

EFFECTS OF CAVE TOURS ON BREEDING *MYOTIS VELIFER*

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Abstract: Human activity in caves can affect bats adversely, especially bats that assemble in maternity colonies where appropriate roosts are restricted to areas with a narrow range of microclimates necessary to raise young. We assessed behavioral responses of a maternity colony of about 1,000 cave myotis (*Myotis velifer*) to experimental cave tours by manipulating 3 factors: size of tour groups, whether tour groups talked, and a combination of light intensity and color used to illuminate trails. We also considered the effects of distances between bat roosts and the tour group as well as season. We measured 4 behavioral responses of bats: number of takeoffs, number of landings, activity level, and vocalization intensity. Light intensity affected bat behavior most; all bat responses were highest in trials with high-intensity white light and lowest in trials with no light. When tour groups talked, takeoffs, landings, and activity level increased. Size of tour groups and treatment interactions did not affect bat behaviors. When bats roosted near the tour route, takeoffs and activity level increased. In addition, all behavioral responses increased as the maternity season progressed. Designing cave tours to minimize short-term effects on bats will require careful consideration of cave lighting and tour frequency, route location, and noise levels.

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As the number of people participating in recreational activities and the number of associated developments increase, so do their effects on wildlife. Identifying, evaluating, and mitigating these effects are necessary to conserve wildlife populations, but can be difficult, especially for wildlife species that are challenging to observe. Cave-dwelling bats, for example, are difficult to locate and observe in their dark roost sites; consequently, assessing effects of human activities on these species poses special challenges for researchers. These efforts are warranted, however, because evidence indicates that human activity in caves can adversely affect bats. For example, activity and energy expenditures of several species of hibernating bats increased in response to various non-tactile disturbances associated with recreational cavers (Speakman et al. 1991, Thomas 1995). Further, some summer colonies of bats stabilized or increased in size when human access to caves was restricted (Stihler and Hall 1993).

Maternity colonies are especially vulnerable to human disturbances because these colonies usually are restricted to 1 roost location for several months as they raise young. Numbers of maternity

roosts may be limited because they must meet specific microclimate requirements for developing young; consequently, colonies show high fidelity to maternity roosts (Lewis 1995). In addition, most bats raise only 1 young per year, so reductions in reproductive success caused by disturbances could be manifested in population-level responses.

We performed a manipulative experiment on the behavior of a maternity colony of cave myotis to assess the effects of tour group size, human voices, and artificial lighting regimes associated with future commercial cave tours. We suggest factors that managers should consider when designing cave tours to minimize effects on maternity colonies of bats.

STUDY AREA

Our study site was Kartchner Caverns in southeastern Arizona, USA, a limestone cave in the foothills of the Whetstone Mountains at an average elevation of 1,434 m. The cavern is >3.2 km long, has large rooms, and is wet (99.5% relative humidity) and live (water percolates into it from the surface). During our study, the cavern was being developed as a state park that would feature guided cave tours for the public.

We studied a colony of about 1,000 cave myotis that uses the cavern as a maternity roost from late April through September. The colony typically roosted in 1 large cluster in 1 room of the cavern.

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Tours will traverse part of this room when it is opened to the public. During our study, no construction occurred in this room.

METHODS

Experimental Design

We manipulated 3 variables of cave tours by using a completely randomized experimental design with a $3 \times 2 \times 4$ factorial treatment structure. Over 2 seasons (1997–1998), we completed 5 replicates of each of the 24 treatment combinations for a total of 120 trials. The first factor we investigated was group size of tours, which had 3 levels: 0, 1–3, and 6–8 people. The second factor was voice intensity of tour groups, which had 2 levels: no talking and everyone talking. The third factor was the combination of light intensity and color used to illuminate the cave during tours, which had 4 levels (listed in order of increasing intensity): no-light, half-white, full-red, and full-white.

