Timing and Variation in the Emergence and Return of Mexican Free-tailed Bats, *Tadarida brasiliensis mexicana*

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Ya-Fu Lee and Gary F. McCracken (2001) Timing and variation in the emergence and return of Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Zoological Studies* **40**(4): 309-316. We investigated the timing and variation in evening emergence and dawn return of a maternity colony of Mexican free-tailed bats, *Tadarida brasiliensis mexicana*, in the summers of 1996 and 1997. In both summers, the onset of evening emergences and the end of dawn returns correlated with sunset and sunrise, respectively. Bats tended to emerge earlier in relation to sunset during late summer than in spring to early summer. Dawn returns ended progressively later in relation to sunrise through the season. Bats emerged much earlier and ended dawn returns later in 1996 than in 1997, coincident with a severe drought in spring to midsummer 1996. Bat captures during different seasons at the cave entrance indicate that patterns of emergence and return were non-random with regard to age, sex, and reproductive classes of bats. Higher proportions of reproductive females emerged earlier in the evening and returned later at dawn. Non-reproductive and post-lactating females and males exhibited an opposite pattern. Higher proportions of juveniles tended to emerge earlier in the evening and to return earlier at dawn. http://www.sinica.edu.tw/zool/zoolstud/40.4/309.pdf

Key words: Activity patterns, Bats, *Tadarida brasiliensis mexicana*.

Avariety of factors may contribute to the timing and patterns of the nocturnal activities of bats (Erkert 1982). Light levels, which closely correlate to the times of sunset and sunrise, typically set the initiation and cessation of nightly activities, respectively. Reduced food availability may result in longer searching times, and thus may advance the onset of emergence (Erkert 1982). Other influential extrinsic factors may include temperature (Catto et al. 1995), cloud cover (Kunz and Anthony 1996), and heavy rain (McAney and Fairley 1988). However, colony size and the age, sex, and reproductive status of individuals can also result in seasonal variation in emergence times (Avery 1986, Rydell 1989, Korine et al. 1994). In addition, the risk of predation may delay the onset of bat emergence (McWilliam 1989), and predation has been suggested as a major reason for bats' nocturnal activity (Speakman 1991).

Large numbers of insectivorous Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) reside in the southwestern United States from spring to early fall. The sizes of their colonies range from several thousands in many man-made structures to tens of millions in some limestone caves (Davis et al. 1962). For cave-roosting bats, passing through orifices of a limited size means that emergence and return must take a considerable amount of time. The evening emergences and morning returns of large Mexican free-tailed bat colonies usually last for 2-3 h, and often occur partially in daylight hours (Davis et al. 1962). Females give birth in early June, and peak energetic demands can cause reproductive females, especially those lactating, to double or even triple their average nightly feeding rate (Kunz et al. 1995). This may influence their patterns of evening emergence and dawn return. As juveniles initiate nightly foraging in mid-late July (McCracken and Gustin 1991), the size of the colony emerging and the demand for food also increase; bats from larger colonies may have to travel longer distances to forage

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(Kunz 1974). Thus, an earlier evening emergence and prolonged dawn return should allow individuals more time to forage, but at a greater risk of predation (Fenton 1995).

In response to energetic needs and the risk of predation, different individuals in these large aggregations may exhibit different temporal patterns of emergence and return. Due to their higher energetic demands, reproductive females may be forced to begin foraging early. In contrast, other classes of adults (e.g., non-reproductive females and males) may be able to emerge later, reducing the risk from diurnal predators, and still meet energy needs. On the other hand, newly volant young may be at greater risk of being caught by predators due to their poorer flying ability, and may have different emergence and return patterns from those of adults (Kunz and Anthony 1996). Herreid and Davis (1966) concluded that the emergence times in relation to sunset of Mexican free-tails do not vary seasonally. Their study, however, presented no data on emergence by bats of different sex, age, and reproductive status. Humphrey (1971) reported that greater proportions of lactating bats emerge earlier than males; however, no data on dawn returns are available.

Our study documents the onset times of evening emergence and the onset and end times of dawn return of a large Mexican free-tailed bat colony over 2 summers, and the temporal distribution and variation among bats of different age, sex, and reproductive classes during emergence and return. We predicted that (1) bats in mid-late summer should initiate their evening emergence earlier and end their dawn return later in relation to the sun than they had earlier in the season, due to increased energetic demands in reproductive females and an enlarged colony size once juveniles are volant; (2) due to their higher energetic demands, greater proportions of reproductive females should emerge earlier and return later than males and non-reproductive females; (3) due to their less adequate flying skills, lack of experience, and potentially higher risk of predation, greater proportions of juveniles should emerge later and return earlier than adults.

