"COOPERATIVE" NURSING BY BIGHORN EWES ON THE NATIONAL BISON RANGE

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ABSTRACT

Observations of individually marked bighorn ewes and lambs (Ovis canadensis) on the National Bison Range in Montana revealed that, in 1982 and 1983, lambs were obtaining 32-85 percentage of suckles from ewes that were not their mothers. Two ewes in each 1982 and 1983 lost their own lambs and continued to nurse all lambs in the nursery band. One ewe in 1982, and 3 ewes in 1983 nursed their own as well as all other lambs. Lamb survivorship was only 10 and 27 percent in 1982 and 1983. Possible effects of kinship, inbreeding, and parasites, and factors influencing lamb survivorship are discussed.

Alloparenting, that is the care of a conspecific young other than one's own, has been reported in some 120 mammalian and 150 avian species (Reidman 1982). Alloparental care ranges from "babysitting" or guarding behavior, in which a female may stay with a group of youngsters while the mothers forage away from the group, to actual adoption of another's young.

Usually considered altruistic, alloparental care may have some selective benefits to the donor in the form of beneficial parental experience, increased inclusive fitness, reciprocal altruism, or exploitation of fostered young (see Reidman 1982). Cooperative care could be favored if the inclusive fitness of the individuals involved was enhanced, and might be expected in groups with relatively high degrees of relatedness between group members (Hamilton 1964).

Alloparenting, especially allomothering, appears to be rare in ungulates, and chiefly consists of "babysitting" behavior (Reidman 1982). "Cooperative nursing" in which a mother knowingly provides milk to an alien young, is distinct from "thief suckles", in which a young mammal obtains milk from an alien mother apparently without her knowledge. Thief suckling is common in reindeer (Rangifer tarandus; Espark 1971) and occasional in giraffes (Giraffa camelopardalis; Dagg 1970, MacClintock 1973). Cooperative nursing has been reported in chital (Axis axis; Schaller 1967), collared peccaries (Tayassu tajacu; Byers and Bekoff 1981), African lions (Panthera leo; Schaller 1972) and both African elephants (Loxodonta africana) and Asiatic elephants (Elaphus maximus; Eisenburg 1972).

Many ungulate females bring their precocial young into so-called "nursery bands" (Espmark 1971, Geist 1971, Estes 1974, Lent 1974, Schaller 1977, Cluttonbrock et al 1981). In many cases, these appear to be groups of unrelated females, characterized by mother and infant attachment and lack of cooperative care (Gubernick 1981b, and references therein). Several authors

have commented on the exclusiveness of the mother-young attachment in wild sheep (Ovis spp.). Urial ewes (Ovis orientalis) reject alien young (Schaller 1977), as do most bighorn ewes (Geist 1971, Shackleton 1973, Horejsi (1976). VOvis Both Shackleton (1973) and Horejsi (1976), working with bighorn sheep in Canada, have commented on the reduction in fitness a ewe would suffer by nursing alien young.

This report documents repeated instances of bighorn ewes nursing alien young, behavior which may or may not fall in the category of "cooperative care" (Hamilton 1964).

METHODS

Study Population

In 1983, fifty-two bighorns, 21 rams and 31 ewes, lived on the National Bison Range. These animals were descendants of 12 sheep that were introduced onto the refuge in 1922. The National Bison Range (NBR), in northwestern Montana, is a National Wildlife Refuge of 7504 ha. (19,000 ac.). The refuge is surrounded by a 2.4 m game fence that prevents immigration or emigration of the wild ungulates. All ungulates maintained within the refuge (elk (Cervus elaphus), bison (Bison bison), pronghorns (Antilocapra americana), mountain goats (Oreamnos americanus), white-tail deer (Odocoileus virginianus), mule deer (O. hemionus), and bighorns) are carefully managed to prevent overgrazing.

The bighorns on the refuge are habituated to people and may be approached to within less that 10m. The herd has been closely observed, year-round, since June 1979. The herd was watched from June 1979 until May 1982 by J. Hogg, and by myself from June 1982 through April 1984.

Identification of Individuals

All of the sheep are individually recognizable by horn characters, physical abnormalities such as torn ears, or ear tags. To facilitate rapid identification, some sheep were splattered with sheep paint, or Nyanzol A dye. Both the paint and the dye were squirted on the animals' coat or horn tips at close range from a hypodermic syringe. This resulted in a variable pattern of splotches that were visible over 1 km away.

Observations during the fall rut yielded approximate conception dates for most ewes. Thorough searches were conducted to find lambs as soon as possible after parturition. Lambs less than 24 hours old were usually catchable. Upon capture, lambs were weighed and ear tagged, and sex was recorded. A ewe in isolation with a lamb less that 5 days old was assumed to be its mother. If the lamb was observed for the first time in the company of more that 1 ewe, it was assigned to the ewe that it reclined next to most often, because lambs recline preferentially with their mothers (Hass, unpub. data). All lambs in 1983 were later sprayed with paint or dye for quick identification. Censuses conducted in early May, and throughout the lambing period, revealed which ewes

were pregnant and how many failed to conceive during rut or lost fetuses during early gestation.

Data Collection

Data presented here were collected during the summers of 1982 and 1983. In both years, the lambing periods on the NBR began in mid-May and almost all ewes had lambed by June 20. All-instances behavioral samples (Altmann 1974) of suckling bouts were obtained during almost daily observations of the nursery bands. In 1982, the sampling period began 22 July and terminated 7 September. The sampling period in 1983 extended from 25 June through 15 September. The lambs were under continuous observation for 4-8 hours during each observation period. A suckling bout began when the lamb was judged to have grasped the teat, and terminated when the lamb moved its head, voluntarily or otherwise, away from the udder.

