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Communal Nesting among Genetically Similar House Mice

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Abstract

From March to October 1986, 35 house mice, *Mus domesticus*, were fitted with radio-transmitters and tracked in and around a Colorado feed shed for an average of 5 (range 2 to 17) days. 5 of 36 simultaneously tracked pairs of lactating females used identical nesting sites. Genotypic similarity at 5 enzyme loci, assayed from biopsies of blood and toes, indicated that these females were more genetically alike than would be expected if pairing occurred randomly among females. We posit that female house mice recognize and preferentially form communal nests with close relatives. Aside from the communally nesting females, minimal overlap occurred among home ranges of lactating females. Only 4 of 10 adult male home ranges appreciably overlapped female home ranges. The home ranges of these 4 males overlapped less than the other adult male home ranges suggesting that males defend one or more females for access to mating. The possibility that communally nesting females are nursing each other's pups is discussed.

Introduction

Evidence is accumulating that some rodents make communal nests. While some species only nest together during the winter (e.g. *Microtus xanthognathus*, WOLFF & LIDICKER 1981), in others, such as *M. arvalis* (BOYCE & BOYCE 1980), *M. californicus* (OSTFIELD 1986), *M. ochrogaster* (L. GETZ, pers. comm.), *M. pennsylvanicus* (MCSHEA & MADISON 1984), *Peromyscus maniculatus* (HOWARD 1949; HANSEN 1957) and *Mus domesticus* (YOUNG et al. 1950), there is evidence from natural populations that more than one female regularly visits a nest during the breeding season. Although communal nesting may have energetic consequences, when it occurs during the breeding season multiple females can potentially share or attempt to exploit lactation. Observations on wild house mice in enclosures (BROWN 1953; SOUTHWICK 1955; CROWCROFT & ROWE 1963; LLOYD 1975; VAN ZEGEREN 1980; BAKER 1981; P. PENNYCUK pers. comm.) and on

inbred strains in the lab (SAYLOR & SALMON 1969, 1971; GANDELMAN et al. 1970; WERBOFF et al. 1970) indicate that females frequently form communal nests and nurse each other's pups. SHERIDAN & TAMARIN (1986) found two different maternally injected radio-isotopes in a single *M. pennsylvanicus* pup indicating that communal nursing also occurs in this species.

Communal nursing is unexpected in natural populations because sharing milk with young other than own offspring should decrease the reproductive success of the donating mother if food is limiting. The potential cost of communal nursing may be large given that energy requirements for many rodent species are doubled during lactation (MATTINGLY & McCLURE 1982; SADLEIR 1984). Consequently, females should either be highly selective about nursing their own pups or they should preferentially share milk with those individuals which enhance their inclusive fitness (HAMILTON 1964). One potential way to increase inclusive fitness is to form communal nests with close relatives. Here we test if communal nesting occurs preferentially among female kin by assessing movement patterns and allelic identity at 5 enzyme loci of radio-tagged lactating commensal house mice. In a future paper genetic differences among populations of wild mice and strains of inbred mice in the propensity to form communal nests will be described.

Methods

Study Area

House mice were trapped and radio-tracked at Heil Valley Ranch, Boulder County, Colorado, elevation 1660 m, between Mar. 1 and Oct. 27, 1986. Most mice were trapped in a double-walled boxcar (12.4 × 2.95 × 2.85 m) in which horse feed, saddles, saddle blankets, miscellaneous supplies and harnesses were stored. The mice stored feed, built nests and moved along horizontal studs within the walls. Nests were also built in saddle blankets or in tunnels beneath the boxcar. Some mice inhabited oat hay bales approximately 100 m from the boxcar until the bales were removed in June. Humans, dogs, cats, skunks, and raccoons were potential predators. One of our radio-tagged females was captured and eaten by a cat and several unmarked pregnant adult females were captured and killed by dogs and ranch hands when some of the hay bales were removed. Rats were poisoned with diphacinone and eliminated from the ranch in 1984. We presume the mice were able to survive the poisoning since the LD50 of mice for diphacinone is about 10 times greater than the LD50 for rats (MEEHAN 1984).

