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Nursing Behavior in Mexican Free-tailed Bat Maternity Colonies

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MCCrackEN, G. F. & GUSTIN, M. K. 1991: Nursing behavior in Mexican free-tailed bat maternity colonies. *Ethology* 89, 305—321.

Abstract

The nursing behavior of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) was examined in two large maternity cave roosts during six nursing seasons. After depositing pups in large creches, adults return to these creches two or more times daily to nurse. Densities, movements, and roosting associations of pups in creches were documented, and a night-vision device and infrared-sensitive video system were used to observe female-pup reunions and nursing affiliations. Densities of young (< 15 d) pups in creches averaged 4000 pups/m². Pups moved independently of one another between milk meals. Stable roosting associations among pups were absent, and females evidently could not predict where a given pup would be relocated. Upon returning to the creche, females searched for and relocated pups using vocal and olfactory cues. Experiments with marked individuals demonstrated that females nursed the same pups on subsequent nights. These same experiments indicated that female/pup recognition was mutual and that the pup participated in reunions by moving toward its putative mother. However, pups also attempted to suckle from other females and 35 instances of apparently successful milk “theft” were observed. Observed milk theft was insufficient to account for the frequency of alloparental nursing that was estimated independently using genotype tests. The high densities of bats within roosts and the lack of stable roosting associations among individuals argue against selection for shared nursing via kin selection and/or reciprocity. Errors in pup recognition, milk-dumping by females, and adoption by mothers whose own pup had died may occur, but high pup survival to weaning suggests that adoption is rare. The estimate of alloparental nursing obtained from genotype tests may be inflated as a result of increased opportunities for milk theft caused by our disturbance of adults. Current evidence suggests that energetic costs to females of alloparental nursing and searching for pups are compensated by mutualistic benefits obtained from aggregative roosting.

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Introduction

Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) give birth and nurse their pups in roosting situations that pose an extreme challenge to selective parental care. In spring, adult females migrate from Mexico to the southwestern

U.S. where they aggregate in large caves in populations that often exceed several million individuals (VILLAR & COCKRUM 1962; DAVIS et al. 1962; COCKRUM 1969). Most females give birth to a single pup in mid-June. Following birth, the female provides her pup with a milk meal, then deposits it with others on the cave walls or ceiling (DAVIS et al. 1962; MCCrackEN 1984). Masses of densely packed pups ("creches") soon cover much of the roosting surface (Fig. 1). Pups remain in these creches until they are volant at about 6 weeks of age. After placing their pups in a creche, females roost in areas of the cave apart from the pups, but they return to the creche and nurse pups two or more times each day.

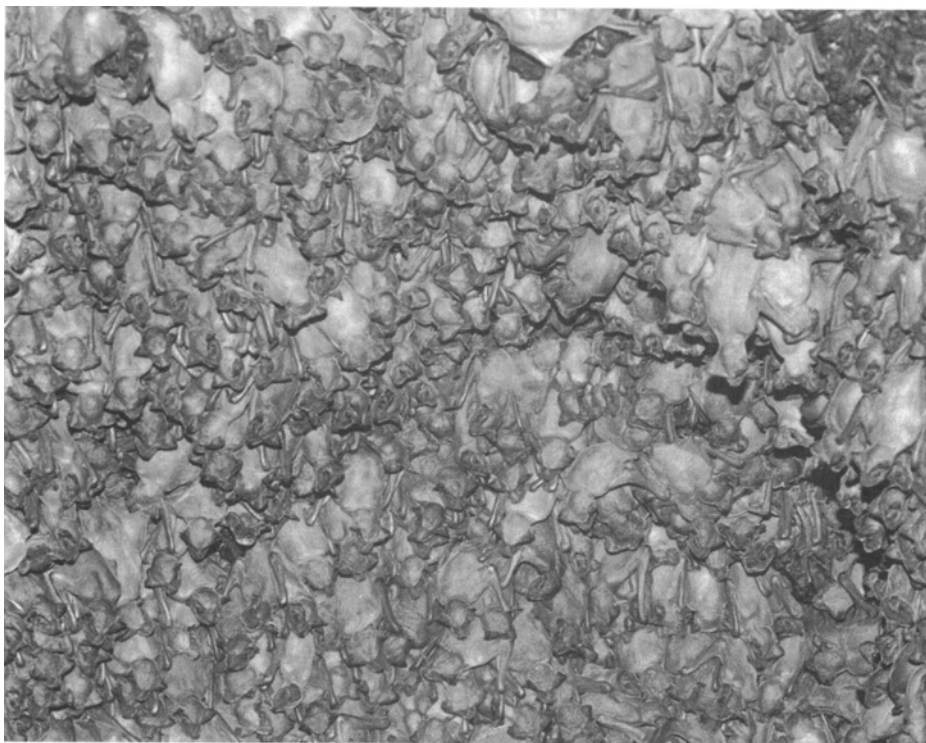


Fig. 1: Photo of massed pups in a creche. Within a few days following the onset of births, single creches can cover areas greater than 100 m² of roost surface and have densities exceeding 4000 pups/m². The photo shows approximately 0.15 m² of roosting area

Because of the cost of location (MILLAR 1977; KUNZ et al. 1983; OFTEDAL 1984; GITTLEMAN & THOMPSON 1988), we expect female mammals to be selective regarding the young that they nurse. Despite conditions in their roosts, and contrary to earlier reports (DAVIS et al. 1962), this expectation was confirmed for Mexican free-tailed bats by examining allozyme genotypes of female-pup pairs taken from a natural maternity roost (MCCrackEN 1984). However, while genotype tests showed nursing to be highly nonrandom, the same tests also showed that, minimally, 17 % of the females examined were nursing pups that

could not be their offspring. Subsequently, our studies on these bats focused on establishing the selective context in which alloparental nursing occurs (see reviews of this topic in RIEDMAN 1982; GITTLEMAN 1985), and determining how female-pup recognition and selective nursing is achieved (GELFAND & MCCrackEN 1985; GUSTIN & MCCrackEN 1986; MCCrackEN & GUSTIN 1987; BALCOMBE 1990).

