Communal nursing in the evening bat, *Nycticeius humeralis*

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Summary. Nursing observations over two summers involving 76 lactating female evening bats, *Nycticeius humeralis*, and 128 pups in an attic in northern Missouri indicate that communal nursing occurs rarely until 2 weeks before weaning during which time over 18% of nursing bouts involve nondescendant offspring. The average relatedness among female pairs nursing non-descendant offspring, based on identity-by-descent estimates using allozyme data, was 0.04 (SE = 0.12). Mitochondrial DNA d-loop sequence comparisons confirm that at most only 2 of 20 female pairs nursing nondescendant offspring came from the same matriline. Thus, females do not nurse matrilineal kin preferentially despite female natal philopatry. In addition, the average degree of relatedness within a colony ($r = 0.01$, SE = 0.03) is too low to provide any indirect benefits from communal nursing. Female error alone is insufficient to explain these observations because females tended to allow female nondescendant young to nurse but excluded nondescendant males, particularly when they had all-male litters. Furthermore, communal nursing bouts did not differ in duration from parental nursing bouts and involved 31% of all banded females and 24% of all banded pups observed nursing. Communal nursing occurred most frequently when pups began hunting on their own and when lactating females attained their lowest average pre-fed body weight. Mortality during this period was higher for male than female pups, and relative weights implicate starvation as the cause. Time-lapse video records of four families of bats in captivity showed that the number of nursing bouts was proportional to daily weight change. I propose that these results are consistent with both immediate and delayed benefits accruing to females which experience variable hunting success. If a female with extra milk reduced her weight by dumping milk prior to her next foraging trip, she could obtain an immediate energetic benefit and maintain maximum milk production. By restricting such milk donations to nondescendant females she may also increase colony size and thereby enhance her future acquisition of information about foraging and roosting sites.

Introduction

The most energetically demanding phase of a female mammal's reproductive life is lactation (Millar 1977; Gittleman and Thompson 1988). If food is limiting, then energy expended on lactation can affect the survival of current offspring, the production of subsequent offspring (Mattingly and McClure 1985; Loudon et al. 1983; Clutton-Brock et al. 1989), or the survival of the mother (Muhlbock 1959; Clutton-Brock et al. 1989). Thus, from an evolutionary perspective the sharing of milk with nondescendant young appears to represent altruistic behavior. Nevertheless, anecdotal reports of communal nursing have been compiled for 120 species (Riedman 1982) and several recent field studies have confirmed frequent communal nursing in some species. For example, 68% of juvenile prairie dogs nurse from more than one female (Hoogland et al. 1989), 87% of adult female Hawaiian monk seals (Boness 1990) nurse other female's pups, and 24% of nursing observed among 2–4 month old fallow deer involved nondescendant fawns (Birgersson et al. 1991).

Phylogenetic regression analysis of the occurrence of communal nursing in 100 mammals derived from questionnaire responses (Packer et al. 1992) indicates that nursing of nondescendant young is associated positively with milk theft in monotocous species and positively with large litter size but negatively with female group size in polytocous species. If the average level of relatedness among females increases as group size decreases, the comparative analysis results for polytocous species support a kin selection explanation for communal nursing in which nursing females provide milk to closely related offspring, as has been reported for lions (Bertram 1976), house mice (Wilkinson and Baker 1988), and prairie dogs (Hoogland et al. 1989). This hypothesis requires that Hamilton's rule be upheld (Hamilton 1964). In other words, after weighting by the degree of relatedness the benefit to the recipient offspring must exceed the cost to the lactating female. If, on the other hand, communal nursing is due to female error, then milk shar-

ing should be infrequent, should have little effect on female or nondescendant offspring reproductive success or survival, and should occur independent of genetic relatedness. If an appreciable cost or benefit of communal nursing exists yet females selectively suckle nondescendant young, then mutualism or some form of delayed mutualism, i.e. pseudo-reciprocity (Connor 1986) or reciprocity (Axelrod and Hamilton 1981; Trivers 1971), may account for the maintenance of this behavior.

In this report I present field and laboratory observations of nursing behavior and genetic tests of relatedness to determine if communal nursing occurs primarily between related evening bats, *Nycticeius humeralis*, or among a random collection of individuals. These 10-g insectivorous vespertilionid bats have been reported (Gates 1941) to nurse young indiscriminately in captivity (but cf. Jones 1967) and in nursey colonies (Watkins and Shump 1981) after pups reach 2 weeks of age. Similar reports of indiscriminate nursing by Mexican free-tailed bats, *Tadarida brasiliensis*, (Davis et al. 1962) have not been confirmed in subsequent work. Even though Mexican free-tailed bat females leave their young in caves containing millions of pups, females successfully find and nurse their own young 83% of the time and do not nurse relatives' pups (McCracken 1984). Communal nursing among related evening bats is possible because females form colonies containing only 15–300 bats and return to their natal colony in either a hollow tree or attic to give birth synchronously to an average of two young every spring (Bain and Humphrey 1986; Humphrey and Cope 1970; Watkins and Shump 1981). In the northern part of the range females, but not males, migrate from winter cave hibernacula to nursery colonies (Humphrey and Cope 1970; Watkins 1970). Besides estimating relatedness I consider the possibility that communal nursing represents either mutualism or delayed mutualism by examining how nursing frequency, adult weight, and juvenile weight might interact to influence juvenile survival before weaning.

Methods

Study sites. The evening bat occurs from southern Iowa east to Maryland, south to Florida and west to northern Mexico. To ensure that geographic variation in behavior could not cause our results to differ from previous work, during the summers of 1987–1990 my assistants and I studied evening bats at seven nursery colonies in northern Missouri and southern Iowa near where communal nursing had been reported (Watkins and Shump 1981). In 1987 we attempted to find the 26 colonies located in this area in the late 1960s (Watkins 1970). Only two sites, the Smith house 10 km south of Princeton, Missouri, containing about 30 adult females, and the Grim house 4 km south of Pulaski, Iowa, with about 65 adult females, still contained bats. In 1987 we also discovered a colony of about 80 adult females in the Zion Baptist Church 5 km east of Cainsville, Missouri. In 1988 we located a colony with about 50 adult females in the Hutton house, 3 km west of Cainsville, and a colony of about 40 adult females in the Thompson house 4 km west of Laredo, Missouri. In 1989 we found two more nursery colonies in northern Missouri: the Busby house 1 km north of Galt containing over 150 adult females and the Easton house 4 km south of New Hampton with over 120 adult females. The Easton house is 200 m from an abandoned house

that contained a nursery colony of evening bats in 1970 (Watkins 1970). Since no bats currently occupy the abandoned house, the Easton colony may represent its descendants. In all cases evening bat nursery colonies occur in the attics of human-inhabited structures that are at least 50 years old.