MATERIALS AND METHODS

Timing of bat emergence and return

Fieldwork took place at Frio Cave (29°25'N, 99°42'W, 354 m in elevation), Uvalde Co., Texas. This limestone cave is located at the boundary between the southern edge of the Edwards Plateau and the South Texas Plains, and is the roost site for a large maternity colony of Mexican free-tailed bats (estimated at ca. 10 million bats; Wahl 1989). During 26 May-6 Aug. 1996, and 19 May-21 Aug. 1997, we visually observed the evening emergence and dawn return of Mexican free-tails, at distances of 10-50 m from the cave entrance. Binoculars (magnification 8 × 35, field 8.6°) were used when necessary. In total, we made 15 evening, 21 dawn, and 9 overnight observations in 1996, and 31 evening and 28 dawn observations in 1997. Evening observations began at 1800-1830 h (CST, and hereafter), and ended at 2100-2130 h when it was totally dark. Dawn observations began at 0400-0430 h, and lasted until ca. 1000 h, ending at least 30 min after the last bats had returned.

Bullock et al. (1987) considered the time when the median number of bats of a colony emerged to be a more realistic estimate of the timing of bat emergence. However, the colony sizes of Mexican free-tails at caves and their densities in emergence and return made accurate counting of individuals almost impossible and the estimate of median emergence time impractical. Instead, we recorded the onset times of evening emergences, and the onset and end times of dawn returns. We defined the onset of the evening emergence as when bats began to emerge as a continuous serpentine stream. Several scattered bats typically left the cave shortly (in most cases, < 1 min) before the onset of a main emergence, and were disregarded. The end times of evening emergences were not recorded, because out-flying bats often mingled with early in-coming bats after dark, and the exact times were difficult to determine. We defined the onset of the dawn return as the point when bats began returning in a continuous column while no or only few bats were leaving the cave. We also visually estimated cloud cover (%) at the cave at each dusk or dawn observation. We noted that clouds usually did not remain stationary, and cloud cover changed frequently at the site. Thus, we defined a cloudy day only when over 50% cloud cover occurred and remained during an observation period.

Bat sampling during emergence and return

We used a hoop net (46.5 cm in diameter and 1 m deep, attached to a 3-m-long aluminum pole) to sample bats as they emerged from the cave in the evening and as they returned at dawn. We restricted sampling to once every 7-10 days to minimize the disturbance to bats and consequential behavioral alterations. Sampling began at the onset of an even-

ing emergence or a dawn return, and continued throughout the evening or morning period of bat activity. During each 10-min sampling session, the hoop net was raised into the bat stream and held still for ca. 20 s. We then transferred all bats caught in 1 sample to an air-circulated container with cotton mesh on the top and sides. Bats were examined immediately for age, sex, and reproductive status, using the criteria of Anthony (1988) and Racey (1988), and released before the next sampling. We found no indication that this procedure damaged bats, and most bats caught were seen flying to join the other bats immediately after release.

Data analysis

Onset and end times of bat emergence and return are presented as the mean (± 1 SE) in minutes relative to the time of sunset or sunrise. All statistical tests were conducted using a 0.05 rejection level, and sample sizes (n) refer to the numbers of evening or dawn observations, unless otherwise noted. We conducted two-way ANOVA to examine the effect of season on onset times of evening emergences, of dawn returns, and end times of dawn returns, between the 2 summers. When the seasonal effect was significant, we used Fisher's PLSD multiple range test to locate differences for paired comparisons (Sokal and Rohlf 1994). We defined the 3 seasonal phases as (I) spring: late May-early June, (II) early summer: mid June-mid July, and (III) late summer: late July-late Aug. The seasonal phases roughly corresponded to the reproductive cycles of bats. In phase I, the majority of females were pregnant. In phase II, most females were lactating but some were still in late pregnancy. While most females were post-lactating in phase III, some continued to lactate, and juveniles began foraging (McCracken and Gustin 1991).