Here we report observations on female-pup reunions and nursing behavior within natural maternity colonies. We also describe aspects of creche demography, including pup densities, their movements, and roosting-group stability. The results reported allow us to account for the alloparental nursing observed, and to discount possible roles of kin selection (e.g. BERTRAM 1975; OWENS & OWENS 1984) or reciprocity (TRIVERS 1971; AXELROD & HAMILTON 1981) in offsetting the costs of alloparental nursing in these bats.

Methods

Dates and Study Sites

Field studies took place from early June to late July of 1981–1985 and 1987, in maternity colonies located in Davis Cave, Blanco Co., Texas, and James River Cave, Mason Co., Texas. In the late 1950's, colony sizes in these caves were estimated at 4×10^6 and 6×10^6 individuals, respectively (DAVIS et al. 1962). Although more recent estimates of colony sizes are unavailable, both caves still house extremely large numbers of Mexican free-tailed bats.

Sex Ratios, Densities, and Roosting Associations

Sex ratios of adults and pups in roosts were obtained from individuals captured for genetic studies (MCCrackEN 1984). Individuals were collected from accessible roost surfaces by hand or using a bucket collector (MCCrackEN & BRADBURY 1981), or they were captured in the cave or at the cave entrance using a butterfly net.

Density estimates of pups in creches were obtained, without detaching pups from their roosthold, by counting all pups encircled within a wire hoop (area = 82 cm²) appressed to the creche. On four nights in late June and early July, 6 counts were taken from accessible creche areas in different locations of Davis or James River Caves (Table 1). The number of pups roosting in 1 m² was extrapolated from these counts. Counts were taken between 22.00 h and midnight, when most adults were foraging outside of the caves.

Table 1: Estimated densities of Mexican free-tailed bat pups in creches in two caves in 1983. Sample size = 6 for each estimate

Cave	Date	$\bar{x}$	Pups/m ² (range)
Davis	26 June	4,134	(3,579–5,307)
James R.	27 June	3,928	(3,209–4,689)
Davis	3 July	3,044	(2,838–3,209)
James R.	5 July	2,859	(2,345–3,085)

Stability of roosting groups and movements of pups within creches were examined by marking adjacently roosting pups and recording individuals' displacements during 24-h periods. To avoid disruption and possible abandonment of creche areas, successful marking required that pups were not detached from the roost and that they were marked with as little disturbance as possible. Dabbing the

heads of pups with water-based, nontoxic, fluorescent paint (Pactra Acrylic Colors) provided an effective mark that persisted for one to several days. These studies took place between 22.00 h and midnight. The location of pups when marked was recorded relative to permanent paint marks on the roost surface. At 24-h intervals, marked pups were relocated using an ultraviolet (UV) light (365 nm wavelength) and their roosting locations were again recorded. Two protocols were employed. First, five groups of 13–15 pups roosting adjacently within areas of $<0.01 \text{ m}^2$ were painted, each group with a different color. These pups were relocated 24 h after marking and the direction and distance of dispersal of each pup were recorded. Second, 26 pairs of adjacently roosting pups were painted, the pups in a pair each with a different color. These individually marked pups were relocated 24 and 48 h after marking and the distance and direction of movement of each pup were recorded. The protocol using pairs allowed us to test whether the disturbance caused by marking pups influenced their movements.

NVD and NVD-Video

In 1983 and 1984, a Javelin Model 221 night-vision device (NVD) was employed to observe female-pup behavior in the maternity creches of Davis and James River Caves. For these observations, the NVD, with an attached zoom lens (70–210 mm, f3.4) and a biocular viewer, was placed on a tripod 1.8–2.1 m from creches located on vertical or nearly vertical roost surfaces. Observation of more horizontal surfaces was prevented by the rapid accumulation of bat guano on the lens. The sole source of illumination was a miner's light (MSA model ML-2), fit with a Wratten-Kodak 87B infrared (IR) filter and a frosted-plastic light diffuser. This was sited along the NVD to provide illumination of the area being observed. This light is beyond human perception and caused no evident disturbance to *T.b. mexicana* females or pups. Studies on light responses in adult females (MISTRY & MCCrackEN 1990) indicate that they do not respond behaviorally to light from this source.

38 h of observation were made between 20 June–19 July 1983 and 19–26 June 1984. While in the cave, observers wore ammonia and dust filtering respirators. Observations took place between 23.00–2.00 h, with observers generally working 1-h shifts per night. It is during this time that females begin returning to nurse pups within creches. After 2.00 h the numbers of adults and the consequent activity on creches are so great that systematic observation of individuals is precluded. Most observations involved focal-animal sampling (ALTMANN 1974) in which a creche was observed until a returning adult landed in the field of view. This bat then was followed until it (1) was lost among other bats, (2) moved outside the possible viewing area of the NVD, (3) flew from the creche, or (4) selected and nursed a pup.

