapping session. Although other species were captured, they were either rare (<5 individuals total) or, in the case of *Eptesicus fuscus*, arrived at water holes after the vast majority of *Myotis* had left. Thus, we feel that bat species of other genera in the area did not have a direct influence on arrival times of the *Myotis* species.

At BCC, 253 individuals of five *Myotis* species were caught: 29 *Myotis ciliolabrum*, five *Myotis evotis*, 121 *Myotis lucifugus*, 61 *Myotis thysanodes* and 37 *Myotis volans*. At SC, 279 individuals of five *Myotis* species were captured: 17 *M. ciliolabrum*, 79 *M. evotis*, 107 *M. lucifugus*, 30 *M. thysanodes* and 46 *M. volans*. Similar overall numbers of bats were captured at each water hole. The number of species present at each water hole was similar. The number of individuals per species varied somewhat between water holes, with captures of *M. evotis* showing greatest disparity between the sites.

Within-species activity patterns across sites

Use curves at BCC and SC were strikingly similar for *M. ciliolabrum*, *M. lucifugus* and *M. thysanodes* (Fig. 1) However, only *M. ciliolabrum* showed almost complete overlap in use at both sites ($G_{\text{adj}} = 0.968$, $V = 1.297$,

$P > 0.05$, d.f. = 5). Intraspecific visitation patterns by other species were significantly different between sites with partial overlap (G_{adj}) by varying degrees. *Myotis lucifugus* showed the highest partial overlap ($G_{\text{adj}} = 0.904$, $V = 20.661$, $P < 0.05$, d.f. = 7), followed by *M. thysanodes* ($G_{\text{adj}} = 0.781$, $V = 19.147$, $P < 0.01$) and *M. volans* ($G_{\text{adj}} = 0.685$, $V = 27.640$, $P < 0.001$, d.f. = 8), the latter two species exhibiting distinctively different patterns across sites. Because only five individuals of *M. evotis* were captured at BCC, we did not compare site-specific use patterns for that species.

Interspecific differences in within-site use

General overlap statistics reveal significant differences among *Myotis* species at BCC (Fig. 2; Table 1, $G_{\text{adj}} = 0.759$). Pairwise species overlap statistics suggest that the greatest overlap is between the use curves of *M. ciliolabrum* and *M. lucifugus* (Table 1). In fact, because the use curve of *M. ciliolabrum* fell almost entirely within that of *M. lucifugus*, there was complete statistical overlap ($SO = 0.870$, Table 1). However, all other species pairs exhibited significant differences in use curves, with the least overlap in use found between *M. volans* and *M. lucifugus* ($SO = 0.252$).

General overlap statistics for SC indicate significantly different use curves for the five *Myotis* species (Table 2, $G_{\text{adj}} = 0.788$). The relationships between *M. ciliolabrum* and *M. lucifugus* use curves were similar to those observed at BCC (Table 2). Use curves were not significantly different when *M. ciliolabrum* was compared with *M. lucifugus* ($SO = 0.812$) or when *M. volans* was compared with *M. evotis*. *Myotis evotis* was the second most abundant species captured at the site and exhibited a broad use curve that peaked at about 54 MAS (Fig. 2); however, its curve was significantly different from all species, except *M. volans*. All other pairwise comparisons for SO were significantly different (Table 2).