Capturing, marking, and aging procedures. We captured adult females with hoop or mist nets as they departed at dusk. For 2 weeks following the appearance of the first pup of the year we entered the Zion attic every other day after dusk to capture and band all infants soon after birth. We usually captured infants by hand while adult females were foraging. We banded each bat on one wing with a unique combination of plastic split-ring bands (canary size, Gey Band and Tag Co., Pittsburgh, PA) which were covered with colored reflecting scotchlite tape and on the opposite wing with a numbered plastic band. For each bat we recorded forearm length, weight to the nearest 0.01 g, relative tooth wear on a scale from 0 (no wear) to 5 (flattened molars and canines), and reproductive condition: pregnant, lactating, or post-lactating. We scored females as lactating if their nipples were bare and distended and milk was visible through their skin from the breast or back. Post-lactating females had bare nipples but no visible milk. Between May 1987 and July 1990 we banded a total of 1353 bats of which we recaptured 1124 at least once.

Because infants are pink only for 1 day (Jones 1967), we were able to assign date of birth directly to some pups. Forearm measurements of 19 female and 26 male pups when recaptured were used to estimate pup age between 2 and 25 days of age using the following two linear regression equations: female age = 1.046 (forearm) − 13.059 (r^2 = 0.87) and male age = 0.954 (forearm) − 11.042 (r^2 = 0.92). The relationship between forearm length and age becomes nonlinear after 25 days of age (Jones 1967). Evening bat pups begin to fly at 21 days of age and attain adult forearm lengths by about 45 days of age (Jones 1967).

Nursing observations. From an observation platform in the Zion attic we conducted 121 h of ad lib observations of nursing in June and July, 1988 and 1989, with the aid of 8 × binoculars and diffuse white light. We attempted to conduct observations at least once every day between 0800 and 2000 hours. On average, observation sessions lasted 1.40 ± 0.91 h (standard deviation here and in all future indications of error). The bats usually clustered at the eastern apex of the attic where we could monitor 20 or more banded adult females through plexiglass windows, but when the attic exceeded 35° C, the bats descended into the walls of the church out of sight. During each observation session we recorded the onset and termination times for all attempted or successful nursing bouts as well as the band combinations of the participating female and pup. However, because bats frequently obscured each other from view, we did not often witness the exact beginning or end of a nursing bout, and focal animal sampling proved impossible. Therefore, we treat nursing bouts as sample units in some analyses, rather than estimate nursing rates, because we could not accurately adjust an individual's nursing time for its time under observation. I assigned maternity to the female that we observed most often suckling each banded pup and scored communal nursing if at least one of the following three criteria was met: (1) a pup suckled from more than one female; (2) two pups suckled from the same female and differed in estimated age by more than 5 days; and (3) pup genotype at one or more enzyme loci (see below) was incompatible with the putative maternal genotype.

Although we never observed a pup nursing from a female more than once during an observation period, we often observed females nursing pups on more than one day. Thus, nursing bouts between the same mother-offspring pair may not represent independent observations. To address this problem I report statistical tests using the number of pups, along with the number of nursing bouts, as the sampling unit. For example, the sex and age distributions of pups nursing from their mothers provide the null hypotheses for the distributions of those attributes among communal nursing pups.

To determine if milk transfer occurs during a nursing bout, in 1990 we kept 30 evening bats captured in Edenton, North Carolina, captive through 4 weeks of lactation. Before parturition all females were trained to feed themselves from dishes containing *Tenebrio* larvae. Then we placed four females and their eight pups in a dimly lit cage with an unlimited supply of mealworms. Nursing behavior was recorded at 30-min intervals over 24 h from time-lapse video tapes on four days: June 8, 11, 15 and 18. On June 8 the four pairs of pups were 3, 5, 5 and 12 days of age. Each pup was weighed to the nearest 0.01 g before and after each video session. We counted the occurrence of any nursing observed within the 5-min period centered on each 30-min interval as one nursing bout.

Estimating relatedness and matriline identity. Blood samples were taken from all adult females at the Zion colony and from at least 19 adult females at each of the other six colonies to estimate average within-colony relatedness using allozyme variation (Queller and Goodnight 1989). We collected approximately 30 µl of blood from each bat by puncturing the propatagial vein with a lancet. After separating the cell fraction from plasma by centrifuging at 5000 g for 5 min, we added an equal volume of distilled water and stored the hemolysate in liquid nitrogen until we performed electrophoresis in the lab. To estimate relatedness between an adult female and the pup that was observed nursing from her, we sampled blood from all Zion pups that were captured after their first flight. To verify the relatedness between a female and her own pup, we used blood from mothers and pups that either had been born in captivity or had been captured in a roost while nursing during the 1st week after birth. Thus, we also genotyped the mother and at least one of her pups from 65 families with 105 pups.

After screening 20 blood enzymes on three buffer systems using horizontal starch gel electrophoresis (McCracken and Wilkinson 1988), we identified six polymorphic allozymes: indophenol oxidase (IPO, EC 1.1.1.1), adenosine deaminase (ADA, EC 3.5.4.4), mannose phosphate isomerase (MPI, EC 5.3.1.8), 6-phosphoglucose dehydrogenase (PGD, EC 1.1.1.1), leucyl-alanine peptidase (PEP, 5.3.1.8) and an esterase (EST, EC 3.1.1.1) using AS-D-napthyl acetate as substrate following standard methods (Harris and Hopkinson 1976). The activity of PEP was sufficiently low in many samples to prevent reliable scoring and was, therefore, excluded from all analyses. Furthermore, the banding pattern of EST was inconsistent with Mendelian expectations for a single locus, multiallelic system and was, therefore, also omitted. The genotypic frequencies of the remaining four allozymes were consistent with Hardy-Weinberg expectations at each colony and exhibited no detectable linkage between any pair of loci. The buffer systems used to resolve each system were continuous tris-citrate II (pH = 8.0) for MPI and PGD and tris-maleate (pH = 7.0) for ADA and IPO.

