

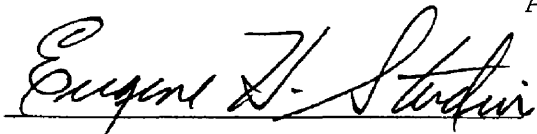
Exit/entry sequences, roost fidelity and transport of young
by big brown bats (*Eptesicus fuscus*)
at a summer roost

by

Sheri Mayrberger

Thesis submitted to the Faculty of the
University of Michigan-Flint
in partial fulfillment of the requirements for the degree
of
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in
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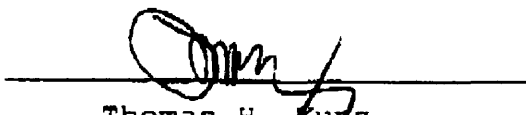
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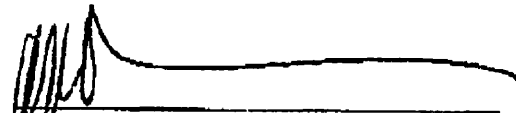
Eugene H. Studier
Committee & Program Chairman
University of Michigan-Flint



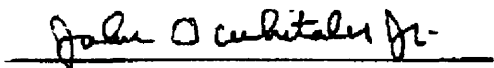
Dennis P. Viele
University of Michigan-Flint



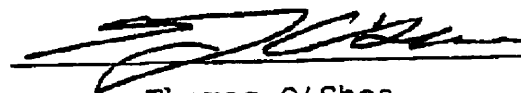
Thomas H. Kunz
Boston University



R. Mark Brigham
University of Regina



John O. Whitaker, Jr.
Indiana State University



Thomas O'Shea
U.S. Geological Survey

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Flint, Michigan

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ABSTRACT

I recorded every exit and entry flight of each member of a sizable big brown bat (*Eptesicus fuscus*) maternity colony using an infra-red camera and VCR at a roost with just a single access/egress hole. I made recordings during 150 consecutive nights in the summer of 2002. Twenty-two bats were fitted with "ball-chain" necklaces bearing unique symbol tags to determine whether maternity colony members exit or re-enter the roost in a specific sequence, i.e., exhibit a fixed hierarchy. I reviewed video tapes in slow-motion and recorded flight times to the nearest second, for all marked and unmarked individuals. Although I found no exact flight sequences, exit patterns at sunset and return patterns at sunrise were not random and certain bats occupied specific

positions within the sunset emergence and sunrise return flights. The lone adult male in the roost routinely emerged after all other bats had exited and regularly returned earlier than all other bats before dawn. In gathering sequence data, roost fidelity data were automatically obtained. Overall fidelity of marked individuals varied between 37% and 93%, although a few individuals exhibited 100% fidelity during some portion of the reproductive period. Average roost fidelity of marked females decreased from 85%, during early pregnancy, to 62% during late pregnancy, increased to 83% during lactation, and then dropped rapidly to 9% during post-lactation. Fidelity, or lack thereof, was affected by females occasionally transporting volant offspring to and from alternate roosts. During a three week period, 0.5% of all flights were with attached young. Babies were always transported singly and transport flights only occurred after the sunset foraging bout was completed. Mothers likely transported large babies only when they could not be disengaged from the teat, and occasionally transported large babies that were probably not their own.

Acknowledgements

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Introduction

Numerous studies have used visual counts of bats exiting at a roost opening to estimate colony size, determine emergence patterns (Swift, 1980, Bullock et al., 1987; Kunz & Anthony, 1996; Viele et al., 2002), and collect re-entry data (McAney & Fairley, 1988). When large numbers of bats are involved, accurate counts are often difficult or impossible (McAney & Fairley, 1988), especially during peak emergence (Lee & McCracken, 2001), or when emerging bats are grouped in clusters (Bullock et al., 1987; Speakman et al., 1995) or bursts (Swift, 1980). Natural and artificial obstructions can also make monitoring difficult (McAney & Fairley, 1988), even when bat numbers are small.

During all-night observations outside a roost opening of pipistrelle bats, Swift (1980) used five minute intervals to record the emergence and subsequent return of all bats, reducing those intervals to 30 seconds during peak emergence. Emerging and returning bats were distinguished from each other by the size and number of flight circles made near the roost entrance.

Speakman et al. (1995) used recorded voice cues, which were later processed by data loggers, to record each

emergence event. In a subsequent year of the same study, events were recorded directly to a laptop computer.

Hope & Bhatnagar (1979) found that the wavelength of infrared light was outside the range of bat retina perception, an observation that was later supported by Barclay & Bell (1988) and Mistry & McCracken (1989), who found that bat activity did not seem to be affected by infrared light.

Several studies have recorded bat activity using low-level red light (Barclay, 1982), far red light (Barclay & Thomas, 1979), night vision devices in conjunction with light sources fitted with infrared filters (Anthony et al., 1981; Burnett & August, 1981; McCracken & Gustin, 1991; Clark et al., 2002) or infrared light sources (Catto et al., 1995) either within the roost or near the roost opening. Clark et al. (2002) used a night vision scope and lamps covered with infrared filters inside cave entrances to periodically videotape activity. Catto et al. (1995) monitored roost access holes using pairs of infra-red light beams connected to a computer. Bat exits and returns were differentiated by the sequence in which the double beams were broken.

Most recently the use of Passive Integrated Transponder (PIT) tags has shown promise as a method of

marking reptiles (Jemison et al., 1995), amphibians (Ott & Scott, 1999), fish (Roussel et al., 2000; Bruyndoncx et al., 2002) and small mammals including ground squirrels (Schooley et al., 1993) and Bechstein's bats, *Myotis bechsteinii* (Kerth & König, 1999). Although methods of monitoring bat activity continue to become more sophisticated, some aspects of monitoring roost activity continue to require direct observation. Reproductive state of females, for example, must be determined by periodic capture, and examination of colony members (Anthony et al., 1981; Rydell, 1989 A&B; Korine et al., 1994; Catto et al., 1995; Arlettaz et al., 2001). Dates of parturition for the colony are often estimated or extrapolated from such examinations (Catto et al., 1995; Arlettaz et al., 2001) or are based on observation of first babies (Whitaker, 1998), or first audible isolation calls (Rydell, 1989A, 1993).