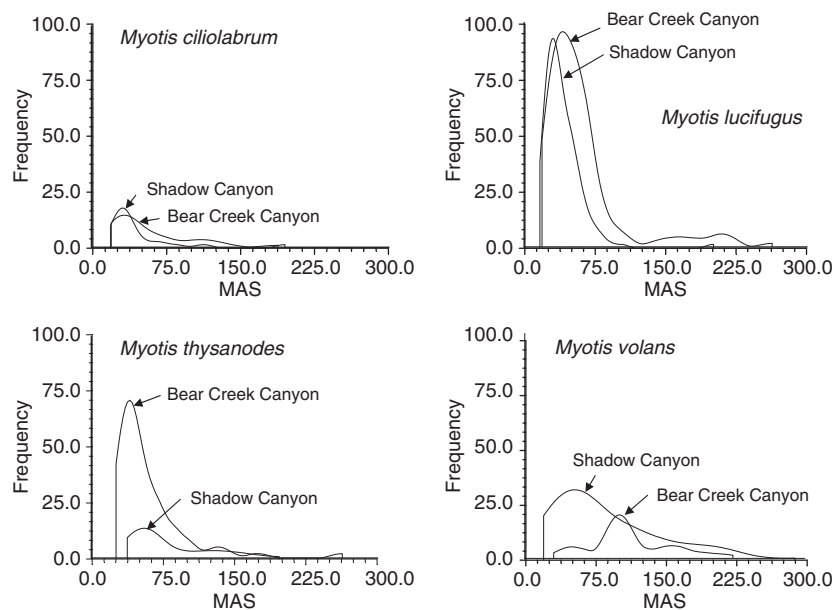


Figure 1 Plots of use curves based upon visitation frequencies (number of individuals captured per species per 10 min time interval) of four species of *Myotis* bats at two water holes in Colorado. MAS, minutes after sunset.

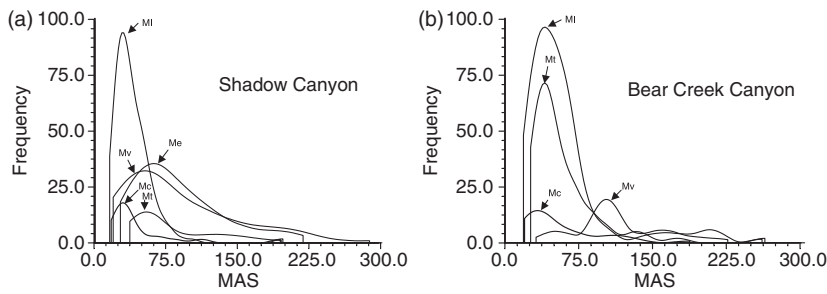


Figure 2 Plots of use curves of (a) five *Myotis* species visiting Shadow Canyon water hole and (b) four *Myotis* species visiting Bear Creek Canyon water hole within the first 300 min after sunset. Mc, *Myotis ciliolabrum*; Me, *Myotis evotis*; ML, *Myotis lucifugus*; Mt, *Myotis thysanodes*; Mv, *Myotis volans*; MAS, minutes after sunset.

Table 1 General overlap and species overlap statistics for Bear Creek Canyon water hole

General overlap statistics					
No. species	GO	G _{min}	G _{adj}	V	d.f.
4	0.829	0.290	0.759	92.241**	21
Specific overlap statistics					
Spp	Pair	SO	U	d.f.	
MYCI	MYLU	0.870	7.509	7	
MYLU	MYCI	0.861	35.345**	7	
MYCI	MYTH	0.651	23.203**	7	
MYTH	MYCI	0.712	40.697**	7	
MYCI	MYVO	0.257	73.302**	7	
MYVO	MYCI	0.342	87.875**	7	
MYLU	MYTH	0.795	54.024**	7	
MYTH	MYLU	0.804	26.113**	7	
MYLU	MYVO	0.301	283.206**	7	
MYVO	MYLU	0.252	112.944**	7	
MYTH	MYVO	0.347	127.077**	7	
MYVO	MYTH	0.427	69.735**	7	

GO, general overlap; G_{min}, minimum overlap; G_{adj}, sample-size adjusted overlap; V, test statistic for GO; d.f., degrees of freedom; SO, specific overlap; U, test statistic for SO. MYCI, *Myotis ciliolabrum*; MYLU, *Myotis lucifugus*; MYTH, *Myotis thysanodes*; MYVO, *Myotis volans*.

**P < 0.001.

Relative abundance across sites

Both *M. ciliolabrum* and *M. lucifugus* occurred in the same relative abundance across sites and showed similar use patterns at both sites (Fig. 1). Captures of *M. thysanodes* were c.75% higher during peak activity periods (n = 24 individuals) at BCC than they were at SC (n = 11 individuals), whereas captures of *M. volans* during peak activity periods were more than 50% higher at SC (n = 18) than at BCC (n = 10). Peak activity times for each species occurred significantly earlier at sites where each was more abundant (Fig. 1; *M. thysanodes*, G_{adj} = 0.781, P < 0.01; *M. volans*, G_{adj} = 0.685, P < 0.001).