For each suckling bout observed, the following were recorded: identity of ewe; identity of lamb; time of suckle (nearest minute); duration of bout (nearest second); whether ewe or lamb initiated bout; whether ewe or lamb terminated bout; and orientation of lamb during bout (left side, right side, or underneath). In 1983, all the above were recorded, plus it was noted whether or not the ewe sniffed the lamb's nose before or rump during the suckle.

Suckle attempts were suckles less than 3 seconds in duration, or obvious and unsuccessful attempts by the lamb to grasp a nipple. Suckle attempts were always terminated by the ewe. Suckle success was the ratio of the number of suckles to the number of suckles and suckle attempts combined.

Ewe suckle rates were obtained by dividing total suckle duration by the number of minutes of continuous observation in an observation period. Suckle rates are a hyperbolic function of lamb age. Suckle rates were inverted (to obtain a linear function) and regressed against lamb age. The equations for the lines obtained by regressing inverted suckles rates against lamb age were then integrated for the period covering 40-100 days of a lamb's age. This integration yielded the area under the curve described by suckle rate vs. age, and resulted in an approximation of the total time a lamb spent suckling between 40 and 100 days of age. This unit was termed "Total Suckle Time" (Hogg 1983). Total Suckle Time was felt to be a valuable measure of post-natal reproductive effort when compared between ewes, between lambs, and between years.

Individual ewes were referred to by two-letter abbreviations of their names, and lambs were referred to by their mother's initials followed by "1" (for lamb).

Ages of ewes were estimated in 1980, ewes older than 5 years cannot be reliably aged in the field (Geist 1966) and were lumped as "older" (5+) ewes (Hogg 1983). Ewes that nursed only their own lambs were referred to as "Own Only" (OO) ewes, those that nursed their own as well as others as "Own Plus" (O+) ewes, and those that had lost their own lambs but continued to nurse other lambs as "Helpers" (H). The use of the term "Helpers" does not imply

function or intent, but is meant to be a description of the behavior observed, as has been established in the literature (Skutch 1961, Brown 1975, Wilson 1975).

RESULTS

In 1982, 24 ewes produced 21 lambs. Of these, only two were still alive when I began censuses in late June. The fates of the missing lambs were uncertain, although predation appeared to be the cause of their disappearances (Hoss 1983, see DISCUSSION). When sampling began in mid-July, it was apparent that 4 ewes were nursing two male lambs. Of the 4, only 1 (DB) nursed only her lamb. OH nursed her own lamb as well as the other lamb. AL and TT, the other ewes, had lost their lambs, but continued to nurse both OHI and DBI until at least September when observations terminated (Fig. 1a). Both lambs received a substantial proportion of suckles from ewes that were not their own mothers (Fig. 1b). In 1982, 53 percent of observed suckles were on alien ewes.

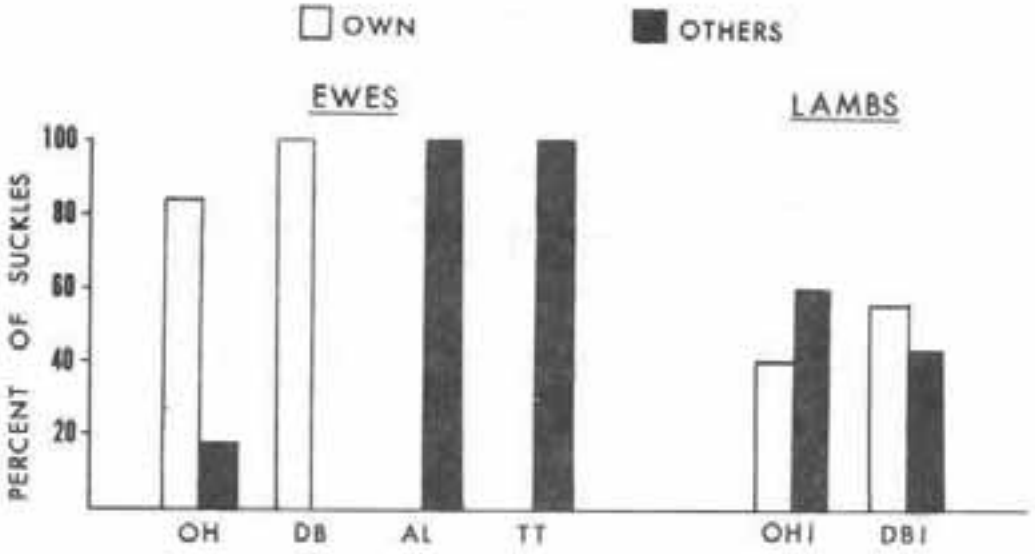

Fig. 1. Percent of suckles observed between own and other lambs and ewes in 1982.

The lambs were not nursed equally by the ewes. OH nursed her own lamb almost 5 times more than DBI, AL nursed OHI almost 3 times more than DBI, and TT nursed both lambs almost equally (G-test, G=1.37, P>0.,50; Table 1).Mean suckle durations on O+ ewes were greater than OO or H ewes, but there were no significant differences in mean suckle durations, whether comparing the OO ewe with the O+ ewe (t=1.77, P>0.05), the OO ewe with the H ewes combined (t=0.31, P>0.90), or the O+ ewe with the H ewes (t=1.71, P>0.05). There was also no significant difference in the mean suckle duration for O+ ewe on her

own lamb vs. the alien lamb (t=1.09, p>0.20).

No significant difference was noted in lamb orientation (side suckled on), for either lamb (OH1: G=2.31, P>0.05; DB1: G=0, P>0.90) or both combined (G=1.25, P>0.10). This is not surprising because lambs can suck from either teat from either side.

Table 1. Number of observed suckles and mean observed suckle duration (seconds) by each lamb on different ewes in 1982.

