

# Nursing of own and foster offspring by Utah prairie dogs (*Cynomys parvidens*)

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**Abstract** From 1995 through 2005, I studied nursing among Utah prairie dogs (*Cynomys parvidens*) living under natural conditions at Bryce Canyon National Park, UT, USA. I observed 850 aboveground nursings, which involved 122 mothers and 248 juveniles from 134 litters. Most of the mothers that nursed aboveground were middle-aged, and most nursing juveniles had been coming aboveground for 1–3 weeks. Most nursings involved a single juvenile, lasted 1–10 min, and occurred between 1800 hours and 2000 hours. Seventy-five percent of nursings (598/796) involved a mother suckling her own juvenile offspring; the other 24.9% (198/796) involved a mother suckling another mother's offspring (i.e., communal nursing). Communal nursings involved juveniles of the home territory, and many communal nursings (74/198=37.4%) involved close kin such as half-siblings, grandoffspring, full-nieces, and full-nephews; other communal nursings (37/198=18.7%) involved more distant kin such as full-second cousins and full-third cousins. Of seven hypotheses that might explain the evolution of communal nursing, evidence supports the importance of two: elevated inclusive fitness via indirect selection and communal nursing as a cost of coloniality.

**Keywords** Coloniality · Communal nursing · *Cynomys parvidens* · Foster offspring · Inclusive fitness · Utah prairie dog

## Introduction

The production of milk by female mammals is essential for the survival of offspring. Milk provides nutrition to juveniles that nurse and also provides antibodies for the constant battle against parasites and diseases (Baker 1984; Roulin and Heeb 1999; Sams et al. 1996). Lactation imposes certain costs for the mother, however. Nursing takes time, for example, and the production of milk requires resources that a mother could otherwise use for maintenance or growth (Boyd 1998; Clutton-Brock et al. 1989; Loudon 1985). These considerations suggest that natural selection should favor mothers who nurse only their own offspring. Consequently, communal nursing—i.e., when a mother (“foster mother” or “allomother”) gives milk to another mother's offspring (“foster offspring”, “alien offspring”, or “allosuckler”)—should be rare. Paradoxically, however, biologists have reported communal nursing for >100 species (Hayes 2000; König 1994a; König 1994b; Packer et al. 1992; Pusey and Packer 1994; Riedman 1982; Roulin 2002; Wilkinson 1992).

Table 1 lists seven hypotheses that might explain communal nursing for wild mammals (Packer et al. 1992; Roulin 2002); Table 1 also shows predictions that follow from these hypotheses. A few other species-specific hypotheses might explain other cases of communal nursing ((Roulin 2002), p. 206), and overcrowding and unlimited food might explain cases of communal nursing among captive mammals (Dittrich 1968; Fogden 1971; Hayes 2000; König 1994a; Packer et al. 1992; Saylor and Salmon 1971).

The seven hypotheses of Table 1 are not mutually exclusive because different mechanisms might work simultaneously and synergistically. By suckling the offspring of other mothers, for example, a mother might increase the probability that the foster offspring will cluster around her

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**Table 1** Hypotheses that might explain why mothers sometimes nurse foster offspring

Hypothesis that might explain communal nursing	Species to which this hypothesis might apply	Predictions from this hypothesis	References
H1, adaptive: communal nursing provides experience to young foster mothers	Dwarf mongooses? Northern elephant seals?	Foster mothers should be young, inexperienced females Young females that do not give birth or lose their unweaned offspring should nurse foster offspring	(Creel et al. 1991; Riedman and LeBoeuf 1982)
H2, adaptive: foster mothers get rid of surplus milk that their own young have not consumed—i.e., via communal nursing, foster mothers lose body mass and are better able to fly, swim, or run	Evening bats, northern elephant seals	Mothers should produce more milk than their offspring can consume Nursing of foster offspring should occur most commonly after a mother has exclusively nursed her own offspring Mothers with small litters should nurse foster offspring more often than mothers with larger litters	(Pusey and Packer 1994; Riedman and LeBoeuf 1982; Roulin 2002; Wilkinson 1992)
H3, adaptive: via indirect selection, foster mothers increase inclusive fitness by nursing offspring of kin	African elephants, African lions, black-tailed prairie dogs, dwarf mongooses, Utah prairie dogs	Foster offspring should be the offspring of kin Foster offspring should be close kin rather than more distant kin	(Bertram 1976; Creel et al. 1991; Dublin 1983; Hoogland 1995; Pusey and Packer 1994); this study
H4, adaptive: via reciprocity, foster mothers rear more offspring when they share nursing of own and foster offspring with other foster mothers	None?	Reciprocal mothers should communally nurse at approximately equal frequencies Foster mothers should suckle foster offspring of only those mothers that nursed the foster mother's own offspring Survivorship of own offspring should be higher for mothers that communally nurse than for mothers that do not	(Pusey and Packer 1994; Riedman 1982; Roulin 2002)
H5, adaptive: communal nursing leads to reduced predation on own offspring because communally nursed foster offspring are more likely to remain near own offspring	Black-tailed prairie dogs		(Hoogland 1995)
H6, adaptive: communal nursing increases the quality and quantity of foster mother's milk and the production of antibodies for the foster mother herself and for her milk	Domestic pig?	Because of more antibodies, foster mothers and their foster offspring should survive better than mothers and juveniles that do not engage in communal nursing Foster mothers should produce more milk of higher quality, and own offspring should therefore survive better	(Auld et al. 2000; Roulin 2003)
H7, non-adaptive: communal nursing is a cost of coloniality—i.e., misdirected maternal care results because mothers cannot, or do not, discriminate between own and foster offspring	Black-tailed prairie dogs, Mexican free-tailed bats, Utah prairie dogs	When juveniles from different litters begin to mingle, mothers should not discriminate between their own and others' offspring The cost of communal nursing should be low	(Hoogland 1995; McCracken 1984); this study

Note that some of the benefits listed here go directly to the foster mother, others go to both the foster mother and the foster mother's own offspring. Scientific names for mammals in this table, in the order presented, are as follows: dwarf mongoose, *Helogale parvula*; northern elephant seal, *Mirounga angustirostris*; evening bat, *Nycticeius humeralis*; African elephant, *Loxodonta africana*; African lion, *Panthera leo*; black-tailed prairie dog, *Cynomys ludovicianus*; Utah prairie dog, *Cynomys parvidens*; domestic pig, *Sus scrofa*; and Mexican free-tailed bat, *Tadarida brasiliensis*.

own offspring, who then will experience higher survivorship versus predation because of the “dilution effect” (Bertram 1978; Hamilton 1971; Hoogland et al. 1989; McKaye 1981; McKaye and McKaye 1977). The same mother might further increase her inclusive fitness via “indirect selection”—which occurs when individuals behave preferentially toward non-offspring-kin such as full-nieces, full-nephews, full-first cousins, and full-second cousins (Brown 1987)—if the clustering foster offspring whom she nurses are the offspring of close kin (Grafen 1982; Hamilton 1964; Maynard Smith 1964; West-Eberhard 1975).

Foster offspring will almost always benefit from receiving milk from foster mothers, so natural selection for juveniles that try to suckle non-mothers is easily explicable. Benefits from communal nursing for the foster mother are more difficult to understand and sometimes go directly to the foster mother (e.g., H1 and H2 of Table 1). Other times, foster mothers gain from communal nursing when benefits go directly to their own offspring (H5), or to both themselves and their own offspring (H6).

Utah prairie dogs (*Cynomys parvidens*) are rare, herbivorous, colonial, ground-dwelling rodents of the squirrel family (Sciuridae) (Hoogland 2003a; Hoogland 2003b; Pizzimenti 1975; Pizzimenti and Collier 1975; Roberts et al. 2000; Wright-Smith 1978). As for other animals (Alexander 1974; Brown and Brown 1996; Hoogland 1979; Hoogland and Sherman 1976), coloniality for Utah prairie dogs involves significant costs, such as increased competition, increased probability of contracting diseases and parasites, and increased probability of misdirected parental care because of the mixing-up of juveniles from different litters. The primary benefit of coloniality for Utah prairie dogs, as for other species of prairie dogs (Hoogland 1981; Hoogland 1995), is most likely lower predation (Hoogland 2003a; Hoogland 2007). When compared to individuals in smaller colonies, individuals in large colonies probably detect predators more quickly, spend less time scanning for predators, and also benefit from “selfish herd” effects (Hamilton 1971; Vine 1971) and “protection by dilution” (Bertram 1978; McKaye and McKaye 1977; Williams 1994).

