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Mother-daughter interactions in American bison (*Bison bison*): Factors associated with individual variation

Green, Wendy Carroll Hortenstine, Ph.D.

City University of New York, 1987

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MOTHER-DAUGHTER INTERACTIONS
IN AMERICAN BISON (*Bison bison*):
FACTORS ASSOCIATED WITH INDIVIDUAL VARIATION

by

Wendy Carroll Hortenstine Green

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1987

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

10 - 6 - 87
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Abstract

MOTHER-DAUGHTER INTERACTIONS IN AMERICAN BISON (*Bison bison*): FACTORS ASSOCIATED WITH INDIVIDUAL VARIATION

by

Wendy C. H. Green

Adviser: Professor Joseph Griswold

To describe developmental changes and individual variation in bison mother-daughter relations, I observed 13 dyads from birth to 1.5 years and collected supplementary data on the first five years for 48 daughters at Wind Cave National Park.

Pre-weaning spatial relations change minimally; mothers and calves follow each other infrequently and are often far apart. Bison appear to be neither hiders nor followers, but incorporate aspects of both strategies. Old and young mothers invest differently in offspring; while older cows provide more nursing care, young mothers contact calves more often. Maternal experience mitigates disruptive effects of tending by bulls on mother-calf relations.

Weaning occurs gradually, with little conflict. The end of weaning varies with the mother's subsequent reproductive status: pregnant cows stop nursing at 9-12 months; barren cows at 17-21. After weaning and the birth of the mother's next calf, daughters spend less time near mothers, but proximity-maintenance behaviors change little. While post-weaning associations with mothers vary in longevity, most continue at least until sexual maturity. Where bonds endure, mothers' efforts at proximity-maintenance are largely responsible.

Bison mother-daughter relationships appear to be polymorphic. Predominant classes reflect maternal and filial independence and maternal nursing tolerance. Bonds end earlier when mothers show aggression in the first few weeks and provide more nursing care. Filial and maternal independence are at opposite ends of a continuum. Calves are most independent when mothers maintain proximity often and nurse patiently.

Younger mothers and later-born calves behave as if to compensate for social and physical disadvantages. Late-born calves and their mothers synchronize movements more than other dyads. Young mothers have closer, longer-lasting relations with daughters. Larger daughters are born earlier, retain natal coats longer, achieve higher rank, and may calve earlier than smaller daughters; they are also more independent of mothers. Prolonged care by barren mothers enhances offspring size and, possibly, reproduction.

Dominance is correlated with age among cows, but with size and age among juveniles. Dominant cows tend to reproduce more than others and provide more nursing care; their daughters develop independence earlier and dominate peers. Dominance among daughters increases with nursing time and early independence.

ACKNOWLEDGEMENTS

I am very grateful to Aron Rothstein for his constant support and his help in many aspects of this study. I also thank Joe Griswold for helping me to organize the dissertation and for his insightful editorial comments. Rich Klukas, Ernest Ortega, Jim Randall, and the staff at Wind Cave National Park helped make the field work possible by providing facilities and considering research needs at roundups. I appreciate the involvement of John Byers, Richard Van Gelder, Carol Simon, Howard Topoff, and Leslie Marcus. Field work was funded by a predoctoral training grant (MH 15341) from the National Institute of Mental Health, and by Sigma Xi.

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PART I: INTRODUCTION AND METHODS

Chapter 1

GENERAL INTRODUCTION

Social organization varies between and within species in relation to environmental differences. In many ungulates, for example, group size increases with the openness of the environment. This relationship has been documented among species of African antelope (Jarman 1974; Estes 1974) as well as within species such as bison (Shackleton 1968; Van Vuren 1983; Rutberg 1984) and white-tailed deer (Hirth 1977). There is also evidence that, in herbivores, populations and closely-related species are more gregarious where food availability is lower (bighorn sheep: Berger 1979a, c; marmots: Barash 1973, 1974, 1977). The latter studies suggest that parent-offspring associations are more extensive where conditions are harsher.

