



Behavioral responses of bats to gates at caves and mines

Geneviève R. Spanjer and M. Brock Fenton

Abstract Gates installed to protect bats at caves and mines have appeared to be more harmful than helpful, but few studies have quantitatively measured the direct impact of gates on bats. To assess bats' responses to gates during pre-hibernation swarming behavior, we recorded flight speeds, flight behavior, and vocalizations at 28 sites (16 with and 12 without gates) from Ontario to Tennessee. We recorded data at unobstructed entrances and passages, at sites with metal gates already in place, and at sites with newly erected mock wooden gates in place. Bats always circled and retreated more often and passed directly through less often at gates (most at mock gates). Higher bat activity and smaller gate size corresponded with more fly-retreat and circling behavior. Echolocation, communicative calls, and flight speed did not differ consistently as a function of gate presence or absence. Bat flight behavior did not differ based on spacing of vertical gate supports, number of entrances, or gate position (entrance or passage), although bats generally circled more and passed directly through less often in passages. To minimize impacts on bats, gates should 1) be erected in large areas, 2) have a bat chute or open top, 3) be placed at entrances (unless predation is a problem), 4) be placed on flat ground (not on an incline), and 5) be erected gradually over a period of several weeks or months when feasible.

Key words bats, behavior, caves, Chiroptera, conservation, echolocation honks, flight speed, gates, mines, swarming

Conservation efforts, however well intended, sometimes may be ineffectual or potentially more harmful than beneficial. One major limitation of effective conservation is a lack of sufficient data about how the organisms to be protected currently behave and how they will be influenced by the conservation measure. This limitation includes some measures intended to protect bats, and research on bat conservation efforts is particularly needed (Racey and Entwistle 2003).

Many bat species are gregarious, most have low reproductive rates (Barclay and Harder 2003), and many require specific roost microclimate for hibernation or rearing young. Many species of bats exhibit fidelity to specific roosts, especially hiber-

nation sites, making them vulnerable to disturbance (Kunz and Lumsden 2003). Approximately 25% of United States bat species hibernate nearly exclusively in caves or mines (Tuttle and Taylor 1998). About 50% of bat species reported from Canada and the United States (21 of 45), including endangered species such as *Myotis grisescens*, *M. sodalis*, and subspecies of *Corynorhinus townsendii*, depend on cave or mine roosts during at least part of the year (Currie 2000, Sherwin et al. 2002). Nontactile human disturbance can harm bats roosting in caves or mines, especially during the hibernation or young-rearing periods of the year (e.g., Fenton 1970, Sheffield et al. 1992, Thomas 1995, Johnson et al. 1998, Mann et al. 2002). Tuttle (1977)

Address for Geneviève R. Spanjer: Department of Biology, York University, 4700 Keele St., Toronto, ON M3J 1P3, Canada; present address: Department of Biology, University of Maryland, College Park, MD 20742; e-mail: gspanjer@umd.edu. Address for M. Brock Fenton: Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada.



reported that some bat populations had declined by as much as 95% as a result of human disturbance.

Gates erected from the 1950s through the early 1970s across cave entrances virtually always resulted in roost abandonment by bats (Tuttle 1977). Design improvements, including gates built with bat chutes (wider openings high up on a gate; Figure 1), have been based largely on observation and abiotic factors (e.g., not restricting airflow; Powers 2002), but the responses of many species to gates are poorly understood, or in some cases negative (Currie 2001). Gates placed in cave passages rather than at entrances have had mixed results (Martin et al. 2000). White and Seginak (1987) compared 3 different gate designs at one cave entrance (showing angle iron [Figure 2] and round steel bar preferable to a funnel design), and Ludlow and Gore (2000) demonstrated that when given the choice, bats use ungated entrances more than gated ones. Although thousands of gates currently block human access to

mine and cave entrances in the United States and Canada (Sherwin et al. 2002), the behavioral responses of bats to gates have been little studied.

Anecdotal observations suggest that bats increase circling when encountering an entrance gate and sometimes land on the gates or even crawl through them, potentially increasing the risk of predation (Tuttle 1977, White and Seginak 1987, Currie 2001). Allende et al. (2003) compared 3 mines with gates in place to 3 newly gated mines (at which they recorded data before and after gate installation) and found bats circled 6-10 times more frequently at gated entrances than at ungated ones. However, Martin et al. (2000) reported a lack of evident circling or increased predation at several dark zone gates.

Swarming is the late summer and early autumn activity exhibited by many bat species that hibernate in caves or mines. During swarming, bats fly in, around, and out of underground sites through most of the night (Poole 1932, Davis and Hitchcock