In 1984 and 1985 a low-light sensitive CCTV camera (Panasonic, Model WV1650) was attached to the NVD to allow video taping of in-creche behavior. As with the NVD studies, all observations were conducted by a person in the cave. Remote observation was precluded because manual manipulation and focusing of the NVD-video was required to follow the rapid movements of adults on the creche. Behavior was observed through a monitor connected to a VHS videocassette recorder (VCR; Cannon Model VR20A). To block the light produced by the monitor, all observations were made from within a small blind. All equipment was battery operated and within reach of the observer in the cave. The video camera, VCR, and power supplies were in sealed containers containing calcium carbonate (drierite) to protect them from the dust, high humidity, and the ammonia and fecal rains within the roost.

A total of 31 h of video recording, made between 19 June–17 July, 1984 and 18–27 June, 1985, was of sufficient quality for analysis. All videotaping took place between 23.00–2.00 h, and on most nights two observers each taped for 1 h. As with the NVD observations, NVD-video studies involved focal animal observations of returning adults.

Infrared Video

The NVD and NVD-video studies of 1983–1985 involved observation of female-pup nursing interactions among individuals for which we knew nothing regarding previous or subsequent nursing affiliations. To establish these affiliations, observation of marked individuals during two or more nursing periods was necessary. This posed logistic difficulties in that a mark must not only identify individuals, but also make them sufficiently conspicuous within the dense masses of other bats in the roost. Young pups weigh as little as 3 g and any mark must be small and lightweight. The mark also

must remain conspicuous between milk meals and, because females return to the cave and nurse throughout the night, it must be possible to monitor a marked pup continuously during this period without disturbing behavior.

In 1987, females and pups were marked with IR reflecting tags (Scotch-light, 3M Co.). Creches were flooded with low intensity IR light, and the movements of tagged bats were monitored using IR-sensitive CCD cameras. Our objective was to monitor the locations of tagged individuals continuously within creche areas of several m², and containing several thousand pups, to observe both searches and female-pup reunions. We found that with low intensity IR light, reflecting tags in the field of view showed as bright spots even though the individual bats were not discernible. Increasing the IR intensity decreased the contrast between the reflection from the tag and the background of the creche, making location of tagged individuals more difficult.

Two cameras (JAI, Model 712 CCD, JAI Electro-Optical Ltd.; Sanyo, Model VDC 3800, Sanyo Electronics) with 12.5–75 mm, f1.2 lenses were used. The JAI camera has greater IR sensitivity, and with it we monitored roost areas of approx. 4 m². The Sanyo camera was used to monitor creche areas of approx. 1.8 m². Miners' lights with IR filters or banks of 3 IR light-emitting diodes (Lightning Bug, Model CW TD00) served as light sources. The cameras were in sealed plastic housings containing drierite and tethered to VCR's and monitors located outside of the cave. All equipment was powered with 12-V gel-cell batteries.

For these experiments, female-pup nursing pairs were collected by hand from accessible creche areas between 23.00 h and midnight. An approx. 1-cm² scotch-light tag was attached using surgical glue (Skinbond Cement) to the head of the pup, and a similar but larger (~ 4 cm²) tag to the back of the female. To avoid leaving odors, we wore surgical gloves when handling bats.

Although tags were seen as reflecting spots, it was possible to distinguish between the tags of females and pups, and among gross differences in tag shape (e.g., square vs stripe) on the video monitor. In addition, we used three colors of scotchlight that can be distinguished in visible light, but not IR. Using a combination of different tag colors and shapes, each individual was given a unique mark distinguishable in visible light.

Tagged pups were returned, within 1/2 h of their removal, to within 10 cm of where they were captured. A camera was focused on that creche area and the tagged female was released at the cave entrance. The creche, with the tagged pup in view, then was monitored for the female's return. On most nights, a camera was used to monitor a single marked pup; however, on three nights two distinctively marked pups were monitored simultaneously. It also proved possible to relocate tagged pups on subsequent nights and to monitor these pups again for possible reunions with the same tagged females.

These experiments were conducted on 11 nights between 26 June–14 July. 14 female-pup pairs were tagged and used in 18 retrieval experiments. Three tagged pairs were monitored on two (2 pairs) or three (1 pair) different nights, the other pairs were monitored for one night. Tagged bats were monitored an average 5.8 h (range 3.3–7.0 h) per night.

Results

Demography and Creche Development

The earliest that pups first were observed in creches was 5 June (James River Cave, 1981) and the latest that pups first were observed was 11 June (Davis Cave, 1982 and 1983). Parturition was highly synchronous. For example, on 10 June 1981, 9 of 66 (14 %) females examined had given birth and the remaining 57 were pregnant, whereas 9 days later (19 June 1981) a sample of 647 females from the same cave consisted of 605 (94 %) that had given birth and only 42 that were still pregnant. These observations agree with DAVIS et al. (1962) who reported that over 90 % of adult *T.b. mexicana* females gave birth within a 15-d period in mid-June.

For several days after births began, clusters of a few to several hundred pups were scattered over the cave walls and ceilings. As more births occurred, clusters rapidly increased in size, and by the third week in June, single creches typically covered areas of 10 to several 100 m². Pups remained densely clustered in creches until they began growing fur at about 4 weeks of age. Unfurred pups found outside of creches invariably appeared sick and emaciated. As pups obtained fur, their roosting densities decreased; however, the distinct segregation of adult and pup roosting locations persisted until weaning, at 6 weeks following birth.

