Communal Nursing in Mexican Free-Tailed Bat Maternity Colonies

Abstract. *Examination of genotypes of female-pup nursing pairs taken from large maternity colonies of the Mexican free-tailed bat in Texas demonstrates that nursing is nonrandom and selective along genetic (kinship) lines. This is contrary to previous reports that nursing in these colonies is indiscriminate. Although nursing is nonrandom, an estimated 17 percent of the females sampled were nursing pups that could not be their offspring. This "nonparental" nursing is an apparent result of the difficulties females face in consistently relocating and selectively nursing their own pups within these enormous colonies.*

Behavior involving costs to an individual performing some action (the actor) and benefits to others (recipients) can be favored by natural selection if recipients are relatives of the actor (kin selection) (*1*) or if recipients provide sufficient aid in the future to the actor or its descendants (reciprocity) (*2*). However, both kin selection and reciprocity require that select recipients realize the benefits of the behavior (*1, 2*). If the behavior is directed indiscriminately, theory requires that it be favored by some form of group selection (*3, 4*). Otherwise, because of its costs, it is maladaptive and evolutionarily unstable (*5*). Examples of kin selection are numerous (*6, 7*), and examples of reciprocity are accumulating (*8*). However, group selection can apparently function only under restricted conditions (*3, 9*), and convincing examples of group selection for such traits are lacking. For this reason, reports of costly behavior with indiscriminately directed benefits are of great interest.

The report of indiscriminate nursing within maternity colonies of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) (*10*) is a widely known example of such behavior. Each spring, pregnant females migrate to caves in the American Southwest and form colonies that often exceed several million individuals (*10, 11*). Most females give birth to a single pup, and within hours of giving birth each female deposits her pup with others on the cave walls or ceilings. Soon, masses of densely packed pups (creches) cover much of the roosting surface. Lactating females enter the creche and nurse pups twice each day, and nursing is reputed to be indiscriminant.

According to Davis *et al.*, "mothers apparently act as one large dairy herd delivering milk passively to the first aggressive customers" (*10*). However, because of the large numbers of bats present, direct observation of marked individuals is extremely difficult, and this conclusion is based largely on circumstantial evidence. Nonetheless, indiscriminate nursing in *T. b. mexicana* is cited frequently in scientific and popular literature (*6, 12–14*).

I now present results of a study on nursing selectivity in Mexican free-tailed bat maternity colonies. My objectives are to (i) use allozyme genetic markers to determine nursing relationships relative to the genotypes of females and the pups they nurse and (ii) consider ways in which natural selection can account for the nursing relationships observed. Samples were collected from the same caves in south-central Texas where the original study describing indiscriminant nursing was conducted (*15*).

Pairs of bats consisting of a lactating female and a firmly attached nursing pup were picked by hand from the roost surface in order to ascertain whether nursing is random relative to female and pup genotypes. Only females and pups that were attached when first sighted and remained together when collected were used. Although pairs were taken from where they could be reached, collections were preferentially at central rather than peripheral regions of creches. A total of 172 nursing pairs was sampled, all from Davis cave (*15*).

Samples taken from adult females included 0.1 cm^3 of whole blood and a small (< 0.1 g) chest muscle biopsy; mortality during sampling was less than 5 percent. Pups were anesthetized with ether and bled from the heart. The preparations of these samples has been described elsewhere (*16*). Horizontal starch-gel electrophoresis and protein staining (*17*) were used to identify several polymorphic allozyme loci, two of which were used in these analyses: malic enzyme (ME) with five alleles and an average frequency of 61 percent for the common allele, and superoxide dismutase (SOD) with six alleles and an average frequency of 70 percent for the common allele.

Table 1. Nonrandom nursing in 167 pairs of *Tadarida brasiliensis mexicana*.*

Result	Nonparental genotype pairs		
	Me	SOD	Loc
Expected (random)	24.3	21.3	42.5†
Observed	5	2	7

*$P << 0.001$ (*G*-test). †Factors out nonparental combinations that would be detected at both loci.

Since paternal genetic contributions to progeny are unknown (*18*), all tests must rely on comparing genotypes of females and pups. One method of analysis involves examining nursing pairs for impossible (nonparental) genotype combinations. For example, in the diallelic situation, an AA homozygote female cannot be the mother of a BB homozygote pup, and vice versa. From the frequency of each genotype of the females and pups in the sample, the number of nonparental combinations expected if nursing is random can be calculated. The observation of significantly less than this expected value will imply selective nursing by females of either their own pup or other pups with similar genotypes. Table 1 gives the results for 167 female-pup pairs at which both the ME and SOD loci were scored. If nursing is random, approximately 43 nonparental genotype combinations are expected; however, only seven occur. Although some females were nursing pups which could not be their own, nursing is, in fact, significantly nonrandom ($P << 0.001$; Table 1) (*19*).