Light levels varied by color, intensity, and location of lights in the cave. Lights used were readily available incandescent bulbs: what we term “white” light was generated by 40-W soft white light bulbs, and our “red” light was generated by 100-W red glass light bulbs. Specifically, the half-white light level consisted of 12 40-W white bulbs placed on the ground along the tour trail. The full-white light level consisted of 19 40-W white bulbs, those of the half-white light level plus 7 additional white lights placed on the ground along another trail located on the opposite side of the room. The full-red light level consisted of the same number and layout of lights as for the full-white level, but bulbs were red and 100-W. Measurements of light intensity (cd/m^2) at locations throughout the roost for the 4 light levels averaged 0 for no-light (range = 0–0), 0.0009 for half-white (range = <0.0001–0.01), 0.006 for full-red (range = <0.0001–0.038), and 0.01 for full-white (range = <0.0001–0.08).

Experimental Procedures

We performed our experiment between late May and mid-August during 1997 and 1998. We refer to the progression of days from late May through mid-August (about 12 weeks) as “season,” a period that spanned pregnancy, lactation, and post-lactation periods of the maternity colony. Experimental tours traversed the cave room in which the maternity colony roosted. Tour groups walked along an unimproved trail over rough terrain for about 30 m, turned, and

exited the room where they had entered. Tours were 25 min in duration. Tour members used headlamps with red lens covers for all trials that required tour groups. We typically performed 2 trials per day, 1 in the morning (between 0830 and 1100 hr) and 1 in the afternoon (between 1300 and 1600 hr). For treatment combinations that required people talking but no tour group present, we placed a tape recorder at the start of the tour trail and played a recording of a talking tour group made during a prior trial.

During tours, an observer (the same person for all trials) videotaped and recorded vocalizations of the bat colony with a battery-powered night-vision apparatus that consisted of a video camcorder (Canon Hi-8 mm ES2500A), night-vision scope (ITT Night Cam 310), objective lens (Angenieux 15–150 mm, f2.8, C-mount), and infrared light source consisting of 168 infrared light-emitting diodes. We assumed that infrared light (>810 nm) did not affect bat behavior during experiments (Hope and Bhatnagar 1979, Mistry and McCracken 1990), and our observations as well as those of others (Burnett and August 1981, McCracken and Gustin 1991, Winchell and Kunz 1996) indicated no apparent behavioral responses of bats to infrared light.

The observer installed videotaping equipment an average of 1 hr prior to tours and used a headlamp with a red lens cover during installation, no light while waiting to begin taping, and only infrared light during taping. The observer was located as far from the colony as videotaping equipment and trail access allowed (range = 3–15 m, \bar{x} = 7.9 m, SE = 0.36 m). Because the observer was present for all trials, any observer influence affected all treatments uniformly.

During the 1998 season, we recorded 5 25-min trials with no observer present using a remotely operated night-vision camera mounted near the maternity roost. We compared data from these observations with those from 5 observations made during “observer-only” trials of the experiment to investigate the effect of the observer on bat behavior.

Data Collection

We quantified 4 behavioral responses of bats: number of takeoffs, number of landings, activity level, and vocalization intensity. We chose to measure these particular responses because they likely are responses of bats to disturbance, they require metabolic expenditures that could adversely affect bats over time, and they could be measured accu-

rately. We counted takeoffs and landings per min. We quantified activity level as the percentage of the colony moving in any way other than flying in 10- to 15-sec scan samples made 3 times per min; these 3 samples were averaged per min. We ranked vocalization intensity relatively as 1 = low, 2 = moderate, and 3 = high in 5-sec scan samples made 3 times per min; these 3 samples also were averaged per min. We judged "intensity" to be a combination of loudness and frequency. The observer who videotaped the bats ranked vocalization intensity subjectively based on prior and continuous exposure to this bat colony, eliminating interobserver variability.