Bucket collections at James River Cave illustrate the extreme segregation of adult and pup roosting areas. 7 collections were made between 7–24 June 1981, and were taken from adult roosting areas. Although 746 lactating, post-parturient, adult females were captured, only 27 pups were taken in the same collections.

Creches typically extend into crevices and other irregularities on the cave surface and estimating their size often is difficult. The estimates of pup density (Table 1) are from creches that were located on relatively flat surfaces where pups could be counted accurately. Other than meeting this criterion, these creches appeared typical of others in these caves. At the time of the 26–27 June estimates most pups present were 1–2 weeks of age. The sex ratio of all pups examined was biased slightly, but not significantly, toward females (421 females/391 males, $n = 812$; $p > .10$, G-test). DAVIS et al. (1962) also reported a slight, but not statistically significant, bias toward female pups.

DAVIS et al. (1962) reported that over 95 % of adult Mexican free-tailed bats present in maternity roosts during June and July were female, and that essentially all of these were parous. In our study, 1,499 adult *T.b. mexicana* were captured in arbitrary samples (those other than female-pup pairs). Of these, 1,449 (97 %) were female and 1,442 (96 %) were pregnant or lactating. Other studies (VILLAR & COCKRUM 1962; COCKRUM 1969) have shown that a large segment of the adult male population remains in Mexico throughout the summer, and that most males that come North roost in alternative sites (DAVIS et al. 1962; SVOBODA & CHOATE 1987).

Although relatively few adult males are present in maternity roosts, there is evidence that the males present are nonrandomly distributed. The arbitrary samples from James River Cave were made using bucket collectors to capture groups of adjacently roosting individuals. The numbers of males taken from different areas within the roost were highly heterogeneous ($p \ll .001$, G-test, SOKAL & ROHLF 1981), with males comprising 0–1 % of the bats present in four collections (total collection sizes (n) = 37–655), and between 6–31 % of bats in the remaining three collections (n = 33–87).

Movements and Roosting Associations of Pups in Creches

Marking studies showed that pups change roosting locations between milk meals. The average distances between relocations were 41 cm (range 13–117 cm, $n = 60$) for pups marked in groups and 45 cm (range 6–107 cm, $n = 37$) for pups marked in pairs (Tables 2, 3). Because pups moving longer distances are

Table 2: Movements during the 24-h period after marking of pups marked in groups within creches. Each group consisted of pups roosting in an area of $< 0.01 \text{ m}^2$. Davis Cave groups were marked on 7 July 1983, James River Cave groups on 28 June 1985. Rayleigh test is from ZAR (1984); p is the probability that dispersal was random in direction

Cave	Group	No. of pups		Net distance moved in cm		Rayleigh Z	p
		marked	relocated	$\bar{x}$	range		
Davis	1	13	13	38.6	12.7—76.6	1.91	$>.10$
Davis	2	13	11	30.7	22.9—66.0	2.23	$>.10$
Davis	3	13	12	47.0	15.2—116.8	10.38	$<.001$
James R.	1	15	14	45.1	17.8—101.6	2.38	$>.05$
James R.	2	15	10	42.7	17.2—94.0	2.92	$>.20$

Table 3: Movements (in cm) during the first and second 24-h periods after marking of pups marked in pairs. Pups in each pair were adjacent when marked. Average distances moved during the 1st versus 2nd 24-h period after marking were not significantly different within any marking period (t-test, $0.10 < p < 0.20$ for June 28—30; $0.50 < p < 0.90$ for July 7—9 and July 11—13). The distances moved in different marking periods differed significantly

Date marked	1st 24 h after marking			2nd 24 h after marking		
	$\bar{x}$	range	n	$\bar{x}$	range	n
28—30 June, 1984	27.7	12.7—45.7	7	44.2	25.4—57.8	3
5—7 July, 1984	36.3	8.3—83.8	11	42.1	6.4—87.0	6
11—13 July, 1983	70.3	36.8—106.	8	79.1	76.8—81.3	2

probably more difficult to relocate, these results may be biased toward more sedentary pups. However, such a bias is probably slight because these studies involved intensive searching of areas of at least 3-m radius, centered on locations where the pups were marked, and a large proportion (87 %) of all marked pups was relocated. The paint marks on pups are ephemeral, and failure to relocate a pup was likely a result of loss of its mark.

Relocation of distinctively marked pups 1 and 2 days after marking showed that the net displacement of pups during the first 24 h after marking was not significantly different from their displacement in the subsequent 24-h period (Table 3), indicating that their movements were not a result of the disturbance caused by marking them. Although the distances moved by pups within a sampling period did not differ during the first or second day after marking, the distances moved during different marking periods differed significantly ($H = 13.348$ ($df = 2$), $p < .001$, Kruskal-Wallis one way analysis of variance; Table 3). Movement distances also were heterogeneous among the three groups of pups marked in Davis Cave ($p \ll .001$, G-test; Table 2). The observation of greater movements in later marking periods (Table 3) suggest that pups may move more as they mature.