Few studies have documented all exit and re-entry events for every bat in a sizable colony over the course of a reproductive season. Many have focused on emergence time and factors controlling it, and/or on emergence patterns such as clustering or age-based exodus (Kunz & Anthony, 1996; Viele et al. 2002). None appear to have focused on the specific sequence in which individuals exit and return to the roost or have provided the exact date of parturition

of specifically identified bats without continued periodic capture.

The purpose of this research was to determine if maternity colony members exit or re-enter the roost in a specific sequence during the periods of pregnancy, lactation, transition (as young are becoming volant) and post-lactation. A maternity colony by name, is a grouping of generations of related adult females. The summer maternity colonies formed by many vespertilionids, including big brown bats, are matriarchal associations in which an absolute or loose hierarchy, as seen in elephants (Sikes, 1971), may be expected. Such a hierarchy may be based on age or size, and may be evidenced as a specific sequence or order of individuals during the sunset emergence or sunrise return flights. I predicted that such a sequence exists.

By recording all exit/entry activity over a period of 150 consecutive nights, transient or rapid changes that might be missed by intermittent data collection would be observed. Voluminous additional data concerning emergence patterns, flight patterns, flight numbers, flight durations, changing colony size, and screech owl predation were automatically obtained and will be reported in future publications. Since sequence potential necessarily relies

on fidelity, data concerning roost fidelity are included here. Year-to-year site fidelity of wintering big brown bats has been studied by Whitaker & Gummer (2000) and short-term individual fidelity was reviewed by Lewis (1995), who focused her work on radio-telemetry studies. Although radiotelemetry can provide short-term fidelity data on individuals, radio tags are usually ephemeral, and certainly do not last an entire reproductive season. Additionally, I recorded events of females carrying young bats, and because transports of young affected roost fidelity, those data are also included here.

Methods and Materials

My study was conducted in Southeast Michigan at a family farm consisting of a two-story clapboard-sided home, circa 1890, a modern home and three outbuildings located near Cass City (N43°36.047', W 083°10.509'). The property owners indicated that a bat colony had occupied the attic of the original home (the study roost) during the summer months for at least 30 years, although the owners had not occupied the home since 1996.

The eight by eight meter attic study roost was defined by four planes of the hip roof that sloped up from the side walls to merge with the ridgepole at a maximum height of 1.5 m above the floor. Bats roosted between crevices of roof boards, behind support beams and in the southerly facing false eaves.

Thorough and repeated inspection revealed only one circular entrance/exit portal, 40 mm in diameter, located near the center of the southerly facing wall on the underside of a 30 cm false eave, 7.5 cm from the building wall and 5 meters above ground level (Figure 1).

I attached a 13 x 18 cm piece of 13 mm plywood, to the false eave flush with the rear edge of the portal, extending downward beneath the portal at an angle 32° from

perpendicular to serve as an entrance/exit ramp for bats, and a background for videotaping. Wooden strips 4 mm square and 5-1/2 cm long were placed horizontally, and parallel to each other at an interval of 13 mm with contact cement and to provide better footing for entering and returning bats (Figure 1).

A standard infrared LED camera (Advance Security Products, Model SSC-1035BR) was mounted 15 cm forward of the ramp and focused on the entrance/exit portal. An analog clock, seven cm in diameter, set to Eastern Daylight Time was mounted adjacent to the portal, in the camera's field of view. Activity was recorded to tape from the infrared camera hard wired to a standard video cassette recorder (VCR) set to super long play (SLP). A television monitor, connected to the VCR provided simultaneous on-site viewing.

I discouraged bats from landing on the eave upside-down and crawling into the portal, an act that would prevent a clear view of the tag to the camera, by placing a block of wood adjacent to the entrance ramp opposite the clock. All equipment was mounted in early April before the local seasonal arrival of bats, except for two lag screws, which were attached to the eave on either side of the



Figure 1- Single exit/entry portal located on the underside of a 30 cm false eave, 5 m above ground level. A standard infrared LED camera was mounted 15 cm forward of the entrance ramp, focused on the portal and an analog clock, 7 cm in diameter. See additional details in text.

camera on 9 August to discourage camera movement by a screech owl that began preying on bats at or near the portal. The lag screws did not impede flight by either the bats or the owl.

Two of the three outbuildings on the property, a 12 x 15.5 m barn and a 4.5 x 8.5 m shed, both within 150 meters of the study roost, also housed bats, however numerous openings prevented video-taping at these additional sites.

I observed the seasonal return of the first bats on 13 April 2002. After allowing several weeks for colony size to stabilize and most returning bats (about 90 bats) to develop roost loyalty, 13 torpid bats (12 females and 1 male), were captured by hand from the ceiling and walls of the roost early on 4 May 2002 and fitted with aluminum "ball-chain" necklaces bearing a unique symbol tag. Unique symbols were painted with white Rustoleum® onto black 11 mm square cotton-reinforced vinyl material. Tags were hand sewn with button thread to the center of necklaces 52 mm in length (15 balls) with clasp, having a total weight of 0.36 grams. On 23 June 2002, nine additional females were caught and similarly fitted with nylon ball necklaces. Nylon necklaces were 50 mm in length with clasp (11 balls), weighed 0.66 grams, and bore two identical symbol tags sewn to the necklace equidistant from both the ends of the

necklace and each other. Mass of necklaces with tags was well less than five percent of the mass of bats (Aldridge & Brigham, 1988), and I observed no evidence that the necklaces affected behavior.

From 4 May to 30 September 2002, all entrance/exit activity was recorded on video tape. Taping and direct observations of roost entrance/exit activity began prior to dusk and continued until 22:00 - 23:00 hrs, at which time taping was switched to a second cassette that provided continuous record until after dawn. Tapes were reviewed in slow motion, and time (to the second) of all exit/entry flights for all bats and identity of any marked bats were recorded. In this thesis I report only data from 4 May until 31 July 2002, the periods of pregnancy, lactation, and the transitional period immediately following lactation.

