

EVENING EMERGENCE BEHAVIOR AND SEASONAL DYNAMICS IN LARGE COLONIES OF BRAZILIAN FREE-TAILED BATS

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Flexible behaviors permit gregarious animals to exploit spatially and temporally favorable conditions for reproduction. Evening emergences of Brazilian free-tailed bats (*Tadarida brasiliensis*) in south-central Texas were recorded to determine changes in colony dynamics and to evaluate hypotheses associated with predator avoidance and seasonal energy demands. In 2007, median parturition date was 18 June and lactation lasted about 54 days. Juveniles commenced flight after 41 days, then continued to suckle for 2 weeks before being weaned. Onset of evening emergence was correlated with sunset, beginning, on average, 11.8 min after sunset (95% confidence interval = 7.1, 16.6), which is later than reported in previous studies. Pregnant females emerged later than their roost mates, consistent with a predator avoidance hypothesis. Lactating females emerged after sunset, but earlier than other bats, consistent with the hypothesis that this is a period of high energy demand. Juveniles emerged later than adult females while they continued to be suckled, but emerged earlier as they matured and were weaned, suggesting a trade-off between predator avoidance and energy demands. Our observations indicate that evening emergence behavior of *T. brasiliensis* varies with environmental cues but is mediated by the energetic demands of reproduction.

Key words: behavioral plasticity, emergence timing, foraging, intraspecific competition, refuging, reproductive timing

Animal behavior is shaped by a variety of physiological, ecological, and social interactions. During breeding periods, gregarious species from several mammalian taxa such as pinnipeds (Boness 1991), rodents (Hayes 2000), bovids (Berger 1992), and bats (Kunz and Hood 2000; Tuttle and Stevenson 1982) exploit environmental and social conditions that optimize reproductive success. Although seasonally and spatially variable food supplies and climate likely influence the timing and location of reproduction (Hoying and Kunz 1998; Kunz 1973), intraspecific competition may limit the advantages of group living (Kunz 1982). Thus, behaviors that enhance an individual's fitness in the context of the group are likely to be favored.

The evolution of nocturnality in bats (reviewed in Speakman 1995) has been attributed to selection to avoid diurnal birds of prey, interspecific competition with aerial-feeding insectivorous birds, hyperthermia during daytime flight, and

echolocation ability. Additionally, foraging behavior of gregarious species may be influenced by energy demands associated with age or reproductive condition (Kunz et al. 1995a) and intraspecific competition for available prey (Kunz 1974). Given that flight is energetically costly, bats should benefit by minimizing flight time (Schmidt-Nielsen 1972; Speakman and Thomas 2003), especially during pregnancy, when female body mass can increase by 25% or more from fetal mass alone (Kunz and Hood 2000; Kunz et al. 1995b). Refuging bats may effectively shorten foraging time by emerging before roost mates have depleted insect prey (Hamilton and Watt 1970; Kunz 1974, 1982). Thus, insectivorous bats must balance trade-offs between environmental cues and intrinsic requirements associated with sex, age, and reproductive status to modulate emergence and foraging behavior (Duvergé et al. 2000; Erkert 1982; Jones and Rydell 1994; Kunz and Anthony 1996; Russo et al. 2007; Rydell et al. 1996; Welbergen 2006).

During summer, Brazilian free-tailed bats (*Tadarida brasiliensis*) aggregate in large colonies comprised almost exclusively of reproductively active females (Cockrum 1969). Their reproductive synchrony coincides with warm weather

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and abundant food resources (Kunz 1974; Kunz and Robson 1995). At this time, many colony members should have similar energetic and behavioral constraints. Although nonreproductive and postreproductive individuals often select less-crowded or cooler roosts (Cockrum 1969; Constantine 1967; Davis et al. 1962), different age or reproductive classes in the maternity colony may lead to partitioning of foraging times.

Evening emergence is correlated with sunset for Brazilian free-tailed bats, but there is daily, seasonal, and annual variation in the onset of emergence (Betke et al. 2008; Herreid and Davis 1966; Lee and McCracken 2001). These differences may reflect climatic conditions, prey availability, or population sizes. Seasonal variation also has been attributed to changes in energy demand during pregnancy and lactation (Kunz et al. 1995a, 1995b; Lee and McCracken 2001; Shiel and Fairley 1999). Factors that contribute to seasonal and annual variation in evening emergence also are likely to affect daily behavior.