The directions individuals dispersed from the centroids of where groups were marked were apparently random in 4 of the 5 groups marked, and highly nonrandom in the remaining group (Fig. 2, Table 2). The case of observed

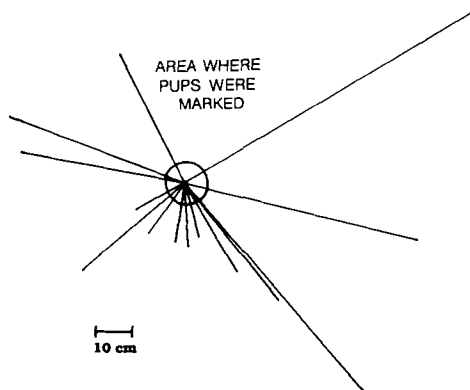


Fig. 2: Net distance and dispersal directions of 14 marked pups in group 1, James River Cave, 24 h after marking (see Table 2)

nonrandom dispersal evidently was a result of cave topography, this group being on the edge of a creche, adjacent to a rock ledge that was devoid of pups. All pairs of pups that were adjacent when marked were not adjacent 24 h later and the movements of these individuals evidently were independent of one another. The average distances between adjacent pups were 42 cm (range 22–99 cm; $n = 8$) after 24 h and 49 cm (range 40–58 cm; $n = 2$) after 48 h.

Female-Pup Behavior on Creches

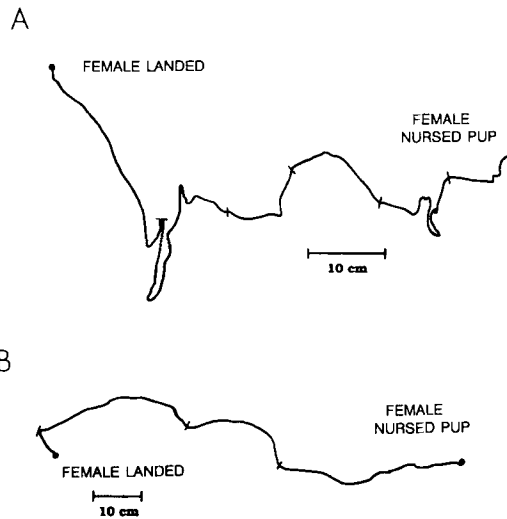
Searches for pups begin when females enter creches by landing on other roosting bats or on adjacent, uninhabited areas of the cave surface. Typically, females vocalize for several s after landing, then begin crawling over and through the masses of pups, continuing to vocalize as they crawl. During a typical search, the female frequently stops crawling and vocalizes intensively for brief periods before resuming her movement. This calling is accompanied by ear-twitching, suggesting that females receive auditory signals as well as broadcast them.

Pups within creches call sporadically when no adults are nearby, and rates of calling appear to increase when adults are on the creche. While a female is on the creche, nearby pups orient toward her and attempt to attach to her teats in evident attempts to get milk. Females are vigilant to suckling attempts by pups and block pups with their folded wings. However, pups frequently are successful in attaching to teats for brief periods. Females repel pups by beating them with their wings, scratching them with their hind feet, and biting. If a search is “successful” the female evinces interest in a pup, touching the top of its head with her muzzle, evidently smelling and exchanging vocalizations with it. These exchanges can persist for a minute or more, before the female raises her folded wing and nudges the pup toward one of her teats.

Search Statistics; NVD and NVD Video

We monitored 170 adults landing on or adjacent to creches. 57 (34 %) of these landings were accompanied by no evidence of searching behavior and the adult flew from view within 5 s. In all other cases ($n = 113$) the adult remained in view for > 5 s and either vocalized, but did not move among pups ($n = 13$), or

Fig. 3: Movements of two lactating females from the location on the creche where they landed to the location of the pups they accepted and nursed. Cross-hatches mark locations where females stopped to call and/or smell. The duration of search A from landing to acceptance of the pup was 7 min 24 s on 5 July 1984, of B 1 min 50 s on 13 July 1984



both vocalized and moved among pups ($n = 100$). 35 of these 113 apparent searches were not observed to their conclusion, in most cases because we lost the adult among other bats. Of the 78 searches that were followed to conclusion, 61 (78 %) ended with the adult flying from the creche without accepting any pup, and 17 (22 %) ended with her settling into the creche and accepting and nursing a pup. An additional 97 adults that already were involved in searching on creches when we first observed them also were followed until they either flew from the creche without selecting a pup ($n = 66$), or selected and nursed a pup ($n = 31$).

For successful searches observed in their entirety, the time elapsed from landing to accepting a pup ranged from 12 s to 9 min 51 s ($\bar{x} = 3$ min 57 s). The time elapsed from when a female and pup made physical contact until the pup appeared to attach to the female's teat ranged from 8 s to 2 min 19 s ($\bar{x} = 32$ s). Unsuccessful searches observed in their entirety ranged from 5 s to 1 min 28 s ($\bar{x} = 21$ s) when the female called but did not crawl through the creche, and from 10 s to 5 min 23 s ($\bar{x} = 1$ min 29 s) when the female both called and moved through the creche. The longest apparent search observed was 25 min 16 s, lasting from when we began watching a female already actively engaged in searching until she flew from view without accepting a pup.

All adult movements were mapped for 11 successful searches (Fig. 3). The total distance moved by females ranged from 0 cm to 260 cm ($\bar{x} = 78.1$ cm). The net distance from where a female landed to the location where she accepted and nursed a pup ranged from 0 cm to 190 cm ($\bar{x} = 45.4$ cm).