Besides the blood sample, we obtained tissue samples from all Zion adult females and at least 14 adult females from each of the other colonies to use for mtDNA sequence analyses (Wilkinson and Chapman 1991). To obtain a tissue sample, the bat's chest fur was clipped, a 3 mm excision was made, and 1–3 mg of pectoral muscle was excised with biopsy scissors while applying ethylene chloride topically as a local anesthetic. Biopsies healed within a week and were undetectable on bats recaptured in subsequent years. Tissue samples were stored in liquid nitrogen until returned to the lab where they were kept at −80° C until DNA was extracted, concentrated, amplified and sequenced (Wilkinson and Chapman 1991).

Although the identity-by-descent method (Queller and Goodnight 1989) can estimate the average degree of relatedness among pairs, when group size is small standard errors on those estimates are typically too large to distinguish between low levels of relatedness (Wilkinson 1985). Therefore, to determine if females selectively nurse matrilineal kin we assigned females to matrilines by using nucleotide sequence variation from d-loop mtDNA. Amplification of d-loop mtDNA revealed both length and sequence variation between individuals. Length variation is caused by an 81 bp sequence that is tandemly repeated five to eight times in this region

(Wilkinson and Chapman 1991). Two randomly chosen individuals with six repeat d-loop regions differ, on average, by 10 base pairs because repeats differ from each other due to past base pair substitutions. Duplication and deletion of repeats occur, on average, once every 100 meiotic events between positions 2 and 5 in the array (Wilkinson and Chapman 1991). Thus, direct comparison of sequence similarity can be misleading because a mother can occasionally have a different nucleotide sequence than her offspring in this region. To overcome this potential problem, we determined the sequence of 27 unique 81-bp repeats in the Zion colony. Then, each female's repeat haplotype was scored, i.e. a five- or six-number code in which each number refers to a unique repeat in the order each repeat occurs in the sequence. We assigned pairs of bats to the same matriline if at least five of the six repeat haplotypes were identical. This procedure correctly classified all 12 captive-born pups for which we had sequence data on both mother and pup into their six separate matrilines.

Statistics. All statistical tests are two-tailed unless stated otherwise. Parametric procedures are used whenever the assumptions of normality and homoscedasticity were met. Computations were performed using SYSTAT version 5.1 (Wilkinson 1989).

Results

Nursing observations in the field

We observed a total of 437 nursing bouts involving 128 pups and 76 adult females at the Zion colony. Of these 437 bouts, 30 occurred between a female that could not have been the mother of the pup that was suckling from her because in 20 cases pups were observed nursing from more than one female, in seven other cases pups whose mother's identity was unknown differed in age from the nursing females' pups by at least 5 days, and in the remaining three cases the pup shared no allele with the putative mother at one or more allozyme loci. My criteria underestimate the incidence of communal nursing because the average relatedness within families was lower at the Zion colony than among families that were born in captivity (see below), indicating that maternity was assigned incorrectly in at least six cases. Given that 62 of the 407 putative parental nursing bouts involved a single nursing bout observation, some of these 62 cases represent additional communal nursing events. Given this caveat, below I examine attributes of known communal nursing females and pups to determine if communal nursing is due to female error.

Communal nursing was not independent of pup age. During most of the first week after birth, pups remained on their mother's nipples whenever their mothers were in the roost. When females returned from foraging, they retrieved pups giving isolation calls. By the end of week 1, pups began crawling away from females and returning for bouts of nursing. We first observed pups suckling from females other than their mothers at 8 days of age (Fig. 1). As pups aged, the relative frequency of communal nursing increased resulting in a significant difference between the ages of descendant and nondescendant nursing pups (17.5 ± 10.6 versus 25.9 ± 8.6 days, respectively; $t = 4.23$, $P < 0.0001$). The frequency of communal nursing peaked at 34 days of age at which time it accounted for over 20% of all nursing bouts.
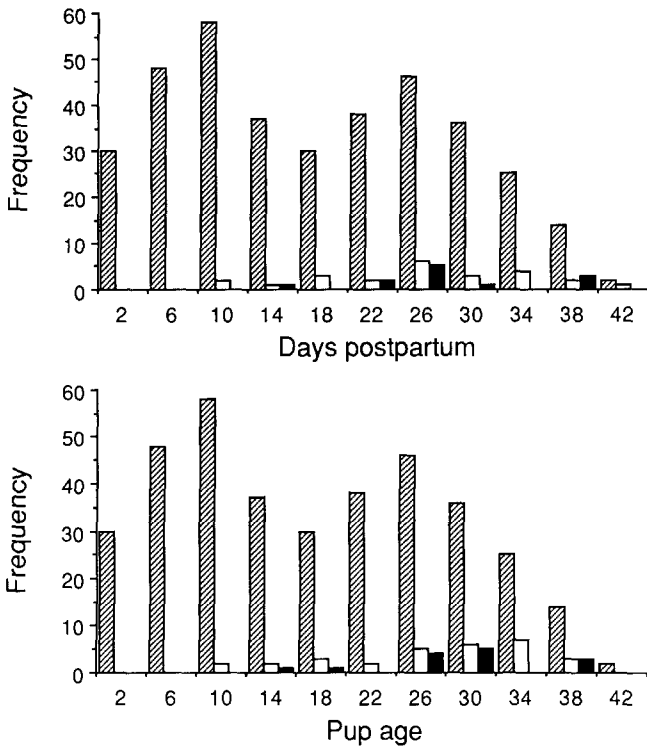
Fig. 1. Number of nursing bouts involving descendant pups (*hatched bars*), nondescendant pups (*open bars*), or rejected nursing attempts (*solid bars*) plotted against the number of days since parturition for the female being suckled (*top*) and against the age of the pup attempting to suckle (*bottom*). See text for criteria used in deciding if pups were nondescendants and for description of a rejected nursing attempt
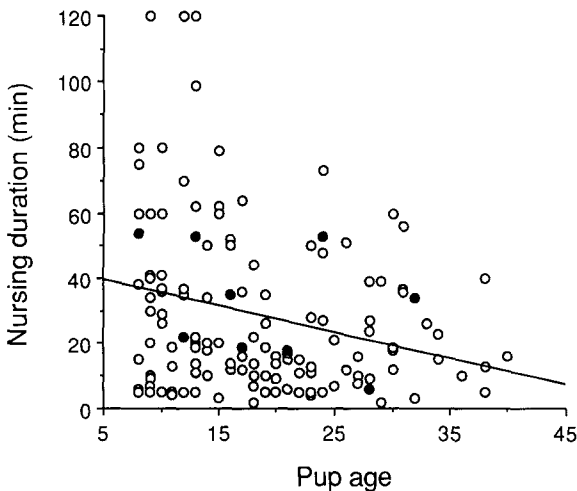
Fig. 2. Duration of nursing bouts between putative mother and her offspring (*open circles*) and between females and nondescendant pups (*closed circles*) as a function of pup age. The regression equation is nursing time $(\min) = 47.7 - 1.0\,x$ (days) $(r^2 = 0.08;\ P = 0.024)$. Only pups 8 days or older are included, to correspond to the period during which communal nursing was observed