Class:		00	0+	H	H
Ewe:		DB	OH	AL	TT
Lambs:					
OH1	No.	0	29	27	17
	Mean dur.	0	21	20	18
DB1	No.	35	6	27	10
	Mean dur.	19	23	19	18

Ewes, for the most part, controlled the suckle bouts (Table 2), initiating and terminating most of them. There were no significant differences among 00, 0+ and H ewes as to the proportion of times that ewes, vs. lambs, initiated suckle bouts (G=0.19, P>0.90) or terminated them (G.052, P>0.50).

Table 2. Percent of suckle bouts that were initated and terminated by each ewe for each lamb in 1982. For example, of the 29 suckle bouts recorded between OH1 and OH, OH intiated 86 percent, or 25, of them.

Lambs:		OH1		DB1		TERM. OH1		TERM. DB1	
Class	Ewe	%	n	%	n	%	n	%	n
00	DB	0	0	100	30	0	0	94	35
0+	OH	86	29	100	6	100	29	100	6
H	AL	89	27	100	10	94	17	91	11
H	TT	75	17	100	10	100	27	100	10

Forty-nine suckle attempts were recorded in 1982. Lambs attempted to suckle more often from ewes that would allow them to suckle at some time, but the correlation was not significant (r=0.54, P>0.05), probably due to small sample size. DB1 was successful 77 percent of the time on DB (00) and 75 per

cent of the time on OH. OH1 was successful in 81 percent of the suckle attempts on his mother. Both were successful 70 percent of the time on the Helpers. There were no significant differences in suckle success among the 3 ewe groups (G=0.90, P>0.05) or between their own and alien lambs on the 0+ ewe (G=0.03, P>0.05).

Total Suckle Time (TST) for ewes ranged from 1.71 to 4.14 hours. DB and TT nursed an estimated 2.69 and 1.91 hours respectively, while AL and OH accounted for the extremes of 1.71 and 4.14 hours, respectively. The per lamb TST averaged 5.23 hours. A large difference was apparent in lamb TST's with OH1 achieving 7.27 hours and DB1, 3.94 hours.

In 1983, 26 of 27 ewes were judged pregnant. Three lambs were found dead (2 died in birth or shortly thereafter (O'Gara, pers. comm.) and one was apparently crushed by the ewe), 12 lambs disappeared within 3 days after they were born (5 of these were handled the day before they disappeared), 2 lambs disappeared when 18-21 days of age and 1 lamb disappeared when approximately 51 days old. As in 1982, predation probably accounted for many of the disappearing lambs. In addition, 2 ewes were seen in unusual distress prior to parturition and were never observed with lambs. Only 6 lambs (23 percent) survived until the end of the summer.

When observations began in late June, 9 ewes were nursing 7 lambs (the lamb that disappeared at 51 days old (BN1) was last seen July 16; some of the data from that lamb are included in subsequent analysis). Of the 9, BR, BN, UM, and LE nursed only their own lambs. OH, DE and TT nursed their own and all other lambs, and AL and FS had lost thier own lambs but continued to nurse all remaining lambs. Suckles of alien lambs accounted for 48-100 percent of total observed suckles (Fig.2 A). BR and LE were each observed letting alien lambs suckle twice (approximately 3 percent of the total observed suckles).

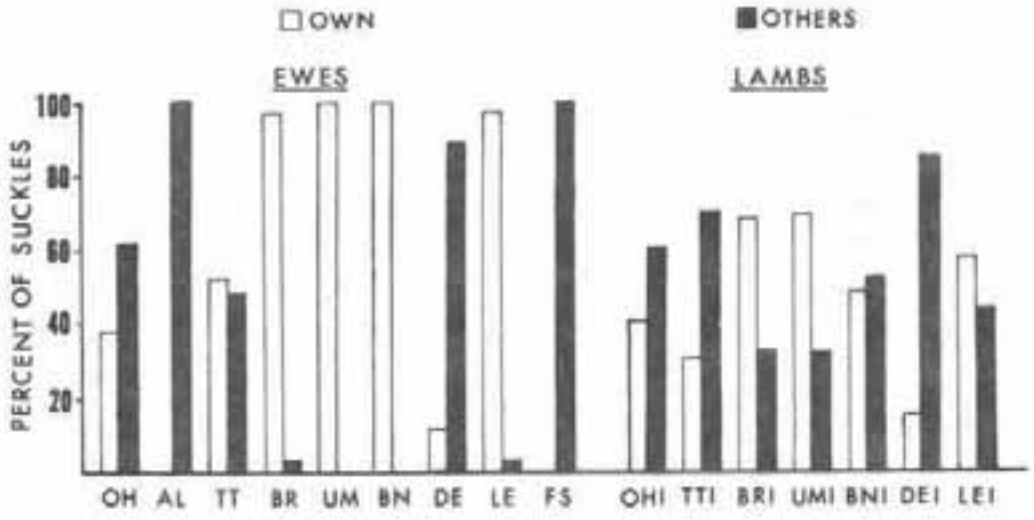

Fig. 2 Percent of suckles observed between own and other lambs and ewes in 1983.

observed suckles). This was judged insignificant and these ewes were considered to suckle only their own lambs. Lambs obtained 32 - 85 percent of suckles from ewes that were not their mothers (Fig. 2b), and 4 of the 7 lambs were observed suckling more often from other ewes. When observations began on June 25, the 3 male and 4 female lambs ranged from 15 to 35 days of age. Again, the lambs were not nursed equally (Table 3). In 1983, a total of 50 percent of all observed suckles were on ewes that were not the lamb's mothers.

For the ewes that nursed other lambs, only FS showed no significant difference among the number of suckles by various lambs ($G=9.94$, $P>0.05$). Of the ewes that still had their own lambs, all except TT discriminated significantly among the lambs that were not their own. Of the 7 ewes that still had their lambs, only 1 (DE) did not nurse her own lamb preferentially (Fig. 2a).

Table 3. Number of observed suckles and mean suckle durations (in seconds) of each lamb on each ewe in 1983.