Females which were in advanced pregnancy had difficulty passing through the exit/entry portal due to greatly increased girth and awkwardness, and were easily distinguished from lactating females. Pregnancy was defined as the period of roost occupancy preceding 19 June, the date at which parturition had occurred in 50% of females. Within the pregnancy period, early pregnancy was defined as the first 20 days of roost occupancy beginning 4

May, middle pregnancy as the following 20 days, and late pregnancy as the next 7 days. Late pregnancy was set at seven days because of dramatic reduction in both flight frequency and duration, which will be discussed in detail elsewhere (unpublished data). Lactation included the 20 days immediately following 19 June, and transition included the 20 days immediately following lactation, the period within which young were becoming volant.

Since a sequence pattern might be most evident during the sunset exit and sunrise return when large numbers of bats pass through the portal, those periods were used to determine if a pattern or hierarchy existed. Sequence data were analyzed using Chi-square tests for independence with critical values set at $P < .05$.

Marked bats necessarily had to be present in the roost to be included in sequencing and fidelity data. Not all marked bats were present in the roost on all days and not all participated in both the sunset exit and sunrise return on all days, resulting in different daily population values. Bats may have exited at sunset and returned before sunrise which included them in sunset exit sequence data, but not in sunrise return sequence data. Individuals that were seen exiting or entering at any time during an

evenings taping were included in fidelity data for that date.

During the transition period, fidelity of marked bats decreased dramatically, resulting in insufficient data to analyze and sequence analysis of the period includes 17 days rather than 20.

Of the 12 females tagged on 4 May, one was never seen again, and two were only seen for the three consecutive nights following tagging and data for those bats are not included here. Of the bats tagged on 23 June, one was only seen for five consecutive nights following tagging and is also not included in results reported here.

Results

Sequence

A chi-square test of independence was performed for pregnant and lactating bats separately in which individual bat order was tallied as first, second, third or last out during sunset emergence or last in, second to last in, third to last in or first in during the sunrise return. Individual 1 during pregnancy, for example, was the first marked bat to emerge at sunset on 13 occasions, the second bat to exit on nine nights, third to exit six times and the last marked bat to leave the roost on one evening (Figure 2). Marked individuals were included in my analysis only when they participated in the sunset flight, the sunrise return flight, or both. On occasions when only three marked bats participated in sunset or sunrise return flights, an individual could be assigned as both the third marked bat out and the last marked bat out (or first in at sunrise). A Chi-square analysis shows a non-random sequence for pregnant bats exiting the roost at sunset ($\chi^2 = 52.3$; degrees of freedom (dF) = 24; $P < 0.001$) and a nearly significant non-random order for pregnant bats at sunrise

Figure 2- Sunset exit (left panel) and sunrise return (right panel) sequences for bats collared on 4 May 2002 (=Julian day [Jday] 124) from 4 May through 19 June (Jday 170), 2002. The entry in the left panel under 1 is the first marked bat to emerge at sunset followed by the second marked bat (under 2), etc. The entry in the right panel under 1 is the last marked bat to return at sunrise. The entry under 2 is the second-to-last bat to return at sunrise, etc. Selected bats have been designated a color to aid in viewing their position in the sunset emergence and sunrise return flights. Dark bordered boxes represent the first day of lactation for those bats whose exact date of parturition is known.

Bats collared on 4 May													Period									
Date	Jday	1	2	3	4	5	6	7	8	9	10	10	9	8	7	6	5	4	3	2	1	Day#
		Sunset Exit										Sunrise Return										
4-May	124	8	13	3	7	6	1	11	9							2	8	7	1	3	1	
5-May	125	1	8	7	3										7	6	2	3	1	8	2	
6-May	126	8	6	12	1	3	2	7					11	7	6	2	12	3	8	1	9	
7-May	127	9	3	6	1	7	12	8	11												13	
8-May	128	9	13	1	6	11	2	8								1	13	2	8	6	5	
9-May	129	7	6	13	1	8															13	
10-May	130	8	14	9	1	7	2	11													8	
11-May	131																				8	
12-May	132																				9	
13-May	133	8	9	7	11														8	2	10	
14-May	134	8	9	2	6	12	7	11											8	2	11	
15-May	135	1	9	8	6	13	11	12	7								12	1	2	8	12	
16-May	136	1	8	7	6	2															13	
17-May	137	1	8	13	6	3														2	9	
18-May	138																				15	
19-May	139																				16	
20-May	140																				17	
21-May	141	7	11	3	12															13	3	
22-May	142	13	6	8	1	7	12	11											8	7	19	
23-May	143	9	13	1	3	7	12	11								11	7	12	1	8	20	
24-May	144	7	1	12	11																1	
25-May	145	1	13	8	7	12	11												13	8	7	
26-May	146	7	1	13	8	11														8	3	
27-May	147	1	6	7	8	11	12													8	4	
28-May	148	1	7	8																	5	
29-May	149	7	8	1	12													7	1	8	6	
30-May	150	6	7	8	3	12	9														7	
31-May	151	9	6	7	8	3															8	
1-Jun	152	6	8	9	1	7	12												8	13	9	
2-Jun	153	7	1	13	8	6															13	
3-Jun	154	6	8	1	12	13													3	13	11	
4-Jun	155	1	13	3	2	8	12													8	12	
5-Jun	156	7	1	8	6	12														3	1	
6-Jun	157	8	12	1	3													12	3	13	14	
7-Jun	158	8	1	13	3													1	3	13	15	
8-Jun	159	1	6	13	3	8													6	1	16	
9-Jun	160	6	3	1															13	6	1	
10-Jun	161	6	1	8	13													8	6	1	18	
11-Jun	162	1	6	8																	3	
12-Jun	163	8	1	3	12	6	2	13													20	
13-Jun	164	1	6	7	13	8															6	
14-Jun	165	1	6	7	12															2	3	
15-Jun	166	3	2	8	6	12													2	13	3	
16-Jun	167	8	1	6	3	13														6	8	
17-Jun	168	8	1	13															13	1	8	
18-Jun	169	6	7	8	11	3	13													11	8	
19-Jun	170	1	9	11	13	3	12												13	9	3	