Communal nursing bouts did not differ in length from parental nursing bouts even though all nursing bouts decreased in duration with pup age (Fig. 2). AN-COVA indicates that the duration of a nursing bout decreased gradually between 8 and 40 days of age ($F =$

4.58, $df = 1$, 145, $P = 0.034$) but did not exhibit a significant interaction with offspring relationship, i.e. nondescendant or descendant ($F = 1.36$, $df = 1$, 145, $P = 0.25$). The regression of nursing duration on pup age indicates that at 8 days of age nursing bouts lasted an average of 40 min and decreased by 1 min per day thereafter. Communal nursing also did not tend to precede or follow parental nursing during the day. The frequency of nondescendant nursing bouts observed during 2-h periods throughout the day did not differ in distribution from the frequency of descendant nursing bouts (Kolmogorov-Smirnov $\chi^2 = 5.60$, $P = 0.237$).

Communal nursing was not due to a few conspicuous females or pups with catholic habits. Of the adult females that were observed nursing any pup 24 allowed a nondescendant pup to nurse; 18 nursed a single non-descendant pup while 6 others nursed two nondescendant pups either on separate days or in one case, in separate years. The incidence of communal nursing was not predicted by the number of nursing bouts we observed for each female ($\chi^2 = 49.6$, $df = 2$, $P < 0.0001$). I obtained the expected frequencies of communal nursing by multiplying the observed number of nursing bouts by the overall proportion of communal nursing, 0.0686, and pooling over all females observed nursing either 0, 1 or 2 nondescendant pups. Altogether 27 different pups nursed from one other female and 3 pups nursed from two females other than their mothers. As for adult females, the incidence of communal suckling was not predicted by how often we observed each pup nurse ($\chi^2 = 128.7$, $df = 1$, $P < 0.0001$).

Females appeared to nurse selectively. Pups initiated nursing by pushing their noses under females' wings. A female willing to nurse would then lift her wing to allow the pup access to her nipple. Rejected nursing attempts occurred when pup nosing behavior was followed by females failing to lift their wings, crawling away, or snapping at persistent pups. We observed females reject pup nursing attempts 15 times throughout the period during which communal nursing was observed (Fig. 1). Females rejected their own pups on three occasions (0.8% of attempts) and nondescendant pups on nine occasions (23.1% of attempts; Table 1). The remaining three rejections involved young that were unbanded or without known mothers and could represent either descendant or nondescendant young. Most rejected nurs-

Table 1. Number of nursing bouts and rejected nursing attempts observed for pups of each sex on putative mothers (descendant offspring) and other females (nondescendant offspring)

Female response	Pup relationship to female	Males		Females	
		Bouts	Pups	Bouts	Pups
Nursed	Descendant	214	71	151	53
Rejected	Descendant	2	2	1	1
Nursed	Nondescendant	12	11	18	18
Rejected	Nondescendant	6	6	3	3

Nursing observations sum to less than 437 because some pups were unbanded and, therefore, are not included in this table

Table 2. Number of nondescendant pups of each sex which were nursed or rejected categorized by the sex composition of the nursing female's litter

Sex composition of litter (n)	Female response	Male	Female	P^a
All male (32)	Nursed	5	9	0.007
	Rejected	7	0	
All female (20)	Nursed	1	3	1.000
	Rejected	1	1	
One male + one female (23)	Nursed	4	4	0.467
	Rejected	0	2	
Unknown (10)	Nursed	2	2	1.000
	Rejected	1	2	

[a] Fisher's Exact Test

ing attempts did not indicate the cessation of lactation. Two of the three pups that were rejected by their mothers were observed nursing from them on a subsequent day. Furthermore, eight females that rejected a pup nursed another pup on the same day including one female that rejected one of her own male pups while later permitting a female nondescendant pup to nurse.

Communal nursing was not independent of pup sex. Overall, we observed significantly more male than female pups nursing (Table 1) given that 49% of the 206 pups banded at the Zion colony were males ($Z = 2.09$, $P = 0.040$), but the average number of nursing bouts (3.0 ± 2.3) observed did not differ between the sexes ($t = 0.21$, $P = 0.83$). However, lactating females appeared to allow nondescendant female pups to suckle more than expected given the nursing bout frequency by each sex ($\chi^2 = 3.93$, $P = 0.047$; Table 1). This result did not quite reach significance ($\chi^2 = 3.53$, $P = 0.060$; Table 1) when we used the number of pups of each sex observed nursing rather than the number of nursing bouts as the sampling unit. In contrast, lactating females rejected both descendant and nondescendant pups at frequencies comparable to those expected given the frequency of parental nursing bouts by each sex ($\chi^2 = 0.40$, $P = 0.53$) or pups of each sex ($\chi^2 = 0.31$, $P = 0.58$; Table 1). Furthermore, those lactating females with all male litters permitted nondescendant females to nurse but excluded nondescendant males (Table 2).

Nondescendant nursing pups were similar in age to the nursing females' own young ($r = 0.69$, $n = 25$, $P < 0.001$) as were rejected nondescendant young ($r = 0.97$, $n = 7$, $P = 0.001$). Similarity in ages of nondescendant and descendant nursing pups is expected, though, because all females in the colony gave birth within a 20-day period in 1988 starting on 30 May and within a 14-day period in 1989 beginning on 9 June. Nevertheless, some nondescendant pups differed in age from the nursing female's own pups by as much as 15 days, which amounted to more than a 50% difference in pup mass. The average age of rejected nondescendant pups did not differ from the age of nursed nondescendant pups (26.4 ± 7.3 versus 25.9 ± 8.5 days, respectively; $t = 0.17$, $P = 0.86$) or from the age of rejected descendant pups

(29.3 ± 5.9 days; $t = 1.0$, $P = 0.34$). Communal nursing females also did not differ in age, as determined directly from banding records or indirectly from the teeth wear index, from females that only nursed their own young (1.89 ± 0.99 years, $n = 28$ versus 1.97 ± 0.91 years, $n = 150$, respectively). The teeth wear index was used to estimate age because it scales isometrically with age among known-aged bats (index $= 1.01$(age)$+ 0.08$, $r^2 = 0.83$, $F_{1,384} = 1849$, $P < 0.0001$). Only 0.25% of adult females captured had a teeth wear index of 5.

