

Communal nursing in prairie dogs

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Summary. Within a natural population of black-tailed prairie dogs (*Cynomys ludovicianus*), 68% of sampled juveniles received milk from foster mothers via communal nursing (Table 1). In proximate terms, communal nursing may result because prairie dog mothers seem unable to discriminate between their own and others' offspring. In ultimate terms, both indirect selection and reduced predation on juveniles resulting from the formation of multilitter groupings have probably been important in the evolution of communal nursing.

Introduction

Black-tailed prairie dogs are large (500–1,000 grams for adults, who are ≥ 2 years old), diurnal, burrowing, herbivorous, colonial, harem-polygynous, cooperatively breeding rodents of the squirrel family (Sciuridae) (King 1955; Hoogland 1981). Colony residents live in contiguous, territorial family groups called coterie (King 1955), which typically contain 1 adult male, 3–4 adult females, and several yearling and juvenile offspring (Hoogland 1986). Our study colony in Wind Cave National Park, South Dakota, USA, is 6.6 hectares in size, and in late spring contains approximately 130 adults and yearlings and 80 juveniles (Hoogland 1983). Because they are highly philopatric, females in the same coterie are almost always close kin, but males disperse from the home coterie before sexual maturity (Hoogland 1982). Prairie dogs in South Dakota copulate in February and March, and gestation lasts for 5 weeks (Hoogland and Foltz 1982).

For the first 5–6 weeks after parturition, prairie dog mothers rear their young in isolated burrow systems which they attempt to defend from all conspecifics (Hoogland 1985). Mothers usually nurse their young during the night or early in the morning before coming aboveground. Unweaned young first emerge from the natal burrow to start feeding on vegetation in May and June. Shortly after they first emerge, young from different litters within the home coterie begin to interact aboveground (Hoogland 1979), and soon start sleeping together at night with one or more mothers. First mixings occur 6.2 ± 4.5 days (mean \pm SD) after the first emergence (range = 0–33, $n = 240$ litters through 1987), and result from the wanderings of the juveniles themselves or when mothers transfer their young from the home burrow to another burrow containing another mother's young. In 1986 and 1987 we investigated the possibility that mothers (foster mothers) might sometimes suckle the post-emergent juvenile offspring of other females (foster offspring) within the home coterie.

Materials and methods

We have seen only 5 cases of aboveground suckling in 15 years. Consequently, we were unable to use behavioral observations to investigate communal nursing. Instead, we used a technique that would allow us to trace the passage of the following uniquely identifiable gamma-emitting radionuclides from mothers to juveniles: ⁶⁰Co, ⁵⁴Mn, ⁷⁵Se, ¹¹³Sn, ⁸⁵Sr, and ⁶⁵Zn (Tamarin et al. 1983; Morimoto et al. 1985). Suspected foster mothers were intraperitoneally injected with 15 microcuries of radionuclide (1 radionuclide per dog per coterie); 2–3 days later (to allow time for transfer of radionuclide from mother to juvenile), scat samples were collected by Hoogland as they were excreted from the relevant juveniles. Within 2–6 weeks after collection, samples were checked for radionuclide at Boston University by Tamarin and Levy, who knew nothing about either the identity of injected prairie dogs or juvenile sleeping patterns.

Table 1. Documentation of communal nursing in prairie dogs in 1987. Sixty-eight percent of all sampled juveniles (25/37) showed evidence of communal nursing, and at least one juvenile communally nursed in 14 of the 16 sampled litters (88%); 25 different foster juveniles, 13 different foster mothers, and 8 different coteries were implicated. At an undetermined frequency, communal nursing was also detected in 1986

Litter designation	Number of babies	Number of babies whose scats were examined for radionuclide	Babies that receive radionuclide from real mother only	Babies that receive radionuclide from foster mother only	Babies that receive radionuclide from both real and foster mother
TSX	4	3			3
WA3X	2	2			2
HBBX	4	2			2
RSX	5	2	1		1
RABX	4	3			2
5X	4	2	1		1
5strX	4	1			1
5SBSX	2	2			2
7X	4	2		1	1
HRSX	5	4		4 ^a	
WA2X	4	4	2		2
6X	4	1		1 ^a	
3SBSX	4	3	1		1
HX	4	1			1
BB8X	3	1			
WAR SX	4	4			
Totals	61	37	5	6	19

^a For these litters, the real mother was not injected with radionuclide

Results

Twenty-five of the 37 prairie dog juveniles (68%) whose scats were examined showed radionuclide from a foster mother (Table 1). At least one juvenile from 14 of the 16 examined litters (88%) showed evidence of communal nursing. As expected, most sampled juveniles also received radionuclide from their own mothers (Table 1). All cases of communal nursing occurred after first juvenile emergencies, when young were at least 6 weeks old. Mothers seemed just as likely to suckle others' offspring as their own offspring when presented with a choice.