Statistical Analyses

We analyzed bat responses to treatments and 4 additional continuous effects (progression of the season, year, distance from the colony center to the tour trail, and time of day) with analyses of variance (ANOVA; $n = 120$). We then used linear contrasts to explore differences among factor levels. In addition, we used Pearson product-moment correlation coefficients to describe correlations among responses and ANOVA to investigate effects of the observer on bat responses. We transformed frequencies of takeoffs and landings using natural logs to meet assumptions for analyses, but report arithmetic means and SE on the scale of the original measurement.

RESULTS

Treatment Effects

Bats responded most to light intensity and color treatments used during experimental tours (Table 1). In general, all responses were highest

Table 1. Results of ANOVA assessing effects of 3 factors on 4 behavioral responses of a maternity colony of cave myotis to experimental tours, Kartchner Caverns State Park, Arizona, USA, 1997–1998.

Treatment	Response	df	F	P
Light intensity and color	Takeoffs (ln)	3, 93	13.95	<0.001
	Landings (ln)	3, 94	11.75	<0.001
	Activity level	3, 93	3.12	0.030
	Vocalization intensity	3, 94	8.00	<0.001
Voice intensity	Takeoffs (ln)	1, 93	5.33	0.023
	Landings (ln)	1, 94	4.44	0.038
	Activity level	1, 93	2.72	0.103
	Vocalization intensity	1, 94	2.06	0.155
Group size	Takeoffs (ln)	2, 93	0.26	0.772
	Landings (ln)	2, 94	0.63	0.534
	Activity level	2, 93	0.34	0.715
	Vocalization intensity	2, 94	1.03	0.363

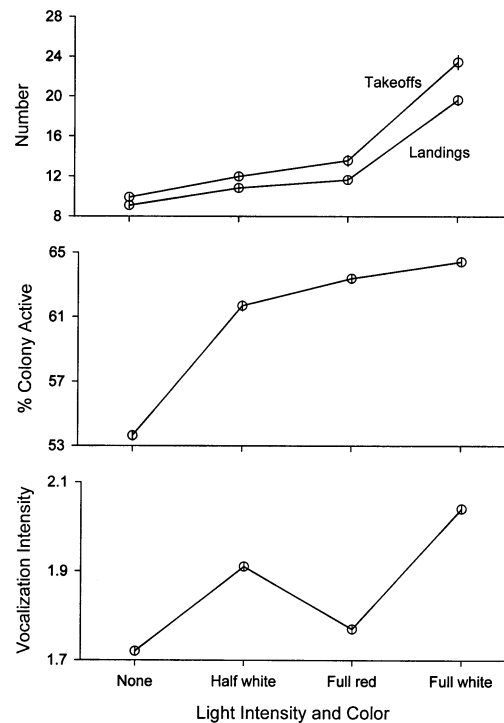


Fig. 1. Effects ($\bar{x}/\text{min} \pm \text{SE}$) of light intensity and color on 4 behaviors of a maternity colony of cave myotis during experimental tours, Kartchner Caverns State Park, Arizona, USA, 1997–1998. Vocalization intensity was ranked as 1 = low, 2 = moderate, and 3 = high.

during full-white light level and lowest during the no-light level (Fig. 1). Both takeoffs ($t = 5.48$, $P < 0.001$) and landings ($t = 5.06$, $P < 0.001$) were higher during full-white light levels compared with all other levels. Specifically, takeoffs increased by 21%, 37%, and 137% and landings by 19%, 28%, and 116% in half-white, full-red, and full-white light levels, respectively, relative to responses in the no-light level (Fig. 1). In contrast, colony activity increased with all 3 light levels similarly (15–20%) compared with the no-light level ($t_3 = 3.05$, $P = 0.003$). Last, vocalization intensity seemed to vary based on light color. Colony activity did not change appreciably (0.03%) in response to full-red light level compared with the no-light level ($t = 0.74$, $P = 0.46$), but did increase in response to both half-white (11%) and full-white levels (19%; $t = 4.22$, $P < 0.001$).