## Weights of nursing pups and adult females

Observations in the laboratory indicate that the amount of milk transferred from females to pups is proportional to the number of nursing bouts. Both the number ($r_s = 0.52$, $P < 0.01$, $n = 29$) and proportion ($r_s = 0.49$, $P < 0.01$) of nursing bouts scored every 30 min from 24 h time-lapse records correlated positively with the amount of weight gained during that period (Fig. 3). Days on which the pups were not observed for more than five intervals were excluded. Pups only nursed from their mothers. Because these data represented four families of pups each weighed on four separate days, I performed on ANCOVA using the age of the pups, number of nursing bouts, and family identity to determine if the correlation between number of nursing bouts and mass change was an artifact of family or age differences. Significant effects for the number of nursing bouts ($F_{1,23} = 8.98$, $P = 0.006$) and family ($F_{3,23} = 3.84$, $P = 0.023$) but not for age ($F_{1,23} = 2.13$, $P = 0.158$) remained after pooling nonsignificant interaction mean squares with the error mean squares.

Recaptures at the Zion, Busby, Grim and Hutton colonies of females with young of known ages departing on their first foraging trip for a night indicated that, on average, females lose weight during lactation (Fig. 4). The slope of the regression for female body mass on
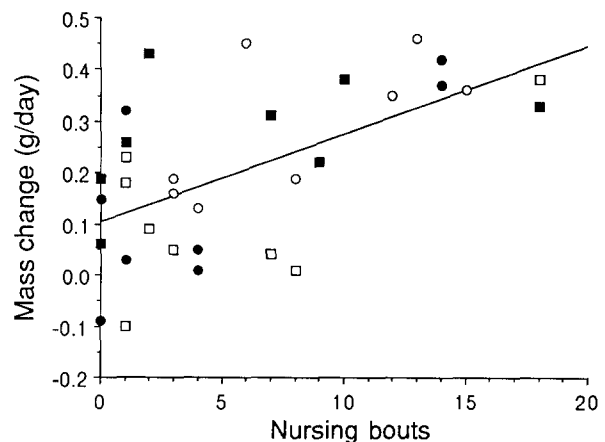
Fig. 3. The mass change of eight pups from four families (indicated by different *symbols*) over four 24-h periods as a function of the number of nursing bouts recorded on time-lapse video tape every 30 min. The regression equation is mass (g) $= 0.017 \, x$ (number of nursing bouts) $+ 0.106$ ($r^2 = 0.33$; $P = 0.0004$). Pups ranged in age from 3 to 22 days
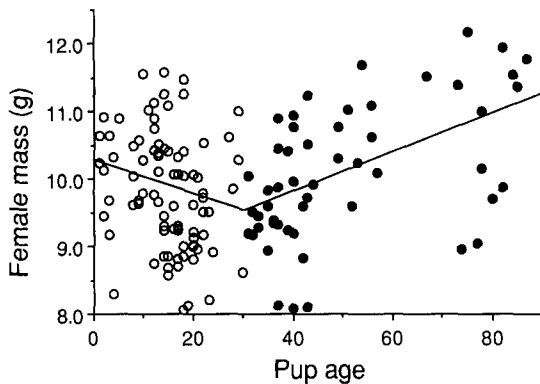
Fig. 4. Mass of females captured as they departed on their first foraging flights of a night as a function of the age of their pups. Data from four colonies are combined. *Open circles* represent data used to estimate the regression for less than 30 days of age and *closed circles* represent data used to estimate the regression above 30 days. Thirty days was chosen as the break-point because it caused the regression lines to hinge

pup age is less than zero between 0 and 30 days of age (mass(g) = $10.29 - 0.03$ (pup age); $n = 85$; $t = 2.25$, $P = 0.027$). Between 31 and 85 days after birth females steadily gain weight (mass (g) = $8.61 + 0.03$ (pup age); $n = 52$; $t = 4.26$, $P < 0.0001$). Even though the lowest average female body weight coincides with the period of most frequent communal nursing, some females exhibit little or no apparent weight loss at this time (Fig. 4).

Preweaning survival

Although the sex ratio of banded pups is 1:1, males are found dead in attics or disappear, even though their sib or mother is present for at least 10 more days, significantly more often than females (Table 3; $\chi^2 = 5.49$, $P = 0.019$). The average age (13.1 ± 12.1 days) of death or disappearance does not differ between the sexes. Even after excluding presumed deaths under 20 days of age, significantly more males than females die or disappear (5 females, 15 males; $\chi^2 = 3.94$, $P = 0.047$).

Examination of the weights of pups recaptured at the Zion colony between 21 and 40 days of age when they where capable of flying indicates that those males

that died or disappeared were either less successful at feeding or received less milk from their mothers or other females. ANCOVA using weight as the dependent variable and forearm as a covariate with preweaning survival as a factor indicate that the slope of the regression between weight and forearm for males that die or disappear was significantly lower than the slope for males that survived (interaction between forearm and survival: $F_{1,54} = 11.02$, $P = 0.002$). This effect was not significant for females.

As with most field studies, the cause of juvenile mortality is unknown, but we did observe a black rat snake (*Elaphus negro*) in the Hutton attic on two occasions and one afternoon a kestrel (*Falco sparverius*) attempted to grab bats from inside the Busby attic by alighting near the crack in the roof where the bats typically departed each night. However, we never observed kestrels flying at dusk when bats depart to feed. Although pups frequently take practice flights within the attics beginning at 21 days of age, after a few days of practice they are competent fliers and would be difficult for a snake to catch. Furthermore, no snake or kestrel was ever observed in or around the Zion colony.

Relatedness among females and nursing pups

To verify the accuracy of our maternity assignments we used allozyme data to estimate relatedness between mother-pup pairs raised in captivity or caught under a week of age while attached to the teat. The average relatedness between 60 female-pup pairs that met those criteria was 0.43 (SE = 0.07), not significantly different from 0.5 as expected. In contrast, the average relatedness between 35 female-pup pairs observed nursing 1 week or more after parturition at the Zion colony and assumed to be mother-offspring because they did not meet any of the communal nursing criteria was 0.23 (SE = 0.06), i.e. significantly less than 0.5. Thus, we have underestimated the frequency of communal nursing. At least 6 of the 35 offspring would have to be unrelated to their putative mothers for the average level of relatedness within the group to drop low enough to fall within the 95% confidence limits of the observed level of relatedness.