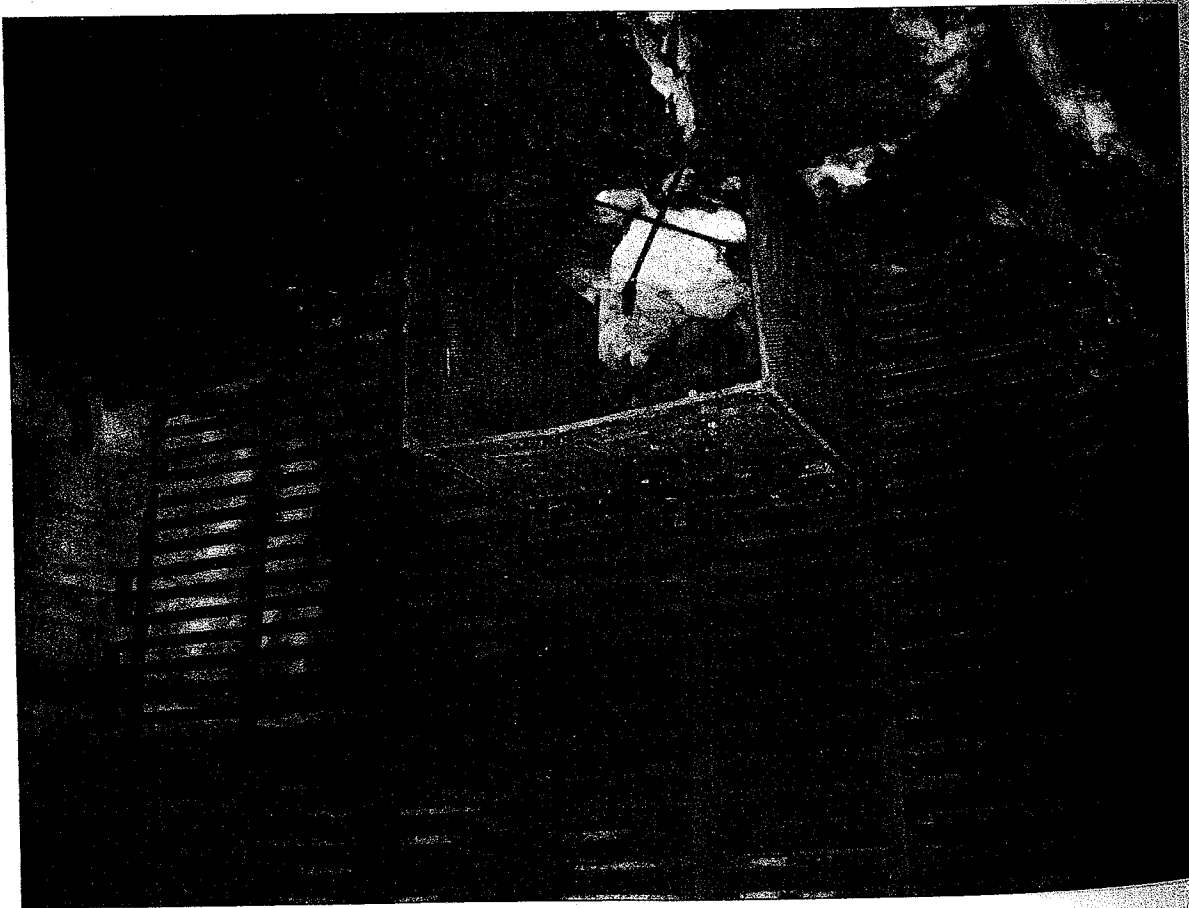


Figure 1. Chute allowing bats easier passage out of cave, in the south gate at Hubbard's Cave, Tennessee.

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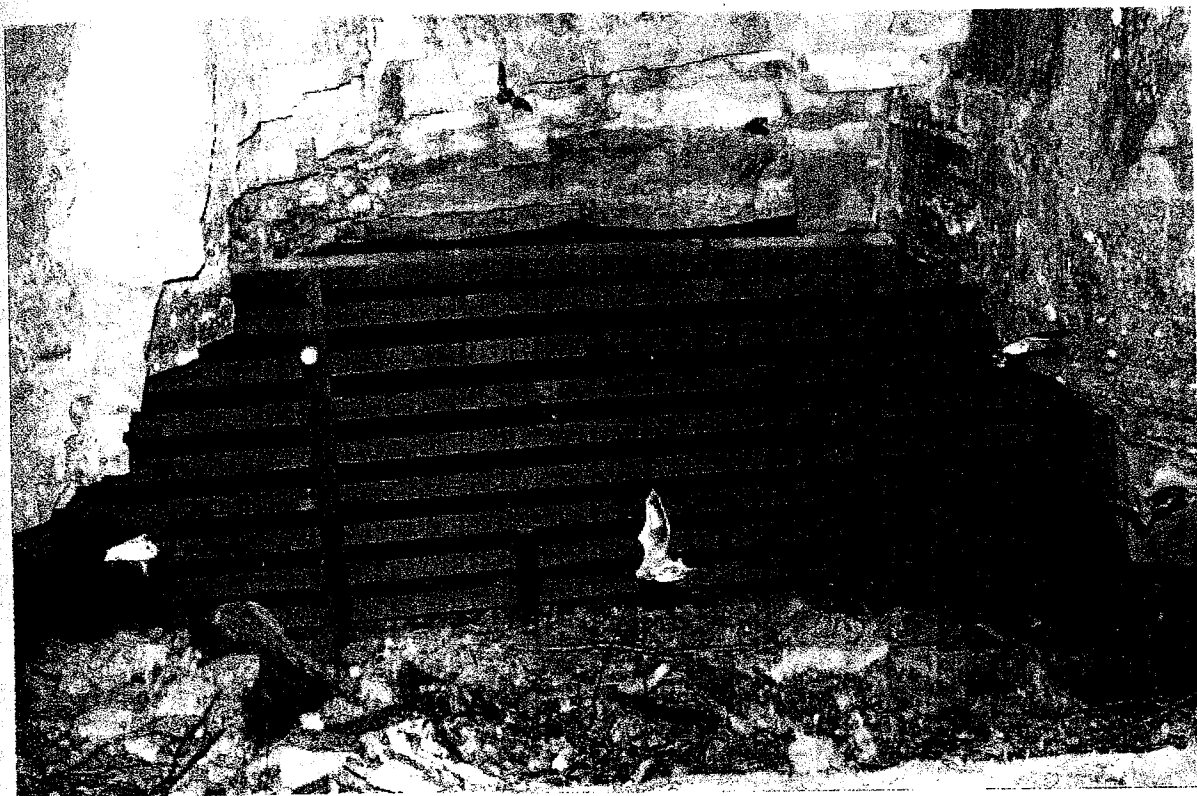


Figure 2. Standard angle-iron gate at Graphite Mine, New York.

1965, Fenton 1969). This behavior has been reported for many species, including *Myotis lucifugus*, *M. septentrionalis*, *M. sodalis*, *Eptesicus fuscus*, *Corynorhinus townsendii*, and *Pipistrellus subflavus* (e.g., Davis et al. 1968, Hall and Brenner 1968, Fenton 1969, Clark et al. 1997). Swarming begins after the young of the year and females leave maternity colonies (Hall and Brenner 1968, Fenton 1969) and continues until bats enter extended bouts of torpor during hibernation. As the swarming season progresses, sexual activity and increasing size of bat populations at swarming sites become evident (Fenton 1969).

During swarming, bats of both sexes and all ages (subadults as well as adults) are present (Fenton 1969). At many sites large numbers of bats, including several species, are active (Davis et al. 1968, Hall and Brenner 1968, Fenton 1969, Cope and Humphrey 1977), and banding studies indicate that a different group of individuals is present each night (Hall and Brenner 1968, Fenton 1969). The brevity of any bat's stay at a swarming site presents the opportunity to study these bats without disturbing them when they are vulnerable. The large num-

bers of bats present at some sites during swarming represents a cross-section of species and ages. Thus, this is an ideal opportunity to collect data about the responses of cave-dwelling bats to gates.

We hypothesized that bats would change their behavior in response to a gate and tested 7 specific predictions: 1) bats decrease their flight speed when approaching gates, 2) bats alter number and type of vocalizations in the presence of a gate, 3) bats change their flight behavior in the presence of a gate, 4) if bats acclimate to a gate's presence, the impact should decline over time, 5) the level of impact of a gate will be greater when a larger number of bats is present (because available flight space per bat is reduced), 6) the size of the gate area and spacing of the vertical supports will influence the impact, and 7) bats will behave differently when flying in a passage versus at an entrance and will thus respond differently to gates placed in passages versus across entrances. To test these predictions, we collected data pertaining to bats' flight speed, flight behavior, and vocalizations in the presence and absence of gates at a variety of cave or mine roosts. We made measurements at caves and mines that were