Class:	OO	OO	OO	OO	O+	O+	O+	H	H
Ewe:	LE	BR	UM	BN	OH	TT	DE	AL	FS
Lambs:									
LE1 No.	64	2	0	0	13	7	4	8	15
Mean Dur.	17	23	0	0	24	20	15	18	16
BR1 No.	0	71	0	0	7	4	7	9	7
Mean Dur.	0	21	0	0	16	17	19	14	16
UM1 No.	0	0	82	0	4	6	10	7	10
Mean Dur.	0	0	15	0	14	21	20	12	13
BN1 No.	0	0	0	16	2	1	9	1	4
Mean Dur.	0	0	0	18	29	11	24	23	13
OH1 No.	0	0	0	0	26	2	24	6	7
Mean Dur.	0	0	0	0	29	13	22	17	17
TT1 No.	0	0	0	0	12	24	24	7	14
Mean Dur.	0	0	0	0	18	20	24	13	16
DE1 No.	2	0	0	0	5	2	10	38	10
Mean Dur.	16	0	0	0	23	21	22	19	17

The suckle duration for 00 ewes was significantly less than 0+ ewes nursing their own (t=7.06, P<0.001) or other lambs (t=4.47, P<0.001). 0+ ewes nursed their own lambs for a longer duration than they nursed alien lambs (t=4.27, P<0.001). There was no significant difference in suckle duration between 00 and H ewes (t=1.09, P>0.20). These results differed from those of 1982 when no difference among groups was found, perhaps due to a much greater sample size in 1983.

As in 1982, there were no significant differences in the orientation for any lambs (OH1: G=0.07, P>0.50; DE1: G=0.14, P>0.50; TT1: G=2.00, P>0.10; BR1: G=2.46, P>0.10; UM1: G=1.61, P>0.10; BN1: G=0.61, P>0.10; LE1: G=0.63, P>0.10) or all lambs combined (G=0.27, P>0.50).

Ewes initiated and terminated most suckle bouts in 1983. There were significant differences among the 3 groups for the proportion of times that ewes vs. lambs initiated suckle bouts (G=11.48, P<0.05), with 00 ewes initiating significantly more bouts that did ewes that nursed other lambs (G=10.32, P<0.05; Table 4). No significant differences were found among the 3 groups as to whether the ewes or lambs terminated bouts (G=0.09, P>0.90).

Table 4. Percent of suckle bouts that were initiated and terminated by each ewe class on own and alien lambs in 1983. See sample in Table 2.

Lamb Class:	INIT.				TERM.			
	Own		Alien		Own		Alien	
Ewe Class	%	n	%	n	%	n	%	n
00	80	202	100	3	88	216	100	3
0+	60	50	66	110	100	53	90	126
H	--	--	71	119	--	--	99	132

In 1983, 467 suckle attempts were recorded. There was a significant correlation between the number of times lambs attempted to suckle from any ewe, and the number of suckles they obtained from that ewe (r=0.77, P<0.01, Fig. 3). Lambs rarely attempted to suckle from ewes that would not permit them to nurse, e.g. alien lambs seldom attempted on 00 ewes, and lambs usually attempted most often on their mothers. Lambs of 00 ewes had a success rate of 72 percent on their mothers, while lambs of 0+ ewes only had a 46 percent success rate on theirs. Aliens were successful 53 percent of the time on 0+ ewes, and 49 percent of the time on Helpers. There were significant differences among the 3 groups in suckle success (G=11.53, P<0.05), with lambs having a higher success rate on their mothers if their mothers were 00 ewes rather than 0+ ewes (G=6.44, P<0.05). There was no significant difference in success rate on 0+ ewes whether the lamb was the ewe's own or an alien (G=0.58, P>0.05).

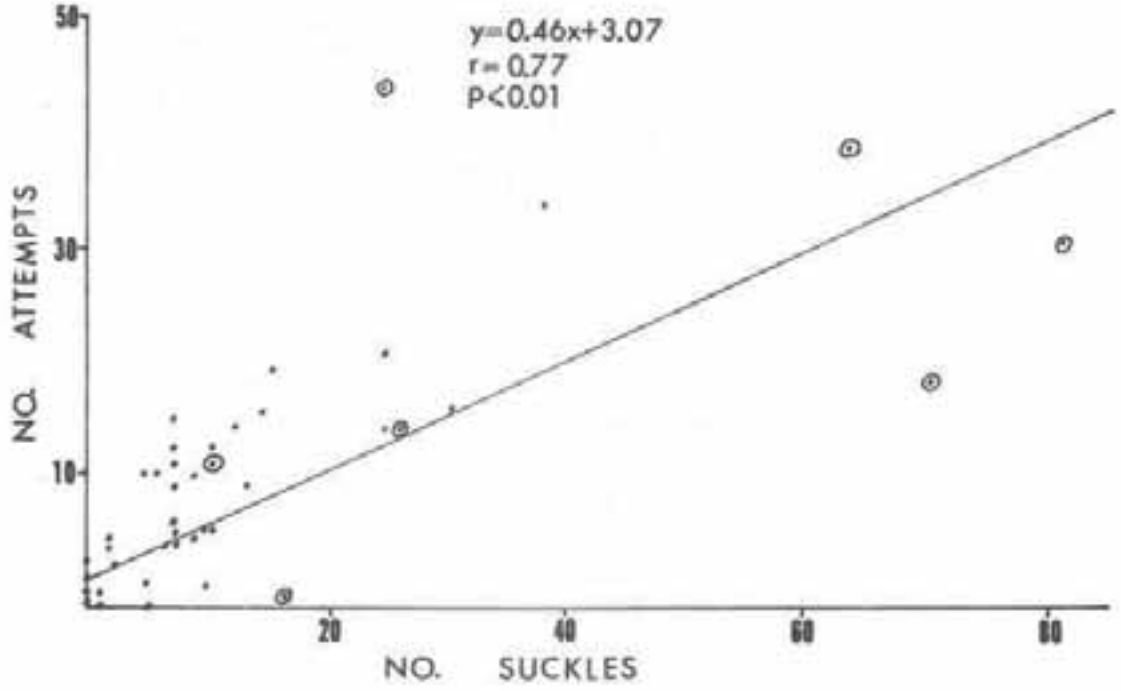

Fig. 3. Relationship between number of suckle attempts and number of suckles for all ewe-lamb pairs in 1983. Circles around points indicate a mother-offspring pair.