Trapping and Tracking Techniques

One night every month from Mar. until Oct. (with the exception of June) we set a minimum of 24 Sherman live-traps inside the boxcar (328 trap-nights). Traps were baited with peanut butter and rolled oats, set between 17.00 and 19.00 h, and checked before 08.00 h. In some months we also set Longworth traps (75 trap-nights), Tincat traps (160 trap-nights), or Ketchall traps (60 trap-nights). Although these trap-night totals included infrequent trapping at other sites (alfalfa hay shed, oat haystack, tool shed, office, and tractor shed) on the ranch, most mice were captured in the boxcar.

An AVM receiver and a Telonix H antenna were used to determine the locations of mice tagged with 148 MHz transmitters that we constructed (WILKINSON & BRADBURY 1987). A 6 cm 0.008 mm metal guitar string antenna and a Mallory 312M hearing-aid battery were attached to each transmitter. The acrylic-encased package weighed 2 g and transmitted for 18–24 days. After anesthetizing each mouse with 60-s exposure to Metofane ether, we attached the transmitter package to the fur on the back of the mouse with colostomy adhesive. We used adhesive, rather than a collar, for attachment so that we could recover the radios. By recovering 7 transmitters a total of 42 times we determined the

accuracy of our location determinations to be within 10 cm. A disadvantage of this technique was that the radio would come off the mouse after a relatively short period (mean = 5, range = 2 to 17 days, N = 35). In Sept. we used plastic "wire-ties" with a locking ratchet mechanism as collars to attach 5 transmitters permanently to ascertain if home range estimates were dependent on number of days tracked. A transmitter was assumed to have fallen off if its location did not change on 3 successive readings and at any later time.

Simultaneous tracking of 1 to 7 radio-tagged mice began 12 to 36 h after transmitter attachment. Most hourly sampling occurred between 16.00 and 24.00 h after human activity in and around the boxcar subsided. At least two samples were taken between 07.00 and 17.00 h to determine if females moved. These sampling procedures resulted in an average of 22 bearings for each radio-tagged mouse. Sign test analyses of the % of 4-h intervals (either A — 08.00 to 12.00 h, B — 12.01 to 16.00 h, C — 16.01 to 20.00 h, or D — 20.01 to 24.00 h) in which a mouse changed position indicated that mice were significantly more active during period C than any earlier period and that activity was comparable at later times (respective comparisons: A vs. B, N = 12, p = 0.34, A vs. C; N = 21, p = 0.02; A vs. D, N = 18, p = 0.29; B vs. C, N = 16, p = 0.03; B vs. D, N = 13, p = 0.15; C vs. D, N = 25, p = 0.36).

Genotype Assessment

After a mouse was anesthetized, approximately 0.1 ml of blood was collected into heparinized capillary tubes by puncturing the suborbital canthal sinus, a unique combination of two toes was taken, and weight, tail length, sex, reproductive condition (i.e. lactating or visibly pregnant) and pelage color and markings were recorded from each animal. The blood and toes were held on ice in the field. In the laboratory, the blood was centrifuged for 4 min at 5,000 rpm to separate the cellular and serum portions. After centrifugation, the cellular fraction was diluted 1:1 with deionized water and the resulting hemolysate and plasma, as well as the toes, were stored at -70 °C, usually for less than 2 months. Prior to electrophoresis, the toes were thawed and then finely minced in an equal volume of cold deionized water in a chilled spotplate. The resulting suspension was spun at 10,000 rpm for 5 min. The toe supernatant, hemolysate and plasma were then subjected to horizontal starch gel electrophoresis following standard procedures (BREWER 1970).