The durations of milk meals observed from when a pup was accepted until the female and pup separated ranged from 9 min 18 s to 27 min 34 s ($\bar{x} = 20$ min 27 s, $n = 8$). All pups observed suckled from both of the female's teats, alternating between teats as many as 5 times during a single meal. Teat switches were accomplished quickly with the evident assistance of the female. Pups remained attached to the cave surface during nursing, and female-pup pairs

moved short distances through the creche during milk meals. Most movement occurred shortly before the female and pup separated, when it often appeared as if the female was dragging the attached pup. In the longest of these observed movements, a female and attached pup traveled a straight-line distance of 28 cm before separating.

Milk Stealing

Most observed attempts to steal milk occurred when pups bit at the teats of females passing close to them. Pups also attempted to take milk from the unoccupied teats of females nursing other pups, and pups evidently attempted to sneak under other pups which were being accepted by females, so as to gain access to those females' teats. Females responded quickly to pup suckling attempts and most pups were repelled almost instantly. Because of the brevity of these interactions, and because our views of teats often were intermittent and obstructed, assessing the success of pup suckling attempts is difficult. However, we observed 35 incidents where pups clearly were successful in attaching to the teats of females, without the sequence of behavior typical in female-pup reunions. 28 incidents involved a pup quickly attaching to the teat of a passing female. On 24 of these occasions the pup was repelled immediately; in the 4 remaining incidents the pup was attached for periods of 8–15 s, with the female beating and scratching the pup until it was repelled. On 5 other occasions we observed a pup attach to the unoccupied teat of a female already nursing another pup. In all cases the second pup was immediately repelled. On two occasions a female-pup pair began apparently typical recognition interactions, but the female repelled the pup and moved away from it when it attached to her. 5 females that repelled pups were observed until they accepted and nursed a different pup, and we observed three different pups attach to one female within a period of 2 min, before she accepted and nursed a fourth pup. We also twice observed adult *T.b. mexicana* attaching to the teats of other adults. In both instances the pair fought and quickly flew from view.

Although our observations do not demonstrate that lactating females actually lose milk during these encounters, indirect evidence indicates that they probably do. Lactating females return to creches with large milk loads (DAVIS et al. 1962; KUNZ, pers. comm.), milk can be expressed easily with the slightest manual pressure, and when the teat of a hand-held female is offered to a pup, the pup attaches and obtains milk immediately (also see DAVIS et al. 1962). The success of milk theft by adults also apparently was documented by DAVIS et al.'s (1962) observations of milk in the stomachs of autopsied adult females.

Female-Pup Reunions: IR Video

Retrieval and nursing of a pup by the same female that nursed it on one or more previous nights were documented in six of the 18 experiments where tagged pups were returned to the creche. These 6 reunions involved four different female-pup pairs. The reunions of one tagged pair were documented on three nights over a 5-night period; the reunions of the three other pairs were documented on one night each. Reunions occurred at all times of night; the

earliest at 0.30 h and the latest at 5.25 h. In 8 other experiments we documented the return of putative mothers to within 1 m of their tagged pups; however, these pairs did not reunite during our observations.

Failure to monitor tagged pups continuously for the return of tagged females was due most frequently to 1) movement of pups beyond our field of view, 2) loss of sight of tags as bats crawled over and under one another, and 3) fouling of the camera lens. Furthermore, as the density of returning adults on creches increased, our ability to discern pup and adult tags decreased, and after ca. 5.30 h, the observation of tags was difficult. Consequently, while observed reunions demonstrated repeated nursing affiliation between the same female and pup, failure to observe female returns or female-pup reunions does not mean that they did not occur.

The IR video studies showed searching patterns similar to those seen with the NVD. In the 14 experiments where a female returned to her presumed pup's vicinity, multiple returns often were observed throughout the night (range 1–11 returns/female, for 52 observed visits). In 38 visits the female landed on or adjacent to the creche within 1 m of the appropriate pup. In the remaining 14 visits the female crawled into the field of view. In 7 of the 38 landings observed the female flew from the creche within 5 s. In another 8 landings the female remained on the creche for > 5 s but did not move within it, and in the remaining 23 landings the female crawled through the creche before either aborting the apparent search and flying or reuniting with the pup. When multiple landings were observed, landing locations often bracketed the location of the tagged pup, suggesting that multiple landings may be used to "triangulate" the pup's position (Fig. 4). Where the female's search could be mapped from her final landing to the reunion ($n = 3$), the average straight-line distance from this landing to the pup's location was 42.7 cm (range 23.1–69.8 cm).

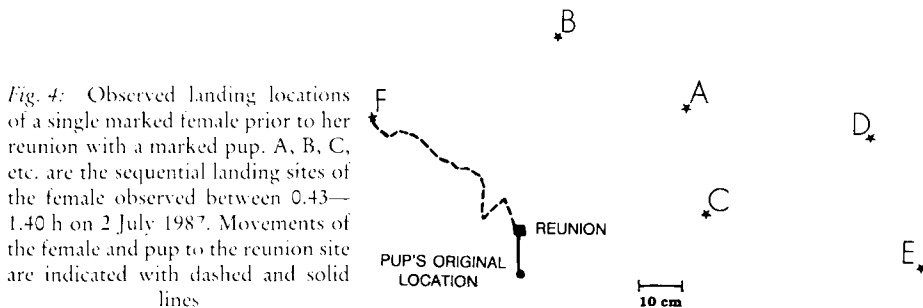


Fig. 4: Observed landing locations of a single marked female prior to her reunion with a marked pup. A, B, C, etc. are the sequential landing sites of the female observed between 0.43–1.40 h on 2 July 1987. Movements of the female and pup to the reunion site are indicated with dashed and solid lines

Because the IR video observations recorded reunions of marked pairs, it was possible to map the movements of pups as well as those of adults (Fig. 5). In all five reunions where pup movements could be mapped, it was evident that not only did the female approach the pup, but the pup also moved toward the female. The mean net distance moved by these five pups as the female approached them was 10.4 cm (range 5.6–17.3 cm).