Utah prairie dog mothers commonly nurse juveniles aboveground and thus differ radically from other species of ground-dwelling squirrels in general (e.g., (Armitage 1984; Dobson et al. 1999; Holmes and Sherman 1982; Michener 1989)) and from other species of prairie dogs in particular (Hoogland 1995; Hoogland 2003a). Utah prairie dogs thus offer an unusual opportunity to study communal nursing. From research that spanned 11 years, I have three objectives in this report: (a) to quantify the details of nursing either own or foster offspring (time of year, time of day, ages of nursing mothers and nursing offspring, and so

forth)—good information on this topic is available for few other mammals and for no other ground-dwelling squirrels; (b) to determine how many aboveground nursings involve foster offspring—i.e., to determine the frequency of communal nursing; and (c) to investigate which hypotheses in Table 1 might help to explain communal nursing among Utah prairie dogs.

## Materials and methods

### The study animal

On a typical day, Utah prairie dogs emerge from their burrows at dawn and forage aboveground until dusk. Within colonies, individuals live in territorial family groups called *clans*, which typically contain one adult ( $\geq 11$  months old) male and two to three adult females (Hoogland 2003a; Hoogland 2007; Wright-Smith 1978). Terrestrial predators include American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), and red foxes (*Vulpes vulpes*); avian predators include golden eagles (*Aquila chrysaetos*), northern goshawks (*Accipiter gentilis*), and prairie falcons (*Falco mexicanus*) (Hoogland et al. 2006).

Female Utah prairie dogs usually attain sexual maturity and mate as yearlings in their first spring after weaning, when they are about 11 months old, but males commonly do not attain sexual maturity until they are 2 years old (Hoogland 2001; Hoogland 2003a; Hoogland 2007). Most females remain in the natal clan territory for life—so that other females of the home clan are usually kin such as mothers, daughters, full-sisters, half-sisters, full-nieces, half-nieces, full-first cousins, and so forth. Males, by contrast, usually disperse from the natal clan territory before mating for the first time. Survivorship in the first year is usually  $<50\%$  for both sexes (Hoogland 2001). Females sometimes live as long as 8 years, and males sometimes live as long as 7 years (unpublished data).

Each mother gives birth underground in an isolated nursery-burrow, and her offspring remain underground in that nursery-burrow for about 5.5 weeks. Juveniles first appear aboveground in late May or early June. Neonates depend almost exclusively on milk for nutrition; older juveniles also depend on milk before first emergence but consume vegetation brought into the nursery-burrow by the mother as well. Weaning is a gradual process that is not complete until 1–4 weeks after juveniles first appear aboveground. All nursings described below occurred aboveground, after juveniles had first emerged from their nursery-burrows.

My study colony of Utah prairie dogs at Bryce Canyon National Park, Utah, inhabited 5.8 ha and, in March of each

year, contained a mean  $\pm$  standard deviation (SD) of  $117.5 \pm 45.5$  adults, who produced a mean  $\pm$  SD of  $158.7 \pm 57.4$  offspring that emerged from their nursery-burrows each spring (Hoogland 2001; Hoogland 2007; Hoogland et al. 2006). Of 1,739 juveniles weaned at the study colony from 1995 through 2005, 887 (51.0%) were males and 852 (49.0%) were females.

#### Capture and marking

Each year, the students and I captured and marked every Utah prairie dog at our study colony. To capture adults, we used double-door live traps ( $15 \times 15 \times 60$  cm), and for juveniles, we used smaller single-door live traps ( $13 \times 13 \times 40$  cm; Tomahawk Live trap Company, Tomahawk, WI, USA). For permanent identification of individuals, we inserted one fingerling ear tag into each ear (National Band and Tag Company, Newport, KY, USA). To identify Utah prairie dogs from a distance, we applied unique markers to the pelage of each adult with Nyanzol-D black dye (Greenville Colorants, Clifton, NJ, USA). We marked all the juveniles from the same litter with the same marking pattern and put a small black “cap” on the head of each juvenile male so that we could distinguish males from females. Using binoculars and 2-m towers, we observed marked individuals everyday from dawn until dusk from March through June of 1995 through 2005 (Hoogland 2001; Hoogland 2007; Hoogland et al. 2004; Hoogland et al. 2006). Because the number and density of Utah prairie dogs were highest around my tower, I observed and recorded >95% of the aboveground nursings summarized below. Verifying the presence (or absence) of a black cap on a marked juvenile’s head was not always possible from a distance, or when a suckling juvenile had its head buried in the fur of the nursing mother; consequently, we could verify the sex of only 68.6% (583/850) of the juveniles that nursed aboveground.

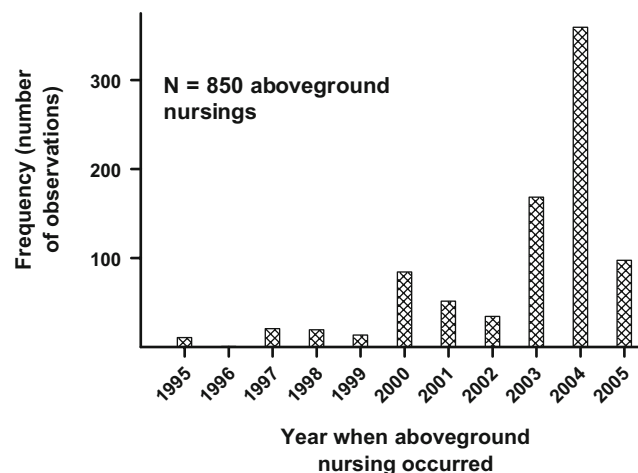
Because Utah prairie dog mothers reared their offspring in separate nursery-burrows, maternity usually was easy to establish. By surrounding entrances to nursery-burrows with live traps on the day after juveniles first appeared aboveground, students and I captured, ear-tagged, and marked >95% of all littermate siblings before they mixed with juveniles from other litters (see also (Hoogland 1995; Hoogland 1999)). We determined the longevity and reproductive success of these juveniles over time and thereby gradually learned kinships among residents of our study colony. For this report, I only use maternally derived kinships. An analysis of paternally derived kinships is underway but is incomplete to this point—in part because Utah prairie dogs have so little genetic variation for biochemical analyses of paternity (Haynie et al. 2003; Roberts et al. 2000). I assumed that littermate siblings were

full-siblings (same mother, same father), but at least some were littermate maternal half-siblings (same mother, different father, born in same year; (Haynie et al. 2003); see also (Hoogland 1995)).

Regarding kinship with the nursing mother, I categorized each juvenile as (a) offspring, for which the coefficient of genetic relatedness,  $r$  (Hamilton 1964), was 0.500; (b) close non-offspring-kin such as non-littermate maternal half-siblings (same mother, different father, born in different years), grandoffspring, great grandoffspring, full- and half-nieces/nephews, full-grandnieces/grandnephews, and full-first cousins, for which  $0.500 > r \geq 0.125$ ; (c) distant kin such as half-first cousins and full-second cousins, for which  $0.125 > r \geq 0.003$ ; or (d) more distant kin for which  $r > 0$ .

Until their offspring appeared aboveground, mothers defended their nursery-burrows from other Utah prairie dogs. Consequently, except when attempting to steal nest-material, mothers did not enter the nursery-burrows of other mothers, and underground nursing of another mother’s pre-emergent offspring evidently did not occur. All nursings reported here occurred aboveground and involved (a) mothers that had their own living juvenile offspring and (b) juveniles that had already first emerged from their nursery-burrows.

From 1995 through 2005, the students and I observed  $\geq 6$  aboveground nursings in every year except 1996 (Fig. 1). From 1995 through 1999, all observations of aboveground nursings were fortuitous, because we were concentrating on experiments to study alarm calling (Hoogland 2007). These experiments were also important in 2000 through 2002,



**Fig. 1** Observations in different years of aboveground nursing among Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005. Sometimes, a mother nursed greater than or equal to two juveniles at the same time (Fig. 7). For this and other figures (except Fig. 7), I scored greater than or equal to two juveniles nursing the same mother at the same time as greater than or equal to two separate cases of nursing



when our emphasis started to switch from alarm calling to aboveground nursing. In 2003 through 2005, our primary focus was aboveground nursing. The higher frequency of aboveground nursings in 2003 through 2005 almost certainly resulted from more attention to this issue in those years.