return ($\chi^2 = 33.6$; $dF = 24$; $0.1 > P > 0.05$). Chi-square analysis for the period of lactation for both the 4 May (Figure 3) and 23 June (Figure 4) marked bats tests show a non-random order during both sunset exit and sunrise return flights ($\chi^2 = 37.0$; $dF = 24$, $P < 0.05$; $\chi^2 = 99.1$; $dF = 24$, $P < 0.001$ and $\chi^2 = 54.6$, $dF = 21$, $P < 0.001$ $\chi^2 = 69.2$, $dF = 21$, $P < 0.001$, respectively). Chi-square analysis for the period of transition from lactation to post-lactation shows a non-random order during the sunset exit ($\chi^2 = 52.6$; $dF = 21$, $P < 0.001$) in the 23 June marked bats (Figure 4).

The tagged male exited last at sunset more often than random during both the periods of female pregnancy, and lactation ($\chi^2 = 14.1$ & 17.0 , $dF = 3$ and $P < 0.001$ in both cases).

Figure 3- Sunset exit (left panel) and sunrise return (right panel) sequences for bats collared on 4 May 2002 (=Julian day [Jday] 124) from 20 June (Jday 171) through 31 July (Jday 212), 2002. The entry in the left panel under 1 is the first marked bat to emerge at sunset, followed by the second marked bat (under 2), etc. The entry in the right panel under 1 is the last marked bat to return at sunrise. The entry under 2 is the second-to-last bat to return at sunrise, etc. Selected bats have been designated a color to aid in viewing their position in the sunset emergence and sunrise return flights. Dark bordered boxes represent the first day of lactation for those bats whose exact date of parturition is known.

Bats collared on 4 May														Period								
Date	Jday	1	2	3	4	5	6	7	8	9	10	10	9	8	7	6	5	4	3	2	1	Day#
		Sunset Exit										Sunrise Return										
20-Jun	171	8	9	1	13											3	9	13	2	6	8	1
21-Jun	172	1	8	3	6	9	13	12	11									no data				2
22-Jun	173	8	6	1	13	9	11	12							13	9	6	11	1	8	3	3
23-Jun	174	6	8	1	13	9						L					13	9	1	6	8	4
24-Jun	175	1	8	6	7	3	13	9	12			A					13	9	6	1	8	5
25-Jun	176	13	1	6	9	8						C							13	8	3	6
26-Jun	177	8	7	1	13	3	6	11				T				13	11	9	1	7	8	7
27-Jun	178	8	13	6	9	1	3					A						13	1	9	8	8
28-Jun	179	8	1	12	9	3	13					T					13	9	1	3	8	9
29-Jun	180	6	9	8	1	13	3					I						13	9	1	8	10
30-Jun	181	8	6	9	13	1	12					O				13	1	9	6	3	8	11
1-Jul	182	13	6	8	3	1	9					N				13	6	1	9	3	8	12
2-Jul	183	9	1	13	7												13	9	1	8	3	13
3-Jul	184	7	8	9	2	1											13	9	1	8	7	14
4-Jul	185	7	8	13	9													13	9	7	8	15
5-Jul	186	7	8	9	3	1												13	1	7	2	16
6-Jul	187	6	7	2	9	1	13	12											13	7	9	17
7-Jul	188	9	6	13	12													13	1	9	6	18
8-Jul	189	6	1	2	9	13													1	9	2	19
9-Jul	190	9	6																		1	20
10-Jul	191	9																				2
11-Jul	192	12	9	6	1																	2
12-Jul	193	9	6	7	1																	3
13-Jul	194	6	9	2	1							T										6
14-Jul	195	1	6	13								R										5
15-Jul	196	1	6									A										6
16-Jul	197	1										N									1	7
17-Jul	198	7										S										8
18-Jul	199	1										I										9
19-Jul	200	9	1	6								T										10
20-Jul	201	9	1									I										11
21-Jul	202	7	1	13								O										12
22-Jul	203											N										13
23-Jul	204																					14
24-Jul	205	9																				15
25-Jul	206	6	9																			16
26-Jul	207																					17
27-Jul	208																					18
28-Jul	209																					19
29-Jul	210	7																			9	20
30-Jul	211											Post Lactation										1
31-Jul	212	13																				2

Figure 4- Sunset exit (left panel) and sunrise return (right panel) sequences for marked bats collared on 23 June 2002 (=Julian day [Jday] 174) from 23 June through 31 July (Jday 212), 2002. The entry in the left panel under 1 is the first marked bat to emerge at sunset followed by the second marked bat (under 2), etc. The entry in the right panel under 1 is the last marked bat to return at sunrise. The entry under 2 is the second-to-last bat to return at sunrise, etc. Selected bats have been designated a color to aid in viewing their position in the sunset emergence and sunrise return flights. Dark bordered boxes represent the first day of lactation for the 21 bats whose exact date of parturition is known.