Bats also responded to voice intensity of tour groups (Table 1). Number of takeoffs increased by 22% when tour groups talked ($\bar{x} = 16.20$, $\text{SE} = 0.42$) relative to when they did not talk ($\bar{x} = 13.25$,

Table 2. Effects of 4 covariables on behavioral responses of a maternity colony of cave myotis to experimental tours, Kartchner Caverns State Park, Arizona, USA, 1997–1998. Responses listed where the factor increased the precision of the ANOVA model ($P < 0.10$).

Factor	Response affected	Estimate ^a	SE	F^b	P
Season ^c	Takeoffs (ln)	0.023	0.003	51.38	<0.001
	Landings (ln)	0.024	0.003	52.62	<0.001
	Activity level	0.171	0.058	8.81	0.004
	Vocalization intensity ^d	0.003	0.002	4.49	0.037
Year ^e	Takeoffs (ln)	0.498	0.157	10.10	0.002
	Landings (ln)	0.635	0.161	15.45	<0.001
	Activity level	-12.874	2.774	21.54	<0.001
Distance ^f	Takeoffs (ln)	-0.022	0.011	3.76	0.055
	Activity level	-1.073	0.198	29.27	<0.001
Time ^g	Vocalization intensity ^d	<0.001	<0.001	3.26	0.074

^a Estimated change in mean response with a 1-unit increase in factor.

^b $df = 3, 93$ for takeoffs and activity level; $3, 94$ for landings and vocalization intensity.

^c Late May–mid-Aug.

^d Ranked: 1 = low, 2 = moderate, 3 = high.

^e Difference between 1997 and 1998.

^f Horizontal distance between center of bat colony and tour trail.

^g 0800–1700 hr.

SE = 0.34). Similarly, number of landings increased by 21% when tour groups talked ($\bar{x} = 14.00$, SE = 0.30) relative to when they did not talk ($\bar{x} = 11.61$, SE = 0.26). In addition, the percentage of the colony active was 5% higher when tour groups talked ($\bar{x} = 62.13$, SE = 0.19) relative to when they did not talk ($\bar{x} = 59.43$, SE = 0.22).

Bats did not respond to group size of tours (Table 1). Likewise, no interactions of experimental treatments affected bat behaviors ($F_{3, 93} < 1.42$, $P > 0.24$ for all responses).

Effects of Other Factors

Although we measured other factors primarily to increase the precision with which we could discern main treatment effects, these covariables also influenced bat responses to treatments in several important ways (Table 2). All responses increased as the season progressed (Table 2). Horizontal distances between the tour trail and the center of the bat colony varied depending on the specific location where bats roosted (range = 2–25 m, $\bar{x} = 13.3$ m, SE = 0.42 m), which in turn influenced bat responses to treatments. Specifically, when bats were closer to the tour trail, number of takeoffs and level of colony activity increased (Table 2).

The number of takeoffs and landings (geometric means) were both slightly higher during 1998 than 1997, by an average of 1.65 ($t = 3.18$, $P = 0.002$) and 1.88 per min ($t = 3.93$, $P < 0.001$), respectively. Overall colony activity, however, decreased by an average of 12.87% (SE = 2.77) from 1997 to 1998 ($t = -4.64$, $P < 0.001$).

Comparing the treatment combinations with only the observer present to those when no one was at the roost site indicated that the observer had little effect on bat responses ($t_0 < 0.26$, $P > 0.49$ for all analyses; Table 3). Power to detect a 20% difference between observations with the observer present versus those with the observer absent was high for activity level (0.99, $\alpha = 0.10$) and was lower for other responses (<0.50; Table 3).

