Temporal resource partitioning by bats at water holes

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Keywords
bats; Myotis; temporal partitioning; resource partitioning; water resources.

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Received 28 June 2005; accepted 23 February 2006
doi:10.1111/j.1469-7998.2006.00152.x

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 rational 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 (≤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 ephemeral, 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 infrascapular region with surgical glue (Barclay & Bell, 1988). We tracked radio-tagged individuals to diurnal roosts using TRX 48S telemetry receivers (Wildlife Materials Inc., Murphyboro, 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 *χ2* 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^θ, where E = \( \sum_{i} T \sum_{j} n_{ij} \left( \ln c_{ij} - \ln p_{ij} \right)/T \), 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). \( c_{ij} \) is the combined portion of cases in which both species used each resource class and \( T = \sum_{i=1}^{T} (t_{ij}) \), where \( t_{ij} \) 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 arrived at water holes after the vast majority of Myotis had left. This suggests that Myotis species were aggregated primarily at water holes.

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 Myotis ciliolabrum, Myotis lucifugus and Myotis thysanodes (Fig. 1). However, only M. ciliolabrum showed almost complete overlap in use at both sites ($G_{adj} = 0.968$, $V = 1.297$, $P > 0.05$, 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 ($G_{adj} = 0.904$, $V = 20.661$, $P < 0.05$, d.f. = 7), followed by Myotis thysanodes ($G_{adj} = 0.781$, $V = 19.147$, $P < 0.01$) and Myotis volans ($G_{adj} = 0.685$, $V = 27.640$, $P < 0.001$, d.f. = 8), the latter two species exhibiting distinctly 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, $G_{adj} = 0.759$). 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, $G_{adj} = 0.788$). 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).
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 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.

\[ \text{Table 1 General overlap and species overlap statistics for Bear Creek Canyon water hole} \]

<table>
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<td>7</td>
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**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, \( G_{\text{adj}} = 0.781, P < 0.01; M. volans, G_{\text{adj}} = 0.685, P < 0.001 \)).

Emergence times

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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, \text{se} = 0.08; M. evotis, n = 2, \bar{x} = 3.84, \text{se} = 0.06; M. lucifugus, n = 2, \bar{x} = 0.41, \text{se} = 0.06; M. thysanodes, n = 2, \bar{x} = 0.52, \text{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.

**Acknowledgements**

Research on live animals was performed in a humane manner and was approved by the Institutional Animal Care and Use Committee. We would like to thank students Jenna Jadin, Krista Fish, Brad Petru, ranger/naturalist Burton Stoner, wildlife biologist Cary Richardson and all the bat volunteers for their help with this project. We thank the City of Boulder Open Space and Mountain Parks Department for allowing us to conduct research. This work was funded by the City of Boulder Open Space and Mountain Parks, the University of Wisconsin-Whitewater and the Colorado Bat Society.

**References**