Bats collared on June 23														Period																			
Date	Jday	1	2	3	4	5	6	7	8	9	10	11	12	13	12	11	10	9	8	7	6	5	4	3	2	1	Day #						
		Sunset Exit										Sunrise Return																					
23-Jun	174	19	17	16	23	18																	18	16	17	19	4						
24-Jun	175	17	18	19	16	21	23															23	18	19	20	16	17	5					
25-Jun	176	19	20	18	17	21	16	23															23	16	19	18	17	6					
26-Jun	177	19	17	23	18	16	21																		23	21	18	19	7				
27-Jun	178	18	19	21	16	23																16	19	18	23	21	20	17	8				
28-Jun	179	20	18	19	23	17	21	16															23	20	16	17	19	18	21	9			
29-Jun	180	19	23	20	18	17	21	16																22	23	16	18	19	17	21	10		
30-Jun	181	18	19	23	17	21	22	16														16	23	22	20	19	18	21	17	11			
1-Jul	182	18	19	23	20	17	21	16															23	22	16	17	20	18	19	21	12		
2-Jul	183	21	17	23	19	16	22	18	20														16	22	21	18	20	23	19	17	13		
3-Jul	184	18	23	21	20	17	19	22	16																	16	18	20	19	21	14		
4-Jul	185	18	21	20	19	17	16																19	22	16	23	21	20	18	17	15		
5-Jul	186	21	19	18	23	17	20	22	16																22	18	20	23	21	17	16		
6-Jul	187	21	23	18	20	17	16	19	22														19	16	22	23	20	18	21	17	17		
7-Jul	188	20	23	19	18	21	17	16																							18		
8-Jul	189	23	18	19	16	17	21	20	22																	16	17	22	19	18	23	21	19
9-Jul	190	23	21	20	18	17	19	16	22																						20		
10-Jul	191	21	20	23	19	17	18	16																							17	1	
11-Jul	192	23	21	20	19	18	17																								2		
12-Jul	193	23	21	20	18	19	17																								3		
13-Jul	194	21	23	20	18	22	19	17																				18	23	21	17	4	
14-Jul	195	19	23	21	18	20	17																								5		
15-Jul	196	21	17	18	23	20																				19	20	18	17	23	21	6	
16-Jul	197	23	21	19	18	20	17																								7		
17-Jul	198	18	17																												8		
18-Jul	199	18	17	19																											9		
19-Jul	200	18	23	19	21	17	22																								10		
20-Jul	201	22	23	21	19	20	18	17																							11		
21-Jul	202	21	23	18	19																										12		
22-Jul	203	21	23	19																											13		
23-Jul	204	23	21	19	18	17																									14		
24-Jul	205	21	18	23	19	17																									15		
25-Jul	206	21	23	18	19	17																									16		
26-Jul	207	23	21	18	19																										17		
27-Jul	208	18																													18		
28-Jul	209	18	23																												19		
29-Jul	210	18																													20		
30-Jul	211	18																													1		
31-Jul	212																														2		

Fidelity

Average fidelity during the periods of early pregnancy, middle pregnancy and late pregnancy averaged 85%, 56%, and 62% respectively. Fidelity increased to 83% during lactation, declined to 46% during transition and dropped to 9% during post lactation (Figure 5).

Individual fidelity varied between 37% and 93%, although a few individuals exhibited 100% fidelity during some portion of the reproduction period (Table 1).

Baby transport

During the weeks that babies were carried, the total number of flights for all bats was 18,120, which includes 102 flights in which young were carried (0.53% of flights), resulting in a net gain at the study roost of 16 babies and 13 adults. Only one baby was carried at a time, never two.

An obvious absence of baby carrying between 9 July and 14 July, was noted (Figure 6).

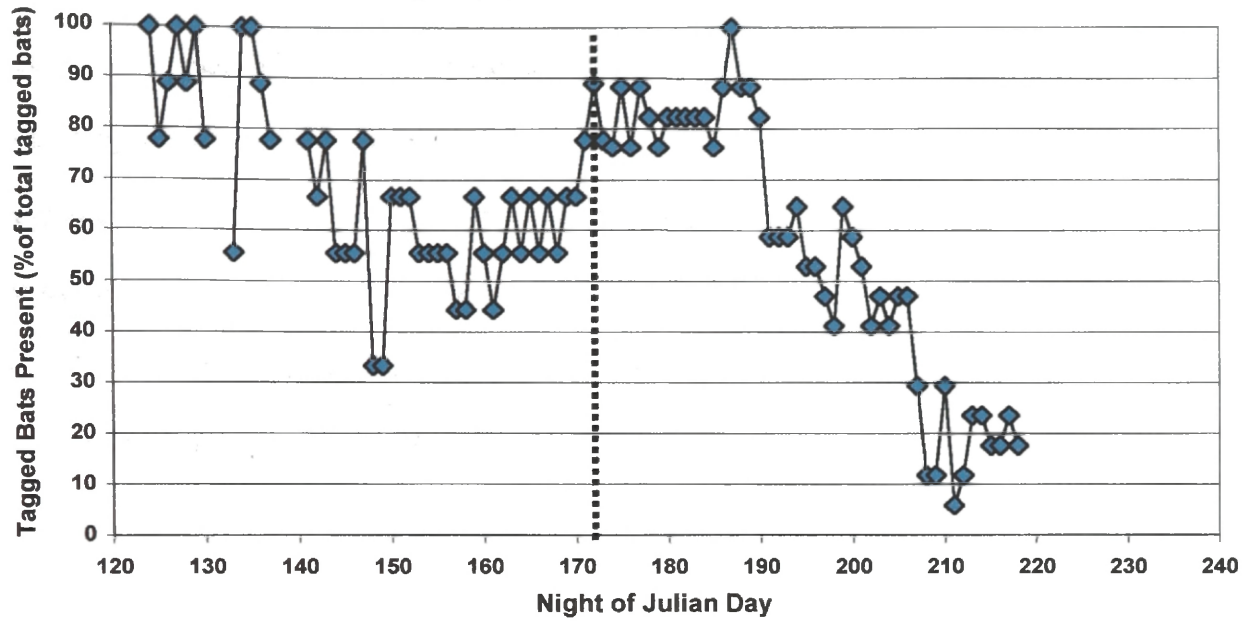


Figure 5. - Percent of tagged bats seen each night beginning 4 May 2002 through 31 July 2002. The dotted line represents the point at which parturition had occurred in 50% of roost occupants. Fidelity was reduced during late pregnancy and again during the period of transition (as young were being weaned).

Table 1 - Data shown represent the percent of days (fidelity) this roost was known to be used by nine marked females whose exact day of parturition was known and that were repeatedly observed after being collared on 4 May (on 23 June for bat 21) 2002. Late pregnancy is defined as the 7 days preceding parturition (4 days for bat 21). Middle pregnancy is the preceding 20 days and early pregnancy is the 14 to 20 preceding days of roost occupancy beginning on 4 May. Lactation is the first 20 days following parturition for each bat and transition is the following 20 days.