Correlations of Responses

All bat responses were correlated positively, suggesting that responses measured similar aspects of behavioral states of the bats. Most correlations were strong: takeoffs and landings ($r = 0.97$, $P < 0.001$), takeoffs and activity level ($r = 0.56$, $P < 0.001$), takeoffs and vocalization intensity ($r = 0.50$, $P < 0.001$), landings and activity level ($r = 0.46$, $P < 0.001$), and landings and vocalization intensity ($r = 0.55$, $P < 0.001$). Activity level and vocalization intensity were correlated less than other responses ($r = 0.27$, $P = 0.003$).

DISCUSSION

Light, Voice, and Distance

Bat responses increased with relative intensity of disturbances created by experimental tours. For example, all behavioral responses were lowest

Table 3. Levels ($\bar{x} \pm SE$, $n = 5$) of 4 behaviors of bats with and without observer present in the cave near the roost (within 3–15 m, $\bar{x} = 7.9$ m, SE = 0.36 m), Kartchner Caverns State Park, Arizona, USA, 1998.

Behavior	Observer present	\bar{x}	SE	Power ^a
Number of takeoffs	No	8.54	1.83	0.47
	Yes	10.24	4.10	
Number of landings	No	8.00	1.53	0.48
	Yes	9.67	3.83	
Percent of colony active	No	52.61	3.11	>0.99
	Yes	46.00	8.62	
Vocalization intensity ^b	No	1.74	0.06	0.34
	Yes	1.76	0.10	

^a Estimated power to detect a 20% difference between observations with the observer present and those with the observer absent at $\alpha = 0.10$.

^b Ranked: 1 = low, 2 = moderate, 3 = high.

when tours were run with no light and highest when run with high-intensity white light. Only vocalization intensity indicated that light color might have affected bat behavior, as bats vocalized more intensely when white light was used relative to when red light was used.

Other cave-dwelling bats have been shown to orient strongly toward light when using a visually guided escape response (Chase 1981, Mistry and McCracken 1990). Although bats tend to orient toward light when confronted with disturbances in caves (Mistry and McCracken 1990), in familiar environments, they may instead move to alternate roost sites (Chase 1981). Bats moved to alternate roost sites during only 3 of our 120 experimental trials; in each of these instances, bats were roosting relatively close (≤ 8 m) to the tour trail. Otherwise, bats seemed to orient toward light to investigate and assess disturbances rather than escape them during our experimental tours.

Acoustic cues also play a role in escape responses of cave bats (Chase 1983, Mistry 1990). Although auditory systems of bats tend to be mechanically and neurologically tuned to the frequencies of their dominant echolocation calls (Kunz and Pierson 1994), hearing in bats ranges from at least 1 to 200 kHz (Henson 1970, Fenton 1985). Therefore, frequencies of human voices (about 0.02–20 kHz) probably are audible to most bats. Cave myotis in our study increased flights and activity level when tour groups talked, but did not respond to differences in the sizes of tour groups we examined; therefore, the volume of voices of large tour groups did not seem to affect bat behavior differently than that of small tour groups. Increases in takeoffs and activity level of bats when tours passed closer to roosts seems to be a function of distance: the closer people were to the bats, the greater the chance of bats seeing, hearing, and responding to people.

Seasonal Changes in Responses

Bat responses to tours increased as the season progressed, suggesting that bats did not habituate to tour activity over time. Seasonal increases in bat responses may have been a result of cumulative effects of experimental tours, or could have been an artifact of natural changes in bat behavior as mothers progressed through phases of maternity and young matured, or may have been due to both factors. Although we could not determine conclusively which factors caused increases in bat responses over the season, we suspect that both natural and tour-caused factors contributed to this pattern.

Natural seasonal changes in behavior for these bats show a general increase in takeoffs, landings, activity level, and vocalization intensity from mid-June through mid-July, then a decline in these behaviors (Mann 1999). This pattern reflects the life history of cave myotis and some other bat species, in which female activity is lowest during pregnancy and parturition in June, highest during peak lactation in July, and declines thereafter (Kunz 1973, 1974; Mann 1999). Other colony-roosting bats have shown similar patterns of physiological demands during the maternity season (Kurta et al. 1987, 1989; Winchell and Kunz 1996; McLean and Speakman 1997).