Radionuclide could possibly transfer from one injected prairie dog to another by means other than nursing. For example, transfer could occur during oral kissing and licking, anal sniffing and licking, or ingestion of urine and feces (King 1955; Hoogland 1986). If so, then our estimates of communal nursing might be meaningless. We investigated this possibility in two ways. First, we looked for, but failed to find, radionuclide in scats of 41 adult males and females that regularly interacted and slept with injected mothers. Second, we injected 7 males and 3 nonlactating females that regularly interacted and slept with recently emerged juve-

niles, and then collected scats from the relevant juveniles. Radionuclide never transferred from any of the males or nonlactating females to any of the 68 juveniles sampled. These results show that the transfer of radionuclide from foster mothers to juveniles occurred by communal nursing rather than by some other route.

Discussion

Communal nursing has been observed in numerous other mammalian species (Bertram 1976; Hrdy 1976; Rood 1980; Reiter et al. 1978; McCracken 1984), but the frequency has always been much lower than the 68% reported here.

In some species that show communal nursing, mothers seem to willingly suckle foster offspring (Bertram 1976; Riedman 1982; Reiter et al. 1978; MacDonald and Moehlman 1982). In other species, communal nursing seems to result because juveniles "steal" milk, surreptitiously or otherwise, from unwilling foster mothers (Hrdy 1976; Reiter et al. 1978). Prairie dog females, as noted above, frequently transfer their just-emerged offspring into a burrow containing juveniles from another litter, and then evidently suckle both their own and foster juveniles. Further, we never saw a

mother reject a foster juvenile that wandered near or into a burrow containing her own offspring. Thus, prairie dog foster mothers seem to be willing participants in communal nursing.

We did not systematically investigate how long suckling of real or foster offspring continues beyond first juvenile emergence. Weaning may be complete for certain litters upon first emergence; for example the BB8X and WAR5X litters in Table 1 evidently did not receive milk from either real or foster mothers after first emergence. On the other hand, juveniles from one litter in 1987 received radionuclide from two different foster mothers as long as 14 days after first emerging.

We assume that there is a cost for mothers associated with communal nursing, since milk dispensed to grandoffspring and nondescendent kin could presumably be channeled directly to offspring. Similarly, we assume that juveniles benefit from additional milk obtained through communal nursing. We did not attempt to measure either the cost to mothers or the benefit to juveniles that results from communal nursing. It is important to remember that communal nursing only occurs after the period of 5–6 weeks of early lactation when juveniles are nursed exclusively by their own mothers. Consequently, any maternal cost of communal nursing associated with lost milk is probably small compared to the cost of producing milk exclusively for offspring for the 5–6 weeks prior to first juvenile emergence.

What are possible benefits of communal nursing, and why does it occur? In proximate terms, communal nursing may result because prairie dog mothers seem unable to discriminate between their own postemergent juvenile offspring and other juvenile kin and seem willing to suckle any juvenile that enters the home burrow (Table 1 and Hoogland 1979, 1986, unpublished data). Perhaps the maternal cost of trying to discriminate between juvenile offspring and other juvenile kin following interlitter mixing outweighs the cost of lost milk. In this scenario, prairie dog foster mothers are similar in some ways to avian foster parents that are victims of intra- or interspecific brood parasitism (Payne 1977; McKaye 1985; Brown 1988). We emphasize that we have not demonstrated here or elsewhere that prairie dog mothers *cannot* discriminate between their own juvenile offspring and other juvenile kin following first juvenile emergences, but only that such discriminative nepotism is not evident from our behavioral observations. In other circumstances where the cost/benefit ratio is different (as when choosing a mate; see Hoogland 1982), perhaps prairie dogs, like other squir-

rels in certain circumstances (Holmes and Sherman 1982; Armitage 1987), *are* able to discriminate between offspring and other types of kin.

Our methodology for investigating communal nursing allowed us to specify that a juvenile *did* or *did not* receive milk from a specific female, but did not allow us to determine *how much* milk was received by each juvenile. It is possible that mothers consistently dispensed more milk to their own offspring than to foster offspring (i.e., discriminative nepotism), but this seems unlikely.