Ewe Total Suckle Time in 1983 ranged from 1.52 to 3.52 hours, with an average of 2.36 hours. Helpers had a mean of 2.47, OO ewes averaged 2.05 hours, and O+ ewes averaged 2.59 hours (Table 5). There was no significant difference between ewes that nursed only their own lambs and those that nursed others (Wilcoxon 2-sample C=12, P>0.10). The per lamb TST averaged 3.14 hours.

Table 5. Total Suckle Times, in hours, for ewes and their lambs in 1983. See METHODS for calculation of TST.

Class	Ewes		Lambs	
OO	LE	1.52	LE1	3.07
OO	BR	2.60	BR1	3.65
OO	UM	2.05	UM1	3.36
O+	OH	2.11	OH1	1.82
O+	TT	2.13	TT1	3.25
O+	DE	3.52	DE1	2.39
H	AL	2.82		
H	FS	2.11		

The lamb TST's ranged from 1.82 to 3.65 hours, with an average of 2.91. This is significantly lower than the 1982 average of 5.69 (Wilcoxon 2-sample C=12, P=0.05).

OO ewes sniffed their lambs significantly more often than did O+ and H ewes (G=52.7, P<0.001), and ewes that still had their lambs (OO and O+) sniffed lambs significantly more often than did Helpers (G=36.8, P<0.001; Table 6).

Table 6. Percent of times that different ewe classes were observed sniffing lamb's nose before or rump during a suckle bout.

Ewe Class:	OO		O+		H	
	%	n	%	n	%	n
	95	201	85	162	64	125

In 1983, 26 instances were observed in which 2 lambs suckled from a ewe simultaneously ("double-suckles"). Thirteen of these cases were on ewes that still had their own lambs (O+), in 8 of those cases, the ewe's own lamb was not one of the 2 suckling. There was a significant difference between the average total duration (both lambs combined) for O+ ewes (35.1 seconds) and for H ewes (22.1 seconds; Wilcoxon 2-sample C=53.5, P<0.05). There was no significant difference in suckle duration for O+ ewes whether nursing 2 lambs at once or their own, (t=1.43, P>0.10) but cumulative suckle duration was significantly greater for 2 lambs, than for a single alien lamb (t=5.18, P<0.05). The cumulative suckle duration for 2 lambs on Helpers was also significantly longer than for a single lamb (t=2.85, P<0.05).

DISCUSSION

Allomothering is usually considered altruistic, due to the high cost of lactation and the resulting decrease in reproductive potential (Reidman 1982). Lactation produces a considerable drain on a female's resources. For most mammals, including sheep, a female that "wastes" her resources on offspring other than her own may jeopardize her own offspring's survival as well as her future reproductive potential (Shackleton 1973, Horejsi 1976, Reidman 1982).

During the summers of 1982 and 1983, all of the lambs on the NBR received a substantial number of suckles from ewes that were not their mothers. Seventy-five percent of the ewes in 1982, and 56 percent of the ewes in 1983 nursed lambs that were not their own. Lambs obtained up to 85 percent of observed suckles from ewes that were not their own mothers. Numerous researchers reported that bighorn ewes would rebuff alien lambs (Geist 1971, Shackleton 1973, Horejsi 1976, Berger 1979), but apparently in none of these

studies were all the lambs and ewes individually known.

Two types of allomothers were present in the NBR herd; ewes that still had their lambs, and those that lost their lambs. Different hypotheses may explain allomothering behavior in each group, so I will discuss the 2 groups separately.

I. Ewes that still had their lambs (0+ ewes).

There are several hypotheses which might explain allomothering in this group:

A. Ewes are failing to consistently identify their own lambs.

The importance of olfaction in lamb recognition by its mother has been reported (Morgan et al. 1975, Grau 1976, Poindron 1976, Poindron and Le Neindre 1980, Gubernick 1981a,b, Rosenblatt and Siegel 1981). Olfactory discrimination by ewes might fail in several ways:

1. Interference during the critical period, preventing formation of an exclusive bond (Poindron and LeNeindre 1980, Rosenblatt and Siegel 1981). This is unlikely because ewes isolate themselves prior to parturition and remain isolated with their lamb for at least 5 days after the lamb is born (pers. obs.). However, the lambs of most of the NBR ewes were handled between 1980-84. Handling was not associated with allomothering behavior, but repeated human disturbance may produce a cumulative effect resulting in poor mother-young bond formation (J. Hogg, Pers. comm.).

2. Anosmia. Domestic sheep (Ovis aries) and goats (Capra hircus) that were experimentally rendered anosmic were unable to discriminate between their own and alien young (Baldwin and Shillito 1974, Klopfer and Famble 1966, Poindron 1976). In one experiment in which ewes were made anosmic prior to parturition, both the ewe's own lamb and alien lambs were less successful in suckle attempts (25 percent compared to 64 percent, by the ewe's own lamb, on intact ewes). Anosmic ewes sniffed lambs during only 50 percent of suckle bouts, compared to 78 percent of the time by intact ewes (Poindron 1976).