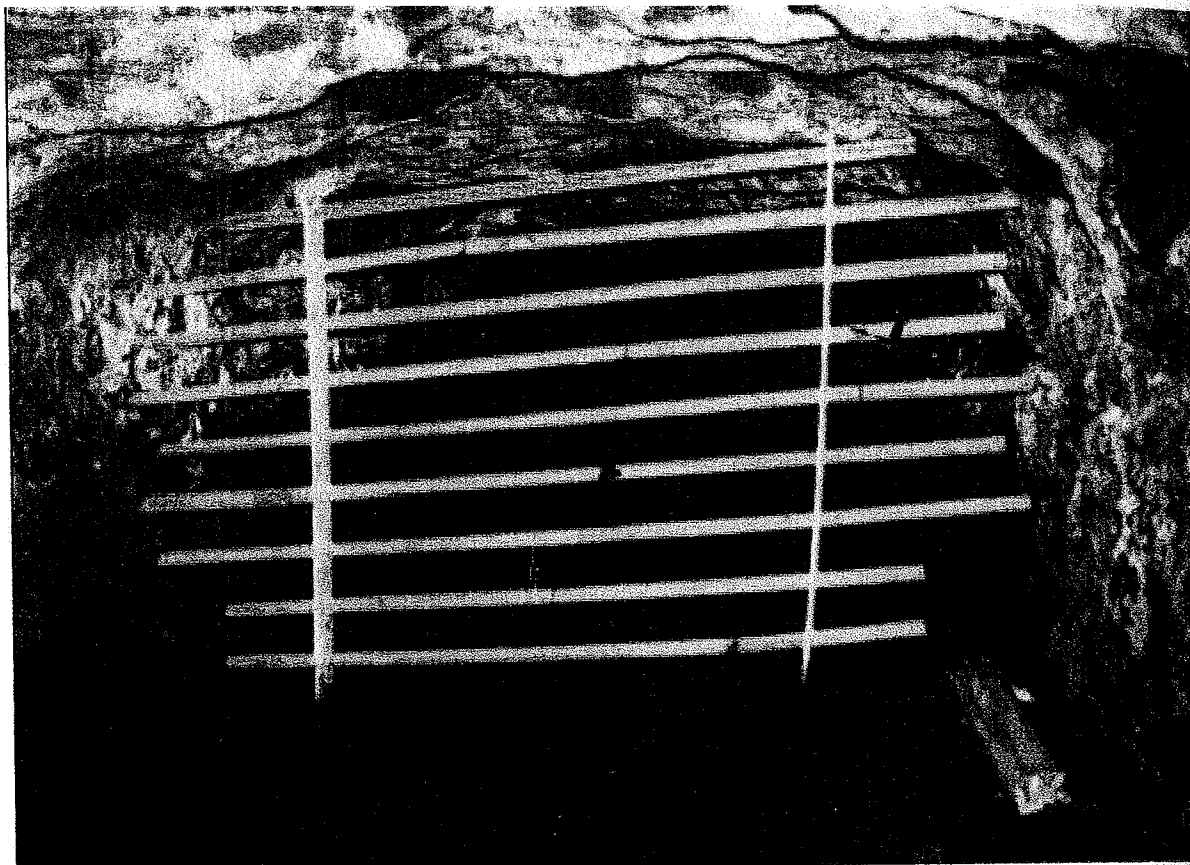


Figure 3. Interior wooden mock gate erected August 2003 perpendicular to the passage of Craigmont Mine, Ontario.

already gated and still supported bat populations to control for the possible effects of habituation.

Study area

From 26 July to 3 October 2003 we visited 33 caves and mines and collected useful data at 28 sites (16 gated). The sites ranged from southeastern Ontario, Canada, to middle eastern Tennessee, United States, and included sites with a variety of gates placed at entrances to caves and mines. They were selected based on previously reported information about the occurrence of autumn swarming behavior or hibernation.

Methods

We collected data at the entrances to caves and mines. At some ungated sites, we installed a mock gate (described below) to assess bats' responses to it. We erected mock gates perpendicular (Figure 3) to the main axis of the passage and sometimes

across the passage at an oblique angle. We erected mock gates either at the entrance or inside the passage at the beginning of the dark zone and left them in place for about 1 hour. The mock gates covered the entrance or passage so that bats entering or exiting the cave (or flying through a passage) were forced to pass through the obstruction to reach their destination. We collected data on multiple nights at 4 sites: Renfrew Mine (Renfrew Co., Ont.), Craigmont Mine (Renfrew Co., Ont.), Mullins Spring Cave (Rockcastle Co., Ky.), and Barton Hill Mine (Essex Co., N.Y.).

Between 26 July and 7 August we tested our operational procedures at the Renfrew Mine (Renfrew Co., Ont.; N 45°18.29'; W 076°54.32'). We recorded echolocation calls and flight speeds at various locations in and just outside the mine, made qualitative observations of behavior, and attempted to record flight speeds with the radar gun positioned various distances from the gate and entrance. We also collected data on 4 nights after installation of a mock gate at the mine's entrance.

Mock gates

We constructed mock wooden gate components from spruce lumber following the spacing specifications and general design of the angle iron gate recommended by the American Cave Conservation Association (ACCA; Tuttle and Taylor 1998; see Figure 2). Horizontal pieces were 7.6-cm angle "iron" and were 2.5 cm thick. Horizontal bars were spaced 14.6 cm apart and were 0.3, 0.6, 1.2, 1.5, 1.8, and 2.5 m in length. Vertical pieces were 15 × 2.5-cm spruce cut into 1.2-, 1.8-, and 2.5-m segments. We used wooden pegs inserted in drilled holes to connect multiple pieces to cover larger areas. We erected mock gates ranging in size from 1.2h × 1.5w m to 2.5h × 2.2w m and 1.8h × 3w m at 11 sites and, at 9, obtained sufficient data for analysis.

Standard data collection protocol

Flight speeds. A K-15 handheld radar gun (beam width 8 degrees from main axis; PB Electronics, Shepherdsville, Ky.), modified to record m/s (Blake et al. 1990) and mounted on a tripod ~1.2 m above the ground ~3.7 m from the gate or entrance, was used to measure flight speeds (Salcedo et al. 1995). We recorded speeds for 5 minutes each with the device facing toward and 180 degrees away from the gate and then repeated the process in both directions approximately 30–60 minutes later.

Vocalizations. We recorded echolocation calls with a Pettersson D980 bat detector (Pettersson Elektronik, AB, Uppsala, Sweden) connected to an F2000 filter unit (Pettersson Elektronik, AB) set to low gain connected to a high-speed sound card (DAQCard-6062E, National Instruments, U.S.) installed in a Dell Latitude laptop computer running BatSound Pro, version 3.31b (Pettersson Elektronik, AB). The bat detector was on a tripod ~1.2 m from the ground ~1.5 m from the gate. We used a recording sampling frequency of 357.1 kilohertz (kHz) and recorded calls for 30 seconds approximately every 10–20 minutes 3–5 times for each situation (unobstructed entrance, unobstructed passage, mock gate[s], real gate[s]) at each site.