Cloudy days were uncommon during the study period, and were particularly rare in the 1996 summer (none in the evening and only 3 at dawn). This prohibited incorporating the factor of clouds in a complete ANOVA. Instead, we used a t-test to compare mean onset times of emergence, and mean end times of return between cloudy and clear days for both early and late summer 1997. We used regression analysis to examine the correlation between onset times of evening bat emergence and times of sunset, and end times of dawn return and times of sunrise. A G-test for the contingency table (bat class vs. time interval) was used to determine if temporal distributions of the relative proportion of different bat classes during emergence and return in the same seasonal phase were independent of time (Sokal and Rohlf 1994).

RESULTS

Timing of bat emergence and return

On average, bats left the cave 23.5 ± 5.6 min before sunset (n = 46) in the evening, and the return ended at 90.7 ± 11.4 min after sunrise (n = 49). However, bats in 1996 left the cave earlier (69.0 ± 5.0 min before sunset) than in 1997 (1.5 ± 3.9 min before sunset; $F_{(1, 40)}$ = 126.4, $p < 0.001$). In addition, the dawn return ended later in 1996 (157.5 ± 16.8 min after sunrise) than in 1997 (40.6 ± 5.3 min after sunrise; $F_{(1, 43)}$ = 121.7, $p < 0.001$). The onset times of dawn returns did not significantly differ between years (40.0 ± 17.9 min before sunrise, 1996; 54.3 ± 8.6 min before sunrise, 1997; $p = 0.5$). The overall seasonal effect on evening emergence was not significant ($F_{(2, 40)}$ = 2.9, $p = 0.07$). Among the 3 sea-
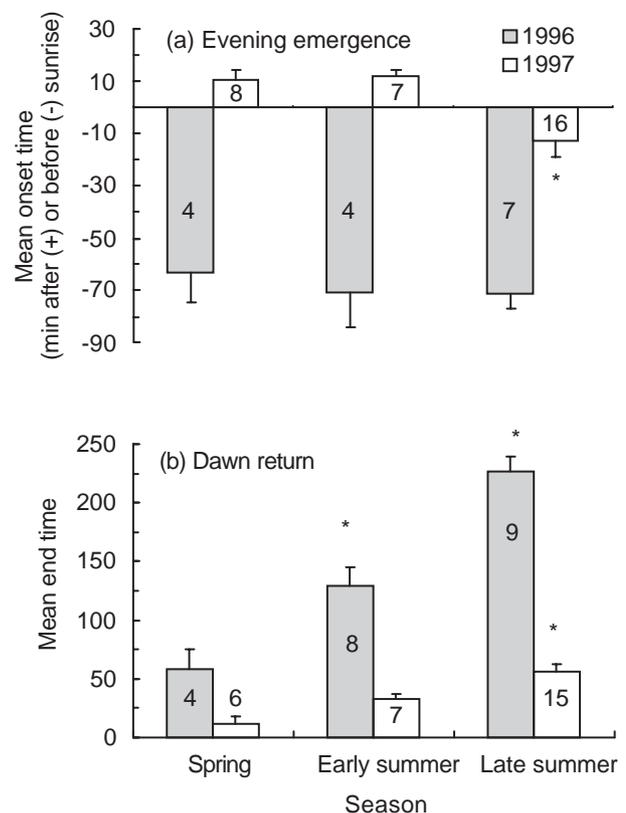

Fig. 1. Mean onset time (± 1 SE) of (a) evening emergences, and mean end time (± 1 SE) of (b) dawn returns, in spring, early summer, and late summer of 1996 and 1997. ∗: Fisher PLSD for paired comparisons across seasonal phases within years, $p < 0.05$. Sample size (# of observations) is in each column.

sonal phases, the onset times of evening emergence did not differ in 1996 ($F_{(2, 12)}$ = 0.24, p = 0.79). In 1997, however, emergence onset was earlier in phase III (13.1 ± 6.1 min before sunset; $F_{(2, 28)}$ = 5.98, p < 0.001) than in phase I (10.5 ± 3.9 min after sunset; III-I = 23.62, PLSD = 17.05, p < 0.05) and phase II (12.0 ± 3.0 min after sunset; III-II = 25.12, PLSD = 18.85, p < 0.05) (Fig. 1a). In contrast, seasonal phases affected the end time of dawn return ($F_{(2, 43)}$ = 45.47, p < 0.001). The mean end time of dawn returns was increasingly later along the seasonal phases in 1996 ($F_{(2, 18)}$ = 28.51, p < 0.001; II-I = 71.25, PLSD = 51.09, III-II = 98.11, PLSD = 40.54; p < 0.05), and in phase III in 1997 ($F_{(2, 25)}$ = 9.32, p < 0.001; III-I = 43.67, PLSD = 21.61, III-II = 23.5, PLSD = 21.61; p < 0.05) (Fig. 1b).