To determine if females identify and preferentially

Table 3. Mortality by sex prior to weaning of banded pups in the Zion attic during 1988 and 1989

Category	Females	Males	Proportion male	P
Banded	105	101	0.49	0.781[a]
Carcasses	4	7	0.64	0.526[b]
Disappeared	5	17	0.77	0.022[b]
Total mortality	9	24	0.73	0.019[b]

Carcasses were found in the attic; disappearances only include those pups under 30 days of age whose mothers or siblings were resighted 10 or more days after the disappearance date

[a] One sample z-test for proportions
[b] χ^2 contingency test

Table 4. Allele frequencies and average relatedness among female-nonoffspring pairs at the Zion colony

Enzyme	n	Groups	Allele frequencies				r	SE
			a	b	c	d		
IPO	40	20	0.090	0.910	0.000		−0.13	0.06
ADA	38	19	0.013	0.913	0.075	0.000	−0.16	0.07
PGD	40	20	0.000	0.625	0.375	0.000	0.17	0.24
MPI	40	20	0.050	0.900	0.050	0.000	0.00	0.12
Mean							0.04	0.12

Standard errors obtained by jacknifing over groups

Table 5. Haplotypes of 21 adult females that provided milk to nondescendants (nursing female) and the mother of the recipient pup (maternal)

Position	Nursing female repeat sequences[a]						Maternal repeat sequences[a]						Repeat similarity
	1	2	3	4	5	6	1	2	3	4	5	6	
	5,	2,	2,	2,	9,	20	5,	11,	11,	12,	2,	17	0.17
	6,	7,	4,	4,	8,	19	5,	2,	2,	2,	15,	17	0.00
	5,	1,	3,	3,	2,	17	5,	1,	2,	2,	2,	17	0.67
	5,	4,	4,	10,	16,	19	5,	2,	2,	2,	2,	17	0.17
	5,	2,	2,	2,	2,	17	5,	11,	11,	2,	2,	17	0.67
	5,	2,	2,	2,	1,	24	5,	4,	4,	4,	4,	26	0.17
	5,	2,	2,	2,	2,	17	5,	11,	11,	2,	2,	17	0.67
	5,	2,	2,	2,	2,	17	5,	1,	3,	3,	3,	17	0.33
	5,	2,	2,	2,	2,	17	5,	2,	4,	4,	4,	17	0.50
	5,	7,	4,	13,	—,	18	5,	1,	2,	2,	2,	17	0.17
	5,	2,	4,	4,	4,	17	5,	4,	2,	3,	—,	20	0.17
	5,	4,	4,	4,	4,	21	5,	2,	2,	2,	2,	17	0.17
	5,	11,	11,	2,	2,	17	5,	3,	3,	3,	10,	22	0.17
	5,	8,	8,	8,	8,	25	5,	11,	1,	2,	14,	17	0.17
	5,	2,	2,	2,	1,	23	5,	2,	2,	2,	1,	23	1.00
	5,	7,	4,	13,	—,	18	5,	2,	2,	2,	2,	17	0.17
	5,	2,	2,	2,	2,	17	5,	2,	4,	4,	4,	17	0.50
	5,	1,	2,	2,	2,	17	5,	7,	4,	13,	—,	18	0.17
	5,	2,	4,	4,	4,	27	5,	3,	2,	4,	4,	18	0.50
	5,	2,	2,	2,	2,	17	5,	7,	4,	13,	—,	18	0.17
	5,	2,	4,	4,	4,	17	5,	2,	4,	4,	4,	17	1.00

Each number corresponds to the position of a unique 81-bp nucleotide sequence in a tandem array in the mtDNA d-loop. Dashes indicate those individuals with only five repeats. Repeat similarity is the fraction of the repeats that are identical. Position refers to the location of each repeat within the d-loop with position 1 being that repeat closest to the proline tRNA gene

[a] The nucleotide sequences corresponding to each numbered repeat are indicated below in reference to one of the repeats:

```
1   ATTAAACTATATTCCACATAAATATTAAACATGTACATAAATATATTAATATTACATAAGACATATAATGTATAATTGTAC
2   ---------------G----------------------------------------------------------------
3   ----------C-------G-------------------------------------------------------------
4   ---------------G-------G--------------------------------------------------------
5   ------T------T------------------------------------------------------------------
6   ------T------T-----G------------------------------------------------------------
7   ----------C---------------------------------------------------------------------
8   ---------------G-------G---------------T----------------------------------------
9   ---------------G--------------------------------------------C-------------------
10  ----------C-------G-------G------------------------------------------------------
11  ----------C---------------------------------------------------------------------
12  ----------C-------G--------------------------------------------------------------
13  ---------------G-------G---------------------------------------------------C----
14  ---------------G-----------------------C----------------------------------------
15  ------T---------G-------G--------------------------------------------------------
16  ----------C-------G-------G------------T----------------------------------------
17  ------T-----A-----G----C--G--A--------C-----G-----------T-----G----CG----C----
18  ------T-----A-----G----C--G--A--------------G-----------T-----G----CG----C----
19  ------T-----A-----G-------G--A--------------G-----------T-----G----CG----C----
20  ------T-----A-----G----C--G--A--------C-----G-----------T-----A----CG----C----
21  ------T-----A-----G----C--G--A--------C-----G------------T---G----CG----C----
22  ------T---C-------G----C--G--A--------C-----G-----------T----------CG----C----
23  ------T-------------------C--G--A--------C-------------------T-----G----CG----C----
24  ------T-----------G----C--G--A--------C-----G-----------T-----G----CG----C----
25  ------T-----A-----G-------G--A--------G-----G-----------T-----G----CG----C----
26  ------T-----A-----G-------G----------T------G-----------T-----G----CG----C----
27  ------T-----A-----G----C--G----------C-----G-----------T-----G----CG----C----
```

nurse related offspring within colonies I estimated the average degree of relatedness between 20 of the 30 known female-nondescendant offspring pairs (Table 4). I could not include the other 10 female-pup pairs because we failed to recapture and bleed the pups in those pairs after the pups became volant. The average level of rela-

tedness between the two bats was not significantly different from zero. However, because sample sizes are small, the standard error associated with this estimate is sufficiently large to prevent rejection of the possibility that these pairs represent second-degree relatives, i.e. half-siblings or grandparent-offspring.