Flight Behavior. After determining which flight behaviors were most frequent, we conducted 5-minute observation periods (1 minute on, 1 minute off) every 5–20 minutes for a total of 3–4 periods in each situation at each site. At sites with low activity, we made observations for 5 consecutive minutes during each period. To observe flying bats, the area of study was illuminated with lights (Coleman lantern [The Coleman Company, Inc., Wichita,

Kans.], Petzl headlight [Petzl America, Salt Lake City, Ut.], and/or General Electric spotlight [General Electric, Fairfield, Conn.], depending on entrance size) covered in clear red to reduce disturbance (Finley 1959). We quantified the number of circles; fly-retreat; pass; chase; collide bat; collide gate; collide person; collide wall, ceiling, equipment, or other; land gate; land other; chatter; and sudden height change (see below).

We included only bats flying between the observer and the gate or entrance in the behavior tally (we did count bats passing out through the entrance or gate from the inside). The observer was always outside the entrance (except when collecting passage data), at a distance that made the entire entrance or passage visible (except in the case of very large gates) but close enough to have an adequate view of bats' flight behaviors while minimizing the impact of observers.

"Circling" was 1 bat flying in ≥ 1 consecutive circles completed between the observer and the gate or entrance. We counted each circling episode as 1. We recorded "fly-retreat" behavior when a bat flying in any direction abruptly changed direction, usually $\sim 180^\circ$, and flew rapidly in the new direction. Each time a bat engaged in one such change in path we counted it as 1. "Pass" was the flight of a bat passing through the gate, entrance, or passage point 1 time. If a bat flew repeatedly in and out of an entrance, we counted each time it passed through as 1. "Chasing" occurred when 1 bat flew rapidly after another (not beside or just above it). We counted each time 2 bats flew in this formation in the observer's field of view as 1. "Sudden height change" was a bat flying at one height level abruptly gaining or losing altitude in a sudden swoop. "Collisions" occurred when a flying bat made physical contact with another bat, gate, cave or mine wall or ceiling, or an observer (including wing brushes, head-on collisions, etc.) but did not land on the object, person, or bat. "Landing" on a gate or other object occurred when a bat touched down and rested briefly on an object. "Chattering" was defined as vocalizations humans could hear when bats were active in the area but did not include the "ticking" sound associated with the production of echolocation (Griffin 1986). Each continuous episode of chattering by a bat counted as 1. If bats engaged in more than 1 activity simultaneously, we counted both activities; for instance, if 1 bat was chasing another while they both flew in a circle, we counted this as 1 chase and 2 circles.

Trapping. At 7 sites we captured bats in a cus-

tom-made 1-m \times 1-m harp trap suspended near the cave or mine entrance and examined them to determine species (when possible), sex, and age (adult or subadult based on ossification of the finger joint; Davis and Hitchcock 1965) before releasing them. At one additional site bats resting on the mine wall were captured by hand.

Data analysis

We used SPSS, version 11.5 (SPSS, Inc. 2002), to conduct statistical analysis. Unless otherwise noted, data (including values given as proportions) met the assumptions of normality and were not transformed prior to analysis. Some data exhibited skewness ≤ -1.0 and, thus, were transformed by squaring each value prior to analysis (Zar 1999).

Flight speeds. For comparison of situations (i.e., forest, passage, in and out for entrance, mock gate, and permanent gate) across sites (e.g., speeds recorded in passages from multiple sites compared with speeds recorded at multiple gates), we only included situations with ≥ 10 flight speeds in the analysis. We referred to the direction in which speeds were recorded as "in" and "out," but we could not determine the direction of flight of bats whose flight speeds were measured. For example, when the radar gun was facing toward the gate from outside the cave, we labeled speeds "gate in," and bats whose speeds we recorded in this set-up were presumably influenced by the gate. When we rotated the radar gun 180° to face away from the gate, we labeled speeds "gate out," and they represented bats we assumed to be unaffected by the gate.

We compared speeds recorded with and without a mock gate for sites with ≥ 3 speed values for each situation. At each site where both perpendicular and angled mock gates were used, we combined flight speed data from the 2 orientations after finding no significant difference between the two for any site.

Vocalizations. Prior to quantitative analysis, we used BatSound Pro to visually examine ≥ 8 recorded call files (30 seconds each) per study site or all files from sites with < 8 recorded, and as many as 35 files for sites where multiple nights were spent or many calls recorded. During this examination, we listened for calls that seemed to be communicative and assessed activity level and other general characteristics. After determining no call features would be lost, we filtered recordings (Butterworth, filter order 8, BatSound Pro) using a high pass of 23 kHz (lower for some files with lower-frequency calls). We then determined duration (DUR in ms),

frequency with maximum energy (FME in kHz), lowest frequency (LF in kHz), and highest frequency (HF in kHz) of each call recorded in each file (30-second sequence). We determined FME, LF, and HF using a power spectrum (Hanning Window, FFT size 256, BatSound Pro), with LF and HF measured at -10 dB from the FME (peak). We compared the parameters of calls we recorded with those reported by Fenton and Bell (1979, 1981), Brigham et al. (1989), Thomas and West (1989), MacDonald et al. (1994), Betts (1998), and Murray et al. (2001) representing various species. We also identified and classified social calls based on descriptions in Fenton (1977), Barclay et al. (1979), Fenton (1985), and Pfalzer and Kusch (2003).

To determine whether honks (calls believed to alert another bat of an impending collision; Suthers 1965) were more prevalent at gated sites, we chose 2 gated and 2 ungated sites, each with high or moderately high activity levels, then determined which call recordings from these sites had calls that were distinguishable from one another (no excessive overlap) and were not saturated. Using data just from these acceptable files, we randomly selected 3 30-second recordings from each gated site and 6 30-second recordings (3 unobstructed and 3 with mock gate) from each ungated site. We then counted number of calls and honks with intensities at least 5% above background noise, based on the time-amplitude display, and clearly distinguishable from background noise on the time-frequency display, in 2 nonconsecutive 200-ms segments from each 30-second recording. We calculated the proportion of calls that were honks for each site, then used a one-way ANOVA to compare this proportion between situations.

Flight behavior. We combined fly-retreats and circles (henceforth referred to as FRCs) for analysis, as each was mutually exclusive to passing directly through. We calculated the ratio of FRC to passes for sites with a mock gate, and the proportion of the total number of behaviors that were passes or FRCs for each site. We then compared these proportions based on real or mock gate presence, passage versus entrance (with and without gates), gate age, bat activity level, gate or passage or entrance size, spacing of vertical supports, whether an entrance was on an incline (qualitatively assessment), and number of cave or mine entrances (1 or > 1). We classified the age of each real gate as ≤ 4 years, 4–6 years, or > 6 years and also tested for a relationship between bat activity and gate age. We

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subjectively assigned each site an activity level: 1) no bats or too few for data; 2) low; 3) moderate; and 4) high, based on visual observation, numbers of behaviors recorded, and overlap between and saturation of recorded calls. Sites with gates were divided into 3 classes based on gate size: $<9.5 \text{ m}^2$ (small), $9.5\text{--}19 \text{ m}^2$ (medium), and $>19 \text{ m}^2$ (large), and unobstructed entrances and passages into 2 size classes: $<\text{or } >4.7 \text{ m}^2$ (small or large). We compared gates with maximum vertical support spacing of $<1.5 \text{ m}$, $1.5\text{--}2.15 \text{ m}$, and $>2.15 \text{ m}$ to one another, and gates with $<1.2 \text{ m}$, $1.2\text{--}1.8 \text{ m}$, and $>1.8 \text{ m}$ average spacing between vertical supports.