Within populations, individual social behavior varies in relation to that of other group members (Slater 1981). Individuals may experience contrasting 'microhabitats.' For example, dominant bison cows forage more efficiently than subordinates (Rutberg 1984, 1986a). Such variation may affect maternal behavior and, through adjustments of mothers and offspring to each others' behavior (Meier 1984), affect the interactions of offspring with mothers and other group members.

For some individuals, social behavior may serve to compensate for disadvantages. Bateson (1976) proposes a model of 'settling for less,' in which handicapped animals readjust their goals in order to maximize available resources. For example, Altmann (1980) found that subordinate yellow baboon mothers restrict their infants' movements more than other mothers. She suggests that this maternal difference is related to the fact that the former have more difficulty in foraging. While such restrictions may retard infant development, they are also likely to decrease the infant's nutritional requirements and thus to increase the mother's ability to provide sufficient nourishment.

In the present study, longitudinal observations of individual bison mother-daughter dyads begin at birth and continue past weaning. Patterns of developmental change in diverse aspects of dyadic interactions are described. Naturally occurring differences in dyadic interactions are examined in relation to such variables as maternal age, offspring birth order, and maternal and filial dominance. Moreover, early and long-term variations are compared in order to describe factors contributing to the longevity of mother-daughter associations.

Bison Natural History

The genus *Bison* includes North American (*B. bison*) and European species (*B. bonasus*). Bison are members of the order Artiodactyla (even-toed ungulates), suborder Pecora (true ruminants), family Bovidae (hollow-horned), and the (oxenlike) tribe Bovini (McDonald 1981). Bovids reflect a trend toward the exploitation of open grassland habitats (Eisenberg 1981), showing adaptions for grazing and running. In particular, the four-chambered ruminant stomach increases microbial fermention of carbohydrates; further adaptations include toughened dental structure for chewing grasses and specialized limbs for running (Romer 1959; Van Gelder 1969; Cloudsley-Thompson 1975). Increased gregariousness also allows bovids to inhabit open regions (Estes 1974); in this respect, bison represent an extreme, having formed enormous herds prior to their decimation (Roe 1951). While bison group size varies with the habitat (Shackleton 1968; Van Vuren 1983; Rutberg 1984), the subjects of this study inhabit a region of predominantly open prairie and correspondingly should be highly gregarious. This is supported by the fact that all cows and juveniles in the park (236 animals in 1984) form one large herd during most of the rut; prior to the rut (January to July), average group size is about 50 (pers. obs.).

Within the United States, wolves are absent in the regions inhabited by bison; however, anti-predator behavior can be observed at Wood Buffalo National Park in Canada. Fuller (1960, 1961, 1966) reports that bison do not appear to alter their behavior in the presence of wolves; they stand or lie down and ruminate, even when a member of the herd is being attacked. These descriptions cast doubt on statements of earlier writers (e.g., Garretson 1938) that bison herds react to wolves' attacks with an organized communal defense. Fuller's observations, in comparison with those of bison in the absence of wolves (e.g., McHugh 1958) indicate that no obvious shift in social organization has occurred since the eradication of predators.

McHugh (1958) and Fuller (1960) describe the sensory capacities of bison. Olfaction seems to be particularly important. Where bison are unaccustomed to humans, human scent causes herds to stampede, even when the source is hidden from view several hundred meters away. The vomeronasal organ is an accessory olfactory system which appears to allow males to detect estrous females in bison and other species (Klemm et al. 1984). Bison also seem to have an acute sense of hearing. Fuller (1960, p. 4) describes a situation which illustrates this point: "On one occasion I was watching a herd of bison and noticed that they began to focus their attention in my direction, but were looking beyond my hiding place. After some time I heard bison vocalizing and later a second herd appeared from the surrounding woods. Since there was a cross wind it is evident that the first herd initially detected the presence of the second by auditory stimuli. It is equally apparent that the bison reacted to the sounds of the second herd long before those sounds were audible to me." Visual perception is probably less acute; however, McHugh (1958) states that bison reacted to the sight of a moving jeep at distances of more than a mile. The relative importance of different sensory modalities may also depend on the context. For example, from a distance, olfaction may be the best way to identify a predator, while audition should be more useful for locating individuals in the herd.