An average of 43 samples was used to resolve 30 enzyme loci using typical staining recipes and buffer conditions (HARRIS & HOPKINSON 1976). 25 enzymes appeared monomorphic despite electrophoresis on a minimum of 2 buffer systems. Four esterase loci (ESa, b, c, d) were biallelic and isocitrate dehydrogenase (IDH) from hemolysate had 3 alleles. ESa, which corresponds to ES-2 (NICHOLS & RUDDLE 1973), and ESb were identified in plasma with a tris-borate buffer (pH 8.0) and a cholinesterase stain (HARRIS & HOPKINSON 1976). ESa was resolved from hemolysate with a LiOH buffer and AS-D-acetate (or methylumbelliferyl acetate) as substrate. ESd was scored using alpha-naphthyl propionate as substrate for the toe supernatant with a tris-maleate buffer (pH 7.4). Only tissue could be obtained from 8 mice killed by dogs or ranch hands which meant that no blood enzymes were scored for these mice.

Data Analysis

We used ANDERSON's (1982) technique on hourly radio-telemetry coordinates to compute a nonparametric estimate of each mouse's spatial utilization distribution (UD). Since this analysis provides the probability associated with being at any x, y position in a specified area, we first transformed our 3-dimensional mouse coordinates to 2-dimensions by extending the x, y plane of the boxcar floor to include all four walls. This transformation retains most of the spatial information since the mice moved primarily across the floor and up and down the walls. Numerous holes into and out of the walls of the boxcar as well as a substantial amount of material (feed bags, saddle blankets, saddles, and trash) on the boxcar floor provided almost continuous habitat for movement and nesting. When using Anderson's PASCAL program to estimate home range areas, limits on the x, y axes, which determine the available area for estimating each UD, were set so that the minimum area circumscribed by the cumulative probability of 0.95 or MAP (0.95) occupied 50 % of the available area. This value was chosen to standardize the effective grid size and avoid boundary problems (ANDERSON 1982).

However, when calculating the overlap in volume between 2 UD's, these axis limits could not be used because they specified different scales. Therefore, to compute UD overlap, axis limits were reset to insure both a constant scale and that the home range area filled a minimum of 10 % of the available grid. We computed the overlap at a specified MAP between all possible pairwise combinations of mouse UD's from mice tracked simultaneously (C source code available from first author). We used MAP (0.95) UD estimates for calculating overlap because these UD estimates are less sensitive to outlying coordinates than MAP (0.99) estimates (ANDERSON 1982).

To assess genetic similarity and, therefore, potential relatedness between pairs of individuals, for each pair of mice we counted the number of alleles which were different at each locus and then summed across all loci. This sum for almost all pairs of mice could range from 0 indicating genotypic identity to 10 meaning complete genotypic dissimilarity. After assuming random mating and independent assortment for the marker loci, both of which we test below, we used this measure to calculate the exact probability of drawing 5 pairs of females all of which were either unrelated or full-sibs. These probabilities were obtained by first determining the probabilities associated with all possible parental genotypic combinations capable of producing either full-sib or randomly-paired offspring that differed by 0, 1 or 2 alleles at a locus as functions of allele frequencies. Using observed allele frequencies these probabilities were then multiplied across all five loci and summed over all possible combinations of allelic identity using the following criteria. No genotypic pair could have more than 3 different alleles and the sum of differences from 5 pairs of genotypes must be less than or equal to 10, the observed sum of differences. We corroborated this analysis by performing a Monte Carlo simulation in which we randomly drew a specified number of pairs of individual genotypes from the observed population of females and then counted the number of times the sum of the differences in allelic identity across all pairs was less than or equal to the observed sum in 10,000 trials. In addition, we estimated the average level of relatedness between communally nursing female pairs using the regression technique of PAMILO (1984).