### Collection of data

When the students and I observed aboveground nursing, we recorded the mother, the juvenile(s) nursing, the time of day, the location within the study colony where the nursing occurred, and the duration of the nursing. All *P* values resulted from two-tailed parametric statistical tests. I considered data from the same female in different years to be independent for my statistical analyses; using only one data point from each long-lived female did not appreciably affect any of the *P* values, all of which were  $>0.050$  (see below and Table 3). Numbers shown in the text and in Table 3 are means  $\pm 1$  SD.

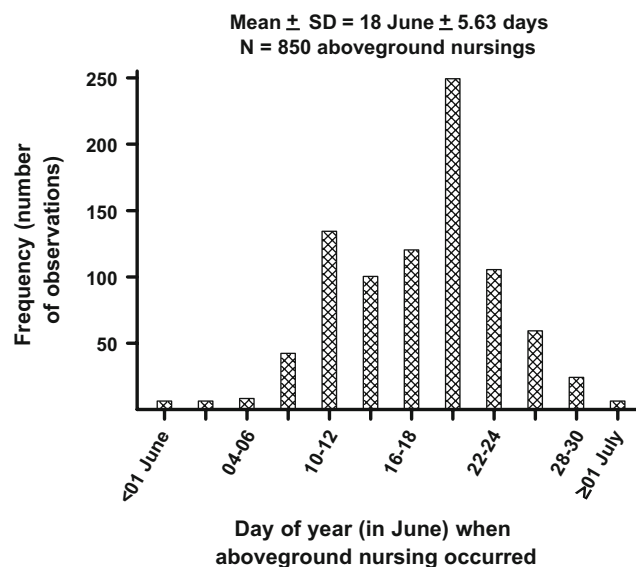
### Results

Over the 11 years (1995 through 2005), the students and I observed 850 aboveground nursings, which involved 122 mothers (25 of whom nursed aboveground in  $\geq 2$  years) and 248 juveniles from 134 litters (Fig. 1). For the 583 cases of aboveground nursing for which we could determine the sex of the suckling juvenile, the numbers of males and females were almost identical (291 males and 292 females).

For 90.1% of the nursings (766/850), nursing stopped aboveground, and the mother and the juvenile separated. For the other 9.9% (84/850), the mother and the nursing juvenile(s) submerged into a burrow together while the juvenile was still nursing, or they submerged together immediately after the aboveground nursing stopped; sometimes the mother and juvenile(s) re-appeared aboveground after several minutes, but other times, they remained underground for the night. For cases involving submergence during or just after aboveground nursing, suckling probably continued underground, but I could not verify such subterranean nursing.

Aboveground nursings occurred as early as 29 May, or as late as 6 July, but most nursings occurred in mid-June (Fig. 2). Most of the mothers that nursed aboveground were middle-aged (i.e., 2–5 years old), but many were yearlings; seven mothers nursed aboveground when they were 6 years old, and two nursed aboveground when they were 7 years old (Fig. 3).

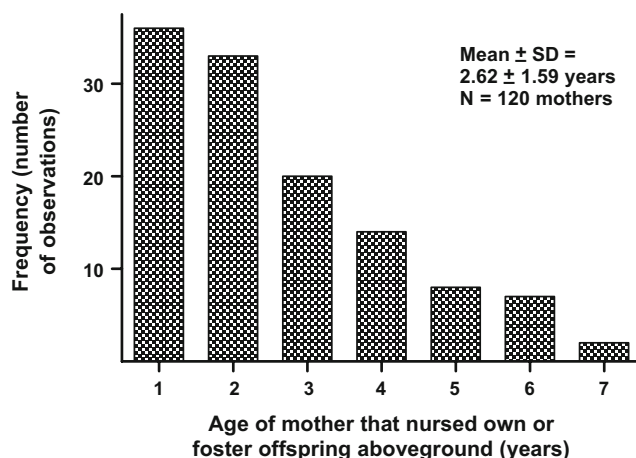
Some of the juveniles that nursed aboveground had been coming aboveground from the home nursery-burrow for as little as 2 days, but other nursing juveniles had been coming



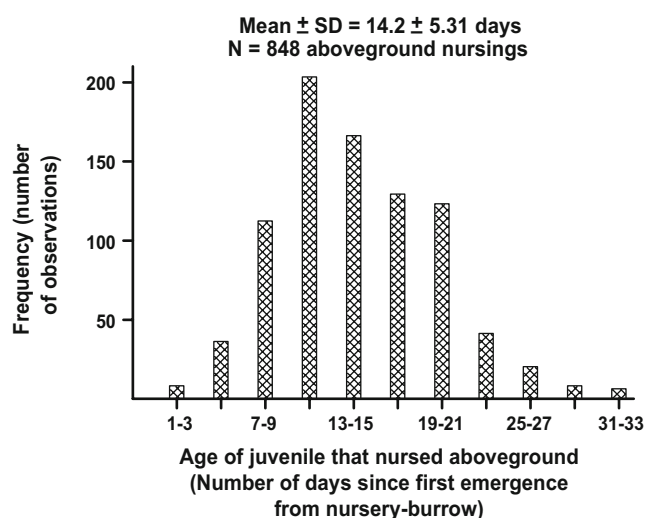
**Fig. 2** Dates when aboveground nursing occurred among Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005

aboveground for as long as 4 weeks (Fig. 4). Most nursings involved juveniles that had been coming aboveground for 1–3 weeks.

For at least 5 weeks after juveniles began to emerge from their nursery-burrows, the students and I recorded aboveground nursings from dawn until dusk. We observed nursings as early as 0900 hours or as late as 2030 hours (Fig. 5). The majority (742/850 = 87.3%) of nursings occurred between 1800 hours and 2000 hours, and 69.3% (589/850) occurred between 1900 and 2000 hours. Some aboveground nursings lasted for only 10 s, but others lasted for as long as 26 min (Fig. 6). Most nursings lasted for 1–10 min. Most commonly, a mother suckled a single juvenile



**Fig. 3** Ages of Utah prairie dog mothers that nursed aboveground at Bryce Canyon National Park from 1995 through 2005



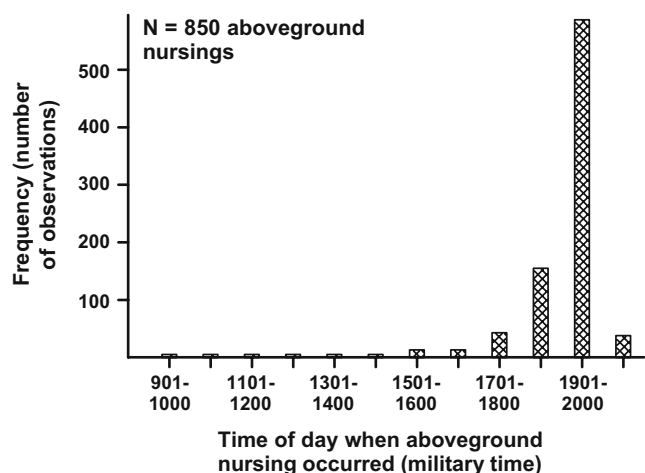
**Fig. 4** Ages of juvenile Utah prairie dogs that nursed aboveground at Bryce Canyon National Park from 1995 through 2005

aboveground, but one mother simultaneously suckled seven juveniles (Fig. 7).

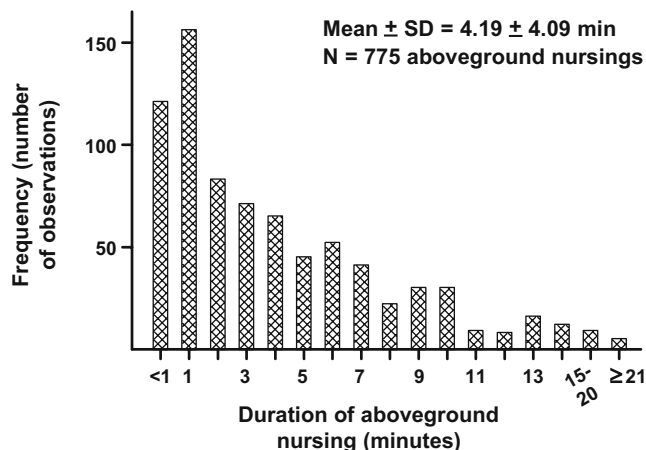
Of 25 mothers that nursed aboveground in greater than or equal to two different years, 20 nursed aboveground in 2 years, three nursed aboveground in 3 years, one nursed aboveground in 4 years, and one nursed aboveground in 5 years.