Bison social organization and mating behavior have been described by McHugh (1958), Fuller (1960), and Lott (1974, 1981). Adult cows and bulls form separate and distinct social units which come together only during the rut. While cows and juveniles form relatively large herds, bulls live solitarily or in small groups. Cows' social interactions are largely dominated by relations with offspring of one or more years (pers. obs.). In contrast, bulls interact primarily with peers after weaning (Rothstein, in prep.), and have no parental role beyond mating. These intersexual differences are reflected in social development. Young males generally stop associating with their mothers soon after weaning and leave the cow-juvenile herd at around 3 years of age (McHugh 1958). In contrast, females remain in the herd. It is the relationship between bison cows and their developing female offspring which is the focus of this dissertation.

Events in the Life Cycle

Before examining bison mother-daughter relations, it is important to consider species- or population-specific events in physical and social development which may influence the bond. The following summary provides an overview of such events, based on three years of field observations. Some of these aspects of development are described as well by McHugh (1958), Egerton (1962), Engelhard (1970), Shult (1972), Mahan (1978), and Lott and Galland (1985).

PARTURITION: After a nine-month gestation period, calves are born singly, beginning in mid April. The birth peak is usually in early May, although calves are born as late as October. During parturition, mothers lie down or stand. Immediately afterward, mothers lick the neonates intensely and may help them to stand by nosing them and/or prodding them with their hooves. Calves generally attempt to stand within the first 10 minutes. In four observed births, calves stood for the first time in 8-18 minutes. By 20-35 minutes, calves began walking, sometimes leaning against the mother. By 15-45 minutes, they began nursing; in one case the first nursing bout continued for 25 minutes. Two calves pronked and ran at 67 and 80 minutes, respectively.

Around the time of parturition, cows leave the herd. Of 14 cows observed during or immediately following parturition, all but one were in, or on the edge of, the herd. After calving they either left the herd or did not follow as the herd moved away. Cows remained alone with their calves for 1-5 days before returning to the herd.

Calving behavior may depend on the age of the cow. Very few multiparous cows, and no cows older than seven, were observed calving. Experienced cows may leave the herd before parturition, as in chamois (Couturier 1938). Many older cows were seen soon after their calves were born in small, mobile cow-calf groups. For the first 1-2 weeks such groups stayed away from the rest of the herd, running at the slightest alarm. In contrast, young cows seemed less wary. Calving within the herd, it was often hard for them to stay with their newborn calves. Other bison crowded around, nosing and occasionally stepping on the calves. As mothers led their calves away they often had to stop them from following other animals. Leaving the herd before birth may be a strategy cows learn through experience, allowing them to avoid post partum interference.

NATAL COATS: Calves are born with orange or light-brown coats, in contrast to the dark brown or black of older animals. Calves began to moult at 5-12 weeks and were fully dark by 10-18 weeks of age (see chapter 12); calves underwent a series of mottled patterns as they moulted. Calves born late in the year generally retained their natal coats until the spring.

ACTIVITY CHANGES: During the first few months, calves spend more time resting than older animals. Calves may interrupt their resting to follow and lie down close to their grazing mothers. Often, however, they remain lying in one spot while their mothers walk as far away as 100m or more to graze. After one or more hours, their mothers may walk back to them and/or call to them; alternatively, when all resting neighbors have walked away, calves may follow them toward their mothers. As they grow older, calves graze with their mothers more often (see chapter 3).