Predation risk increases when bats emerge in daylight (Baxter et al. 2006; Fenton et al. 1994; Fox et al. 1976; Gillette and Kimborough 1970; Lee and Kuo 2001; Rydell and Speakman 1995; Speakman 1991, 1995; Speakman et al. 2000). However, Brazilian free-tailed bats regularly emerge in dense flocks well before sunset, followed by a lull before the remaining colony emerges at or after dusk (Betke et al. 2008; Lee and McCracken 2001). This highly gregarious and pulsed behavior may reduce predation risk to individuals that emerge in daylight (Duvergé et al. 2000; Lee and Kuo 2001; Speakman and Tallach 1998; Swift 1980). We predicted that bats with elevated energetic demands would comprise this early group. Lactating females were expected to emerge earliest because they experience the highest energy demands and have better flight ability. Pregnant and juvenile bats whose flight abilities are poorer due to greater wing loading or inexperience should emerge later (Jones and Rydell 1994; Kunz 1974; Kunz and Anthony 1996; Norberg and Rayner 1987). We expected this pattern especially during early flights by suckling juveniles (Jones 2000). The specific purpose of our study was to document annual variation in evening emergence behavior of Brazilian free-tailed bats and to evaluate these results within the framework of hypotheses regarding predator avoidance and energetics.

MATERIALS AND METHODS

Study sites.—We documented evening emergence behavior from early April through late September 2007 at 3 limestone caves located <160 km from each other in south-central Texas: Ney Cave, Davis (Blowout) Cave, and Frio Cave. In midsummer, Ney and Davis caves house upwards of 400,000 bats, whereas Frio Cave has upwards of 1,000,000 individuals (Betke et al. 2008). The landscape in the vicinity of these caves is a semiarid savannah, dominated by oak (*Quercus*), mesquite (*Prosopis*), and diverse grasses. Fields of corn, cotton, and sorghum occur within the likely foraging range of *T. brasiliensis* at Ney and Frio caves, but not Davis (Horn and

Kunz 2008). Mean annual temperature in the region is 17.8°C. Mean annual precipitation is 828 mm with mean monthly high of 108 mm in May (National Oceanic and Atmospheric Administration 1950–2006; <http://www.noaa.gov>).

Study species.—Brazilian free-tailed bats range from Argentina northward to Oregon and eastward to North Carolina in the United States (Wilkins 1989). This species is migratory, and seasonally forms maternity colonies in caves and bridges in south-central Texas. The diet consists of a variety of flying insects, dominated by Lepidoptera, Coleoptera, and Hemiptera, including important agricultural pests (Cleveland et al. 2006; Kunz et al. 1995b; Lee and McCracken 2005; Whitaker et al. 1996). Mean body mass and length of forearm were 11.3 g and 43.0 mm, respectively, for nonpregnant females ($n = 30$).

Colony composition.—Bats were captured at cave openings with 0.5-m-diameter hand nets (BioQuip, Rancho Dominguez, California) or 1.0 × 1.5-m double-frame harp traps (G5 Cave Catcher; Bat Conservation and Management, Inc., Carlisle, Pennsylvania). Once bats began to emerge steadily, nets or traps were elevated into the emerging column until 25 individuals were captured (usually 2–5 min). We positioned the trap in the center of the emerging column to reduce trap avoidance. Sex, age, and reproductive condition were assessed based on external characteristics (Anthony 1988; Racey 1988). Adult females, unless lactating, were classified as nonreproductive if no fetus could be palpated. Given that most adult females trapped in spring likely carried small fetuses, hereafter, “pregnant” refers to palpably pregnant females. Lactation was based on our ability to express milk by palpation.

Bats were released beneath the emerging column away from the cave so that they were encouraged to join the dispersing bats without reentering the cave. Sampling was repeated at 10-min intervals until emerging bats were too scarce to capture 25 individuals within 10 min, or a large number of bats began to return. All protocols followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), and were approved by Boston University’s Institutional Animal Care and Use Committee.

We captured a total of 5,620 bats on 23 nights from 2 April to 19 September 2007. Ney Cave and Davis Cave were sampled twice monthly, whereas Frio Cave was only sampled twice because a similar study occurred in 1996 and 1997 (Lee and McCracken 2001). Bimonthly sampling provided adequate data about population trends without appearing to influence normal emergence.

Temperature and relative humidity loggers accurate to 0.5°C and 0.6% relative humidity (iButton Hygrochron DS1923; Maxim Integrated Products, Dallas Semiconductor, Sunnyvale, California) were placed inside and outside caves to record data at 15-min or 30-min intervals. Light levels near cave openings were recorded at 15-min intervals (HOBO Pendant UA-002-64; Onset Computer Corporation, Pocasset, Massachusetts). Additional climate data were obtained from the National Oceanic and Atmosphere Administration (<http://>

www.noaa.gov) from stations nearest to sample locations. Sunset times were taken from *The Old Farmer's Almanac* (<http://www.almanac.com>).