Bat#	Pregnancy				Lactation	Transition	Total Mean
	Early	Middle	Late	Average			
1	89	100	86	93.3	100	85	92.9
2	100	30	14	48.7	35	30	40.7
3	75	60	71	66.7	95	50	69.6
6	83	55	86	71.1	70	60	68.2
8	94	100	100	97.7	100	35	83.1
9	79	25	0	43.5	100	75	63.9
11	83	30	14	48.9	35	10	36.5
13	76	70	71	72.7	100	30	69.0
21			100	100	100	80	90.9
average	84.9	58.8	60.2	71.4	81.7	50.6	68.3

12(♂)	50	55	43	51.1	70	5	43.7
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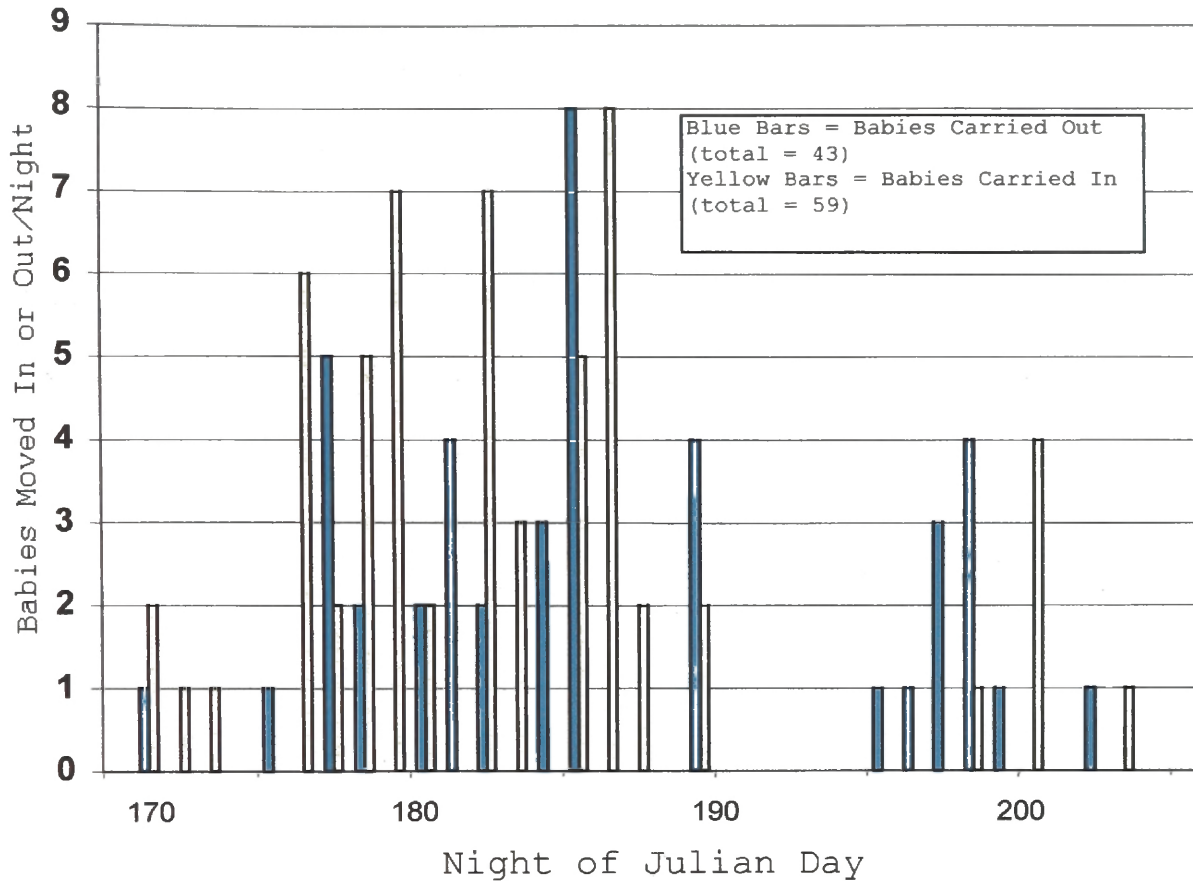


Figure 6 - Incoming and outgoing flights by big brown bat adults carrying young, from 19 June, the date of the first transport flight until 19 July, the date of the last transport flight.

Discussion

I observed no absolute exit or entry sequences during pregnancy (Figure 2), lactation, or transition (Figures 3 & 4). Although no exact sequence patterns exist, exit and entry were not random and flight sequence was significantly affected by reproductive condition with certain individuals contributing significantly to the non-random order.

Bat number 1 for example, was the first marked bat to exit at sunset far more frequently than expected at random while pregnant, ($\chi^2 = 10.6$, $dF = 3$, $P < 0.05$). While number 1 exited at random during lactation, it was significantly the third to last bat to return at sunrise ($\chi^2 = 19.3$, $dF = 3$, $P < 0.001$). Bat 11 was disproportionately the last bat to leave at sunset during both pregnancy and lactation ($\chi^2 = 16.4$ & 9.0 ; $dF = 3$ and $P < 0.05$ in both cases) and bat 6 exited at sunset in the number 1 or number 2 position during pregnancy more frequently than random ($\chi^2 = 9.1$, $dF = 3$, $P < 0.001$). At sunrise return during lactation, bat 8 was disproportionately the first marked bat to return ($\chi^2 = 19.1$, $dF = 3$, $P < 0.001$) and bat 13 was most frequently the last marked bat to return ($\chi^2 = 39.8$, $dF = 3$, $P < 0.001$). During the period of transition, bat 17 was more likely to be the last bat to exit at sunset ($\chi^2 = 18.0$, $dF = 3$, $P < 0.001$), and bats 21 and 23 exited first and second

respectively more frequently than random ($\chi^2 = 8.3$, $dF = 3$, $P < 0.001$ in both cases).