We found no cloud effects on onset times of evening emergence (cloudy days: 14.8 ± 7.3 min after sunset; clear days: 9.7 ± 2.2 min after sunset; t = 0.9, d.f. = 15, p = 0.38) in spring-early summer. We recorded only 1 cloudy day in late summer, and a similar analysis could not be performed. Clouds also had no effects on end times of dawn returns, either in spring-early summer (cloudy days: 23.3 ± 9.4 min

after sunrise; clear days: 22.9 ± 5.8 after sunrise; t = 0.03, d.f. = 11, p = 0.49) or in late summer (cloudy days: 63.2 ± 9.6 min after sunrise; clear days: 52.2 ± 9.3 after sunrise; t = 0.63, d.f. = 13, p = 0.24).

The time of evening emergence correlated with the time of sunset in 1997 (r^2 = 0.77, $F_{(1,29)}$ = 94.6, p < 0.001), but not in 1996 (r^2 = 0.02, $F_{(1,13)}$ = 0.27, p = 0.6) (Fig. 2a-b). In 1996, bats emerged intermittently on 10 of 15 evenings, during which their emergence was interrupted for ca. 4-44 min, followed by a 2nd emergence. This behavior was not observed in 1997. The onset of the 2nd emergence in 1996 correlated with the time of sunset (r^2 = 0.55, $F_{(1,8)}$ = 11.62, p < 0.01) (Fig. 2a). The end times of dawn returns correlated with the times of sunrise in both 1996 (r^2 = 0.77, $F_{(1,19)}$ = 63.56, p < 0.001) and 1997 (r^2 = 0.82, $F_{(1,26)}$ = 121.73, p < 0.001) (Fig. 3a-b).

Temporal patterns among bat classes in emergence and return

Over the 2 summers, we captured a total of 8142 bats. This included 5720 adult females (70.2%) in different reproductive conditions (preg-
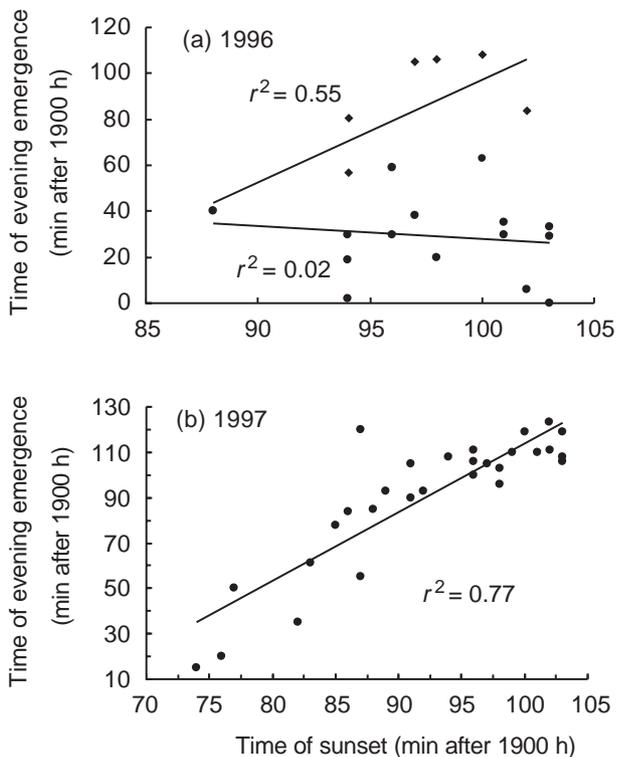