Results

Swarming and other observations

Based on captures at 8 sites, at least 6 species, representing 3 genera were involved in swarming at the study sites (*Myotis grisescens*, *M. leibii*, *M. lucifugus*, *M. septentrionalis*, *Eptesicus fuscus*, *Pipistrellus subflavus*). The echolocation calls we recorded appeared to represent at least 7 species and 3 to 4 genera. The calls we recorded corresponded with previously described calls of *Myotis lucifugus*, *M. leibii*, *M. sodalis*, *M. septentrionalis*, *M. grisescens*, *Eptesicus fuscus*, *Nycticeius humeralis* (possibly), *Pipistrellus subflavus* (possibly), and *Corynorhinus rafinesquii* (Fenton and Bell 1979, 1981; Brigham et al. 1989; Thomas and West 1989; MacDonald et al. 1994; Betts 1998; Murray et al. 2001). At all sites we recorded calls from at least 2 species, and at 23 of 28 sites at least 3 species. It is possible that some bats whose calls were recorded at sites were merely passing by and were not actively swarming at the site.

Flight speeds

Of the 12 mock-gate versus no-gate comparisons (we compared "in" and "out" separately), flight speeds were significantly slower in the presence of a mock gate in 4 situations (3 sites; right-tailed *t*-tests with $P \leq 0.05$ for each comparison). When comparing speeds by location type (all sites combined), "entrance in" differed significantly from all other situations, including mock perpendicular in. Entrance out also differed from gate in; gate in also differed from passage, mock perpendicular in, and mock perpendicular out; and gate out differed from passage ($F_{7, 1303} = 27.31$ [subscript numbers represent df and error df], overall $P \leq 0.001$; all *P* values ≤ 0.01 using Dunnett T3 post hoc test). It should be

noted that when comparing speeds within a single situation but among various sites, there was a significant difference in 26 of 56 comparisons (ANOVAs for 8 situations; $P \leq 0.05$; $n = 1,311$ total individual speeds recorded at 14 sites on 24 separate nights). Overall, average flight speed was highest when bats exited an ungated entrance ("entrance in"; $X = 5.14 \text{ m/s} \pm 1.04$; $n = 225$ individual speeds, 6 sites and 12 nights sampled) and lowest when bats left an entrance with a real gate in place ("gate in"; $X = 4.06 \text{ m/s} \pm 0.66$, $n = 98$, 4 sites and 11 nights sampled).

Vocalizations

Based on data presented in Lawrence and Simmons (1982) and assuming a large object, a call frequency of $\sim 40 \text{ kHz}$, and a sound pressure level of 110 dB (Griffin 1986), bats we studied potentially could detect a gate's presence via echolocation at a range of $\sim 27 \text{ m}$. Based on subjective examination, there were no obvious differences in calls recorded in the presence and absence of real or mock gates. Bats produced a variety of echolocation calls, including honks and buzzes (higher pulse repetition rates). There was no significant difference in the proportion of honks recorded at sites with high and low activity based on the presence or absence of real or mock gates ($F_{2,12} = 0.13$, $P = 0.88$), and honks comprised 11–12% of calls for each situation ($n = 254$ calls for gates, 152 calls for mock gates, and 166 calls for unobstructed areas). At swarming sites we also recorded a variety of other vocal signals associated with social situations (Barclay et al. 1979), whether the sites were ungated or gated with real or mock gates, and whether activity was high or low.

Flight behavior

Bats' reactions to mock gates based on their flight behavior varied between sites from low or almost nonexistent to very perturbed. At sites where the latter was true, this reaction did not lessen after the gate had been in place for ≥ 30 minutes. Some bats changed direction as they neared a gate and did not appear to return. At gates with an opening (i.e., small door closed during only part of the year, and open during swarming) or a bat chute, bats appeared to fly through the opening(s) more frequently than through the remainder of the gate.

There was a significant increase in the number of fly-retreat or circles (FRCs) and a decrease in direct passes when a gate was present, and activity level, gate size, and location of a gate at a hill bottom all

corresponded to a change in behavior, while spacing of vertical supports and passage versus entrance gate position were not correlated with significant changes in proportion of FRCs or passes. For all sites with a mock gate, the ratio of FRC to pass was higher with the mock gate in place than before the mock gate was installed or after it had been removed (Figure 4). The proportion of all behaviors that were FRC ($F_{2,56}=21.97$, overall $P \leq 0.001$) or passes ($F_{2,56}=23.29$, overall $P \leq 0.001$) differed significantly among locations with no gate, a real gate, and a mock gate (Tukey HSD post hoc test, all P values ≤ 0.025 ; Table 1).

Bats circled or flew and retreated significantly more (right-tailed t -test; $t_{44}=4.04$, $P \leq 0.001$) and passed less (left-tailed t -test; $t_{44}=-4.23$, $P \leq 0.001$) at entrance gates (real or mock, $n=29$) than at unobstructed entrances ($n=17$). The proportion of passes at passage gates (real or mock, $n=5$) was significantly lower (left-tailed t -test; $t_{5,69}=-2.43$, $P=0.027$) than in unobstructed passages ($n=6$), and the proportion of FRCs was significantly higher when a gate was in place (right-tailed t -test; $t_{5,35}=2.29$, $P=0.034$, no assumption of equal variances for either).

Among unobstructed entrances and passages, there were no significant differences in the proportion of behaviors that were passes (data transformed, $F_{2,20}=1.39$, $P=0.27$) or FRC ($F_{2,20}=0.92$, $P=0.41$) between sites according to bat activity level,

Table 1. Summary of bat flight behaviors for each situation based on proportion of total behaviors observed.^a All data was collected between July and October 2003 from sites in Ontario, New York, Vermont, Ohio, Kentucky, and Tennessee.

Situation ^b	% passes	% fly-retreat + circle
No gate (23, 19, 14)	68	23
Real gate (22, 22, 14)	50	37
Mock gate (14, 10, 9)	25	60

^a Numbers do not add up to 100% because other behaviors (not passes or FRCs) were also observed.