### Results that pertain specifically to communal nursing

Seventy-five percent of aboveground nursings (598/796) involved a mother suckling her own juvenile offspring. The other 24.9% (198/796) involved a mother suckling foster offspring on the foster mother's home territory (i.e.,

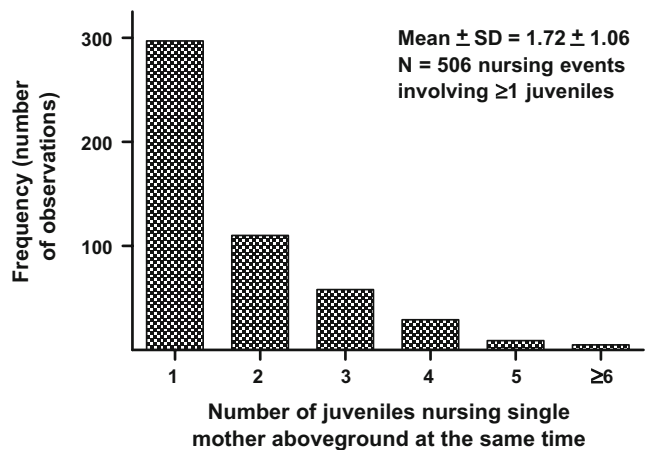


**Fig. 5** Time of day when aboveground nursing occurred among Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005



**Fig. 6** Duration of aboveground nursing among Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005

communal nursing). For 54 of the 850 cases of aboveground nursing, the students and I could not determine if the mother suckled own or foster offspring because of uncertain maternity when juveniles from different litters mixed before we could capture and mark them (Hoogland 2007). Of the 122 mothers that we observed nursing aboveground at least once, 67 nursed only their own offspring (54.9%), and 55 (45.1%) nursed foster as well as their own offspring. Beneficiaries of communal nursing included 91 juveniles from 64 litters. In 2004 (the year when the students and I observed most cases of communal nursing; see Fig. 1), 67.7% of mothers (21/31) nursed foster offspring at least once. For the 139 cases of communal nursing for which we could determine the sex of the suckling juvenile, the numbers of males and females were almost identical (68 males and 71 females).



**Fig. 7** Number of juveniles that nursed single mother aboveground at the same time among Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005

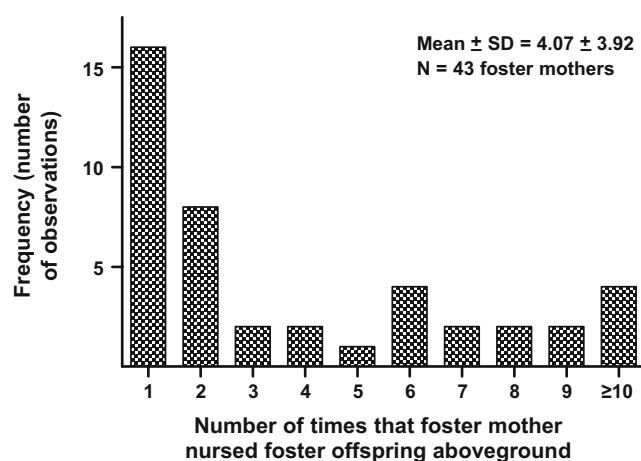
I observed less than five cases (i.e., <1% of all above-ground nursings) in which a mother aggressively chased, or fought with, own or foster offspring that tried to suckle. For those mothers that were nursing aboveground, I never saw a mother that refused an additional own or foster offspring that tried to suckle—i.e., willing mothers evidently did not discriminate between own versus foster offspring, and they frequently suckled offspring of mothers who did not themselves engage in communal nursing.

Females that did not give birth never engaged in communal nursing, nor did females that lost all their unweaned, pre-emergent offspring to predation or infanticide. Until weaning of own offspring was complete, foster mothers always continued to nurse own offspring.

Mothers varied in the frequency of aboveground communal nursing. Many foster mothers nursed foster offspring only once, but one mother nursed foster offspring on 17 occasions in 2003 (Fig. 8).

For 56.1% of communal nursings (111/198), I was able to determine the kinship between the foster offspring and the nursing mother (Table 2). Many beneficiaries (74/198 = 37.4%) of communal nursing were close non-offspring-kin (half-siblings, grandoffspring, great grandoffspring, full- and half-nieces/nephews, full-grandnieces/grandnephews, and full-first cousins; for all these,  $r \geq 0.125$ ). Other beneficiaries (37/198 = 18.7%) were kin ( $0.125 > r > 0.000$ ) such as half-first cousins and full-second cousins (Table 2). For the other 43.9% of communal nursings (87/198), beneficiaries were more distant kin for which  $r$  was probably  $>0$  because the beneficiaries were almost always juveniles born to female kin in the foster mother's home territory.

A comparison of mothers that nursed own offspring only versus mothers that nursed both own and foster offspring



**Fig. 8** Frequency at which foster mothers nursed foster offspring aboveground among Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005. This figure only shows data from foster mothers that nursed foster offspring at least once

**Table 2** Genetic relationship of foster offspring to foster mother for Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005

Relationship	Number
Half-sibling	12
Grandoffspring	17
Great grandoffspring	14
Full-niece or full-nephew	4
Half-niece or half-nephew	21
Full-grandniece or full-grandnephew	2
Half-grandniece or half-grandnephew	8
Full-first cousin	4
Half-first cousin	5
Full-first cousin once removed	2
Half-first cousin once removed	4
Full-first cousin twice removed	3
Half-first cousin twice removed	1
Full-second cousin	1
Half-second cousin	4
Half-second cousin once removed	2
Half-second cousin twice removed	1
Full-third cousin	4
Half-third cousin once removed	1
Full-grandniece twice removed	1
Total	111

These kinships derive from maternal genetic relationships only; determination of paternal genetic relationships is still underway. For this table, I assumed that offspring of the same litter were full-siblings but recognize that littermate siblings were sometimes maternal half-siblings (same mother, different father, born in same year). The offspring of a full-first cousin is a full-first cousin once removed; the grandoffspring of a full-first cousin is a full-first cousin twice removed; and so forth. For 87 other communal nursings, the exact coefficient of genetic relatedness between mother and foster offspring was unknown, but  $r$  was probably  $>0$  because the beneficiaries were almost always juveniles born in the foster mother's home territory

revealed no statistically significant differences regarding maternal age, maternal body mass, probability of maternal survivorship until the following spring, litter size when juveniles first emerged from the nursery-burrow, or percentage of offspring in litter that survived for  $\geq 1$  year after first emergence (Table 3). The percentage of offspring in a litter that survived for  $\geq 1$  year did not differ between litters that did and did not have greater than or equal to one juvenile that suckled from a foster mother ( $30.2\% \pm 27.9\%$ ,  $N=38$  versus  $27.3\% \pm 25.8\%$ ,  $N=30$ ;  $P=0.654$ ,  $t$  test). The number of times that a mother communally nursed varied directly, though not significantly, with the cumulative number of offspring reared to first emergence by all mothers in the home territory (i.e., with the maximal number of potential foster offspring in the home territory

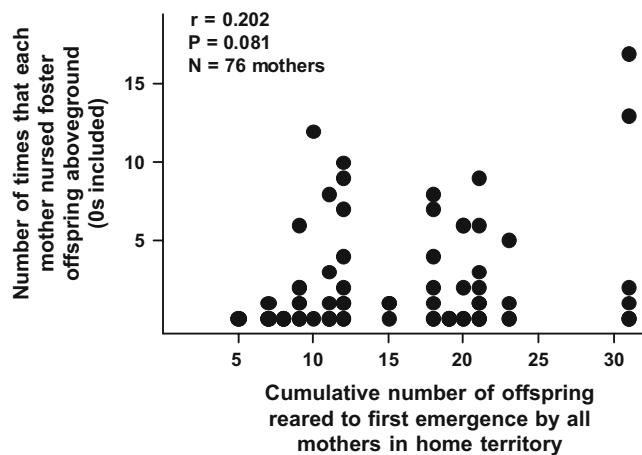
**Table 3** Comparison of mothers that nursed only their own offspring versus mothers that nursed both their own and foster offspring

	Mothers that nursed own offspring only	Mothers that nursed both own and foster offspring	Statistical significance of this difference
Maternal age (years)	2.51±1.46 N=45	2.51±1.62 N=43	$P=0.999$ $t=0.002$
Maternal body mass (grams) when mother's juveniles first emerged from nursery-burrow	762±69.2 N=44	783±73.2 N=42	$P=0.169$ $t=1.388$
Percentage of mothers that survived until following spring	61.3%±49.1% N=62	65.2%±48.2% N=46	$P=0.676$ $\chi^2=0.175$ df=1
Litter size when juveniles first emerged from nursery-burrow	3.84±1.28 N=45	3.95±1.05 N=41	$P=0.675$ $t=0.421$
Percentage of offspring in litter that survived for ≥1 year after emergence from nursery burrow	26.7%±27.5% N=35	31.6%±28.4% N=32	$P=0.472$ $t=0.724$

Numbers are means±SD.  $P$  values are from the  $t$  test or the  $2 \times 2$  chi-square test

(Pearson correlation,  $r=0.202$ ,  $N=76$  foster mothers,  $P=0.081$ ; Fig. 9).