Fig. 2. Relationship between times of evening emergences and times of sunset in (a) 1996 (●: first emergence, n = 15; ♦: second emergence, n = 10) and (b) 1997 (n = 31). There were split emergences in 1996 but not in 1997.
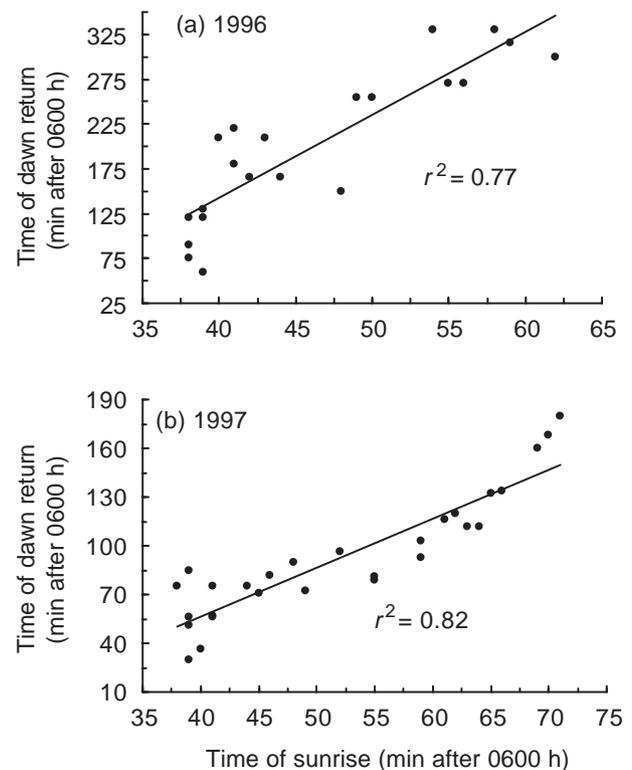

Fig. 3. Relationship between ending times of the dawn returns and times of sunrise in (a) 1996 (n = 21) and (b) 1997 (n = 28).

nant or lactating: 4613, non-reproductive: 266, post-lactating: 841), 1397 adult males (17.2%), and 1025 juveniles (12.6%). The temporal distribution of captures of the different bat classes during both evening emergences and dawn returns in each seasonal phase was non-random. In spring (seasonal phase I), pregnant bats were most abundant earlier in the evening emergences, while the relative proportions of males and non-reproductive females increased as the emergence progressed (G = 58.79, d.f. = 3, p < 0.001). In contrast, the relative proportions of pregnant bats increased later in the morning, and the relative proportions of males and non-reproductive females decreased later in the morning (G = 9.47, d.f. = 5, p < 0.1) (Fig. 4a).

We observed a similar pattern in early summer (phase II), when most reproductive females were lactating (emergence: G = 118.61, d.f. = 4, p < 0.001; return: G = 72.15, d.f. = 5, p < 0.001) (Fig. 4b). In late summer (phase III), many post-lactating females appeared, and young began nightly foraging. Higher proportions of lactating bats continued to emerge at an earlier time, as did juveniles; whereas the relative proportion of other adult classes (i.e., males and post-lactating females) emerging increased during later time intervals (G = 93.22, d.f. = 6, p < 0.001). Lactating females also showed an increase in pro-

portion later in the dawn returns, while higher proportions of juveniles and other adults returned earlier (G = 281.34, d.f. = 10, p < 0.001) (Fig. 4c).