^b Number of data sets (location-time combinations), # locations, # caves and mines.

but these data may not be representative of most sites, because 4 of the 5 values with high activity were obtained at a single site (2 locations for 2 nights each). Among gated sites, bats exhibited a significantly higher proportion of passes at gates with moderate activity (only 1 site had low activity, so it was not included) than at gates with high activity (right-tailed t -test; $t_{12,82}=4.66$, $P \leq 0.001$, equal variances not assumed; Table 2). Likewise, the proportion of FRC was significantly lower at sites with moderate activity than at sites with high activity (left-tailed t -test; $t_{18}=-6.45$, $P \leq 0.001$; Table 2).

The proportion of behaviors that were passes did not differ significantly based on gate size (data transformed, $F_{2,19}=1.77$, $P=0.20$), but the proportion of behaviors that were FRCs was significantly

lower for large gates (>19 m², $n=7$) compared with small gates (<9.5 m², $n=8$) ($F_{2,19}=5.94$, overall $P=0.01$, $P=0.021$; Table 2). However, for unobstructed passages and entrances, there was no significant difference in the proportion of behaviors that were FRCs (2-tailed t -test; $t_{21}=-0.25$, $P=0.81$) or passes (2-tailed t -test; data transformed, $t_{21}=0.09$, $P=0.93$) between those classified as small (<4.7 m², $n=12$) and large (>4.7 m², $n=11$; Table 2).

In general, unobstructed areas were smaller than gated areas. There was no significant difference in the proportion of behav-

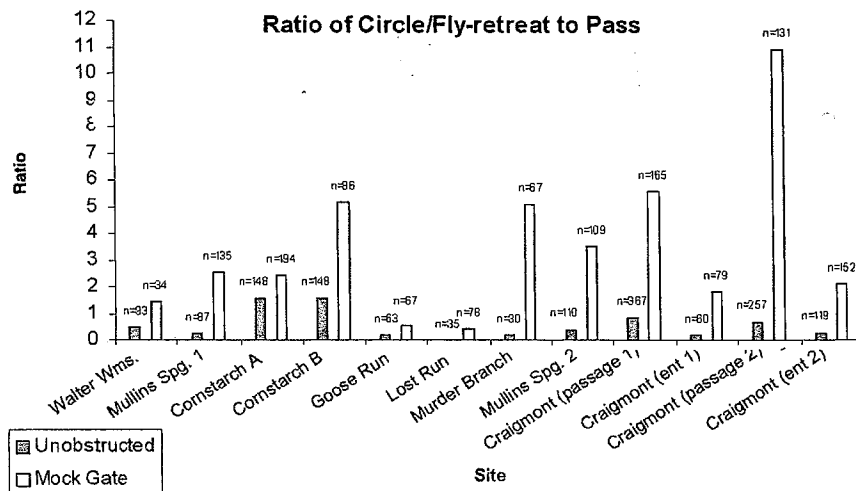


Figure 4. Bat flight behaviors in presence and absence of wooden mock gates. Numbers (1 and 2) indicate different nights at the same location. Letters (A and B) indicate 2 different gate orientations at the same location on the same date. Locations: Walter Williams Preserve Mine, Ulster Co., New York; Mullins Spring Cave, Rockcastle Co., Kentucky; Craigmont Mine, Renfrew Co., Ontario; Cornstarch Cave, Fentress Co., Tennessee; Goose Run Mine, Athens, Co., Ohio; Lost Run Mine, Perry Co., Ohio; Murder Branch Cave, Menifee Co., Kentucky.

Table 2. Variables associated with significant differences in bats' flight behavior. Proportions indicate proportion of total observed behaviors that were passes or fly-retreat or circles (FRCs).

Variable	Proportion of behaviors that were passes	Proportion of behaviors that were FRCs	Comments
Gate size* or passages	No difference	Higher at small gates*	No difference based on size in unobstructed entrances
Spacing of vertical supports	No difference	No difference	All ≥ 0.6 m apart
Gate age*	Higher at newer gates*	No difference	Activity lower at newer gates*
Gate at hill bottom vs. flat ground*	Lower at hill bottom*	No difference	
Gate location (passage vs. entrance)	No difference	No difference	
Bat activity level*	Lower when activity was higher, at gated sites only*	Higher when activity was higher, at gated sites*	No difference at ungated sites
Number of entrances	No difference	No difference	

* Indicates variables that were significant in the context of flight behavior.

iors that were passes (data transformed, $F_{2,19}=0.21$, $P=0.81$) or FRC ($F_{2,19}=0.81$, $P=0.46$) based on maximum spacing between vertical supports or average spacing of vertical supports ($F_{2,18}=0.39$, $P=0.68$ for pass (data transformed); $F_{2,18}=0.001$, $P=0.99$ for FRC; Table 2). At Aeolus Cave, which had vertical supports more closely spaced than any other site (0.6m), bats displayed a relatively high collision rate of 6%, but activity level also was unusually high.

There was no significant difference in bat flight behavior (2-tailed t -tests; $t_{21}=-1.12$, $P=0.28$ for % FRC; $t_{21}=1.09$, $P=0.29$ for % pass [data transformed]) between unobstructed entrances ($n=17$) and unobstructed passages ($n=6$) or between entrance gates (mock or real, $n=29$) compared with passage gates (mock or real, $n=5$) (2-tailed t -tests; $t_{32}=-1.06$, $P=0.30$ for % pass; $t_{32}=1.52$, $P=0.14$ for % FRC; Table 2), although sample sizes were highly uneven.

We never saw any bat collision in the absence of a gate (even at sites with high activity), but at 54.5% (12 of 22) of real gates and 50% (7 of 14) of mock gates, at least 1 collision was observed (including at 1 gate with low activity). Collisions accounted for 2% of all activities recorded at real and mock gates.

There was no significant difference in the proportion of behaviors that were passes (data transformed; left-tailed t -test; $t_{20}=-0.52$, $P=0.31$) or FRCs (right-tailed t -test; $t_{20}=0.28$, $P=0.39$) between sites with a single entrance ($n=6$) compared with multiple entrances ($n=16$; Table 2). The proportion of bat passes was significantly higher at gates located on flat ground ($n=15$) than at those located at the bottoms of hills ($n=6$; right-tailed t -test; $t_{19}=2.04$, $P=0.028$), but there was no significant difference in

proportion of behaviors that were FRCs based on a gate's location relative to a hill (left-tailed t -test; $t_{19}=-1.6$, $P=0.065$; Table 2).

Discussion

It has been hypothesized that bats are more vulnerable to predators at gated cave and mine sites than at ungated sites (MacGregor 1993, Tuttle 1977, White and Seginak 1987) partly because they slow down as they approach gates. Overall, our data do not support this suggestion; rather, bats generally appeared to use directional changes to avoid collision with obstacles. We rarely witnessed bats landing on gates, which may be due to gate designs with larger flight spaces or the fact that bats present during swarming were typically not newly volant (Hall and Brenner 1968, Fenton 1969). We never observed a bat taken by a predator or saw any predator in the study areas; however, our presence may have deterred potential predators.