Bat behaviors during our experimental tours increased from June through July, following this natural seasonal pattern. After mid-July, however, takeoffs and landings continued to increase rather than decrease through the end of July and the rest of the season. Because increases were steady rather than abrupt, as might be expected if associated with distinct points during the maternity season (parturition, peak lactation, volancy, weaning), we attribute them more to cumulative effects of tours than natural patterns of behavior. However, increases could be attributed at least partially to young becoming more active and independent and consequently more able to respond to disturbances as the season progressed.

MANAGEMENT IMPLICATIONS

We found that light intensity, noise, day of season, and distance between tours and roost locations most disturbed the bats that we studied. Therefore, we suggest that cave tours be designed to minimize effects of these factors on bats. The most important period of the season in which to minimize disturbance is from parturition through peak lactation (mid-Jun–mid-Jul for this colony) because energetic costs of females likely are highest during this period. If possible, no tours should be allowed during the maternity period in those portions of the cave inhabited by bats. If females expend much energy responding to disturbances from tours during this period, they may not be able to meet energy needs of themselves and their young, jeopardizing the persistence of the colony. Increases in flights could be especially expensive because flight in some bats requires almost twice the maximum metabolic capabilities of similar-sized terrestrial mammals (Thomas 1975). These recommendations may apply to other species of bats that form maternity colonies in caves and have similar physiological requirements.

Strategies used or suggested to protect bats in commercial caves have focused on limiting visitor access and impact during important phases of bat life cycles, such as raising young and hibernation (Sheffield et al. 1992, Gurnee 1994, Jagnow 1998). An alternative approach is to restrict or eliminate human activity in caves or areas of caves where bats are vulnerable to disturbance (McCracken 1989, Arita 1996). Carefully controlled tours and cave-development strategies may explain increased abundances of bats in some commercial caves (Arita 1996, Johnson et al. 1998). Moreover, educating visitors about the ecology of bats and their importance in ecosystem function could be critical to meet conservation goals (Sheffield et al. 1992, Gurnee 1994, Fenton 1997).

Management actions to conserve bat maternity roosts in commercial caves probably will be most successful if they are species- and site-specific, and based on empirical data. Managers must first understand the specific habitat requirements for the species of concern, then identify and protect caves or areas within caves that meet these requirements. Additionally, cave characteristics, such as cave volume and topography, can greatly influence how bats perceive disturbances associated with tours.

Because suitable maternity roosts are likely limited (Lewis 1995), they clearly are important for maintaining bat populations. Functional loss of roost habitat due to human disturbances could lead to insularization of bat populations that would then be more vulnerable to local extinction events (Gates et al. 1984). Finally, all management plans for maternity roosts should include continuous monitoring efforts designed to detect biologically meaningful changes in colony size over time.

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LITERATURE CITED

ARITA, H. T. 1996. The conservation of cave-roosting bats in Yucatan, Mexico. *Biological Conservation* 76:177–185.