Results

Spatial Analyses

We captured a total of 93 mice (48 females and 45 males), recaptured 11 females and 10 males, and attached 35 transmitters. Since we estimated 35 home ranges from 5 to 68 x, y readings (samples) taken on 2 to 17 days per mouse, both number of samples or days radio-tracked might influence home range estimates. However, Spearman rank correlations were nonsignificant both for number of samples and home range size ($p = 0.18$ for MAP [0.5]; $p = 0.31$ for MAP [0.95], $N = 35$) and for number of days each mouse was radio-tracked and home range size ($p = 0.22$ for MAP [0.5]; $p = 0.15$ for MAP [0.95], $N = 35$). These results suggest that home range estimates based on just a few days of radio-tracking did

Table 1: Age and sex class estimates of mean home range (S.E.) in m²

	Male		Female		Kruskal-Wallis H
	Juvenile	Adult	Juvenile	Adult ¹⁾	
MAP (0.5)	0.57 (0.21)	0.73 (0.19)	0.37 (0.17)	0.23 (0.10)	9.86*
MAP (0.95)	1.65 (0.43)	2.66 (0.79)	1.12 (0.52)	0.75 (0.35)	9.73*
N	3	10	6	15	

* $p < 0.05$

¹⁾ Lactating or visibly pregnant. Excludes one non-lactating female.

Table 2: % overlap in MAP (0.95) utilization distributions for each age/sex combination

Age/sex combination	Mean (%)	S.D. (%)	N
Juv male — juv male	15.3	0.0	1
Juv male — ad male	15.8	17.3	9
Juv male — juv female	0.0	0.0	4
Juv male — ad female	11.8	11.5	6
Ad male — ad male	11.8	10.2	9
Ad male — juv female	4.6	11.2	8
Ad male — ad female	7.1	9.2	32
Juv female — juv female	0.0	0.0	1
Juv female — ad female	3.6	6.5	17
Ad female — ad female	8.5	12.0	36

not appreciably underestimate home range estimates derived from a week or more of data.

Although home ranges did not differ significantly between spring (Mar.—May, $N = 12$), summer (Jul.—Aug., $N = 15$), and fall (Sep., $N = 6$; Kruskal Wallis $H = 4.13$ for MAP [0.95]), we did find major differences between home range areas used by each age/sex category (Table 1). Lactating females or those in late pregnancy have small home ranges, i.e. MAP (0.95) < 1 m², whereas adult male home ranges exceed those of lactating females by a factor of 3.5. Since female house mice have a post-partum estrus, these differences in home range area suggest that polygamy could occur when females nest near each other as has been reported by others (CROWCROFT & ROWE 1963; REIMER & PETRAS 1967; LIDICKER 1976).

A significant difference in the location of home ranges over time occurred for 1 adult female and 3 adult males which were radio-tracked on two occasions separated by 6 months. Therefore, overlaps between UD's were calculated only for mice radio-tracked simultaneously, i.e. 123 pairs of mice. Although significant variation ($F = 1.99$, $p = 0.038$) among arcsine-squareroot (angular) transformed overlap estimates existed between the age/sex combinations, no obvious pattern can be discerned from the mean overlaps (Table 2).

An indication of the potential for polygamy can be obtained by counting the number of lactating or pregnant female UD's which have significant overlap with each simultaneously tracked adult male UD. If the resulting distribution of overlaps is clumped, this implies that few males had access to reproductively active females. Since the males we radio-tracked each month had different numbers of potential females to overlap, we calculated the proportion of radio-tagged female home ranges which had an overlap greater than 0.10 with each of the 10 adult males. For 6 of these males the proportion was 0, one male had a proportion of 0.25, and 3 males had proportions of 1. This distribution is nonrandom, i.e. it differs significantly from a Poisson distribution ($\chi^2 = 9.79$, $p < 0.01$). Thus, less than half of the adult males may be visiting females for mating. Although the difference in mean pairwise overlaps (mean 5.0 %, sd = 8.9 %)

between the 4 males with access to females and all other simultaneously tracked adult males (mean = 10.5 %, S.D. = 10.0 %, N = 8) is not significantly different (after angular transformation, $t = 1.506$, $p = 0.165$), the smaller overlap between males with access to females may imply that these males defend territories. In support of this idea, we noticed numerous smelly mounds of dried urine located along obvious mouse runways which might serve as signposts to demarcate individual males' territories (HARRINGTON 1976).