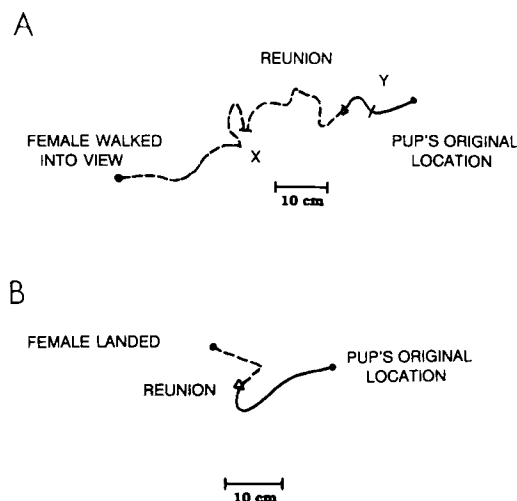


Fig. 5: Joint female-pup movements leading to the reunions of two marked pairs. Movements of adults: dashed lines, pup movements: solid lines. A: between 3.32–3.40 h (search duration 7 min 35 s) on 30 June 1987. B: between 5.21–5.25 h (search duration 3 min 25 s) on 14 July 1987. On A the pup reached location Y as the adult reached location X, suggesting that the pup discriminated its presumed mother at a distance of at least 40 cm

Discussion

The Frequency and Context of Alloparental Nursing

Although we observed frequent attempts by pups to steal milk, our videotapes of focal animals include 4.3 h of suckling following searches and apparent acceptance of a pup, but only a total 1.3 min of suckling following apparent milk thefts. The latter is less than 0.5 % of the total suckling observed. While we have almost certainly underestimated the number of attempts at milk theft that were successful, these statistics suggest that milk theft alone cannot account for the relatively high frequency of alloparental nursing (ca. 17 %) indicated by genetic tests (McCracken 1984). A possible explanation for this discrepancy is that milk theft is only one source of alloparental nursing, and females also may accept and nurse pups other than their own.

Where information is available, all relevant features of *T. b. mexicana*'s biology argue against selection for alloparental nursing through kin selection (RIEDMAN 1982; GITTLEMAN 1985) or reciprocity (TRIVERS 1971; AXELROD & HAMILTON 1981; WILKINSON 1988). Stable associations among related individuals are a common if not universal feature accompanying the evolution of kin-biased interactions (WEST-EBERHARD 1975; GREENWOOD 1983; HOLMES & SHERMAN 1983). In *T. b. mexicana*, the density and independent movements of pups and adults (OKONIEWSKI 1986) demonstrate that persistent associations among individuals do not occur within roosts. The lack of stable roosting associations also suggests that a female cannot monitor the nursing affiliations of other females and pups known to her, and this eliminates the possibility of selection for shared nursing via reciprocity (TRIVERS 1971; WILKINSON 1988). Information on the genetic structure of pups and adults within colonies further corroborates the conclusion that, except for nursing mother-pup pairs, roosting associations of kin are absent in these roosts (McCracken 1984). Banding studies (DAVIS et al. 1962;

VILLAR & COCKRUM 1962; CONSTANTINE 1967; COCKRUM 1969) documented the movements of individuals among different maternity roosts, and also appear to obviate the possibility that interdemic selection (WADE 1978) acts to favor alloparental nursing in these bats.

Helping to raise unrelated young could still be advantageous to females if females received benefits such as improved social status, better integration into social units, or from learning (e.g. HRDY 1976; BROWN 1978; ROOD 1978). However, the lack of stable groups in *T. b. mexicana* also appears to eliminate the first two of these possible benefits. High mortality among the pups of certain mothers (e.g., young mothers), could provide a class of females that would benefit from helping if the experience gained made them better mothers in the future. However, HERREID (1967) estimated preweaning pup mortality in Davis Cave at only 1.3 %. The estimated high survival of pups through weaning indicates that success at raising pups is not likely to increase because of learning.

In some cases, adoption following the loss of a female's own offspring may occur because continued nursing is important for maintaining a female's post-weaning estrus and mating cycle (LEBOEUF et al. 1972; RIEDMAN & LEBOEUF 1982). This is improbable in *T. b. mexicana* because whether or not they nurse a pup through weaning, females will not mate again until the following spring (DAVIS et al. 1962). Furthermore, the estimated high survival rate of pups suggests that even if females that lose their pup adopt another, this could explain only a fraction of the alloparental nursing suggested by our genetic results.

If adoption is common, most adoptions would require that a female either abandon her own living pup or that she raise two pups. Abandonment of her own for the benefit of an unrelated pup is implausible. We do not know whether a female can provide sufficient milk for nursing two pups, but females pregnant with twins are extremely rare (DAVIS et al. 1962). It is not known how frequently the birth of live twins occurs, or if the female can raise both pups. Work in progress on pup growth and the energetic demands of lactation (KUNZ, pers. comm.) should address these issues.