Emergence times

Of the 14 radio-tagged individuals, we located 10 roost sites of four *Myotis* species. Roost sites for three radio-tagged female *M. volans* were never located. Because we have no

Table 2 General overlap and species overlap statistics for Shadow Canyon water hole

General overlap statistics					
No. of species	GO	G _{min}	G _{adj}	V	d.f.
5	0.838	0.235	0.788	101.419**	36
Specific overlap statistics					
Spp	Pair	SO	U	d.f.	
MYCI	MYEV	0.469	30.278**	9	
MYEV	MYCI	0.556	93.964**	9	
MYCI	MYLU	0.812	8.339	9	
MYLU	MYCI	0.820	42.917**	9	
MYCI	MYTH	0.355	41.410**	9	
MYTH	MYCI	0.396	59.304**	9	
MYCI	MYVO	0.682	15.312	9	
MYVO	MYCI	0.686	34.624**	9	
MYEV	MYLU	0.451	127.346**	9	
MYLU	MYEV	0.445	174.882**	9	
MYEV	MYTH	0.734	49.476**	9	
MYTH	MYEV	0.764	17.213*	9	
MYEV	MYVO	0.828	30.149**	9	
MYVO	MYEV	0.842	15.778	9	
MYLU	MYTH	0.409	193.104**	9	
MYTH	MYLU	0.468	48.543**	9	
MYLU	MYVO	0.679	83.550**	9	
MYVO	MYLU	0.669	36.995**	9	
MYTH	MYVO	0.700	22.786*	9	
MYVO	MYTH	0.689	34.311**	9	

Abbreviations are the same as in Table 1, MYEV, *Myotis evotis*.

*P < 0.005.

**P < 0.001.

evidence of multispecies use of rock crevice roost sites in the area, we assumed that roost sites are species specific. Multiple observations were made at roosts and the mean emergence time was based on the mean in MAS for each emergence event. There was no significant difference in mean emergence times among four *Myotis* species (Kruskal–Wallis, n = 15, P = 0.142).

Mean emergence times (in MAS) from roost sites were as follows (n represents the number of observed outflight events per species): *M. ciliolabrum*, n = 4, \bar{x} = 28.4, standard errors (SE) = 8.34; *M. evotis*, n = 2, \bar{x} = 29.7, SE = 10.77; *M. lucifugus*, n = 4, \bar{x} = 36.1, SE = 7.05; *M. thysanodes*, n = 5, \bar{x} = 30.8, SE = 5.62.

Distance from roost sites to water holes

Mean distances (km) and SE between roost sites and water holes of capture were as follows: *M. ciliolabrum*, $n = 4$, $\bar{x} = 0.29$, $SE = 0.08$; *M. evotis*, $n = 2$, $\bar{x} = 3.84$, $SE = 0.06$; *M. lucifugus*, $n = 2$, $\bar{x} = 0.41$, $SE = 0.06$; *M. thysanodes*, $n = 2$, $\bar{x} = 0.52$, $SE = 0.06$. There was no significant difference in distance between water holes and roost sites among *Myotis* species (Kruskal–Wallis, $n = 10$, $H = 10.20$, $P = 0.065$). Furthermore, distance was not significantly correlated with arrival times ($n = 10$, $r = 0.64$, $P = 0.358$), and roost sites appeared clustered near water holes.

Discussion

The temporal niche axis (i.e. temporally based resource partitioning among species) has rarely been studied as a mechanism for resource partitioning in mammals (Kronfeld-Schor & Dayan, 1999; Kronfeld-Schor *et al.*, 2001). In the present study, we show separation of arrival times among *Myotis* bat species visiting two small water holes to drink. Where relative abundance was consistent for a species at both sites, temporal use patterns did not vary. However, where relative numbers at peak visitation times of a species were higher at one site versus the other, earlier visitation times coincided with higher relative abundance at each site (Fig. 1). Thus, our data support the hypothesis that bat species structure use patterns temporally at water holes that are small and do not afford spatial partitioning. The patterns of use exhibited by *Myotis* species at our two water holes were not apparently due to differences in emergence times or in distance of roost sites from the water holes. Most *Myotis* species established roost sites in proximity to the water holes, as has been concluded by other authors (Speakman *et al.*, 1991). The exception was *M. evotis*, for which known roost locations were not proximate to the water holes studied.