In the NBR bighorns, lambs were successful 77 and 72 percent of the time on their mothers, if their mothers were 00 ewes, and 81 and 46 percent of the time if their mothers were 0+ ewes (values for 1982 and 1983 respectively). Aliens were successful 0 and 16 percent on 00 ewes, and 75 and 53 percent on 0+ ewes. The higher values for 1982 are probably due to a lower lamb-to-ewe ratio (2 lambs and 4 ewes in 1982 compared to 7 lambs and 9 ewes in 1983). In 1983 lambs were successful more often on 00 ewes and less successful on 0+ ewes and Helpers. This was not the case in 1982, so on the basis of suckle success, I hesitate to make any conclusions. However, 0+ ewes did not discriminate between their own and alien lambs and 0+ sniffed lambs significantly less often when suckling than 00 ewes. The lack of discriminatory ability in the 0+ group of ewes may be due to anosmia.

Bighorn sheep on the NBR are infested with sheep nasal bots (Oestrus ovis; O'Gara pers. comm.), which have been present in the herd since at least 1936 (Capelle 1966). Sneezing, coughing and nasal discharge are evident

throughout the summer months. Nasal bots in domestic sheep may produce minute hemorrages, mucosal defects at the site of attachment, and constant irritation and thickening of the nasal mucous membranes (Jubb and Kennedy 1970, Capelle 1971). Female bot flies deposit larvae on the nostrils of sheep during the summer months. The first-instar larvae (about 10 millimeters in length) remain in the nasal passages for 1-9 months. Second-instar larvae (3.0 - 14.5 millimeters, Fallis 1940, cited in Capelle 1966) migrate into the frontal sinus and develop rapidly. Third-instar larvae (24 - 30 millimeters in length) migrate out the nostrils and are sneezed out by the sheep and pupate in the ground (Capelle 1966). Nasal bot larvae might render bighorn sheep partially or completely anosmic through cumulative scarring, due to either the constant irritation of the first-instar larvae or subsequent minor infections. The presence of large numbers of second- and third-instar larvae might also inhibit a ewes olfactory ability enough to disrupt the imprinting process soon after parturition. Second- and third-stage larvae have been reported in the Wildhorse Island and Sun River herds in late May (Capelle 1966). The effects of nasal bots on the olfaction of bighorn sheep is not known; they apparently do not affect olfaction in domestic sheep (T. Bunch, pers. comm.). Nasal bot-induced secondary infections leading to severe osteolysis and death is common in desert bighorns (Paul and Bunch 1978, Bunch 1980) but has only been reported once in a Rocky Mountain bighorn (Turner 1982).

Nasal bot-induced anosmia might explain why some ewes are not discriminating their own from alien lambs in this herd. Ecological factors might result in differential levels of infestion, which might explain why there were no O+ ewes observed in 1980-81 (J. Hogg, Pers. comm.).

3. Inbreeding effects. The bighorn sheep currently inhabiting the NBR are all decendants of a group of 12 animals that were introduced over 60 years ago. Refuge records do not indicate any additional transplants. The population has fluctuated from 10-100 animals, but has remained between 40-70 animals for the last 20 years (National Bison Range Refuge Narrative Reports 1922-1984). The coefficient of inbreeding in this herd is undoubtedly high (see Soule 1980). The exact effects of inbreeding in bighorn sheep are unknown. The herd falls under Geists' (1971) definition of a high quality population with regard to age at first reproduction, size, and yearling development. It remains possible that the lambs are so closely related that they cannot be distinguished from one another. This hypothesis fails to explain why some ewes still discriminated against alien lambs.

B. Kin selection.

Hamilton (1964) put forth the idea of "inclusive fitness", that is, the sum of an individuals reproductive success, plus that of its relatives, represents the individuals "inclusive fitness". According to Hamilton's genetical theory of social behavior (1964), a social act that increases the inclusive fitness of the performer will be promoted by natural selection.

Bighorn ewes usually live in groups consisting of adult females, yearlings and lambs. In many populations, rams shift to separate bachelor herds when 2-4 years of age, but ewes remain with their maternal band (Geist 1971). Ewes may actually associate in extended matriarchies of closely related individuals, rather than in allied groups of unrelated females as previously

suggested (Geist 1971, Gubernick 1981b). African and Asiatic elephant females are reported to exist in extended matriarchies; infants are allowed to nurse from any lactating female in the group, although the mother provides most of the care for her own infant, (Eisenberg 1972). African lions also exist in matriarchal groups where lactating females allow any cubs to suckle (Schaller 1972). Among ungulates, those that live in small, discrete units reportedly cooperate in defense against predators, while those in large, unallied groups generally do not (van Lawick-Goodall and van Lawick-Goodall 1970, Kruuk 1972). Cooperative defense has been reported in bighorns (Shank 1977). On the NBR all of the ewes associate in an extended matriarchy. Whether this is substantially different from a more natural situation that allows immigration and dispersal of individuals is not known.

Coyote predation may have accounted for most, if not all, of the disappearing lambs. Coyotes were frequently sighted in the lambing areas in 1982-83, and many coyote scats contained bighorn lamb hair. The NBR lacks the rugged, cliffy areas in which mountain sheep ewes in other populations retreat to lamb (Spencer 1943, Geist 1971, Pitzman 1971, pers. obs.). Lamb survivorship was significantly less in 1982 and 1983 (10 and 23 percent) than in 1980 and 1981 (50 and 53 percent, Hogg 1983; $G=6.35$, $P<0.05$) when no 0+ ewes were observed (J. Hogg, pers. comm.). Low survivorship of the lambs may prompt some ewes to "cooperatively" care for the surviving young, with the theoretical result that lambs have a better chance of surviving than if cared for by only 1 ewe. This "group selection" of related individuals is then a form of kin selection (West Eberhard 1975, Wilson 1975).

0+ ewes tended to be older than 00 ewes (Table 7). An increase in age results in a decrease in reproductive potential. A 10-year-old ewe will produce potentially fewer lambs in her remaining reproductive lifetime than

Table 7. Classes and ages of lactating ewes in 1982 and 1983. (+)=ewes that were estimated to be at least 5 years old in 1980.