At present, we suspect that the costs would be extremely high if a female with a living pup were to adopt another. PIEROTTI & MURPHY (1987) have proposed a model that could favor adoption of unrelated individuals as a result of selection acting both on individuals and through "soft altruism" (WILSON 1980). However, the model of PIEROTTI & MURPHY (1987) requires that costs to the adopting parent(s) are low, a condition that almost certainly does not hold for *T. b. mexicana*.

We know that female *T. b. mexicana* often abandon searches without accepting and nursing a pup. Female elephants that have difficulty locating their calf may nurse another calf to reduce their milk load (LEE 1987). We have seen no evidence of "milk dumping" in *T. b. mexicana*. Observed nursing was always preceded by either the sequence of mutual interactions suggesting recognition, or by aggressive or covert attempts by pups to attach to the female. In no case did we see a female allow a pup to nurse without apparent mutual vocal and olfactory exchange. However, milk dumping remains a possibility.

Alloparental care often has been attributed to parental "mistakes", such mistakes being more common in colonies with dense populations (RIEDMAN 1982; KOVACS 1987). The extreme challenge for recognition that *T. b. mexicana* face suggests that mistakes are likely. Two instances that we counted as milk thefts began with typical female-pup recognition behavior, but the pup was repelled after it attached to the female's teat. Females also often stop during searches and appear to "check" a particular pup before passing by it. The potential for parent error clearly exists. We did not, however, observe any case where a female accepted a pup and nursed it, only later to repel it.

As a final possibility, FODGEN (1971) attributed earlier reports of "adoptive" nursing in gray seals (SMITH 1968) to disturbance caused by human observers. The discrepancy between the observed frequency of milk theft and our genetically-based estimates of alloparental nursing could be due, in part, to disturbance caused in obtaining the genetic estimates. While on the creche, adult females are vigilant to the suckling attempts of pups; any lapse in this vigilance is likely to present nearby pups with an opportunity to attach to the female. Visible light, which was used during our sampling of nursing pairs, is disturbing to both adults and pups, but perhaps more so to adults. Although we spent minimal time in the roost and sampled only females and pups that were firmly attached when first sighted (MCCRACKEN 1984), it is possible that our presence reduced the vigilance of adults and increased the likelihood of successful milk theft by pups (as pickpockets take advantage of disturbance in a crowd). It is difficult to imagine how this possibility can be eliminated. NVD goggles and IR light could be used while pairs are collected. But we know from our observations in creches that even without visible light roosting adults are disturbed by the nearby presence of large moving bodies, which they presumably detect using echolocation.

The roosting habits of *T. b. mexicana* result in costs to females, minimally, from the milk lost to pups other than their own, and from the activities required to relocate pups and selectively nurse them. Two questions that arise are; 1) why are maternity colonies so large, and 2) why do these bats roost in such high density?

T. b. mexicana are known to roost in much smaller colonies in buildings, mine shafts, train tunnels, and beneath bridges (DAVIS et al. 1962; pers. obs.), but such roosts rarely include nursing females and pups. The fact that maternity colonies are almost always restricted to caves that can accommodate millions of bats, suggests they gain benefits in these roosts that compensate for the resultant costs (other likely costs of large aggregations include increased susceptibility to ectoparasites (MARSHALL 1982) and infectious disease (CLARK 1981), and long commuting distances for resources (DAVIS et al. 1962).

Aggregation in large populations provides thermal benefit. Temperatures within maternity roosts are at 35–40 °C, as an apparent consequence of accumulated metabolic heat. MCCrackEN (1989) argued that there may be a "threshold" population size which is sufficiently large to raise in-roost temperatures. However, this does not necessarily account for dense clustering. In some caves (e.g. James River) all roost surface appears to be occupied by bats; however, in other caves (e.g. Davis) much roost surface is unoccupied and less dense aggregation

seems possible, but does not occur. In this regard, HERREID (1963a, b) has demonstrated that dense clustering by both adult and juvenile free-tailed bats elevates and stabilizes body temperatures and reduces the metabolic costs of thermoregulation.

Evidently, females aggregate in large numbers and place pups in dense creches to gain these and other possible mutual benefits. In so doing, they must tolerate the other costs of such behavior. These costs appear to be unavoidable consequences of their roosting behavior.

The Role of Pups in Female-Pup Reunions

Many studies on bats have concentrated on female recognition of pups (BROWN 1976; SCHMIDT et al. 1982; BROWN et al. 1983; ROTHER & SCHMIDT 1985; THOMSON et al. 1985), but for a few species evidence exists that pups also discriminate among females (TURNER et al. 1972; KOLB 1977). Although it is not yet established that *T. b. mexicana* pups discriminate among the calls (BALCOMBE & MCCrackEN 1991) or odors (LOUGHRY & MCCrackEN 1991) of females, the infrared-video recordings of reunions between tagged females and pups suggest that mutual recognition occurs, and that pups actively participate in reunions by moving toward their presumed mother. These pup movements were seen in all reunions monitored, and in one reunion, the pup's movement was greater than that of the adult (Fig. 5B). The observation that a pup began movement toward the appropriate female when the female and pup were as far as 40 cm from one another implies mutual acoustic recognition.

Acknowledgements

We thank M. LANDON, P. GIBSON, D. MIRANDA, J. BALCOMBE, S. MISTRY, and T. BURNETT for help in the field, and G. DAVIS and R. C. SCHULZE for access to caves on their properties. This work was supported by NSF grants BSR-8207042 and BSR-8700425.

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Received: September 17, 1990

Accepted: June 20, 1991 (G. Barlow)