Analytical methods.—For each sampling night, the onset and end of emergence were recorded. We calculated the proportion of pregnant, lactating, nonreproductive (hereafter, including undetectably pregnant and postlactating) females, adult males, and juveniles. To determine the overall reproductive composition of the colony, standard Gaussian curves were fitted to the proportions of adult females that were in early pregnancy (undetectably pregnant females), in late pregnancy (detectably pregnant females), that were lactating, and that were postlactational. Median duration of lactation was estimated from the span during which lactating females comprised the majority of adults (see Kunz 1971, 1973). Minimum age to achieve flight was estimated as the span from the 1st night when lactating females were captured on consecutive sample days to the 1st night when juveniles were captured.

Multiple linear regression with a backward elimination procedure using $\alpha = 0.15$ for retention in the model was calculated using onset of emergence as the dependent variable and time of sunset (sunset), daily minimum temperature (T_{\min}), daily maximum temperature, occurrence of precipitation in the previous 24 h (24-h rain, binary), and time of moonrise as independent variables. Median emergence times for each cohort were computed across the entire study period and within seasonal phases.

Emergence times were normalized as a percentage of the duration of emergence to adjust for varying durations. Contingency tables were created for the relative proportion of a given cohort emerging within 10% time intervals. Pearson's chi-square was calculated to test for independence between the relative proportion of each cohort emerging (e.g., lactating versus other, juvenile versus other, etc.). We described emergence patterns with logistic regression, using percentage of emergence time elapsed to predict the relative abundance of a particular cohort compared to the rest of the colony emerging at the same normalized time. All statistics were performed with JMP 5.0.1 (SAS Institute Inc., Cary, North Carolina) and OriginPro 8 (OriginLab Corp., Northampton, Massachusetts). Unless otherwise indicated, values are reported as mean (95% confidence interval).

RESULTS

Seasonal colony dynamics.—Reproductively active adult females comprised >88% of individuals ($n = 2,923$) in the colonies from 8 May to 24 June, before the 1st flights of juveniles (Fig. 1). During the same period, the proportion of males was negatively correlated with date ($r = -0.77$, $P < 0.002$). After 4 July, adult males were essentially absent. Juveniles were captured in greater numbers than adults beginning 17 July (Fig. 1).

Early spring (2 April–8 May) corresponded with early pregnancy, when nonreproductive or undetectably pregnant females represented 64.2% (61.3, 67.0) of individuals caught.

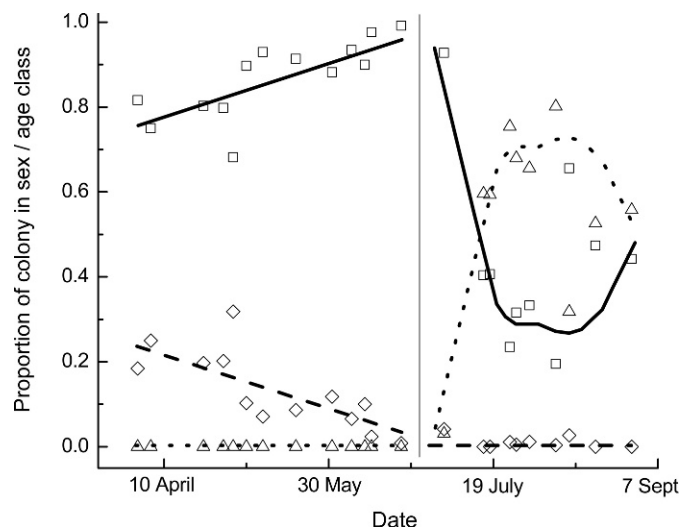


FIG. 1.—Relative proportions of adult male (diamonds, dashed line) and female (squares, solid line) Brazilian free-tailed bats (*Tadarida brasiliensis*) during evening emergences from 3 caves in south-central Texas fit linear trends before juveniles (triangles, dotted line) 1st fly (left of vertical line): proportion of males = $-0.0027(\text{Julian day}) + 0.494$ ($R^2 = 0.593$, $P < 0.002$) and proportion of females = $0.0027(\text{Julian day}) - 0.506$ ($P < 0.002$, $R^2 = 0.593$, $P < 0.002$). After juveniles begin to fly (right of the vertical line), trend lines were estimated by 10-point Savitsky-Golay estimation. Adult males were effectively absent when the 1st juvenile was captured. Volant juveniles were 1st captured on 4 July 2007 at Ney Cave. Juveniles became more abundant than adult females on 17 July.

Late spring (8 May–18 June) corresponded to pregnancy, when 80.2% (78.3, 82.1) of bats were palpably pregnant. Early summer (18 June–11 August) corresponded to lactation, when lactating females made up only 38.1% (36.2, 40.1) of bats captured, whereas juveniles comprised 53.0% (51.0, 55.0). Late summer corresponded with the postreproductive period, when 45.5% (40.8, 50.3) were nonreproductive or postlactating, whereas 54.5% (49.7, 59.2) were juveniles (Fig. 2).