Non-random patterns of emergence in big brown bats have been reported previously by Viele (1994), and Brigham & Fenton (1986), observed non-random departures of radiotagged individuals in pair-wise comparisons.

Brigham and Fenton (1986) also found that radiotagged members of a colony of *Eptesicus fuscus* excluded from one roost site, moved to another as a socially interacting unit.

Non-random exit/entry patterns may be the result of individual differences in perception or responsiveness to intrinsic or extrinsic synchronizing signals or Zeitgebers, which regulate evening emergence. Zeitgebers have been studied in a number of animal species (O'Farrell & Studier, 1975; Reeb & Mrosovsky, 1990; Erkert, 2000; Colman et al., 2001). Reichle et al. (1965) studied nocturnal rhythms of cave crickets and found that portions of the study population were more active each night than others, suggesting that individual differences exist within groups in response to common behavior-influencing factors.

Kunz (1982) and Erkert (2000) have suggested that light is the most important factor in determining emergence time of bats, and Jones and Rydell (1994) reviewed the

available data for possible reasons for interspecific variation in emergence time. If consistent individual differences exist within a bat colony in their perception and response to common Zeitgebers, such as light intensity, then loose exit and re-entry sequences may be explained.

Other explanations for the non-random sequences may be more simplistic. Individuals that exit first may fly to premium foraging areas first, may fly the furthest to forage, or might roost nearest the exit portal. Such explanations must assume that those individuals that forage furthest or roost nearest the portal do so regularly. It has been found that little brown bats travel greater distances while pregnant than when lactating (Henry et al., 2002), and non-reproductive and post lactating female Townsend's big-eared bats consistently fly greater distances to forage than males (Fellers and Pierson, 2002).

In advanced pregnancy, girth of females became very large and bats entered the roost with greatly increased awkwardness. The tagged male was the only bat observed during the period of female pregnancy with a necklace, a noticeably small girth, and superior agility upon entering the portal, and I conclude that it was the only male in the roost. Adult males are often solitary in summer (Davis et al., 1968).

The non-random exit pattern of the male in my study agrees with the findings of Lee & McCracken (2001), who observed that male Mexican free-tailed bats exited after reproductive females at sunset, and as in their findings, the lone male in this roost returned earlier before dawn than other bats. The exit last/return first pattern of the male may be one of the reasons that his presence was tolerated by the females.

Little is known, however, about intraspecific differences or preferences as possible explanations for non-random exit and return sequences and should be open for future study.

Roost fidelity is variable among chiropteran species, however, bat colonies are more loyal to roosts with greater permanency, such as buildings (Lewis, 1995). Brigham and Fenton (1986) found that *Eptesicus fuscus* roosting in buildings were loyal over a reproductive season. If a single roost provides a variety of microclimates (Licht and Leitner, 1967), a favorable roost may reduce the need for alternate roost sites. The 4-sided roof in this study was exposed to sun or shade for different periods of time each day, and provided numerous crevices, and several false eaves in which bats could roost. Roost fidelity, however, was rarely 100% (Figure 5). Fidelity was highest during

early pregnancy, presumably as bats became re-established in their summer roost after returning from winter hibernacula. Fidelity then decreased during middle and late pregnancy, before rising during lactation. Only 10-20% of marked bats were observed during transition, although colony number averaged 147, indicating that many adults were using alternate roosts and that most bats present were juveniles.

During this study, marked individuals occasionally transported babies. The shortest time interval between exit of a marked adult without a baby attached, and reappearance with a baby was less than 90 seconds. The shortest time interval within a single evening of a marked adult entering the roost with a baby, exiting the roost alone, and re-entering with another baby was about 10 minutes. Such short intervals between lone exits and returns of the same bat with young indicate that the mother was not foraging while carrying a baby, but rather that young were being transported to and from nearby alternate roosts. Two other outbuildings, both within 150 meters of the study roost, also housed bats and likely served as additional shelter options for one cohesive colony, as Willis (personal communication) found of big brown bats in aspen tree cavities.

Willis found that a single group of bats dynamically intermingled nightly between several aspen trees. Frequent splitting (fission) and rejoining (fusion) of a single colony of bats among several shelter options has also been reported by Kerth and König (1999). Solitary red bats do not exhibit high fidelity to particular a roost, but use many roosts within a small geographic area (100 m from each other) over consecutive nights (Mager & Nelson, 2001). Nearby alternate roosts would likely provide additional shelter options within a familiar area, in the event of roost destruction.

Roost fidelity for specific individual marked bats, whose exact date of parturition was known (Table 1), closely followed the trends seen for all marked bats. Fidelity was high in early pregnancy, decreased as parturition neared and rose again during lactation. Except during the obligate suckling period for their infants, mothers are not required to roost at specific sites. Some pregnant females were extremely loyal to the study roost, while others apparently used alternate roosts progressively more often and in progressively greater numbers as pregnancy neared parturition. After parturition, six of nine lactating females showed high fidelity to this natal roost and one (#3) was fairly loyal, but two mothers (#'s 2

and 11) occupied this roost only about 1/3 of the time. Although an occasional entrance or exit of these 2 bats may have been missed, both bats exhibited less than 100% fidelity during primary lactation. Less than 100% fidelity during the lactation period, when mothers typically return 1 to 2 times per times per night to the roost to nurse young (Henry et al., 2002) is surprising. Because very young big brown bats are heterothermic (Audet & Fenton, 1988), they may be able to survive short periods without being nourished by suspending neonatal growth for that period. Although I am unaware of documented examples in big brown bats, a mother could suckle a young baby other than her own. *Nycticeius humeralis* mothers indiscriminately nurse babies older than two weeks (Watkins and Shump, 1981). Death of babies, before or after parturition would also eliminate the necessity of those females to return to the roost each night. Mortality of big brown bat babies prior to weaning is 7 - 10% (Kunz, 1974).

Part of reduced fidelity during lactation might also be explained by movement of babies, which was seen here, to nearby alternate roosts. Movement of non-volant young by mothers has been described in pipistrelles by Whitaker (1998).