I was unable to determine whether communal nursing increased either the production of antibodies by foster mothers or the quality/quantity of foster mothers' milk.



**Fig. 9** Number of times that foster mother communally nursed aboveground versus the cumulative number of offspring reared to first emergence by all mothers in the home territory (i.e., versus the maximal number of potential foster offspring in the home territory) for Utah prairie dogs at Bryce Canyon National Park from 1995 through 2005. The  $r$  and  $P$  values are from the Pearson correlation test. Data shown here are only from territories that contained greater than or equal to two litters that emerged from their nursery-burrows—i.e., I excluded territories containing only one litter, in which communal nursery was highly unlikely because foster offspring were almost always from the home territory. When two of the 76 foster mothers had the same values for the  $x$  and  $y$  variables, data for both mothers are shown as a single circle. Because the purpose of this figure is to show the number of communal nursings versus the potential number of foster offspring in the home territory, I have included data from mothers that did and did not nurse foster offspring aboveground

## Discussion

Hypotheses that might explain communal nursing among Utah prairie dogs

**Hypothesis 1 (H1): communal nursing provides experience to young foster mothers** To improve nursing skills, natural selection might favor mothers who suckle foster offspring (Roulin 2002). Three lines of evidence indicate that H1 does not apply to Utah prairie dogs. First, H1 predicts that foster mothers should most often be young, inexperienced females. Utah prairie dog foster mothers, however, were usually older females that had weaned greater than or equal to one litter, and ages of mothers that did and did not nurse foster offspring were almost identical (Table 3). Second, H1 predicts that young females that do not give birth should nurse foster offspring and also that young females that lose their unweaned offspring to predation or infanticide should nurse foster offspring. I did not observe either of these phenomena among marked Utah prairie dogs. Third, H1 is unlikely to apply to Utah prairie dogs because communally nursing mothers always nursed their own as well as foster offspring—even though nursing own offspring alone should have been sufficient to gain experience.

**Hypothesis 2: foster mothers get rid of surplus milk that their own young have not consumed** If mothers sometimes produce more milk than their own offspring can consume and if retaining surplus milk imposes a handicap—e.g., because it inhibits running away from predators—then, natural selection might favor mothers who nurse foster offspring (Beck et al. 2000; Lee 1987; O'Brien and Robinson 1991; Riedman and LeBoeuf 1982; Roulin 2002; Wilkinson 1992). Three lines of evidence indicate that H2 does not apply to Utah prairie



dogs. First, I detected no evidence that mothers ever produce more milk than their offspring can consume. Offspring of mothers that communally nursed commonly nursed foster mothers, for example—thereby indicating that they were not satiated with milk from their own mothers. Second, H2 predicts that communal nursing should occur most commonly after a mother has exclusively nursed her own offspring. Just before sunset on a typical evening in mid-June, however, Utah prairie dog mothers commonly nursed foster offspring while simultaneously—or sometimes before—nursing their own offspring. Third, H2 predicts that mothers with small litters should nurse foster offspring more often than mothers with larger litters—because the former should have more milk to spare if the quantity of milk is independent of litter size (Plesner Jensen et al. 1999; Pusey and Packer 1994). Utah prairie dogs did not show this trend (Table 3).

*Hypothesis 3: via indirect selection, foster mothers increase inclusive fitness by nursing offspring of kin* Sometimes, mothers might increase inclusive fitness more by suckling hungry, desperate full-nieces and full-nephews (or other close kin) than by nursing their own well-fed offspring (Hayes 2000; König 1994a; Roulin 2002). Foster Utah prairie dog offspring were usually the offspring of kin (Table 2), and this trend indicates that indirect selection has been important in the evolution of communal nursing. Utah prairie dog mothers sometimes fall victim to predation within a few days after their offspring first emerge from the nursery-burrow (unpublished data; see also (Hoogland et al. 2006)), and indirect selection for nursing foster offspring by grandmothers, full-aunts, half-aunts, full-first cousins, and so forth is probably especially important when mothers die in June when communal nursing might occur.

*Hypothesis 4: via reciprocity, foster mothers rear more offspring when they share nursing of own and foster offspring with other mothers* If mother A and mother B nurse their own and the other's offspring, then such reciprocity will mean that mother A's offspring will have access to mother B's milk if mother A experiences a temporary shortage or depletion of milk or if mother A dies. Further, offspring of each mother probably will receive unique antibodies from the other mother's milk (Roulin 2002; Roulin and Heeb 1999). Despite these possible benefits, reciprocity probably does not explain communal nursing among Utah prairie dogs for at least two reasons. First, for communal nursing to evolve via reciprocity, all mothers should communally nurse at approximately equal frequencies (Axelrod and Hamilton 1981; Roulin 2002). Utah prairie dog mothers varied substantially regarding the frequency of communal nursing, however (Fig. 8). Many mothers never nursed foster offspring, but others commonly

nursed foster offspring over several years (see also (Knight et al. 1992; McCracken and Gustin 1991; Murphey et al. 1995; Plesner Jensen et al. 1999; Pusey and Packer 1994)). Further, foster mothers frequently suckled offspring of mothers who did not themselves engage in communal nursing, and foster mothers were not obviously more likely to suckle the offspring of other foster mothers of the home territory who engaged in reciprocal communal nursing at about the same frequency (although I did not rigorously investigate this possibility). Second, reciprocity, in general (Alexander 1974; Axelrod and Hamilton 1981; Trivers 1971), and reciprocity regarding communal nursing, in particular (Pusey and Packer 1994; Roulin 2002), is vulnerable to cheating—i.e., natural selection will usually favor mothers who maximize nursing of own offspring and minimize, or completely avoid, nursing of foster offspring whenever possible. The role of reciprocity in the evolution and maintenance of communal nursing among Utah prairie dogs probably has been minimal.

*Hypothesis 5: communal nursing leads to reduced predation on own offspring because communally nursed foster offspring are more likely to remain near own offspring* For the 3–4 weeks after they first emerge from their nursery-burrows, Utah prairie dog juveniles cannot run as fast as adults, are still learning the importance of responding to alarm calls, and are not familiar with the location of all burrow-entrances within the home territory. Consequently, recently emergent juveniles are especially vulnerable to predation (Hoogland et al. 2006). By nursing foster offspring, a mother increases the probability that those foster offspring will cluster around her own offspring before, during, and after communal nursing. Communal nursing also increases the probability that foster offspring will spend the night with the foster mother and the foster mother's own offspring. The foster mother's own offspring, therefore, might be safer from predation because of the multi-litter group's increased awareness of predators (Bertram 1978; Hoogland 1981; Hoogland and Sherman 1976; Patterson 1965), because of "selfish herd" effects (Hamilton 1971; Vine 1971) and because of "protection by dilution" (Bertram 1978; McKaye and McKaye 1977; Williams 1994). In this scenario, natural selection might favor Utah prairie dog mothers that pay the costs of communal nursing so that their own offspring will be less vulnerable to predation. If so, then survivorship of own offspring should be higher for mothers that communally nurse than for mothers that do not. My results do not support this prediction (Table 3).