Parturition occurred over approximately 28 days from 6 June to 4 July, when pregnant bats were last captured. Median parturition date was 18 June. Median length of lactation was 54 days (Fig. 2). Volant juveniles were 1st captured on 15 July at Davis Cave and 18 July at Ney Cave, approximately 40 days after lactating bats were 1st trapped on consecutive sample nights. For the period from April through August 2007, mean monthly ambient temperature (Fredericksburg, Texas) was 27.9°C and total rainfall was 1,069 mm (<http://www.noaa.gov>).

Timing of evening emergence.—All emergences consisted of a single event with no breaks. Onset of emergence was significantly correlated with sunset and minimum ambient temperature (Table 1). After removing 1 outlier from the analysis, sunset explained most variation in onset of emergence (slope = 1.40, $R^2 = 0.83$, $d.f. = 21$, $P < 0.0001$), with overall mean onset of emergence 11.8 min after sunset (7.1, 16.6; Fig. 3). Onset of emergence relative to sunset did not differ among caves (1-way analysis of variance, $F = 0.383$, $d.f. = 2, 20$, $P = 0.813$). Mean emergence duration was 92.0 min (76.8, 107.1), ranging from 31 to 150 min.

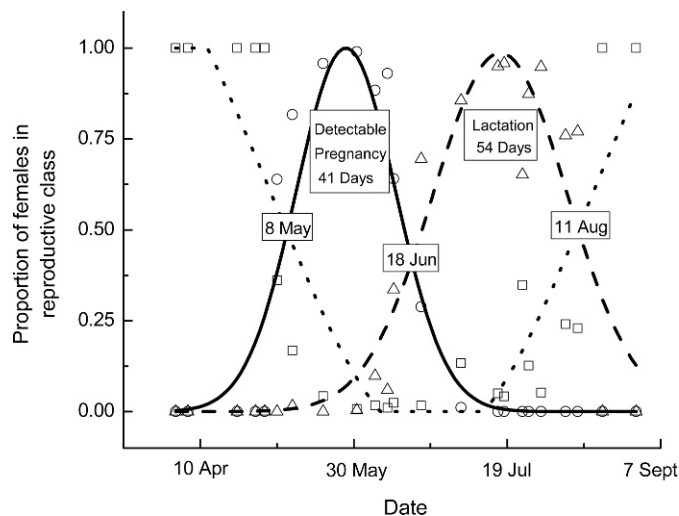


FIG. 2.—Relative proportions of female Brazilian free-tailed bats (*Tadarida brasiliensis*) in different reproductive conditions captured during evening emergence at 3 caves in south-central Texas. Proportions of females in different reproductive classes are based on the total number of adult females captured each night (males and juveniles are excluded). Curves are Gaussian standard curves fitted to pooled nonreproductive, undetectably pregnant, and postlactating females (squares, dotted line; adjusted $R^2 = 0.755$, $d.f. = 19$); palpably pregnant females (circles, solid line; adjusted $R^2 = 0.897$, $d.f. = 19$); and lactating females (triangles, dashed line; adjusted $R^2 = 0.875$, $d.f. = 19$). Curve intersections indicate the median end date of a reproductive (or seasonal) phase. The palpably pregnant phase (late spring) began on 8 May, lactation (early summer) began on 18 June. Median period of lactation was 54 days, ending 11 August. Before 8 May (early spring) corresponded with early pregnancy and after 11 August (late summer) was the postlactation period.

Median emergence time relative to sunset differed among reproductive and age cohorts over the study period and within seasonal phases (Table 2). Median emergence time was earliest for nonreproductive or undetectably pregnant females in early and late spring, for pregnant females during early summer, and for juveniles during late summer. Pregnant females in early spring, adult males in late spring, juveniles and postlactating females in early summer, and adult females in late summer had the latest median emergence times. Over the entire study, median emergence time was earliest for nonreproductive adult females and latest for pregnant females.

Relative abundances of dominant cohorts differed among normalized emergence time intervals (Table 3). During early

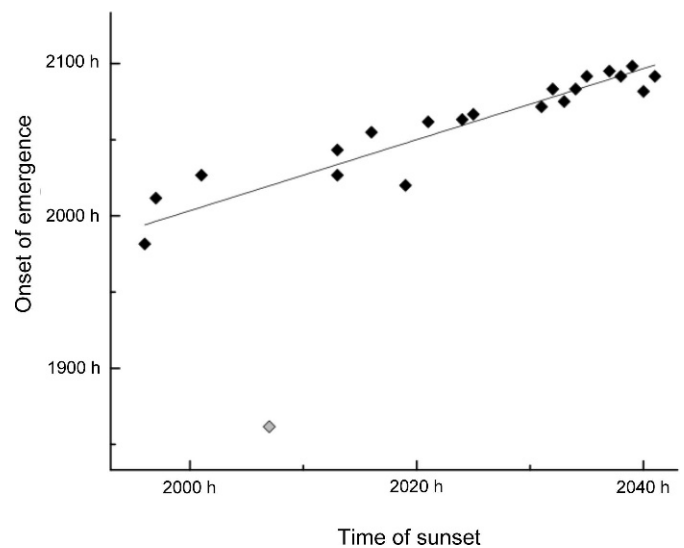


FIG. 3.—The onset of evening emergence by Brazilian free-tailed bats (*Tadarida brasiliensis*) at 3 caves in south-central Texas was correlated with sunset. The outlier (gray diamond) was excluded from regression calculations: onset of emergence = $1.398(\text{sunset}) - 477$ ($R^2 = 0.827$, $P < 0.0001$). The model was calculated using minute of the day for times.