We observed a behavioral gradation in bat flight behavior from ungated to gated situations and differences between permanent and mock gates, indicating that while bats may adjust somewhat to new gates, their behavior continues to be affected over time. Even at sites where gates have been in place for ≥ 10 years (e.g., Renfrew Mine, Aeolus Cave), bat flight behavior differed from that observed in ungated situations (more FRCs, fewer passes), despite gated entrances or passages generally being larger than ungated ones. Bats' apparently more negative reaction to smaller gates was probably the result of restricted access thereby creating a bottleneck as many bats were forced to pass through a

smaller area. Since there were no significant differences in flight behavior based on size at ungated areas, the presence of an obstacle may be a key component in bats' responses in smaller areas. Flying in the presence of a gate could be analogous to flying in clutter (e.g., within a forest), and such conditions may force bats to pay more careful attention to their surroundings and possibly expend energy actively avoiding collisions via less direct flight paths (e.g., sudden direction changes, circling). The lack of differences in flight behavior based on spacing of vertical supports may reflect vertical spacing of at least 0.6 m, the minimum recommended by the American Cave Conservation Association (ACCA; Tuttle and Taylor 1998).

We found no evidence that bat flight behavior was less affected by dark zone (passage) than by entrance gates (e.g., B. Howard, National Speleological Society member, personal communication). While bats did engage in more FRCs and fewer passes proportionally in passages (with or without a gate) than at entrances (with or without a gate), the differences were not statistically significant. These differences indicate less hindered flight at entrances than in passages, perhaps because adding an obstacle (e.g., gate) to an already enclosed space creates a "third wall" for bats to negotiate physically and acoustically.

We suspect that gates impose a real cost to bats in terms of increased flight times and higher energy expenditures or exclusion from important sites rather than through the direct impact of collisions. The abundance of directional changes and circling, as well as recovering from collisions, cost energy and time that could be used to seek a mate, find an ideal hibernation spot, or forage. Loss of energy could be especially detrimental to bats just before the hibernation period, and loss of time may be especially harmful for swarming bats visiting multiple potential hibernation sites. Numerous reports, beginning with Tuttle (1977), describe bats abandoning newly gated roosts, and some of the bats we saw fly away from a gate did not appear to return. A gradual return of bats to gated roosts has been observed in some instances (e.g., D. Dalton, Gating Consultant, personal communication), supporting the idea that bats may habituate somewhat to the presence of a gate.

Management implications

Over the past 40 years, the gating of caves and

mines used by bats has advanced greatly with regard to abiotic factors (air flow, resistance to humans, etc.), and these advances should be the basis for further modifications reflecting the behavior of bats. Policies about gating should be applicable to all bat species in the region, not the 1 or 2 listed as Endangered because many roosts are used by multiple species at least some time during the year (e.g., Hitchcock 1965, Rodriguez-Duran 1998, Wohlgenant 1994, data from this study). Use of night vision or infrared viewing devices and real-time video recordings may be useful for future studies regarding flight behavior at gates, and larger mock gates could isolate the variables of gate size and newness.

Since bats seem to react more to newer gates (Table 2), assembling gates gradually over a period of several months, when possible, might give bats a chance to adapt, and make them less inclined to flee a newly gated roost. Finally, we recommend, based on our data, that a bat-friendly gate should 1) be placed at as large an area as possible (i.e., gates not be placed at smaller points in a passage, or where the entrance has begun to taper), 2) always have a bat chute, open top, or further-spaced horizontal bars higher up when possible, 3) be placed at an entrance, rather than in a passage, when possible (unless predation is a known problem), and 4) be placed on flat ground rather than an incline.

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Literature cited

- ALLENDE, C., J. BECK, N. ERVIN, J. TAYLOR, AND K. GRANDISON. 2003. Monitoring and evaluating the results of bat protection efforts. Page 18 in the Program and Abstracts of the Thirty-third Annual North American Symposium on Bat Research, 8-11 October, 2003, Lincoln, Nebraska, USA. Abstract.
- BARCLAY, R. M. R., M. B. FENTON, AND D. W. THOMAS. 1979. Social behavior of the little brown bat, *Myotis lucifugus*, II. Vocal communication. *Behavioral Ecology and Sociobiology* 6: 137-146.
- BARCLAY, R. M. R., AND L. D. HARDER. 2003. Life histories of bats: life in the slow lane. Pages 209-253 in T. H. Kunz and M. B. Fenton, editors. *Bat ecology*. University of Chicago, Chicago, Illinois, USA.
- BETTS, B. J. 1998. Effects of interindividual variation in echolocation calls on identification of big brown and silver-haired bats. *Journal of Wildlife Management* 62: 1003-1010.
- BLAKE, R. W., R. KOLOTYO, AND H. DE AL CUEVA. 1990. Flight speeds of the barn swallow, *Hirundo rustica*. *Canadian Journal of Zoology* 68: 1-5.
- BRIGHAM, R. M., J. E. CEBEK, AND M. B. C. HICKEY. 1989. Intraspecific variation in the echolocation calls of two species of insectivorous bats. *Journal of Mammalogy* 70: 426-428.
- CLARK, B. K., B. S. CLARK, AND D. M. LESLIE, JR. 1997. Seasonal variation in use of caves by the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*) in Oklahoma. *American Midland Naturalist* 137: 388-392.
- COPE, J. B., AND S. R. HUMPHREY. 1977. Spring and autumn swarming behavior in the Indiana bat, *Myotis sodalis*. *Journal of Mammalogy* 58: 93-95.
- CURRIE, R. R. 2000. Federally listed threatened and endangered species of importance to mining. Pages 51-56 in K. C. Vories and D. Throgmorton, editors. *Proceedings of bat conservation and mining: a technical interactive forum*. United States Department of the Interior, Carbondale, Illinois, USA.
- CURRIE, R. R. 2001. An overview of the response of bats to protection efforts. Pages 173-183 in K. C. Vories and D. Throgmorton, editors. *Proceedings of bat conservation and mining: a technical interactive forum*. United States Department of the Interior, Carbondale, Illinois, USA.
- DAVIS, W. H., R. W. BARBOUR, AND M. D. HASSELL. 1968. Colonial Behavior of *Eptesicus fuscus*. *Journal of Mammalogy* 49: 44-50.
- DAVIS, W. H., AND H. B. HITCHCOCK. 1965. Biology and Migration of the bat, *Myotis lucifugus lucifugus*, in New England. *Journal of Mammalogy* 46: 296-313.
- FENTON, M. B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* 47: 597-602.
- FENTON, M. B. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. Pages 1-34 in *Life Science Contributions*, Royal Ontario Museum, Number 77, Ontario, Canada.
- FENTON, M. B. 1977. Variation in the social calls of little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology* 55: 1151-1157.
- FENTON, M. B. 1985. *Communication in the Chiroptera*. Indiana University, Bloomington, USA.
- FENTON, M. B., AND G. P. BELL. 1979. Echolocation and feeding behavior in four species of *Myotis* (Chiroptera). *Canadian Journal of Zoology* 57: 1271-1277.
- FENTON, M. B., AND G. P. BELL. 1981. Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy* 62: 233-243.
- FINLEY, R. B. JR. 1959. Observation of nocturnal animals by red light. *Journal of Mammalogy* 40: 591-594.
- GRIFFIN, D. R. 1986. *Listening in the dark: The acoustical orientation of bats and men*. Cornell University, Ithaca, New York, USA.
- HALL, J. S. AND F. J. BRENNER. 1968. Summer netting of bats at a cave in Pennsylvania. *Journal of Mammalogy* 49: 779-781.
- HITCHCOCK, H. B. 1965. Twenty-three years of bat banding in Ontario and Quebec. *Canadian Field-Naturalist* 79: 4-14.
- JOHNSON, A. J., 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., AND L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Pages 680-743 in T. H. Kunz and M. B. Fenton, editors. *Bat ecology*. University of Chicago Press, Chicago, Illinois, USA.
- LAWRENCE, B. D., AND J. A. SIMMONS. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation. *Journal of the Acoustical Society of America* 71: 585-590.
- LUDLOW, M. E., AND J. A. GORE. 2000. Effects of a cave gate on emergence patterns of colonial bats. *Wildlife Society Bulletin* 28: 191-196.
- MACDONALD, K., E. MATSUI, R. STEVENS, AND M. B. FENTON. 1994. Echolocation calls and field identification of the eastern pipistrelle (*Pipistrellus subflavus*: Chiroptera: Vespertilionidae), using ultrasonic bat detectors. *Journal of Mammalogy* 75: 462-465.
- MACGREGOR, J. 1993. Responses of winter populations of the federally endangered Indiana bat (*Myotis sodalis*) to cave gating in Kentucky. Pages 364-370 in D. L. Foster, editor. *National cave management symposium proceedings*. American Cave Conservation Association, Horse Cave, Kentucky, USA.
- MANN, S. L., R. J. STEIDL, AND V. M. DALTON. 2002. Effects of cave tours on breeding *Myotis velifer*. *Journal of Wildlife Management* 66: 618-624.
- MARTIN, K. W., W. L. PUCKETTE, S. L. HENSLEY, AND D. M. LESLIE, JR. 2000. Internal cave gating as a means of protecting cave dwelling bat populations in eastern Oklahoma. *Proceedings of the Oklahoma Academy of Science* 80: 133-137.
- MURRAY, K. L., E. R. BRITZKE, L. W. ROBBINS. 2001. Variation in search-phase calls of bats. *Journal of Mammalogy* 82: 728-737.
- PFAIZER, G., AND J. KUSCH. 2003. Structure and variability of bat social calls: implications for specificity and individual recog-