Year	Ewe	Class	Age
1982	DB	00	6
	OH	0+	7+
	AL	H	7+
	TT	H	6
1983	LE	00	8+
	BR	00	3
	UM	00	2
	BN	00	2
	OH	0+	8+
	DE	0+	7
	TT	0+	7
	AL	H	8+
	FS	H	8+

will a 5-year-old ewe. A ewe may increase her inclusive fitness (Hamilton 1964) more by investing in not only her own lamb, but also the other lambs (her relatives), provided she can do this without detriment to her own offspring.

Ewes that nursed alien lambs may be hurting their own lambs. In 1983, but not in 1982, lambs of O+ ewes had lower TST's than lambs of OO ewes, but this difference was not significant (Wilcoxon 2-sample C=5, P>0.10). However, all lambs "cooperatively" nursed in 1982 and 1983 were still alive and in good shape as of April 1984. The cost of lactation was evident in the poor coat and general body condition of lactating ewes compared to non-lactating ewes, but all ewes that nursed alien lambs in 1982 produced healthy lambs in 1983, and all ewes that nursed aliens in 1983 appeared pregnant in April 1984.

Cooperative nursing in chital may be related to high levels of predation (Schaller 1967) and cooperative nursing in collared peccaries is one of several cooperative behaviors exhibited in their familial groups (Byers and Bekoff 1981).

C. Rare or isolated event.

It remains possible that the allomothering witnessed in the last two summers on the NBR is simply an error that occurs too infrequently for natural selection to act upon (Dawkins 1976). So many authors have commented on the exclusiveness of the mother-young bond in ungulates (Geist 1971, Shackleton 1973, Horejsi 1976, Schaller 1977, Shillito Walser 1977, Gubernick 1981a, b, Reidman 1982) that it would be easy to view this allomothering as an isolated event. What appear to be patterns may actually be coincidences.

II. Ewes that had lost their lambs (Helpers).

Predation was probably the proximate cause for the occurence of all Helpers in this herd, particularly if they had lost their lambs when at least several days old and the ewes were not physiologically "primed" for the peak lactation period (Moen 1973, Hanwell and Peaker 1977). Also, the pain of an overfull udder might motivate ewes to nurse alien lambs to alleviate the discomfort. Domestic ewes that lost their own lambs sometimes adopted aliens (Arnold and Morgan 1975). Both AL and FS lost their lambs when at least 10 days old in 1983, similar data are not available for 1982. Two helpers were also present in the NBR herd in 1980 and 1 in 1981 (J. Hogg, pers. comm.). The continuation of nursing behavior throughout the lactation period could be a cooperative effort on the part of the Helpers to aid in the survival of the remaining lambs (their relatives; see Kin Selection above). Ewes control the suckle bouts by initiating and terminating them, presumably Helpers could wean lambs any time they chose to. Flexibility in the length of the weaning period has been described by Berger (1979). The fact that Helpers nursed all lambs in the nursery band, instead of adopting a particular lamb, may support either the Kin Selection or the Anosmia hypothesis.

Ewes on the NBR have nursed more than 1 lamb, apparently without jeopardizing their reproductive fitness. The end result, whether intentional or not, appears to be cooperative care, with the lambs receiving more milk. Most of

this is due to the additional milk provided by the Helpers. This study does not permit discrimination among the hypotheses presented here.

Further detailed research on the NBR herd, and other herds is necessary to determine the extent of allomothering behavior in bighorn sheep.

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LITERATURE CITED

Altmann, J. 1974. Observational study of behavior; sampling methods. Behav. 49:227-267.

Arnold, G.W. and P. D. Morgan. 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. Appl. Anim. Ethol. 2:25-46.

Baldwin, G. A. and E. Shillito. 1974. The effects of oblation of the olfactory bulbs on the parturition and maternal behavior in Soay sheep. Anim. Behav. 22:220-223.

Berger, J. 1979. Weaning conflict in Desert and Mountain bighorn sheep (Ovis canadensis): An ecological interpretation. Z. Tierphychol. 50:188-200.

Brown, J. L. 1975. The evolution of behavior. W. W. Norton Co. NY. 761 pp.

Bunch, T. D. 1980. A survey of chronic sinusitis in the bighorns of California. Trans. Desert Bighorn Counc. 24:14-18.

Beyers, J. A. and M. Bekoff. 1981. Social, spacing and cooperative behavior of the collared peccary. Tayassu tajacu. J. Mammal. 62:767-785.

Capelle, K. J. 1966. The occurence of Oestrus ovis L. (Diptera: Oestridae) in the bighorn sheep from Wyoming and Montana. J. Parasitol. 52:618.

Capelle, K. J. 1971. Myiasis. Pages 279-305 in J. W. Davis, R. C. Anderson, eds. Parasitic Diseases of Wild Animals. Iowa State Univ. Press, Ames, Iowa.

Cluttonbrock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red Deer: Behavior and Ecology of Two Sexes. Univ. Chicago Press, Chicago, 378 pp.

Dagg, A. I. 1970. Tactile encounters in a herd of captive giraffe. J. Mammal 51:279-287.

Dawkins, R. 1976. The Selfish Gene. Oxford Univ. Press, NY. 224 pp.

Eisenburg, J. F. 1972. The Elephant: life at the top. Pages 191-207 in P. R. Marler, ed. The Marvels of Animal Behavior. National Geographic Society, Washington, D.C.

Espmark, Y. 1971. Mother-young relationship and ontogeny of behavior in Reindeer (Rangifer tarandus L.). Z. Tierpsychol. 29:42-81.

Estes, R.D. 1974. Social organization of the African Bovidae. Pages 166-205 in V. Geist and F. Walther, eds. The Behavior of Ungulates and its Relation to Management, IUCN, Morges, Switzerland.

Fallis, M. 1940. Studies on Oestrus ovis. Can. J. Res. 18:442-446.

Geist, V. 1966. Validity of horn segment counts in aging bighorn sheep. J. Wildl. Mgmt. 30:634-635.