Table 6. Allele frequencies and average relatedness among adult females within colonies

Enzyme	Year	n	Groups	Allele frequencies					r	SE
				a	b	c	d	e		
IPO	1988	289	5	0.089	0.910	0.001			0.09	0.06
	1989	168	6	0.090	0.910	0.000			0.18	0.07
ADA	1988	294	5	0.015	0.905	0.073	0.008		−0.06	0.10
	1989	170	6	0.022	0.897	0.079	0.002		−0.10	0.06
PGD	1988	294	5	0.036	0.543	0.412	0.008	0.001	0.00	0.02
	1989	170	6	0.016	0.528	0.425	0.032	0.000	0.01	0.04
MPI	1988	294	5	0.020	0.919	0.049	0.007	0.005	0.08	0.07
	1989	170	6	0.010	0.942	0.044	0.004	0.000	−0.11	0.09
Mean	1988	289	5						0.02	0.03
	1989	168	6						0.00	0.03

Standard errors obtained by jacknifing over groups

To evaluate the possibility that some female-nondescendant offspring pairs at the Zion colony were matrilineal kin, all six 81-bp repeats for 37 adult females were sequenced. These 37 bats were sequenced because they were either females observed to suckle pups other than their own or were the mothers of pups that had nursed from other females. To obtain corresponding fragments from heteroplasmic individuals, polymerase chain reaction products containing only six repeat fragments were cut from gels, cleaned, amplified and sequenced directly (Wilkinson and Chapman 1991). From these sequences we identified a total of 27 different repeat haplotypes (Table 5). Eight of the 37 bats shared the same haplotype and thus almost certainly were related through a common maternal ancestor, three pairs of bats each had a different haplotype, and the remaining 23 bats had unique haplotypes in which the 81-bp sequence for at least two repeats was different. In each of 12 families, the pup repeat haplotype was identical to the maternal repeat haplotype. Among the sample of 37 individuals were the mothers of 21 of the 30 female-nondescendent offspring nursing pairs. Two of those 21 pairs showed identical repeat haplotypes and, therefore, were almost certainly matrilineal kin (Table 5). These two are not evidence for selective nursing by level of relatedness, however, because 1000 Monte Carlo randomizations indicates that with 27 haplotypes and 37 individuals, two or more identical haplotypes should occur by chance in 25 percent of samples containing 21 pairs. Furthermore, in comparing the six repeats within an individual, the average number of identical repeats was 2.29 among the 21 pairs. This value does not differ from expectation (2.13±0.33) if 21 pairs are selected at random 1000 times from the 37 sequences.

Female natal philopatry coupled with mating within colonies could cause colonies to diverge genetically resulting in an average level of relatedness that might favor communal nursing within a colony by kin-group selection (Wade 1980). I tested this possibility by estimating the average level of relatedness within a colony on each of the two years. In neither 1988 nor 1989 was average relatedness significantly greater than zero (Table 6).

Discussion

In contrast to a previous report (Watkins and Shump 1981), our observations indicate that evening bats do not nurse nondescendant young indiscriminately. The vast majority of our nursing observations involved a pup attached to the teat of its mother. However, most communal nursing does occur after the young are nearly 2 weeks of age, as was reported previously (Watkins and Shump 1981). Even though females return to their natal colonies, both allozyme and mitochondrial DNA sequence information indicates that females do not nurse matrilineal relatives preferentially as predicted by kin selection. Furthermore, genetic differentiation of colonies does not occur, presumably because all males disperse and mate with females from other colonies (Wilkinson, unpublished) and females live no longer than 5 years. Consequently, females are no more closely related to a pup selected at random from their own colony than to one from another colony. If communal nursing bouts do result in milk transfer, as the positive correlation between weight gain and nursing bout frequency recorded in the laboratory and the absence of any difference between communal and parental nursing bout durations observed in the field indicate, then the simplest alternative explanation is that communal nursing is nonadaptive because females mistakenly identify and suckle nondescendant young on rare occasions.

Female error

Female error has been invoked to explain communal nursing in species that historically have not needed to nurse selectively but are currently forced to nurse offspring in proximity, such as in captivity (Packer et al. 1992; Eales et al. 1988) or after recent reduction in suitable nursing habitat (e.g., Fogden 1971; Boness 1990). However, communal nursing is not always observed among captive evening bats (Jones 1967; this study). While the number of *N. humeralis* in attic nursery colonies may occasionally be greater than in historical tree-

hollow colonies, we have located tree-hollow roosts with over 100 bats (Wilkinson 1992). Furthermore, because attics are often larger and more abundant than tree hollows, evening bats may have experienced an expansion, rather than contraction, of available nursing habitat.

Three additional lines of evidence cast doubt on the female error hypothesis. First, females exhibited selectivity when nursing as evidenced by active rejection of some nondescendant pups and acceptance of others. Because we observed most females nurse pups after a rejection, rejections do not indicate the cessation of lactation. We suspect we have underestimated the frequency of rejections because they occur quickly and often involve subtle movements. Despite the possibility that our observation methods might have over-represented the behavior of conspicuous individuals, the females and pups we observed nursing most frequently were not more likely to nurse communally. Although communal nursing was rare in comparison to all nursing bouts observed, it was relatively common, i.e. as much as 20% of all nursing bouts, during the period that pups were learning to feed themselves.

Second, sufficient acoustic information is available in pup isolation calls for us, and presumably lactating females, to assign 100% of 306 isolation calls to 38 pups using cross-validation discriminant function analysis (Scherrer and Wilkinson 1992). During the first week after parturition females that return from foraging rely on these calls to locate young (Wilkinson, unpublished). As pups age, the characteristic frequency modulation pattern that distinguishes pups remains intact while the overall frequency increases and the duration decreases (Scherrer and Wilkinson 1992). Because isolation calls become completely ultrasonic after the young reach 2 weeks of age, we do not know if they are produced during the period that communal nursing is most common. However, isolation calls have been recorded from other bat pups, e.g. *Phyllostomus discolor*, as old as 45 days (Esser and Schmidt 1989).