DISCUSSION

Timing and variation in emergence and return

In all bat species studied to date, except for the black-bearded tomb bat (*Taphozous melanopogon*) in India, the nocturnal activity of bats has been largely synchronous with the timing of sunset and sunrise (e.g., reviewed in Erkert 1982, McAney and Fairley 1988, Isaac and Marimuthu 1993, Catto et al. 1995, Kunz and Anthony 1996). Our results generally agree with the majority of these studies. There was, however, considerable variation, both in the onset times of evening emergences and in the end times of dawn returns among seasonal phases. Similar patterns of an earlier emergence relative to sunset in mid-late summer than in spring-early summer have been found for other bats (e.g., little brown bats, *Myotis lucifugus*, Kunz and Anthony 1996). Indeed, the late summer emergences of Mexican free-tails that we documented are the earliest ever reported for bats (see reviews in Jones and Rydell
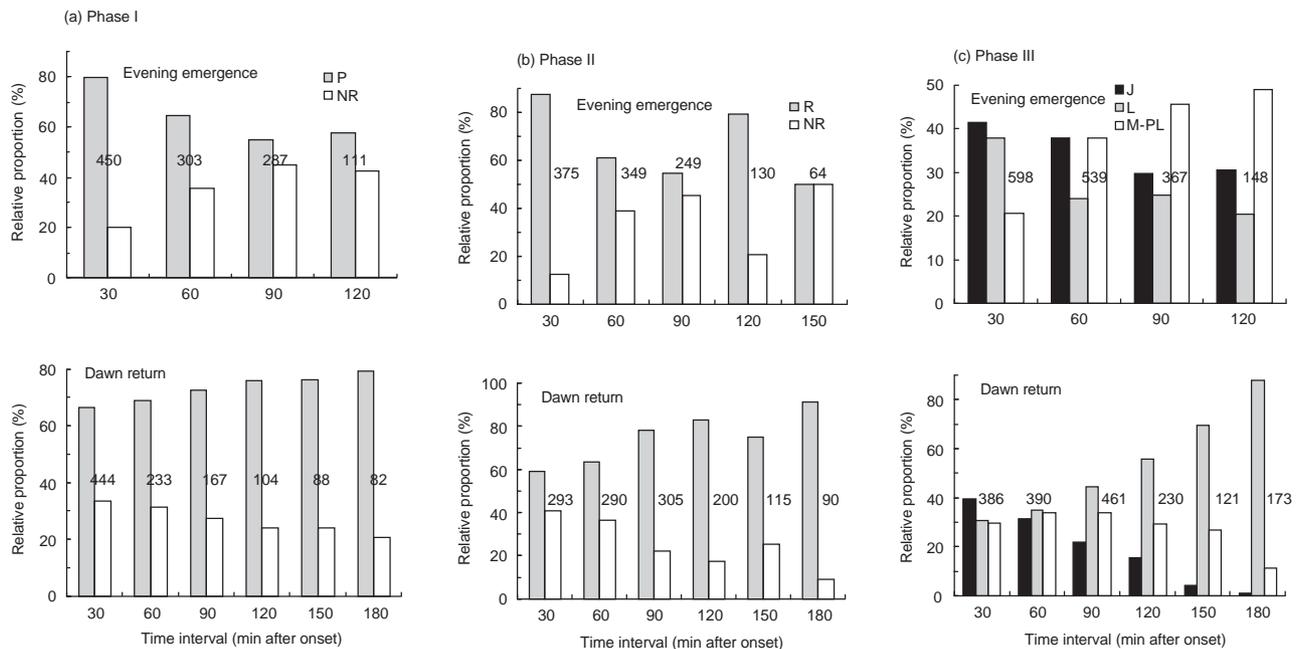

Fig. 4. Temporal distribution of different bat classes captured in seasonal phase (a) I (*n* = 5), (b) II (*n* = 5), and (c) III (*n* = 7) in the evening emergence and dawn return. The number in each time interval is the total number of bats captured. P: pregnant bats, NR: other adults (males and non-reproductive females), R: reproductive females (pregnant and lactating), J: juveniles, L: lactating bats, and M-PL: other adults (post-lactating females and males).

1994).

We found a significant difference in onset times of evening emergence between the earlier and later seasonal phases in 1997 but not in 1996. This result does not fully support our prediction that bats in mid-late summer should emerge earlier and end their dawn return later relative to the sun than earlier in the season; however, the power of the test also was weakened by smaller sample sizes in 1996. Nevertheless, the much earlier emergence by bats in 1996, especially in spring-early summer, invites explanation. There was no evidence that the colony size at the cave differed between the 2 summers. The striking year-to-year variation we observed might have been due to the drought that occurred in south-central Texas from the fall of 1995 through late summer 1996. The drought was the longest and most severe in the region during the past 2 decades. In the area where Frio Cave is located, the mean monthly precipitation during Jan.-Apr. 1996 (ca. 7.6 mm) represented only ca. 20% of the typical mean monthly precipitation during the same period over the past 30 years. Through July, the mean monthly precipitation (ca. 17.8 mm) in 1996 was still only ca. 30% of the "normal" precipitation (NOAA 1969-1999).

Drought can influence the growth of vegetation, and in turn may affect the activities, e.g., feeding, reproduction, and development, of many insects and negatively impact their populations (Wellington and Trimble 1984). The drought of 1995-1996 may have reduced numbers and total biomass of insects available to bats in spring and summer 1996. This likely forced bats to travel longer distances and prolong foraging times (Erkert 1982) by advancing emergence and delaying return. We suggest that the drought and reduced food supply would have affected different individual bats to varying degrees, depending on their energy demands and nightly feeding success. This may explain the split emergences observed in 1996, in which a portion of bats emerged exceptionally earlier, and the onset of these early emergences did not correlate with the times of sunset.