spring (Fig. 4A), the probability of trapping a pregnant female increased from about 12% to 25% as emergence progressed (logistic $\beta_1 = -1.06$, $\chi^2 = 16.94$, $P < 0.0001$, $n = 1,109$), and the probability of trapping an undetectably pregnant or nonreproductive female decreased from 72% to 53% (logistic $\beta_1 = 0.83$, $\chi^2 = 17.02$, $P < 0.0001$, $n = 1,109$). During late spring (Fig. 4B), a similar pattern existed for pregnant females, with the probability of trapping a pregnant female increasing from 66% to 81% (logistic $\beta_1 = -1.10$, $\chi^2 = 10.52$, $P = 0.001$, $n = 1,695$). The probability of trapping lactating females during late spring decreased from 16% to 4% (logistic $\beta_1 = 1.61$, $\chi^2 = 30.32$, $P < 0.0001$, $n = 1,695$). During early summer (Fig. 4C), lactating females were more abundant early in the evening, decreasing from 59% to 20% as emergence progressed (logistic $\beta_1 = 1.74$, $\chi^2 = 156.42$, $P < 0.0001$, $n = 2,394$), and the probability of trapping juveniles increased from 32% to 74% as emergence progressed (logistic $\beta_1 = -1.80$, $\chi^2 = 176.31$, $P < 0.0001$, $n = 2,394$). In late summer (Fig. 4D), however, the likelihood of trapping juveniles decreased from 73% to 35% as emergence progressed (logistic $\beta_1 = 1.58$, $\chi^2 = 25.96$, $P < 0.0001$, $n = 422$), whereas the likelihood of trapping adult females

TABLE 1.—Summary of best 3 independent variables in multiple linear regression predicting onset of emergence ($n = 23$). Sunset time and onset of emergence were converted to minute of the day for calculations. T_{\min} is the daily minimum ambient temperature. 24-h rain is a binary variable where 1 indicates >0 mm rain fell the day before the emergence and 0 indicates no rain in that period. R^2 is cumulative for each added independent variable.

Parameter	Estimate	SE	t -ratio ($d.f. = 22$)	P	R^2
Intercept	-356.30	434.32			
Sunset	1.26	0.37	3.46	0.003	0.59
T_{\min}	2.38	1.12	2.12	0.048	0.66
24-h rain	-12.82	8.14	-1.57	0.130	0.70

TABLE 2.—Median emergence times (minutes after sunset) for different reproductive cohorts of Brazilian free-tailed bats (*Tadarida brasiliensis*) at 3 caves in south-central Texas. During early and late spring, nonreproductive and undetectably pregnant females (NR/undetectable) emerged earlier than others. Pregnant females (although relatively rare) had the earliest median emergence time during early summer. Juveniles emerged earlier than others during late summer. Dashes indicate that no individuals in the cohort were captured during that seasonal phase. The sample size for each cohort is indicated in parentheses.

	Seasonal phase				
	Early spring	Late spring	Early summer	Late summer	May–September
NR/undetectable	10 (712)	34 (56)	69 (22)	53 (192)	26 (982)
Pregnant	82 (184)	80 (1,360)	29 (36)	—	78 (1,580)
Lactating	—	50 (147)	47 (912)	—	47 (1,059)
Postlactating	—	—	76 (127)	—	76 (127)
Adult male	22 (213)	88 (132)	62 (29)	—	42 (375)
Juvenile	—	—	76 (268)	39 (230)	72 (498)

increased from 27% to 65% (logistic $\beta_1 = -1.58$, $\chi^2 = 25.96$, $P < 0.0001$, $n = 422$).

DISCUSSION

Seasonal colony dynamics.—Peak mating season for Brazilian free-tailed bats in south-central Texas occurs from late March through early April (Keeley and Keeley 2004). Our estimated median parturition date was approximately 80 days after the mating period proposed by Keeley and Keeley (2004), concurring with gestation estimates derived from dissections (Davis et al. 1962). However, pregnancy can only be detected from external observations during the 2nd half of gestation when the fetus is large enough to detect by manual palpations (Hayssen and Kunz 1996; Racey 1988). Later in the summer when suckling ends, adult females leave maternity roosts and juveniles become more abundant than adults during emergences. Similar increases in the relative abundance of young bats were reported by Cockrum (1969) and Constantine (1967).