Previous studies that documented high levels of evaporative water loss in insectivorous bat species under laboratory conditions of high temperature and low humidity (Studier, 1970; Studier *et al.*, 1970; O'Farrell *et al.*, 1971; Studier & O'Farrell, 1976; Webb, 1995; Webb *et al.*, 1995) clearly indicate that bats emerging from diurnal roosts, especially in hot, arid environments, would be motivated to drink at nearby water holes to replenish diurnal losses. These data were instrumental in us testing the hypothesis of resource partitioning at water holes proximate to roost sites where large numbers of bats congregate to drink at small (<2 m diameter) water holes. In particular, lactating females face particular challenges because entering torpor (a potential water-saving mechanism) slows the production of lactate, whereas remaining homeothermic maintains lactate production but induces greater evaporative water losses (Kurta *et al.*, 1989a,b, 1990; McLean & Speakman, 1999; Wilde, Knight & Racey, 1999). These factors may be the reason why maternity roosts are commonly located very close to a water source (Speakman *et al.*, 1991). Thus, for females living in arid environments, seeking out appropriate roost

sites near standing water may be confounded by overcrowding at proximate water holes too small to allow for spatial separation for simultaneous use among individuals and species. Indeed, Adams & Simmons (2002) documented that bats drinking at the two water holes studied herein organize a single distinctive flight pathway that more than 95% of bats approaching to drink use, apparently to avoid collisions with other bats. The orchestration mimics an airport landing strip design. Thus, it appears that bats drinking at small water holes structure use of the resource on several levels, one of which is to temporally space visitations across species, perhaps to avoid overcrowding.

For *M. ciliolabrum* and *M. lucifugus*, we found a high degree of similarity between use patterns regardless of water hole location (Fig. 1). Both species arrived early to drink. We note the disparity between capture numbers of these two species; that is *M. lucifugus* was the most abundant species, whereas *M. ciliolabrum* was least abundant at our study sites and perhaps this disproportion facilitates their temporal co-occurrence. *Myotis ciliolabrum* is the smallest bat and ecophysiology theory predicts that individuals would require a drink immediately upon emergence, which brings it into direct contact with the more abundant and larger bodied *M. lucifugus*. We hypothesize that some dynamic associated with differences in body size and temporal co-occurrence at water holes is responsible, in part, for abundance patterns at our study area.

We recorded relatively large differences in captures at peak activity times of *M. thysanodes* and *M. volans* between sites, as well as significantly different intraspecific use curves (Fig. 1). These two species appeared to shift their visitation patterns relative to one another, wherein the more abundant species visits significantly earlier in the evening (Fig. 2). If earlier visitation times are being selected for, this may account for temporal asymmetry between those of similar ecophysiology, and this asymmetry may be driven more or less by relative population numbers. Possibly, a sort of 'pecking order' based upon species-specific colony sizes and population numbers may exist that establishes the proximate sorting among species drinking at any given water hole.

However, other causes of temporal asymmetry between species across water holes might be in play. For example, the addition of a relatively abundant fifth species (*M. evotis*), present at SC, may have caused a change in the interaction among species using the site. In addition, the size and shape of water holes could influence visitation patterns. SC is slightly smaller but accommodates more bats of more species than does BCC; more temporal precision in visitation for some species is warranted and presents greater efficiency in use of the resource. Although we could not discern distance of roost site from water hole and emergence times as variables related to arrival times at water holes, this does not mean that these variables may not be a factor in other areas. However, if the location of maternity sites is predisposed to be proximate to water holes as suggested by Speakman *et al.* (1991), and supported by our data, then the distance to water holes would in most cases cancel out among species using a particular water source. In addition,

where natural and/or artificial water sources are large enough to allow for spatial separation, temporal partitioning would predictably not be apparent. In our study area, no large water sources lie in proximity to known natural roost sites.

The patterns we describe provide support for the hypothesis that small water holes are important influences on the temporal nature of bat activity. We find that bats, typically separated when roosting and feeding due to ecomorphological differences, are brought into contact at small, discrete water sources and that bat species drinking at a particular site temporally partition drinking times. We feel that further investigations into temporal patterns of water use by bats will provide useful information for understanding further community and population dynamics of mammals, as well as in conservation and management goals.

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