Five of the 36 pairs of lactating or visibly pregnant females that were radio-tracked simultaneously nested in identical locations. In one of these cases, both radios were recovered in a single nest. In the four other cases, one radio came off away from the nest site; however, in each case a nest was found where we inferred one was located. These 5 pairs of females had significantly higher MAP (0.95) overlaps (median = 20.4 %) than the other 31 pairs of simultaneously lactating or pregnant females (median = 3.1 %, $t = 2.86$, $p < 0.01$, Mann-Whitney U test). This frequency (5/36 or 14 %) of communal nesting is a minimal estimate because nonradio-tagged females could have shared nests with radio-tagged females.

In addition to the 5 pairs of radio-tagged females that communally nested, we have direct observations which implicate communal nesting in a sixth pair of mice. On Sep. 23 we pruned open the boards in the wall of the boxcar in search of an unattached transmitter and found a nest containing four 3-4-day-old pups. While looking at the pups two adult females approached the nest from within the wall. One of these females had a bare patch on her back revealing that she recently carried a transmitter and was lactating. The second female was pregnant (within 2 days of parturition) and had all her toes indicating that she had not been captured. These two females took turns carrying the pups from the exposed nest. Their cooperation, lack of hostility, and the impending parturition suggest that these two females subsequently reared both litters in a communal nest.

Genotypic Analyses

The genotypes at each of the five loci did not differ from Hardy-Weinberg expectations and the mean of the inbreeding coefficients ($F = 0.045$, S.E. = 0.055, standard error calculated by jackknifing z-transformed estimates of F , cf. SOKAL & ROHLF 1981) was not significantly greater than zero (Table 3). Furthermore, there was no evidence of gametic disequilibria since none of the 10 G-tests

Table 3: Genotype counts, allele frequencies, and inbreeding coefficients

Locus	Genotype Count				Allele Frequency			F
	FF	MF	MM	SM	F	M	S	
ESa	15	53	25		0.446	0.554		-0.153
ESb	87	4	2		0.957	0.043		0.071
ESc	33	44	17		0.585	0.415		0.036
ESd	51	24	6		0.778	0.222		0.143
IDH	34	39	20	1	0.569	0.426	.005	0.141

Table 4: Genotypic similarity between 5 pairs of suspected communally nursing females

Julian Date	Genotype at each locus					No. of different alleles
	ESa	ESb	ESc	ESd	IDH	
63	SF	FF	SF	SF	SS	2
	SF	FF	SF	FF	SF	
188	FF	FF	FF	FF	FF	3
	SF	FF	SF	FF	SF	
218	FF	FF	SF	FF	SF	1
	SF	FF	SF	FF	SF	
258	FF	FF	SF	FF	SF	1
	FF	FF	SS	FF	SF	
260	FF	FF	SF	FF	SF	3
	FF	FF	SF	SS	FF	

for association between each pair of loci were significant. These results are consistent with the assumptions of random mating and independent assortment.