The first flight of a female carrying young occurred on 19 June, and the last on 21 July. Babies were always carried individually, although on 10 occasions a marked female separately carried two babies into or out of the roost on the same evening, including an evening in which the adult twice carried a baby from the roost and then made two return transport flights several hours later. Observations in this study of one-at-a-time baby transport agree with observations made by Davis (1970), who found that *Antrozous pallidus* also carried babies individually after giving birth to twins.

During incoming transport flights, adults often showed signs of fatigue, occasionally pausing on the entrance ramp before entering the portal. Babies were always dangling from the adult's teat, although most moved their rear legs in a climbing motion when they contacted the entrance ramp.

Many short flights by the female both into and out of the roost often preceded transport flights. The most extreme example included six separate flights within three hours preceding a transport. Additionally, transport of young was always undertaken after the sunset foraging flight, suggesting that the high energy demands of lactation (Studier et al., 1973; Kurta et al., 1989) had priority over transport activity.

After spending daylight hours in the roost, the lactating female's milk supply should be lowest near evening emergence time, a condition that may promote easier removal of a small baby from the teat by the mother. During the period of transition, as babies were becoming volant, several observations were made of mothers shaking their own bodies and biting at babies as they exited the portal in an obvious effort to dislodge the baby from their teat. Some of those efforts failed, and the baby remained attached during flight, whereas others resulted in the baby being left behind, or on one occasion, subsequent flight of the baby. Subsequent flight of the baby, which had just been dislodged from the mother's teat, demonstrates that some pups will continue suckling if the opportunity arises, even though they are capable of flying. The lactation period (32 to 40 days) of big brown bats is longer than the length of time that is required for babies to become volant at 18 to 35 days (Kurta & Baker, 1990), indicating that volant young have access to lactating mothers (Brigham & Brigham, 1989). Insects captured by juvenile big brown bats (1.2 g insects/hour) are much less than those taken by adults at 2.7 g insects/hour (Gould, 1955), implying that newly volant young use their mother's milk as supplemental nutrition while becoming experienced foragers as Mumford

and Whitaker (1982) found of red bat juveniles, whose stomach contents consisted of both milk and insects. Decreased dependency on mother's milk by volant young may be related to decreased roost fidelity by the mother. Reduced fidelity during the period of transition has been reported for other species (Vaughan & O'Shea, 1976; Krull et al., 1991).

The low percentage of transport flights to total flights agrees with Davis's (1970) conclusion that insectivorous bats generally do not carry young while foraging. Davis (1970) also found that *Antrozous pallidus* babies could only be removed by researchers from the mother's teat by prying the babies jaws open, and in part because of their tenacious grip, suggested that most examples of transport of young bats occurred as the result of disturbance. Davis suggested that in cases of disturbance, the mother was not able to hurriedly remove the baby, although he agreed that normal transport may occur in some species as a possible survival advantage. Since there were no disturbances during the course of this study, I suggest that occasions of young transport during early lactation were normal, and because of the short time intervals involved, were made between the study roost and the two other known roosts on the property. Those

transports that occurred during the period of transition, as babies were being weaned, happened only when the mother was unsuccessful in disengaging the larger baby. Newly volant big brown bats have a body mass at 75% of adult mass and a forearm length that is essentially equal, making newly volant juveniles nearly as large as adult females (Burnett & Kunz, 1982). The inability of a mother to remove a baby almost as large as itself, would help explain some transports made by some bats, such as bat 23, who transported two babies into the roost on 4 July of early lactation, and exited with one on 16 July of late lactation.

Babies were also transported over a period of days. Bat 17, for example, made two transport flights from the roost 26 June and remained away from the roost until the following evening when she made two return transport flights. Bat 20 left with a baby on 23 June, and remained away until the following evening, when she returned with the baby. She made several lone exits and returns after the 24 June transport return, but again carried a baby from the roost on 25 June. The same female again made four entrances and four exits on 26 June, before returning with babies in two separate flights on 27 June. Leaving the roost with one baby, but returning on separate occasions

with two babies was not an isolated case. Bat 22 removed a baby from the roost 3 July, and twice returned with a baby 4 July. Parturition had occurred in all females by 27 June, which presents the question as to why an adult female would leave with one baby, but return with two.

Although a mother and volant baby might leave the study roost separately, reencounter each other at an alternate roost and return to the study roost with the baby attached to the mother, the more likely explanation for an adult leaving with one baby and returning with two is that she was carrying a baby that was not her own. Mexican free-tailed bat young attempt to "steal" milk from females other than their own mother by attaching themselves to the teat of the passing adult, or to the second teat of an adult already nursing another pup. Despite the adult's efforts to cover her teats with a folded wing, non-offspring were occasionally successful (McCracken and Gustin (1991). Pestering of adult females in late lactation by large volant young may be a significant factor in encouraging adults to abandon the natal roost, which may further explain reduced fidelity during the transition period.

Fidelity data necessarily relied on whether a particular bat was using the roost on any given day, and

therefore, upon recording the unique symbol tag. On 6 July during the period of lactation, which was over two months since the first tagging, fidelity of marked bats reached 100% (Figure 5), indicating that all tagged bats were alive, using the study roost, and all tags were visible. Over the course of the study, a tag may have occasionally been missed due the individual's orientation upon entering (up-side-down), or exiting (sideways), which prevented a clear line of sight to the camera. Future work would begin with nylon ball necklaces, which were easier to place on bats, and double-tags, which reduced the possibility of camera misses. Other misses may have occurred due to tag or necklace damage, or removal of same by the marked individual or another bat. On one occasion, a bat was observed pulling a marked individual by the symbol tag. A bat may also have been present in the roost on a particular day, but did not forage, and was therefore included in fidelity data as absent. Additional unforeseen elements may have affected fidelity data, such as the Eastern Screech Owl that appeared and was recorded capturing bats at the entry/exit portal. While no marked bats were observed being captured, predation may have occurred while bats were out of camera range.

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