Although *T. brasiliensis* is relatively dexterous at birth, presumably to cling to the mother and the roost substrate (Hermanson and Wilkins 1986), the young experience slow skeletal (Papadimitriou et al. 1996) and muscular growth

TABLE 3.—Results of contingency table analyses testing for independence of the relative proportion of reproductive cohorts of Brazilian free-tailed bats (*Tadarida brasiliensis*) emerging and normalized emergence times (10% intervals). Pearson chi-square is computed from a comparison of the indicated reproductive cohort to all other cohorts combined. NR = nonreproductive.

Seasonal phase	Cohort	Pearson's χ^2 (d.f. = 9)	P
Early spring	NR/undetectable	26.55	0.002
	Palpably pregnant	32.66	<0.001
Late spring	Palpably pregnant	55.76	<0.001
	Lactating	81.44	<0.001
	Adult male	21.09	0.012
Early summer	Lactating	213.83	<0.001
	Juvenile	226.71	<0.001
Late summer	Juvenile	36.37	<0.001
	NR/postlactating	36.37	<0.001

(Hermanson 2000), which delays the onset of flight relative to other species. Our estimate of approximately 40 days to achieve flight is consistent with previous reports (Kunz and Robson 1995). However, volant juvenile bats, in general, are not immediately independent of their mothers (Kunz 1973, 1974; Rolseth et al. 1994; Swift and Racey 1983). We observed that Brazilian free-tailed bats continue suckling for 2 weeks after they begin flying outside their roosts.

During 6 sample nights in July and early August, 50.3% of juveniles were female ($\chi^2 = 0.027$, $P = 0.87$, $n = 915$), an observation that is consistent with a 1:1 sex ratio at birth in south-central Texas (Davis et al. 1962; Kunz and Robson 1995). However, on 4 sample nights in late August and September, proportions of juvenile males and females were significantly different (62.3% females:37.7% males; $\chi^2 = 35.44$, $P < 0.001$, $n = 583$). Whether this reflects a decrease in young males due to differential dispersal or mortality, or an influx of young females from other natal roosts during autumn migration remains unclear. Because there was no corresponding increase in abundance of adult bats, we expect that these behavioral differences are characteristic of young males and females. Further research is needed to determine the causes.

Many males of Brazilian free-tailed bats presumably remain at winter roosts in Mexico (Davis et al. 1962; Glass 1982). The maternity colonies that we examined consisted of >20% males in early April, suggesting potential mating activity. Over subsequent weeks, the number of adult males declined to near 0 by the time juveniles began flying. Males and nonreproductive females that vacate maternity roosts (Glass 1982; Hermanson and Wilkins 1986) may benefit from lower foraging competition at alternate roosts (also see Kunz 1974) while coincidentally easing intraspecific competition at crowded maternity roosts.

Variation in timing of evening emergence.—The onset of evening emergence was highly correlated with sunset, differing by >15 min from expected on only 3 nights. Although most environmental factors were not significant predictors, we suggest that precipitation and temperature contributed to the nightly disparities. The most disparate emergence occurred on 22 April at Davis Cave, beginning 95 min before the expected time. On this evening, nearly all bats had dispersed 25 min before sunset. Although daily