When all simultaneously tracked pairs of mice are considered, no relationship exists between genotypic similarity and UD overlap. The Spearman rank correlation between MAP (0.95) UD overlap and the sum of allelic differences across all 5 loci was not significant ($r = 0.04$). However, the five pairs of females which nested communally had overlapping UD's and significantly similar genotypes (Table 4). The Monte Carlo simulation gave a probability of 0.04 that 5 pairs of genotypes which were as or more genetically similar than the genotypes of the 5 pairs of communally nesting mice would occur together by random sampling. Given the population allele frequencies and assuming random mating and independent assortment, the probability of randomly drawing 5 pairs of mice with no pair having more than 3 different alleles at all 5 loci and the sum of differences from all 5 pairs being less than 10, as was observed, is 0.03. If all 5 pairs were full-sibs, the probability of obtaining this or greater similarity is 0.81. Thus, the Monte Carlo simulation confirms that communally nesting females are more genetically similar than expected by chance but not significantly more or less similar than full-sibs. Note that these genotype pairs are undoubtedly compatible with some levels of relatedness less than 0.5. The regression technique of PAMILO (1984) estimates that the average coefficient of relatedness within each of the 5 pairs is 0.13 (S.E. = 0.11). Given the small number of individuals per group and the small number of groups, this probably underestimates the true relatedness (WILKINSON & McCracken 1985).

Discussion

This study provides evidence for genetic assortment among communally nesting females. Several mechanisms, such as assortative dispersal, natal philopatry, and phenotype matching among females, might operate to explain

these data. Unfortunately, we have very little information on dispersal patterns. We tracked one adult female 45 m away from the boxcar on one night, but all other radio-tracked females remained in or near the boxcar. The one female which we tracked again 6 months later nested on the opposite side of the boxcar during the second tracking session. Average recapture distance for females living in buildings has been reported as 11 feet (YOUNG et al. 1950), 3.78 m (BROWN 1953), and 12.13 m (MACLEOD 1959). Clearly, even though a female may have a small home range during lactation, she does not necessarily remain in a small area all her life. Thus, locally stable breeding groups probably do not occur in our or many other populations (MYERS 1974, FITZGERALD et al. 1981). Our inability to detect significant inbreeding is consistent with this interpretation. Given the relatively small area in which our females were breeding, their single food source and apparently successive nest movements (also reported by SINGLETON 1983) we doubt that natal philopatry could be sufficient to explain the nesting patterns we observed. We conclude that some female mice actively choose nursing partners based on past association or a phenotypic cue. Direct assessment of genotypic similarity by smell by adult females is plausible given that congenic female mice differentiate between potential mates on the basis of H-2 (YAMAZAKI et al. 1976) and t-allele (LENINGTON & EGID 1985) haplotypes.

Communal nesting could provide a relative reproductive advantage to both participants if 1) communal litters have improved heat retention which improves pup survival or growth, 2) fewer pups are lost to predators because the nest is guarded at more times than if only one mother cared for pups or 3) communally reared pups grow faster due to increased milk production by two females which share nursing duty (SAYLOR & SALMON 1969, 1971). While hypothesis 1 cannot be dismissed, it appears insufficient to account for communal nests in months (Table 4) which differ in mean temperature by more than 20 °C. In *M. pennsylvanicus* some thermoregulatory advantage is more plausible since communal nesting is more common in the colder months (MADISON et al. 1984). Predation on pups from non-conspecific predators is probably rare because nests were either inside a wall or underground. Hypothesis 2 may be important, however, if communal nesting aids in the defense of litters from infanticidal males or females, which has been observed in laboratory populations of wild (LABOV 1980; JAKUBOWSKI & TERKEL 1982) and inbred house mice (reviewed in VOM SAAL 1984). In a captive situation, males are not tolerated near a communal nest and are attacked by the nursing partners (PARMIGIANI 1984; VOM SAAL 1984). For the third hypothesis to operate, food must be non-limiting. Even though horse feed was always available within the shed, litter size for three nests located in the field was much less (2, 3 and 4 pups) than the number of fetuses in three pregnant females killed by dogs (5, 6 and 7 fetuses) or the number of pups born to wild Colorado mice in the lab (mean = 7.0, S.D. = 1.6, N = 5). Although these samples are small, they suggest that either appropriate food is limiting, or there is some cost, such as a higher risk of predation, associated with increased food intake in the field which would limit this advantage of communal nursing.