Geist, V. 1971. Mountain Sheep: A study in Behavior and Evolution. Univ. Chicago Press, NU.

Grau. G. 1976. Olfaction and reproduction in ungulates. Pages 219-242 in R. L. Doty, ed. Mammalian Olfaction, Reproductive Processes and Behaviour. Academic Press, NY.

Gubernick, D. J. 1981a. Mechanisms of maternal "labelling" in goats. Anim. Behav. 29:305-306.

Gubernick, D. J. 1981b. Parent and Infant Attachment in Mammals. Pages 243-305 in D. J. Gubernick and P. H. Klopfer, eds. Parental Care in Mammals. Plenum Press, NY.

Hamilton, W.D. 1964. The genetical theory of social behavior, I and II. J. Theor. Biol. 7:1-52.

Hanwell,A. and M. Peaker. 1977. Physiological effects of lactation on the mother. Pages 297-312 in M. Peaker, ed. Comparative Aspects of Lactation. Proc. Zool. Soc. Lond. Symp. Academic Press, NY.

Hogg, J. T. 1983. A study of social organization, social behavior, and population dynamics in Rocky Mountain bighorn sheep on the National Bison Range, Moiese, Montana. MT Fish, Wildlife and Parks Res. Rep. P. R. Proj. W-120-R-13. 56 pp.

Horejsi, F.L. 1976. Suckling and feeding behavior in relation to lamb survival in bighorn sheep (Ovis canadensis canadensis Shaw). PH.D. Thesis, Univ. Calgary, Calgary, Alberta. 265 pp.

Jubb, K.V.F., and P. C. Kennedy. 1970. Pathology of Domestic Animals, 2nd ed. Academic Press, NY, Vol. 1, 543 pp.

Klopfer, P.H. and L. Gamble. 1966. Maternal "imprinting" in goats: role of the chemical senses. Z. Tierphychol. 23:588-592.

Kruuk, H. 1972. The Spotted Hyena. Univ. Chicago Press, Chicago. 335 pp.

Lawick-Goodall, H. Van, and J. van Lawick-Goodall. 1970. Innocent Killers. Ballentine Books. NY, 222 pp.

Lent, P. C. 1974. Mother-infant relationships in ungulates. Pages 14-55 in V. Geist and F. Walther, eds. The Behavior of Ungulates and its Relation to Management. IUCN, Morges, Switzerland.

MacClintock, D. 1973. A natural history of giraffes. Charles Scribners Sons, NY, 134 pp.

Moen, A. N. 1973. Wildlife Ecology. W. H. Freeman Co., San Francisco, CA 458 pp.

Morgan, P. D. and C. A. P. Bundy, G. W. Arnold and D. R. Lindsay. 1975. The roles played by the senses of the ewe in the location and recognition of lambs. App. Anim. Ethol. 1:139-150.

National Bison Range Refuge Narrative Reports 1922-1984. On file at refuge headquarters, National Bison Range, Moiese, Montana.

Paul, S. R. and T. D. Bunch. 1978. Chronic frontal sinusitis and osteolysis in desert bighorn sheep. J. Am. Vet. Med. Asso. 173-1178-1180.

Pitzman, M. S. 1971. Birth behavior and lamb survival in mountain sheep in Alaska. Unpub. M. S. Thesis, U. Alaska, Fairbanks, Alaska, 116 pp.

Poindron, P. 1976. Mother-young relationships in intact or anosmic ewes at the time of suckling. Biol. Behav. 2:161-177.

Poindron, P. and P. Le Neindre. 1980. Endocrine and sensory regulation of maternal behavior in the ewe. Pages 75-119 in J. S. Rosenblatt, R. A. Hinde, C. Beer, and M. C. Busnel, eds. Advances in the Study of Behavior, Vol. 11, Academic Press, NY.

Reidman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. Quat. Rev. of Biol. 57:405-435.

Rosenblatt, J. S. and H. I. Siegel. 1981. Factors governing the onset and maintenance of maternal behavior among nonprimate mammals: the role of hormonal and nonhormonal factors. Pages 243-305 in D. J. Gubernick and P. H. Klopfer, eds. Parental Care in Mammals, Plenum Press, NY.

Schaller, G.B. 1967. The Deer and the Tiger. Univ. Chicago Press, Chicago, 370 pp.

_____. 1972. The Serengeti Lion: A study of predator-prey relations. Univ. Chicago Press, Chicago. 480 pp.

_____. 1977. Mountain Monarchs: Wild sheep and goats of the Himalaya. Univ. Chicago Press, Chicago, 425 pp.

Shackleton, D. M. 1973. Population Quality and Bighorn Sheep. PhD. Thesis, Univ. Calgary, Calgary, Alberta, 226 pp.

Shank, C. C. 1977. Cooperative defense by bighorn sheep, J. Mammal. 58:243-244.

Shillito Walser, E. 1977. Maternal Behavior in Mammals. Pages 313-331 M. Peaker, ed. Comparative Aspects of Lactation. Proc. Zool. Soc. Lond. Symp. Academic Press, NY.

Skutch, A. F. 1961. Helpers among birds. Condor 63:198-226.

Soule, M. E. 1980. Threshold for survival: maintaining fitness and evolutionary potential. Pages 151-170 in M. E. Soule and B. A. Wilcox eds. Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer, Sunderland, ME.

Spencer, C. C. 1943. Notes on the life history of Rocky Mountain Bighorn Sheep in the Tarryall mountains of Colorado. J. Mamm. 24:1-11.

Turner, J. C. 1982. Chronic cranial osteitis in a Rocky Mountain bighorn sheep. J. Wildl. Dis. 18:373-379.

West Eberhard, M. J. 1975. The evolution of social behavior by kin selection. Quat. Rev. Biol. 50:1:33.

Wilson, E. O. 1975. Sociobiology. Belknap Press, Harvard; 697 pp.