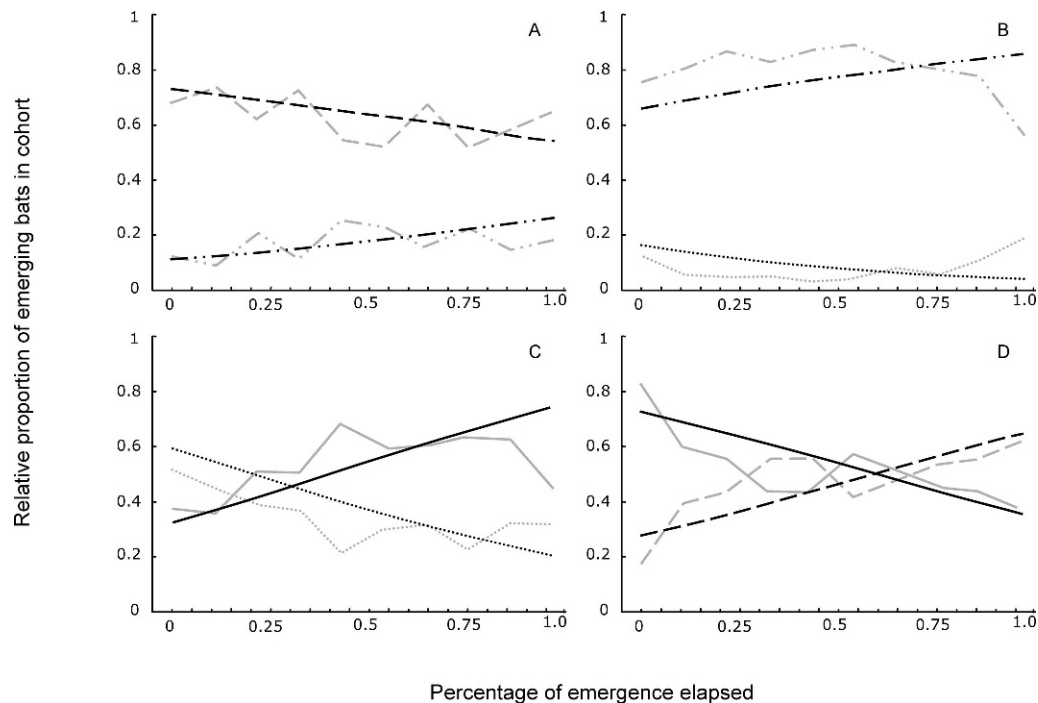


FIG. 4.—The relative abundance of Brazilian free-tailed bats (*Tadarida brasiliensis*) in different reproductive and age cohorts changed as the emergence progressed within seasonal phases. Logistic regressions (black lines) represent the relative abundance of the cohort predicted from elapsed emergence based on summarized data (gray lines). A) During early spring, the likelihood of trapping pregnant females increased (dash-dot-dot), and undetectably pregnant or nonreproductive females decreased (dashed). B) During late spring, the likelihood of trapping pregnant females increased and lactating females decreased (dotted) as the emergence progressed. C) During early summer, the likelihood of trapping lactating females decreased and juveniles increased (solid) as emergence progressed. D) During late summer, the likelihood of trapping juveniles decreased and nonreproductive females increased (dashed) as the emergence progressed. Reproductive, age, and sex cohorts not depicted within a seasonal phase were not present or had no significant relationship with time.

minimum temperature that day was near the monthly mean, the 2 previous nights were unseasonably cold. Low temperatures of 0.6°C and 2.2°C, respectively, likely decreased insect availability and limited foraging success on these nights (also see O'Donnell 2000). Cold ambient temperature also would lead to high energy costs associated with thermoregulation (Speakman and Thomas 2003). Thus, the return to more typical ambient conditions likely prompted earlier than normal foraging bouts. No rain occurred on sample nights, although rain on the previous nights may have a similar effect on emergence times.

In 2007, mean onset of emergence time was $11.8 \text{ min} \pm 2.3 \text{ SE}$ after sunset. Herreid and Davis (1966) reported similar timing of emergence onset ($\pm \text{SE}$): $11.0 \pm 2.5 \text{ min}$ after sunset in 1957–1960 at Davis Cave. However, variation in onset of emergence among years is evident: $69.0 \pm 5.0 \text{ min}$ before sunset and $1.5 \pm 3.9 \text{ min}$ before sunset in 1996 and 1997, respectively, at Frio Cave (Lee and McCracken 2001). Differences in climate and prey availability are likely at least partly responsible (Erkert 1982; Lee and McCracken 2001). Many insect populations decrease during dry weather (Hawkins and Holyoak 1998). However, the summer of 2007 was in the 90th percentile historically, with 524 mm rainfall from June to August. In contrast, summer rainfall totals in 1957–1960, 1996, and 1997 were 259 mm, 152 mm, and 271 mm, respectively. All 4 study periods averaged near-

normal summer temperatures ($26.4^\circ\text{C} \pm 0.9^\circ\text{C SD}$, 1971–2000—<http://www.noaa.gov>). On average, the latest emergences occurred during the wettest summer, 2007, and the earliest emergences occurred during the driest summer, 1996. In 2007, we did not observe early emergences consisting of substantial pauses in activity between 2 or more emerging pulses, as has been reported at these sites in previous years (Betke et al. 2008; Lee and McCracken 2001). Thus, we conclude that Brazilian free-tailed bats delay emergence during wet years when weather likely favors insect populations. In dry years, bats emerge well before sunset, risking predation during daylight flight to increase foraging chances.

Population declines of bats can lead to lower intraspecific competition for prey near the roost and a reduced benefit of early emergence. Only 57 mm of rain fell in south-central Texas during June, July, and August of 2006. Although the impact of this drought has not been quantified, there is evidence for large annual fluctuations in colonies based on NEXRAD Doppler radar data on reflectivity of dispersing Brazilian free-tailed bats in the study area (Horn and Kunz 2008). Later emergence times in 2007 were consistent with the behavior expected after colony declines.

Timing of emergence among reproductive cohorts.—Pregnant Brazilian free-tailed bats may emerge earlier than roost mates (Lee and McCracken 2001), although we observed the opposite in early and late spring of 2007. Pregnant bats in the

later half of gestation are vulnerable to predation by raptors due to their reduced agility (Gillette and Kimborough 1970; Hayssen and Kunz 1996; Jones and Rydell 1994; Norberg and Rayner 1987). Variation in timing of emergence by pregnant bats relative to others suggests they modify behavior in response to environmental and social cues. Thus, we observed that undetectably pregnant and nonreproductive bats emerged earlier than roost mates that are farther along in pregnancy.