- BURNETT, C. D., AND P. V. AUGUST. 1981. Time and energy budgets for dayroosting in a maternity colony of *Myotis lucifugus*. *Journal of Mammalogy* 62:758–766.
- CHASE, J. 1981. Visually guided escape responses of microchiropteran bats. *Animal Behaviour* 29:708–713.
- . 1983. Differential responses to visual and acoustic cues during escape in the bat *Anoura geoffroyi*: cue preferences and behaviour. *Animal Behaviour* 31:526–531.
- FENTON, M. B. 1985. *Communication in the Chiroptera*. Indiana University Press, Bloomington, USA.
- . 1997. Science and the conservation of bats. *Journal of Mammalogy* 78:1–14.
- GATES, J. E., G. A. FELDHAMER, L. A. GRIFFITH, AND R. L. RAESLY. 1984. Status of cave-dwelling bats in Maryland: importance of marginal habitats. *Wildlife Society Bulletin* 12:162–169.
- GURNEE, J. 1994. Management of some unusual features in the show caves of the United States. *International Journal of Speleology* 23:13–17.
- HENSON, O. W., JR. 1970. The ear and audition. Pages 181–263 in W. A. Wimsatt, editor. *Biology of bats*. Volume 2. Academic Press, New York, USA.
- HOPE, G. M., AND K. P. BHATNAGAR. 1979. Electrical response of bat retina to spectral stimulation: comparison of four microchiropteran species. *Experientia* 35:1189–1191.
- JAGNOW, D. H. 1998. Bat usage and cave management of Torgac Cave, New Mexico. *Journal of Cave and Karst Studies* 60:33–38.
- JOHNSON, S. A., V. BRACK, JR., AND R. E. ROLLEY. 1998. Overwinter weight loss of Indiana bats (*Myotis sodalis*) from hibernacula subject to human visitation. *American Midland Naturalist* 139:255–261.
- KUNZ, T. H. 1973. Population studies of the cave bat (*Myotis velifer*): reproduction, growth, and development. *Occasional Papers of the Museum of Natural History, The University of Kansas* 15:1–43.
- . 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* 55:693–711.
- , AND E. D. PIERSON. 1994. Bats of the world: an introduction. Pages 1–46 in R. M. Nowak. *Walker's bats of the world*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- KURTA, A., G. P. BELL, K. A. NAGY, AND T. H. KUNZ. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology* 62:804–818.
- , K. A. JOHNSON, AND T. H. KUNZ. 1987. Oxygen consumption and body temperature of female little brown bats (*Myotis lucifugus*) under simulated roost conditions. *Physiological Zoology* 60:386–397.
- LEWIS, S. E. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* 76:481–496.
- MANN, S. L. 1999. *Investigations to conserve a maternity colony of cave myotis (Myotis velifer) in southern Arizona*. Thesis, University of Arizona, Tucson, USA.
- MCCRACKEN, G. F. 1989. Cave conservation: special problems of bats. *Bulletin of the National Speleological Society* 51:47–51.
- , AND M. K. GUSTIN. 1991. Nursing behavior in Mexican free-tailed bat maternity colonies. *Ethology* 89:305–321.
- MCLEAN, J. A., AND J. R. SPEAKMAN. 1997. Non-nutritional maternal support in the brown long-eared bat. *Animal Behaviour* 54:101–108.

- mal Behaviour 54:1193–1204.
- MISTRY, S. 1990. Characteristics of the visually guided escape response of the Mexican free-tailed bat, *Tadarida brasiliensis mexicana*. *Animal Behaviour* 39:314–320.
- , AND G. MCCrackEN. 1990. Behavioural response of the Mexican free-tailed bat, *Tadarida brasiliensis mexicana*, to visible and infrared light. *Animal Behaviour* 39:598–599.
- SHEFFIELD, S. R., J. H. SHAW, G. A. HEIDT, AND L. R. McCLENAGHAN. 1992. Guidelines for the protection of bat roosts. *Journal of Mammalogy* 73:707–710.
- SPEAKMAN, J. R., P. I. WEBB, AND P. A. RACEY. 1991. Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology* 28:1087–1104.
- STIHLER, C. W., AND J. S. HALL. 1993. Endangered bat populations in West Virginia caves gated or fenced to reduce human disturbance. *Bat Research News* 34:130.
- THOMAS, D. W. 1995. Hibernating bats are sensitive to nontactile human disturbance. *Journal of Mammalogy* 76:940–946.
- THOMAS, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. *Journal of Experimental Biology* 63:273–293.
- WINCHELL, J. M., AND T. H. KUNZ. 1996. Day-roosting activity budgets of the eastern pipistrelle bat, *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 74:431–441.

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