Third, female error does not predict a female bias in the young allowed to nurse. Although we observed male pups nursing more often than female pups, we did not see more nursing bouts by male pups than by female pups. Females with all-male litters preferentially nursed female young. Therefore, the apparent sex bias in communal suckling is unlikely to be due to females being more conspicuous than males or to confusion over identity among pups of the same sex. In contrast to the variation among pups in isolation calls, acoustic characteristics do not differ between the sexes (Scherrer and Wilkinson 1992). If lactating females preferentially allow female young to nurse, they must use other information, such as olfactory cues (Watkins and Shump 1981), to discriminate between pups of different sex.

Mutualism and delayed mutualism

Our observations indicate that those male pups that die or disappear weigh less than the male pups that survive, suggesting that they fail to obtain sufficient food to survive. We have no evidence indicating that the suspected predators, kestrels and rat snakes, could cause such a sex bias in mortality. Because male-biased preweaning mortality occurred at the same time that apparent female-biased communal nursing was observed, communal nursing could be causally related to the difference in preweaning survival. Communal nursing and rejected nursing attempts occurred most often when female body weight was lowest (Fig. 4) as expected if communal nursing is the result of hungry pups seeking food from other females. While low-body-weight females should always reject communal nursing attempts, females in good condition that hunt successfully could benefit by sharing milk if improving the survival of unrelated female young positively affects their survival. Several lines of evidence suggest that communal nursing may provide both immediate and delayed benefits to females under some situations.

Females that have enjoyed above-average hunting success may produce more milk than their offspring can consume in a day, especially if those young have also hunted successfully. Evening bat females are impressive milk producers and secrete half their body weight in milk per day at peak lactation (Steele 1991). Consequently, variation in hunting success must affect milk production. In red deer, daily milk yield varies by more than a factor of two between hinds kept on high quality grass-clover pasture and poor quality hill pasture (Loudon and Kay 1984). Well-fed female bats could benefit immediately from milk sharing if, by allowing nondescendant pups to nurse, they decreased the weight they must carry on their next foraging trip. If their own young need milk on a later day when hunting is poor, milk dumping may help to maintain milk production and prevent infections. Milk retained in the mammary gland exerts a negative chemical feedback to reduce milk synthesis (Mepham 1976). In cows, incomplete milking not only decreases milk yield, but also decreases fat yield and percentage (Bailey et al. 1953) and increases the incidence of mastitis (Schalm and Mead 1943).

This mutualism hypothesis predicts that communal nursing should occur most often when young have begun to fly and feed themselves, and when foraging success is highly variable. By examining the palates of young bats, Steele (1991) noted that insect prey are first captured at 24 days of age. Thus, 73% of the communal nursing bouts involved females whose pups had already begun to hunt. By focusing a video camera above a balance positioned at the entrance to the Zion colony, we were able to record departures, arrivals and weights of evening bats throughout the 1989 lactation period (Wilkinson 1992). These video tapes show that 20% of returning lactating female evening bats fail to gain any weight while 8% gain more than 4 g on a foraging trip (Wilkinson 1992). By simultaneously sampling spatial variation in insect prey density every night in 1989, we also found that communal nursing occurred most frequently during the 3-day period when both the average and the variance in prey density reached its annual peak (Wilkinson 1992). Because evening bats feed on small flies and beetles that occur unpredictably in rich patches that persist for 1–4 days, our observations are consistent

with some females being successful foragers and having milk to share while others are unsuccessful and cannot satisfy their own pups' needs. Although we failed to obtain the individual weights necessary to determine if those females that returned after gaining an above-average amount were more likely to nurse communally, variation in hunting success is the most plausible explanation for why some females failed to wean any pups while others were able to wean three pups, why communal nursing is infrequent, and why we did not observe communal nursing in captivity.

However, the milk dumping hypothesis by itself does not predict any sex bias in communal nursing. Female-biased communal nursing is expected, however, if it enhances pup survival and all bats benefit by roosting in a larger colony, i.e. by delayed mutualism (Connor 1986). Colony size is increased more by helping females than males because males disperse from their natal colonies in late August (Watkins and Shump 1981) while females remain together and continue to gain weight until the entire colony migrates in late September or early October (Baker et al. 1968). Because females return to their natal colony to breed in subsequent years, any benefits to living in a larger group can accrue over the life of a bat. While many benefits to group living are possible, video-tape records, radio-telemetry, prey density dispersion patterns, and two roost exclusion experiments indicate that evening bats transfer information about rich foraging and alternative roosting sites (Wilkinson 1992). Unsuccessful foraging bats follow previously successful foragers and improve their prey capture. Such following behavior involves all bats in the colony including some adult females following 8-week-old females (Wilkinson 1992). Because female evening bats are never found alone and apparently take advantage of the experience of colony members to find roosting, feeding, and hibernating sites, sharing milk with nondescendant female young may result in delayed benefits to a lactating female. The extent to which increasing colony size will improve a female's ability to find ephemeral food warrants further theoretical and empirical study but is likely to depend on the spatio-temporal variation in food, on the searching patterns of the bats, and on the degree to which information transfer occurs.

By the mutualism and delayed mutualism hypotheses just described, female-biased communal nursing should be independent of the sex of a female's own litter yet we observed females with all-male litters excluding nondescendant males and nursing nondescendant females. However, examination of Table 2 shows that females with all-female litters were just as likely to nurse nondescendant females as were females with all-male litters, and even females with one male and one female pup did not differ significantly from females with all-male litters in the proportion of females nursed. Unfortunately, the power of these comparisons is weak given the small sample sizes. Thus, the importance of the sex of a female's own litter in determining her propensity for communal nursing requires further study.

The combination of direct and delayed benefits to communal nursing proposed here is consistent with the finding that communal nursing is more common among polytocous mammals in which female group size is small (Packer et al. 1992). In polytocous species, each offspring takes a smaller fraction of a female's total milk output than in monotocous species so the potential cost to the female is less. Any delayed benefit of the behavior is likely to correlate negatively with group size because the biggest relative improvements in foraging efficiency or predator avoidance come as small groups increase in size. For example, if increasing group size is not costly but dilutes the per capita predation rate, then the individual benefit from increasing group size by one individual will be proportional to $1/n - 1/(n+1)$. Communal nursing should, therefore, be directed at those offspring, whether they are related or unrelated, that remain in the social group and be most common in small groups. Identification of the sex and dispersal patterns of nondescendant nursing offspring in prairie dogs (Hoogland et al. 1989), capybara (MacDonald 1981), cavies (Rood 1972), pigs (Bryant and Rowlinson 1984), or water buffalo (Tulloch 1979) coupled with direct measurements on individual foraging success and rate of communal nursing would provide an independent test of these hypotheses.

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