*Hypothesis 6: communal nursing increases the quality and quantity of the foster mother's milk and the production of antibodies for the foster mother herself and for her*

*milk* When compared to mothers that nurse less often, mothers that frequently nurse produce more milk in some species, and they also produce more antibodies for themselves and for their milk (Matera 1996; Roulin 2003). If so, then H6 predicts that both the mother and her own offspring should survive better when the mother suckles foster offspring. Further, foster offspring should survive better than offspring that nurse only their own mothers—unless foster offspring nurse foster mothers only when they are close to starvation or in poor health (and thus unlikely to survive even with milk from foster mothers). I could not directly measure either levels of different antibodies within adult and juvenile Utah prairie dogs or the quantity and quality of milk produced by different mothers, but I was able to examine the probability of survival until the following spring for mothers and juveniles. Mothers that nursed both own and foster offspring did not survive better than mothers that nursed only their own offspring (Table 3), own offspring of foster mothers did not survive better than offspring of mothers that did not nurse foster offspring (Table 3), and offspring that nursed both own and foster mothers did not survive better than offspring that nursed only their own mothers. These results do not support H6.

*Hypothesis 7: communal nursing is a cost of coloniality* As for other species of ground-dwelling squirrels (Armitage 1984; Barash 1989; Hoogland 1979; Leger and Owings 1978; McCarley 1966; Michener 1973; Slade and Balph 1974), juveniles from one litter of Utah prairie dogs began to interact with juveniles from other litters within the home territory within a few days after first emerging from the nursery-burrow. Within a week or so, inter-litter interactions were frequent. Further, juveniles of one litter sometimes spent the night with juveniles of another litter as soon as 4–5 days after first emergence from the nursery-burrow. Many of these interactions resulted fortuitously because juveniles of different litters were all looking for forage in the same home territory, and others probably resulted because natural selection presumably favors juveniles that play, fight, and chase with numerous other juveniles in preparation for adulthood. Because of all these interactions, I could not accurately identify (unmarked) littermate siblings soon after first emergences of litters from their nursery-burrows. Perhaps Utah prairie dog mothers had the same problem. If so, then, in proximate terms, regular communal nursing might have resulted because mothers were unable to easily discriminate between their own offspring versus foster offspring. Before juveniles first appeared aboveground, mothers probably could easily discriminate between their own nursery-burrows (with only their own offspring) and other nursery-burrows (with potential foster offspring). Following first emergences of

juveniles from their nursery-burrows and the widespread mixing of juveniles from different litters, however, mothers might have found discrimination between their own and others' offspring too difficult or too costly—so that communal nursing began. Utah prairie dog mothers also did not seem to discriminate between own and others' juvenile—and adult—offspring in behavioral interactions such as kissing, chasing, fighting, and territorial disputes (unpublished data; see also (Hoogland 1995)).

Notice that the first six hypotheses of Table 1 that might explain communal nursing implicate adaptation because they involve benefits to the foster mother, her offspring, or both. H7, however, implies that communal nursing is a non-adaptive cost of coloniality that foster mothers pay in return for the benefits of reduced predation within colonies for themselves and their offspring (Manning et al. 1995; McCracken 1984; McCracken and Gustin 1991; Packer et al. 1992; Pusey and Packer 1994).

Why don't mothers discriminate between own and foster offspring?

When the consequences of misdirected parental care are serious or when competition between parents and non-offspring-kin is severe (Alexander 1974; Hamilton 1964; West et al. 2002), natural selection sometimes favors parents that can discriminate between own and foster offspring, offspring that can discriminate between own and foster parents, or both. Such parent-offspring recognition helps to re-direct parental effort to own offspring and occurs within myriad colonial species (Balcombe 1990; Balcombe and McCracken 1992; Beecher et al. 1986; Trillmich 1981), including several species of ground-dwelling squirrels (Holmes and Mateo 2007; Holmes and Sherman 1982; Michener 1974). So why haven't Utah prairie dogs evolved parent-offspring recognition following emergences of juveniles from their nursery-burrows so that communal nursing should be rare? I have no answer for this vexing question. Note, however, that communal nursing does not commence until juveniles appear aboveground, when their dependence on milk is declining. From birth until first emergence about 5.5 weeks later, juveniles receive milk only from their own mothers. Consequently, any maternal cost of communal nursing associated with lost milk must be small compared to the cumulative cost of producing milk exclusively for own offspring for the 5.5 weeks between birth and first emergence. Perhaps the costs of communal nursing are smaller than the costs associated with parent-offspring recognition—e.g., development of individually specific calls/odors of parents, offspring, or both; time associated with finding own offspring; identification and rejection of foster offspring; and so forth. Further, because foster

offspring are typically the offspring of kin (Table 2), costs of communal nursing are usually offset, at least partially, by gains in inclusive fitness via indirect selection.

### General discussion

Communal nursing occurs in many contexts. Foster mothers usually have their own offspring ((Bertram 1976; Dublin 1983; Pusey and Packer 1994; Taber and Macdonald 1992; Wilkinson 1992); this study), for example, but sometimes they do not (Creel et al. 1991; Lawick 1974; MacDonald and Moehlman 1983; Packard et al. 1985; Rood 1980; Rood 1990). The type of beneficiary of communal nursing also varies. Foster offspring, frequently, are the progeny of close kin ((Bertram 1976; Creel et al. 1991; Dublin 1983; Pusey and Packer 1994); Table 2), but foster offspring sometimes are unrelated, or only distantly related, to their foster mothers (McCracken 1984; Reiter et al. 1981; Riedman and LeBoeuf 1982; Watkins and Shump 1981; Wilkinson 1992). Finally, communal nursing varies regarding the willingness of the foster mother. Some foster mothers encourage nursing by foster offspring ((Bertram 1976; Birgersson et al. 1991; Creel et al. 1991; McCracken 1984; Rood 1980); this study). In other cases, communal nursing results when juveniles surreptitiously “steal” milk from unknowing foster mothers (LeBoeuf and Briggs 1977; Reiter et al. 1978; Reiter et al. 1981; Taber and Macdonald 1992).

For many mammals, communal nursing is difficult for humans to quantify. One problem is that the study animals are sometimes mobile and, thus, difficult to locate each day (Harcourt et al. 1981; Hrdy 1977; Packard et al. 1985). A second problem is that nursing sometimes occurs at night, underground, or in dark dens (Hoogland 1995; McCracken 1984; Wilkinson 1992). A third problem is that documentation requires individuals that are marked (Hoogland 1995) or have distinctive natural markings (Festa-Bianchet 1988; Lee 1987; Pusey and Packer 1994). Consequently, with a few notable exceptions (e.g., (Creel et al. 1991; McCracken 1984; Pusey and Packer 1994; Reiter et al. 1981; Wilkinson 1992)), observations of communal nursing are elusive and usually anecdotal. Here, I report the first detailed observations of communal nursing for rodent species living under natural conditions.

Most cases of aboveground nursing among Utah prairie dogs occurred under the following circumstances: a mother went to the mound at the entrance to her nursery-burrow about 30–60 min before sunset, stood upright on her hind feet, and allowed her own and foster offspring to suckle. This scenario implies that mothers were willing participants in nursing their own and foster offspring.

Aboveground nursing of own and foster offspring by Utah prairie dogs was not limited to a few idiosyncratic individuals. Rather, the students and I observed above-

ground nursing by 122 mothers; 55 of these 122 mothers (45.1%) nursed foster offspring at least once. Two hundred and forty-eight juveniles from 134 litters nursed aboveground; 91 of these 248 juveniles (36.7%), from 64 litters, nursed foster mothers. In the year when we observed most cases of communal nursing (2004), 67.7% of mothers (21/31) nursed foster offspring at least once. These numbers and frequencies for nursings are all for aboveground nursings that the students and I observed and, therefore, are underestimates that do not include either aboveground nursings that we did not detect (because of tall vegetation, for example) or underground nursings.

I assume that a juvenile that nursed aboveground for 20 min obtained more milk than a juvenile that nursed for only 15 min, but as for species such as African lions (*Panthera leo*), house mice (*Mus musculus*), Norway rats (*Rattus norvegicus*), and red deer (*Cervus elaphus*) (Cameron 1998; Loudon et al. 1983; Mendl and Paul 1989; Pusey and Packer 1994), juvenile Utah prairie dogs might have suckled longer when less milk was available. If so, then amount of milk received did not vary directly with time spent nursing.