- nitition. *Journal of Zoology* (London) 261:21-33.
- POOLE, E. L. 1932. A survey of the mammals of Berks County, Pennsylvania. *Bulletin of Reading Public Museum and Art Gallery* 13:5-74. (As cited in Fenton 1969).
- POWERS, R. D. JR. 2002. The angle iron bat gate. *Proceedings of the Bat Gate Technical Interactive Forum*, Austin, Texas, USA. E-proceedings. Available online at: www.mcrc.org/bats. [Date accessed: 25 October 2002].
- RACEY, P. A., AND A. C. ENTWISTLE. 2003. Conservation ecology of bats. Pages 680-743 in T. H. Kunz and M. B. Fenton, editors. *Bat ecology*. University of Chicago Press, Chicago, Illinois, USA.
- RODRIGUES-DURAN, A. 1998. Nonrandom aggregations and distribution of cave-dwelling bats in Puerto Rico. *Journal of Mammalogy* 79:141-146.
- SALCEDO, H. C., M. B. FENTON, M. B. C. HICKEY, AND R. W. BLAKE. 1995. Energetic consequences of flight speeds of foraging red and hoary bats (*Lasiurus borealis* and *Lasiurus cinereus*; Chiroptera: Vespertilionidae). *Journal of Experimental Biology* 198:2245-2251.
- 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.
- SHERWIN, R. E., J. S. ALTENBACH, AND S. HAYMOND. 2002. The responses of bats to gates. *Proceedings of the Bat Gate Technical Interactive Forum*, Austin, Texas, USA. Available online at: www.mcrc.org/bats. [Date accessed: 25 October 2002].
- SPSS, INC. 2002. SPSS for Windows, Version 11.5.0. SPSS, Inc., Chicago, Illinois, USA.
- SUTHERS, R. A. 1965. Acoustic orientation by fish-catching bats. *Journal of Experimental Zoology* 158:319-348.
- THOMAS, D. W. 1995. Hibernating bats are sensitive to nontactile human disturbance. *Journal of Mammalogy* 76:940-946.
- THOMAS, D. W., AND S. D. WEST. 1989. Sampling methods for bats. A. B. Carey and L. F. Ruggiero, technical editors. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station. *Wildlife-habitat relationships: sampling procedures for Pacific Northwest vertebrates*. General Technical Report PNW-GTR-243. Portland, Oregon, USA.
- TUTTLE, M. D. 1977. Gating as a means of protecting cave dwelling bats. Pages 77-82 in T. Aley and D. Rhodes, editors. *National Cave Management Symposium Proceedings*. Speleobooks, Albuquerque, New Mexico, USA.
- TUTTLE, M. D., AND D. A. R. TAYLOR. 1998. Bats and Mines. Revised edition. Bat Conservation International, Resource Publication Number 3. Austin, Texas, USA.
- WHITE, D. H., AND J. T. SEGINAK. 1987. Cave gate designs for use in protecting endangered bats. *Wildlife Society Bulletin* 15:445-449.
- WOHLGENANT, T. J. 1994. Roost interactions between the common vampire bat (*Desmodus rotundus*) and two frugivorous bats (*Phyllostomus discolor* and *Sturnira lilium*) in Guanacaste, Costa Rica. *Biotropica* 26:344-348.
- ZAR, J. H. 1999. *Biostatistical Analysis*. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.



Genevieve R. Spanjer (top) obtained her B.S. in biology from Berry College, where she conducted research on cave-dwelling crayfish, and her M.Sc. from York University, where her cave-related studies focused on bats. Her primary research interests are bat behavior, ecology, and conservation, and studies of these animals have taken her to a variety of locations from British Columbia to Belize. In fall 2005, Genni began her Ph.D. in biology at the University of Maryland. **M. Brock Fenton** (bottom, with camera) obtained his honours B.Sc. in biology from Queen's University and his M.Sc. and Ph.D. from the University of Toronto. He has held faculty appointments in the Departments of Biology at Carleton and York Universities and the University of Western Ontario. His research on bats has concentrated on their behavior and ecology and has involved fieldwork in many parts of the world, the Americas as well as Africa, China, and Australia. Brock is currently professor and Chair of Biology at the University of Western Ontario.



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