Temporal patterns among bat classes in emergence and return

Higher proportions of reproductive females tended to leave early in the emergence, but returned later at dawn. Reproductive females, particularly those lactating, have higher energetic demands, and likely spend more time foraging (Barclay 1989, Catto et al. 1995). In contrast, non-reproductive and post-lactating females and males presumably have lower energetic demands. These individuals tended to leave the roost later, but returned earlier at dawn. An advantage of later emergence and earlier return appears to be a reduction in the risk of predation (Speakman et al. 1995, Rydell et al. 1996). This may be particularly important for Mexican free-tails, because of the generally early and long emergence and long morning return by this species, both of which extend into daylight hours. Thus, the temporal distribution of activity patterns among classes of Mexican free-tails may reflect a consequence of balancing the need to forage with avoiding the risk of predation.

Higher proportions of juveniles consistently returned earlier than did adults at dawn. Juveniles are poorer flyers, and may be more easily attacked by predators. Diurnal raptors (e.g., Red-tailed Hawks, *Buteo jamaicensis*, and Peregrine Falcons, *Falco peregrinus*) have a higher success rate attacking Mexican free-tails at times in the summer after juveniles begin foraging (Lee and Kuo 2001). Thus, predation appears to pose a larger threat for juveniles, and an earlier return by juveniles at dawn may minimize this risk. In the evening, however, higher proportions of juveniles also emerged earlier. This is in contrast to the findings that newly volant young tend to emerge later than adults until a certain developmental stage (e.g., mouse-eared bats *Myotis myotis*, Audet 1990; *M. lucifugus*, Kunz and Anthony 1996), presumably due to their slower and less agile flight (Hughes et al. 1995), the fact that their energy needs are supplemented by milk from their mothers (Jones et al. 1995, Kunz and Stern 1995), or to minimize acoustic clutter from adults (Buchler 1980).

Juvenile *M. lucifugus* become indistinguishable from adults in emergence within 2 wk of 1st flight (Buchler 1980). The forearm length of Mexican free-tails reaches average adult size in the 6th wk after birth (Kunz and Robson 1995), which is in late July. Our data in this period came mostly between the last week of July and mid Aug., and it is possible that we missed the earlier stage of juvenile volancy. In some species, after the early stage in volancy development, young bats may advance emergence to follow their mothers when foraging (e.g., vampire bats *Desmodus rotundus*, Wilkinson 1985; big brown bats *Eptesicus fuscus*, Brigham and Brigham 1989; reviews in Kunz and Hood 2000), perhaps being attracted to conspecific echolocation calls, for learning, or acquiring information about foraging sites. However, there is no available evidence supporting the possibility that Mexican free-tail juveniles following adults to forage. Further studies are required to evaluate this speculation.

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墨西哥游離尾蝠(*Tadarida brasiliensis mexicana*)出入洞之時間
與組成變異

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　　本研究以觀察及捕捉取樣的方式，記述穴居性墨西哥游離尾蝠傍晚出洞及清晨入洞之時間與相對組成的變異，希望瞭解蝠群個體組成的變化(例如性別，母蝠生殖狀況，幼蝠開始覓食)對蝠群出入洞時間的影響。墨西哥游離尾蝠傍晚出洞的起始及清晨入洞的終止時間，分別與日落及日出之時間成正相關。但其在夏季中、晚期(母蝠泌乳，幼蝠開始出洞覓食)之出洞時間，相對於日落時間，顯著提前；而其清晨入洞的終止時間，相對於日出時間，亦顯著延後。捕捉取樣的結果顯示，在春末至夏末的不同時期，該蝠出入洞時，蝠群內個體組成之相對比例在時間上呈非隨機性分布。較高比例之懷孕及泌乳母蝠出現在出洞初期與清晨入洞的末期；公蝠及無生殖狀況或已終止泌乳之母蝠則呈現相反趨勢；而不論出洞或入洞，較高比例之幼蝠均出現在初期。從蝙蝠個體的能量需求、幼蝠的成長與行為發展、及蝠群受掠食壓力等角度探討，此結果支持我們的預期。