These data also allow calculation of a minimum estimate of how frequently females nurse pups that are not their own. Considering the large number of females and pups in a colony, the chance that a female would nurse her pup if nursing were random would be approximately zero, and all 167 females in the sample would almost certainly be nursing pups other than their own. Using the ME and SOD loci, I expected to detect about 0.25 (the ratio of the nonparental genotype combinations and the number of pairs) of these. Given that seven nonparental combinations were actually detected, I estimated that a minimum of 28 of the 167 pairs, or about 17 percent, actually involved mothers nursing pups that were not theirs. This is a minimum estimate because it is based on the assumptions that (i) when a female is not nursing her own pup she nurses at random relative to pup genotypes, and (ii) genotypes are distributed randomly within the colony. If genetic structuring occurs within the colony, or if a female preferentially nurses her own pup and others with similar genotypes, this is an underestimate of nonparental nursing.

It has not been possible to assess directly whether females that are not nursing their own pups nurse at random or whether they preferentially nurse particular pups. The latter would suggest that kin selection or reciprocity are involved. However, studies on movements of marked pups within creches demonstrate that, over 24-hour periods, pup dispersion has a mean net displacement of 37.6 ± 23.6 cm with a range of 2 to 117 cm ($N = 36$) (*20*) and that individuals marked while roosting adjacently move independently of one another. Because of the high densities of pups within creches ($\overline{Y} = 40$ pups per 100 square centimeters when the data were collected), these results indicate that stable roosting associations of less than several hundred juveniles do not occur. Such assemblages are much too large to function as effective kin or reciprocation groups. Examination of the spatial distributions of alleles at the ME and SOD loci, both for pups within creches and for day-roosting adult females, also indicates that individuals are distributed at random within cave colonies relative to these genetic markers (*21*). Although these genetic tests may not have the sensitivity to detect a mosaic of small kin groups within roosts (*22*), these results agree with the observation that stable roosting associations of either related or unrelated individuals do not exist within colonies. Genetic tests also show homogeneity in allele frequencies among colonies (*21*), indicating that the among-colony genetic variance required if group selection (*3*) were to favor communal nursing does not occur. This is the expected result since reports on female movements (*10*) suggest that gene flow among colonies is substantial.

Considering the information now available, the most likely explanation for the observed pattern of nursing is that creching makes it impossible for a female always to relocate and selectively nurse her own pup. On the basis of the high density of pups and their aggressiveness toward lactating females returning to the creche (*10, 23*), it can be argued that females actually do well to find and nurse their own young as frequently as 83 percent of the time. Nonetheless, the high energetic expense of lactation (*24*) ensures that nonparental nursing involves a cost to females, and this cost should be accounted for in some fashion. It has been demonstrated that dense clustering of both adult and juvenile Mexican free-tailed bats elevates and helps stabilize body temperatures and reduces the metabolic cost of thermoregulation (*25*). Females may deposit their pups in large creches and tolerate the cost of occasionally nursing pups other than their own because of these or other possible mutual benefits. With this explanation, selection actually acts against communal nursing, but the balance of selective forces acting on an individual make this system superior to roosting singly or in smaller groups where nonparental nursing need not occur.

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15. Davis cave houses an estimated 4 million free-tailed bats; James River cave, 6 million; Bracken cave, 20 million; and NEY cave, 10 million (*10*).
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18. Mating occurs prior to female arrival at maternity roosts, and the mating system of these bats is undescribed.
19. Another analysis which corroborates these results is as follows. Mothers homozygous for a given allele must give it to their pups. Pups of mothers heterozygous for a given allele have a 50 percent chance of receiving it from the mother plus a chance of receiving it from the father. Assuming that paternal alleles are contributed at the frequency at which they occur in the adult population, the number of nursing female-pup pairs expected to share a given allele if females nurse only their own pup or if they nurse at random can be calculated. Observed associations of alleles in the female-pup pairs sampled were intermediate between these expectations.
20. Pups were marked in situ using nontoxic fluorescent paints. Mean movements during the first 24 hours after marking were no different ($0.5 < P < 0.9$; *t*-test) than in subsequent 24-hour periods, indicating that greater than normal movements do not result from disturbance caused by marking.
21. Four groups of pups were collected from widely separated areas of the creche in Davis cave and four groups of roosting adult females from widely separated areas in James River cave. Each pup group consisted of 25 individuals roosting within an area of less than 50 cm^2. Adult female groups ranged from 33 to 41 individuals, and each group was taken from an area of less that 1200 cm^2. There was no significant heterogeneity in allele frequency at the ME or SOD loci among either set of groups ($0.5 < P < 0.9$ at both loci for adults, $0.1 < P < 0.5$ at both loci for pups; *G*-test for heterogeneity). Standardized genetic variances (F_{st}) among each set of groups were also small for both loci ($\overline{F}_{st} = 0.011$ for adults; $\overline{F}_{st} = 0.007$ for pups), and in no case were they significantly larger than zero. Collections of 40 to 143 adult females taken at random from four different maternity colonies (*15*) also show no significant genetic heterogeneity among colonies ($0.1 < P < 0.5$ at ME; $0.5 < P < 0.9$ at SOD), and F_{st} values are again small ($\overline{F}_{st} = 0.003$) and not significantly different from zero. Observed genotype frequencies in all collections agree with Hardy-Weinberg expectations, with no consistent patterns of heterozygote deficiency or excess.
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23. Preliminary observations with a night vision scope within roosts have shown that pups swarm returning females, and I have observed up to four different pups attaching sequentially to the teats of a single female.
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