Nursing of juvenile black-tailed prairie dogs occurs almost exclusively underground (Hoogland 1995). The same is true for nursing among Gunnison's prairie dogs (*Cynomys gunnisoni*; (Hoogland 1999; Hoogland 2003a); but see (Rayor 1988) for occasional exceptions), white-tailed prairie dogs (*Cynomys leucurus*; (Clark 1977); J. L. Hoogland, unpublished data), and most (all?) species of ground squirrels (*Spermophilus*; e.g., (Dobson et al. 1999; Holmes and Sherman 1982; Michener 1989)) and marmots (*Marmota*; e.g., (Armitage 1984; Barash 1989; Blumstein and Armitage 1999)). So why do Utah prairie dog mothers nurse their own and foster offspring aboveground so frequently? I have no answer to this intriguing question nor do I know why the vast majority of aboveground nursings occur just before sunset.

A typical clan of Utah prairie dogs contains a single sexually mature male, who usually mates with all the females in that clan (Hoogland 2007). Before or after mating with the resident sexually mature male of the home territory, a female commonly mates with additional males from other territories (Hoogland 2007). Consequently, juveniles from different litters within the same territory in the same year are frequently non-littermate paternal half-siblings (same father, different mother, born in the same year). The single sexually mature male within a territory—and an invading male that also mated with females in that same territory—probably benefits when his juvenile offspring can obtain milk from all mothers within the home territory. Perhaps natural selection has favored paternally expressed alleles that suppress the ability of mothers to discriminate between own and foster offspring within the

home territory (Roulin and Hager 2003)—so that communal nursing is common.

Of the seven hypotheses that might explain the evolution or maintenance of communal nursing among Utah prairie dogs (Table 1), circumstantial evidence supports the importance of H3 (elevated inclusive fitness via indirect selection) and H7 (communal nursing as a cost of coloniality). H3 and H7 might both be relevant to today's colonies of Utah prairie dogs, but perhaps only one was important in the early stages of the evolution of communal nursing. Mechanisms responsible for the evolutionary origin of communal nursing are not necessarily the same mechanisms responsible for the evolutionary maintenance of communal nursing within extant populations (Hoogland 1995; Packer et al. 1992).

The number of times that a mother communally nursed correlated positively, though not significantly, with the cumulative number of offspring reared to first emergence by all mothers in the home territory. This relationship might result because communal nursing is a cost of coloniality, and this cost should be greater when the number and density of potential foster offspring in the home territory are high. Conversely, the relationship might occur because a large number of potential foster offspring in the home territory offers more opportunities for reaping benefits from communal nursing via indirect selection.

For comparisons of mothers that did nurse foster offspring versus mothers that did not (Table 1), statistical tests were not significant for maternal age, maternal body mass, maternal survivorship until the following spring, litter size at first emergence from the nursery burrow, or juvenile survivorship in the first year (Table 3). Notice, however, that trends for the last four comparisons in Table 3 were in the direction predicted if communal nursing is adaptive. Perhaps the benefits of communal nursing for Utah prairie dogs are large enough for natural selection to favor the suckling of foster offspring but so small that unequivocal demonstration with statistical significance will require huge sample sizes. If communal nursing is primarily a non-adaptive cost of dense coloniality, however, then we should not expect to find clear advantages for foster mothers. Indeed, if compensatory benefits of communal nursing have not evolved in this latter scenario, then we should expect to find disadvantages for mothers that suckle foster offspring.

I agree with (Roulin 2002) that careful experiments will be necessary for a better understanding of the ultimate causation of communal nursing. I also agree that designing and completing these experiments will be a formidable task because communal nursing is so difficult to document for mammals living under natural conditions.

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## References

- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383
- Armitage KB (1984) Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. In: Murie JO, Michener GR (eds) *The biology of ground-dwelling squirrels*. University of Nebraska Press, Lincoln, NE, pp 377–403
- Auldist B, Carlson D, Morrish L, Wakefield CM, King RH (2000) The influence of suckling interval on milk production of sows. *J Anim Sci* 78:2026–2031
- Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211:1390–1396
- Baker JR (1984) Mortality and morbidity in grey seal pups (*Halichoerus grypus*). Studies on its causes of environment, the nature and sources of infectious agents and the immunological status of pups. *J Zool* 203:23–48
- Balcombe JP (1990) Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Anim Behav* 39:960–966
- Balcombe JP, McCracken GF (1992) Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? *Anim Behav* 43:79–87
- Barash DP (1989) *Marmots: social behavior and ecology*. Stanford University Press, Stanford, CA
- Beck CA, Bowen WD, Iverson SJ (2000) Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J Exp Biol* 203:2323–2330
- Beecher MD, Medvin MB, Stoddard PK, Loesche P (1986) Acoustic adaptations for parent-offspring recognition in swallows. *Exp Biol* 45:179–183
- Bertram BCR (1976) Kin selection in lions and evolution. In: Bateson PPG, Hinde RA (eds) *Growing points in ethology*. Cambridge University Press, Cambridge, UK, pp 281–301
- Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*, 1st edn. Sinauer, Sunderland, MA, pp 64–96
- Birgersson B, Ekvall J, Temrin H (1991) Allosuckling in fallow deer, *Dama dama*. *Anim Behav* 42:326–327
- Blumstein DT, Armitage KB (1999) Cooperative breeding in marmots. *Oikos* 84:369–382
- Boyd IL (1998) Time and energy constraints in pinniped lactation. *Am Nat* 152:717–728
- Brown JL (1987) *Helping and communal breeding in birds*. Princeton University Press, Princeton, NJ
- Brown CR, Brown MB (1996) Coloniality in the cliff swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, IL
- Cameron EZ (1998) Is suckling behavior a useful predictor of milk intake? A review. *Anim Behav* 56:521–532
- Clark TW (1977) *Ecology and ethology of the white-tailed prairie dog (Cynomys leucurus)*, Publications in biology and geology No. 3. Milwaukee Public Museum, Milwaukee, WI, pp 1–97



- Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262
- Creel SR, Montfort SL, Wildt DE, Waser PM (1991) Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature* 351:660–662
- Dittrich L (1968) Keeping and breeding gazelles at Hanover Zoo. *Int Zoo Yrbk* 8:139–143
- Dobson FS, Risch TS, Murie JO (1999) Increasing returns in the life history of Columbian ground squirrels. *J Anim Ecol* 68:73–86
- Dublin HT (1983) Cooperation and reproductive competition among female African elephants. In: Wasser SK (ed) *Social behavior of female vertebrates*. Academic, New York, NY, pp 291–313
- Festa-Bianchet M (1988) Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. *Anim Behav* 36:1445–1454
- Fogden SCL (1971) Mother-young behaviour at grey seal breeding beaches. *J Zool (Lond)* 164:61–92
- Grafen A (1982) How not to measure inclusive fitness. *Nature* 298:425–426
- Hamilton WD (1964) The genetical evolution of social behaviour. *J Theor Biol* 7:1–52
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Harcourt AH, Fossey D, Sabater-Pi J (1981) Demography of *Gorilla gorilla*. *J Zool (Lond)* 195:215–233
- Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Anim Behav* 59:677–688
- Haynie ML, van den Bussche RA, Hoogland JL, Gilbert DA (2003) Parentage, multiple paternity, and breeding success in Gunnison's and Utah prairie dogs. *J Mammal* 84:1244–1253
- Holmes WG, Mateo JM (2007) Kin recognition in rodents: issues and evidence. In: Wolff JO, Sherman PW (eds) *Rodent societies*. University of Chicago Press, Chicago, IL, pp 216–228
- Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in two species of ground squirrels. *Am Zool* 22:491–517
- Hoogland JL (1979) Aggression, ectoparasitism, and other possible costs of prairie dog (*Sciuridae: Cynomys* spp.) coloniality. *Behaviour* 69:1–35
- Hoogland JL (1981) The evolution of coloniality in white-tailed and black-tailed prairie dogs (*Sciuridae: Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252–272
- Hoogland JL (1995) The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, IL
- Hoogland JL (1999) Philopatry, dispersal, and social organization of Gunnison's prairie dogs. *J Mammal* 80:243–251
- Hoogland JL (2001) Black-tailed, Gunnison's, and Utah prairie dogs all reproduce slowly. *J Mammal* 82:917–927
- Hoogland JL (2003a) Prairie dogs. In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild mammals of North America*. Johns Hopkins University Press, Baltimore, MD, pp 232–247
- Hoogland JL (2003b) Sexual dimorphism in five species of prairie dogs. *J Mammal* 84:1254–1266
- Hoogland JL (2007) Alarm calling, multiple mating, and infanticide among black-tailed Gunnison's, and Utah prairie dogs. In: Wolff JO, Sherman PW (eds) *Rodent societies*. University of Chicago Press, Chicago, IL, pp 438–452
- Hoogland JL, Sherman PW (1976) Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecol Monogr* 46:33–58
- Hoogland JL, Tamarin RH, Levy CK (1989) Communal nursing in prairie dogs. *Behav Ecol Sociobiol* 24:91–95
- Hoogland JL, Davis S, Benson-Amram S, LaBruna D, Goossens B, Hoogland MA (2004) Pyraperm halts plague among Utah prairie dogs. *Southwest Nat* 49:376–383
- Hoogland JL, Cannon KE, DeBarbieri LM, Manno TG (2006) Selective predation on Utah prairie dogs. *Am Nat* 168:546–552
- Hrdy SB (1977) *The langurs of Abu*. Harvard University Press, Cambridge, MA
- Knight MH, Vanjaarsveld AS, Mills MGL (1992) Allo-suckling in spotted hyaenas (*Crocuta crocuta*): an example of behavioural flexibility in carnivores. *Afr J Ecol* 30:245–251
- König B (1994a) Communal nursing in mammals. *Verh Dtsch Zool Ges* 87:115–127
- König B (1994b) Fitness effects of communal rearing in house mice: the role of relatedness versus familiarity. *Anim Behav* 48:1449–1457
- Lawick H (1974) *Solo: the story of an African wild dog*. Collins, London, UK
- LeBoeuf BJ, Briggs KT (1977) The cost of living in a seal harem. *Mammalia* 41:168–195
- Lee PC (1987) Allomothering among African elephants. *Anim Behav* 35:275–291
- Leger DW, Owings DH (1978) Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. *Behav Ecol Sociobiol* 3:177–186
- Loudon ASI (1985) Lactation and neonatal survival of mammals. *Symp Zool Soc Lond* 54:183–207
- Loudon ASI, McNeilly AS, Milne JA (1983) Nutrition and lactational control of fertility in red deer. *Nature* 302:145–147
- MacDonald DW, Moehlman PD (1983) Cooperation, altruism, and restraint in the reproduction of carnivores. In: Bateson PPG, Klopfer P (eds) *Perspectives in ethology and ontogeny*, volume 5. Plenum Press, New York, NY, pp 433–467
- Manning CJ, Dewsbury DA, Wakeland EK, Potts WK (1995) Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. *Anim Behav* 50:741–751
- Matera L (1996) Action of pituitary and lymphocyte prolactin. *Neuroimmunomodulation* 4:171–180
- Maynard Smith J (1964) Group selection and kin selection. *Nature* 201:1145–1147
- McCarley H (1966) Annual cycle, population dynamics and adaptive behavior of *Citellus tridecemlineatus*. *J Mammal* 47:294–316
- McCracken GF (1984) Communal nursing in Mexican free-tailed bat maternity colonies. *Science* 223:1090–1091
- McCracken GF, Gustin MK (1991) Nursing behavior in Mexican free-tailed bat maternity colonies. *Ethology* 89:305–321
- McKaye KR (1981) Natural selection and the evolution of interspecific brood care in fishes. In: Alexander R, Tinkle D (eds) *Natural selection and social behavior*. Chiron Press, New York, NY, pp 177–183
- McKaye KR, McKaye NM (1977) Communal care and kidnapping of young by parental cichlids. *Evolution* 31:674–681
- Mendl M, Paul ES (1989) Observations of nursing and sucking behaviour as an indicator of milk transfer and parental investment. *Anim Behav* 37:513–515
- Michener GR (1973) Field observations on the social relationships between adult female and juvenile Richardson's ground squirrels. *Can J Zool* 15:33–38
- Michener GR (1974) Development of adult-young identification in Richardson's ground squirrel. *Dev Psychobiol* 7:375–384
- Michener GR (1989) Reproductive effort during gestation and lactation by Richardson's ground squirrels. *Oecologia* 78:77–86
- Murphey RM, Paranhos da Costa MJR, da Silva RG, de Souza RC (1995) Allonursing in river buffalo, *Bubalus bubalis*: nepotism, incompetence, or thievery? *Anim Behav* 49:1611–1616
- O'Brien TG, Robinson JG (1991) Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour* 119:30–50
- Packard JM, Seal US, Mech LD, Plotka ED (1985) Causes of reproductive failure in two family groups of wolves (*Canis lupus*). *Z Tierpsychol* 68:24–40
- Packer C, Lewis S, Pusey A (1992) A comparative analysis of non-offspring nursing. *Anim Behav* 43:265–281



- Patterson IJ (1965) Timing and spacing of broods in the black-headed gull *Larus ridibundus*. Ibis 107:433–459
- Pizzimenti JJ (1975) Evolution of the prairie dog genus *Cynomys*. Occas Pap Mus Nat Hist Univ Kans 39:1–73
- Pizzimenti JJ, Collier GD (1975) *Cynomys parvidens*. Mamm Spec 52:1–3
- Plesner Jensen S, Siefert L, Okori JJJ, Clutton-Brock TH (1999) Age-related participation in allosuckling by nursing warthogs (*Phacochoerus africanus*). J Zool 248:443–449
- Pusey AE, Packer C (1994) Non-offspring nursing in social carnivores: minimizing the costs. Behav Ecol 5:362–374
- Raylor LS (1988) Social organization and space-use in Gunnison's prairie dog. Behav Ecol Sociobiol 22:69–78
- Reiter J, Stinson NL, LeBoeuf BJ (1978) Northern elephant seal development: the transition from weaning to nutritional independence. Behav Ecol Sociobiol 3:337–367
- Reiter J, Panken KJ, LeBoeuf BJ (1981) Female competition and reproductive success in northern elephant seals. Anim Behav 29:670–687
- Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. Q Rev Biol 57:405–435
- Riedman ML, LeBoeuf BJ (1982) Mother-pup separation and adoption in northern elephant seals. Behav Ecol Sociobiol 11:203–215
- Roberts WM, Rodriguez JP, Good TC, Dobson AP (2000) Population viability analysis of the Utah prairie dog. Environmental Defense Report, Washington, DC pp 1–49
- Rood J (1980) Mating relationships and breeding suppression in the dwarf mongoose. Anim Behav 28:143–150
- Rood JP (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. Anim Behav 39:566–572
- Roulin A (2002) Why do lactating females nurse foster offspring? A review of hypotheses and empirical evidence. Anim Behav 63:201–208
- Roulin A (2003) The neuroendocrine function of allosuckling. Ethology 109:185–195
- Roulin A, Hager R (2003) Indiscriminate nursing in communal breeders: a role for genomic imprinting. Ecol Lett 6:165–166
- Roulin A, Heeb P (1999) The immunological function of allosuckling. Ecol Lett 2:319–324
- Sams MG, Lochmiller RL Jr, Qualls CW Jr, Leslie DM, Payton ME (1996) Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. J Mammal 77:179–190
- Saylor A, Salmon M (1971) An ethological analysis of communal nursing by the house mouse (*Mus musculus*). Behaviour 40:62–85
- Slade NA, Balph DF (1974) Population ecology of Uinta ground squirrels. Ecology 55:989–1003
- Taber AB, Macdonald DW (1992) Communal breeding in the mara, *Dolichotis patagonum*. J Zool 227:439–452
- Trillmich F (1981) Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour 78:21–42
- Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57
- Vine I (1971) Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. J Theor Biol 30:405–422
- Watkins LC, Shump KA (1981) Roosting behavior in the evening bat, *Nycticeius humeralis*. Am Midl Nat 105:258–268
- West SA, Pen I, Griffin AS (2002) Conflict and cooperation—cooperation and competition between relatives. Science 296:72–75
- West-Eberhard MJ (1975) The evolution of social behavior by kin selection. Q Rev Biol 50:1–33
- Wilkinson GS (1992) Communal nursing in the evening bat, *Nycticeius humeralis*. Behav Ecol Sociobiol 31:225–235
- Williams TD (1994) Adoption in a precocial species, the lesser snow goose: intergenerational conflict, altruism or a mutually beneficial strategy? Anim Behav 47:101–107
- Wright-Smith MA (1978) The ecology and social organization of *Cynomys parvidens* (Utah prairie dog) in south central Utah. MS thesis. Indiana University, Bloomington, IN