In captivity some wild *M. domesticus* females take turns nursing each other's pups in a communal nest (pers. obs.). Since we tracked 5 pairs of lactating females

to the same nest site, we strongly suspect that both mice nursed either a single litter or a joint litter. If true, this is surprising even if one of the mutual advantages to communal nesting listed above is operating. Whatever the advantage, a conflict over nursing duty is expected since all females in an outbred population should, in an evolutionary sense, prefer multiple mothers for their own pups but not for potential competitors' pups. Outcomes of this conflict could be all females being selfish and nursing their own offspring as predicted by individual selection, all females in a small area cooperating independent of relatedness or prior association within groups as predicted by group selection (WADE 1978), or differential communal nursing based either on relatedness as predicted by kin selection (HAMILTON 1964) or on probability of future association as predicted by reciprocity (TRIVERS 1971; AXELROD & HAMILTON 1981).

If the females which used the same nesting site did nurse each others' pups, the genotypic data implicate kin rather than group selection as one mechanism favoring communal nursing among house mice. Furthermore, the home range data fail to support the existence of small, socially-isolated groups as required for either inter- or intra-demic selection to operate. But, could reciprocity also operate? Long-term reciprocity would require that two females combine litters often during their lifetimes. Reciprocity on this time-scale would exert a much weaker selective pressure than kin selection because the magnitude of the selective advantage will be proportional to the number of opportunities for reciprocation (WILKINSON 1988). This number should be small since most female house mice probably produce few litters during their lifetimes. Short-term reciprocity, on the other hand, may ensure cooperation between lactating partners. Females could monitor each other's nursing periods to ensure that neither "cheats" by expending less milk than the other. Such behavior would result in reciprocal feeding bouts of similar duration. In the laboratory, communally nursing wild mice appear to alternate roles in just this way (unpubl. data). Such reciprocal nursing would be further facilitated if the young are of equal age because the energetic demands of the pups from each litter would be similar. Communal nursing could, therefore, provide a previously unrecognized selective advantage for induced estrous synchrony such as occurs in some female rodents that nest in close proximity (J. EISENBERG pers. comm.) and in evening bat nursery colonies where all females give birth within a 36-h period and are reported to nurse communally (WATKINS & SHUMP 1981).

Communal nursing has been reported for an ecologically diverse assemblage of species (see reviews by HRDY 1976; RIEDMAN 1982; GITTLEMAN 1985). Careful recent work on some of these species has revealed that females rarely share much milk with offspring other than their own. For example, McCracken (1984) has shown that only 17% of adult female-pup Mexican free-tailed bat pairs represented mothers nursing pups other than their own. Captive experiments have demonstrated that even though these females deposit their young in creches containing thousands of pups, they use acoustic (GELFAND & McCracken 1986), olfactory (GUSTIN & McCracken 1987) and presumably spatial information to locate and identify their young. Communal nursing appears to occur as pups try

to steal milk from mothers searching for their young (McCracken 1984). Similarly, LEE (1987) reports that out of 1865 nursing bouts observed in African elephants only 3.7 % involved a female nursing another's calf. We do not believe, however, that all suspected examples of communal nursing are invalid. Regular sharing of nursing duty clearly does occur in capybara (MacDONALD 1981), wild boar (DELCROIX et al. 1985), meadow voles (McSHEA & MADISON 1984; SHERIDAN & TAMARIN 1986) and lion (BERTRAM 1976) in addition to house mice. In these cases some females appear to be expending substantial resources in feeding offspring other than their own. Although we agree with GITTLEMAN (1985) that communal care often correlates with protracted development and delayed sexual maturity, the rodent examples clearly contradict that trend. Thus, we urge other field workers to look for evidence of communal nursing particularly in species which form communal nests. Recall that a rare behavior, such as predation, can be selectively important. The important evolutionary question, therefore, is not how often individuals nurse each other's young, but what are the costs and benefits of communal nursing.

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