Although still emerging mostly after sunset, the relative proportion of lactating females decreased as the emergence progressed during late spring and early summer. Lactating females experience higher energy demands and are lighter than pregnant females (Kunz et al. 1995b; Kurta et al. 1989; Oftedal 1985). They emerge earlier than both nonreproductive and pregnant bats (Lee and McCracken 2001; Welbergen 2006), consistent with the hypothesis that high energy demands lead to earlier foraging. Lactating females also reduced predation risk in 2007 by emerging after sunset even when flocking behavior and fast flight provide them some protection in daylight. Emergence times for mothers also may be influenced by feeding schedules of offspring, but the favorable weather during our study likely allowed lactating bats to delay emergence until after sunset without compromising foraging success.

Variation in emergence activity by juveniles between early and late summer exemplifies their flexible behavior. Flight conditions are often crowded at the constricted openings to large maternity roosts (Kalcounis and Brigham 1994). Considering the relatively brief parturition period, a large number of inexperienced juveniles risk colliding in congested cave openings (Kunz 1974; Kunz and Anthony 1996; Kunz et al. 1995a; Speakman and Tallach 1998). Such collisions often result in bats falling to the ground, leading to injury or death (Gillette and Kimborough 1970; Winkler and Adams 1972). Inexperienced juveniles also are poorer at avoiding avian predators (Lee and Kuo 2001; Perry and Rogers 1964). Moreover, initial flights by juveniles are more important for practicing skills than for meeting energy demands because they are still suckling (Kunz 1974; Kunz and Anthony 1996). Together these factors may have delayed the emergence of juveniles relative to roost mates during early summer.

Once juveniles are weaned, they forage to fulfill nutritional needs independently. Improved strength and navigational abilities of older juveniles should allow better flight in crowded conditions and the ability to flock to reduce predation risk (Duvergé et al. 2000). In late summer, juveniles began to emerge earlier in the evening, which is consistent with observations of a convergence in foraging behavior with adult patterns within 2 weeks of the onset of flight (Kunz 1974; Kunz and Anthony 1996).

Timing of nightly activity by Brazilian free-tailed bats appears to be influenced by environmental cues, developmental stage, predation risk, and variable metabolic demands. On a nightly basis, we suggest that emergence times are most influenced by recent foraging success and predation risk. Conversely, on a seasonal basis, we suggest that variation in

emergence times is related to reproductive state or maturity, which in turn interact with energetic demands and availability of prey. Finally, annual variation in population size and prey availability can further influence emergence behavior. When resources are sufficient to satisfy nutritional needs of the colony, we suggest that individuals deploy behaviors that minimize risks associated with diurnal activity. However, when competition is intense due to limited prey or large colony size, individuals may employ more risky behaviors, such as emergence before sunset, to meet increased energy needs. Thus, Brazilian free-tailed bats succeed in large aggregations by modifying their emergence behavior to match energy demands to current environmental, physical, and social situations.

RESUMEN

Los comportamientos flexibles permiten a animales gregarios explotar condiciones espacial y temporalmente favorables para la reproducción. Se monitoreó la emergencia (o salida del refugio) de los murciélagos brasileños de cola libre (*Tadarida brasiliensis*) al atardecer, en la región centro-sur de Texas para determinar los cambios en la dinámica de la colonia y para evaluar hipótesis asociadas con la evasión de depredadores y la demanda energética estacional. En 2007, la fecha media de parto fue el 18 de junio y la lactancia duró alrededor de 54 días. Los juveniles comenzaron a volar después de 41 días y continuaron siendo amamantados por dos semanas antes de ser destetados. El comienzo de la emergencia al atardecer estuvo correlacionada con la puesta del sol, empezando, en promedio, 11.8 minutos después de la puesta del sol (intervalo de confianza del 95% = 7.1, 16.6), lo cual es más tarde que lo reportado en estudios previos. Las hembras preñadas salieron del refugio más tarde que los demás miembros de la colonia, consistente con una hipótesis de evasión de depredadores. Las hembras lactantes salieron del refugio después de la puesta del sol, pero más temprano que otros murciélagos, consistente con la hipótesis de que éste es un período de alta demanda energética. Los juveniles salieron del refugio más tarde que las hembras adultas mientras eran amamantados, pero salieron más temprano al madurar y ser destetados, sugiriendo una compensación entre la evasión de depredadores y la demanda energética. Nuestras observaciones indican que el comportamiento de emergencia del refugio de *T. brasiliensis* al atardecer varía con los estímulos ambientales, pero es mediado por la demanda energética de la reproducción.

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