In ultimate terms, communal nursing may lead to increased reproductive success in two ways. The first way concerns predation, which is especially heavy on recently emerged juveniles (Hoogland 1981). By mixing with young from other litters and thereby forming large multilitter groupings within the home coterie, young probably reduce predation on themselves through increased awareness of predators (Hoogland 1981), “selfish herd effects” (Hamilton 1971), or “protection by dilution” (Bertram 1978; McKaye 1981, 1985). By suckling the juveniles of other females, a mother increases the probability that these foster juveniles will cluster around her own offspring. Thus, prairie dog mothers may willingly pay the cost of communal nursing in order to obtain the benefits of multilitter groupings for their own offspring. Multilitter groupings will only be beneficial if predators typically take one member of, rather than the entire, grouping (Hamilton 1971; McKaye and McKaye 1977), and this is the case for prairie dogs (Hoogland 1981, unpublished data).

Since females within the same coterie are always close kin (Hoogland 1982, 1986), beneficiaries of communal nursing are genetically related to their foster mothers. Thus, selection involving grandoffspring as well as indirect selection (kin selection [Hamilton 1964; Maynard Smith 1964] involving nondescendent kin only [Brown 1987]) may be a second ultimate explanation for communal nursing in prairie dogs. For example, mothers may sometimes increase inclusive fitness (Hamilton 1964) more by suckling hungry juveniles of close kin than by suckling their own well-fed offspring. Juvenile kin that suckle foster mothers would not only receive the benefit of additional milk, but would also experience those benefits from multilitter groupings realized by the foster mothers’ own offspring. Indirect selection for communal nursing may be especially important in those cases when the mother disappears shortly after her offspring first emerge from the natal burrow, as occurred for 9 of 352 litters (3%) that emerged at the study colony in 1975–1987.

Among ground-dwelling squirrels (*Marmota* spp., *Spermophilus* spp., *Tamias* spp., *Eutamias* spp., *Cynomys* spp.), which are among the best studied of mammals in terms of social behavior, the mixing of young from different litters shortly after the first emergences from underground nests seems to be ubiquitous (Hoogland 1979; Murie and Michener 1984). Further, two or more lactating mothers sometimes share the same burrow from parturition through first juvenile emergence – so that communal nursing would be especially likely and the cost of lost milk might be especially high – in yellow-bellied marmots (*Marmota flaviventris*) (Armitage 1984), Richardson's ground squirrels (*Spermophilus richardsonii*) (L.S. Davis, personal communication), Gunnison's prairie dogs (*Cynomys gunnisoni*) (Rayor 1988), and white-tailed prairie dogs (*Cynomys leucurus*) (Hoogland, unpublished data). For these reasons, we hypothesize that communal nursing is not limited to black-tailed prairie dogs, but rather that it is widespread among other species of ground-dwelling squirrels as well.

In our same population where females suckle the postemergent offspring of close kin (Table 1), lactating females often kill the pre-emergent offspring of close kin within the home coterie (Hoogland 1985). Infanticide in this context leads to the partial or total elimination of 30% of all litters born ($n=57$ cases at the study colony through 1987, involving 33 different killers). Our data from 19 foster mothers indicate that certain females are killers who do not later become foster mothers, while other females are foster mothers who never kill. Although extreme variation in the behavior of individuals toward kin has been documented in insects (Hamilton 1972), birds (Koenig and Mumme 1987), and mammals (Hausfater and Hrdy 1984), variation of the magnitude reported here for prairie dogs – from infanticide to communal nursing – may be unique. One explanation for the shift from infanticide to communal nursing may be related to parent-offspring recognition, as suggested above. When young juveniles of different litters are isolated in burrow systems, it is probably easy for the mothers to discriminate between their own home burrows containing their own offspring (as targets for nursing) and other home burrows containing the offspring of other females (as targets for infanticide). Following the first emergences of older juveniles and interlitter mixing, it may be too costly for mothers to discriminate between their own and others' offspring... with the result that infanticide ceases and communal nursing becomes common. Another possible explanation for

the shift is that the usefulness of others' offspring varies with time. Early in lactation (March–April) when herbaceous food is especially scarce (King 1955), others' offspring may be most useful as sources of sustenance from the cannibalism that typically follows infanticide (Hoogland 1985). Later in lactation (May–June) when herbaceous food is abundant and juveniles are larger and more difficult to kill, others' offspring may be most useful for the formation of multilitter groupings with one's own offspring via communal nursing. In this explanation, both infanticide and communal nursing represent selfish behaviors by which mothers attempt to rear their own offspring at the expense of others' offspring.

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