THE RUT: In July the rut begins. Bulls circulate through the herd, roaring, fighting, and displaying to each other. They frequently approach cows, nosing their vulvae and performing flehmen to test cows' reproductive conditions. Mature cows who are close to estrus are tended by bulls. A tending bull keeps the cow as far away from the herd as possible, and drives away other bulls. For the few days during which the cow is in estrus, she is frequently chased by 10 or more bulls; mating often occurs at the end of such chases (see also Lott 1974, 1981).

Most cows come into estrus when their calves are four months old. Tending generally interrupts the mother-calf relationship (chapter 5). Calves are driven away from mothers, and mothers are driven away from calves. Calves stop following mothers and behave more independently. Mothers often try to follow their retreating calves, but are cut off by tending bulls.

LATER DEVELOPMENT: Weaning is completed during the first winter except when mothers do not calve the next year (chapter 6). Daughters usually calve at three years (appendix A). Physical growth continues beyond sexual maturity; for example, horns continue to increase in thickness and curvature. However, the fourth year seems to represent a physical plateau, being the age at which cows acquire all their adult teeth (Fuller 1959), and reach maximum weight (appendix C).

In this investigation, mother-daughter relations are examined in relation to aspects of both early and later stages of development.

Chapter 2

GENERAL METHODS

I. Subjects and Field Techniques

The Study Site

This study was conducted at Wind Cave National Park, located in the southeastern foothills of the Black Hills, in Custer County, South Dakota. The park covers 11,335 ha (approximately 70 square km); the terrain consists of rolling hills intersected by canyons. About 20% of the vegetation is coniferous forest dominated by ponderosa pine (*Pinus ponderosa*). The rest is mixed grass prairie, including western wheatgrass (*Agropyron smithii*), needlegrasses (*Stipa* spp.), bluegrasses (*Poa* spp.), grama grasses (*Bouteloua* spp.), bluestems (*Andropogon* spp.), and sedges (*Carex* spp.). Forbs include scurfpeas (*Psoralea* spp., goldenrod (*Solidago* spp.), sweetclover (*Melilotus* spp.), and fetid marigold (*Dyssodia papposa*). Fringed sage (*Artemisia frigida*), wild rose (*Rosa* spp.), lead plant (*Amorpha canescens*) and snowberry (*Symphoricarpos occidentalis*) comprise the major shrubs. Average annual precipitation is about 46 cm.

The Study Herd:

The Wind Cave bison herd includes about 230 cows and juveniles and about 100 bulls. Bison range throughout the enclosed park, but spend most of their time away from wooded areas, on flatter, grassy rolling hills. They frequently share grazing areas with pronghorn antelope (*Antilocapra americana*), elk (*Cervus elaphus*), and black-tailed prairie dogs (*Cynomys ludovicianus*). During the summer, especially, bison spend much of their time in prairie-dog towns. These bison have no non-human predators. While coyotes are frequently within or near bison herds, they are virtually ignored by herd members. Only when calves are less than 2 weeks old do cows chase away coyotes.

Bison are native to this region but were nearly eliminated before 1913, when the New York Zoological Society reintroduced 14 animals (Shult 1972). To this group a few bison from other areas were added later. The herd has recently been found to be among the most outbred of those tested so far in the United States (Stormont, pers. comm.). This is probably due to the proximity of a larger bison herd in Custer State Park, which shares WCNP's Northern border and is separated in several places only by cattle guards.

The Wind Cave bison are managed only in the sense that their range is limited by the park fence and that they are subjected to periodic roundups. The latter permit the culling of excess animals and insertion of small, numbered eartags for identification. Roundups occurred at two-year intervals until late 1983, when the park began a program to eliminate brucellosis (a disease that affects cattle but not bison; it is believed to pass from bison to cattle when the two species are kept together). Since then, roundups have been held each year and a greater effort has been made to round up all bison. All are tested for brucellosis, and the reactors shot.

The primary subjects of the study were 13 female calves and their mothers, who were observed from birth (or soon after) in spring and early summer, 1983, until August, 1984, when most were 17 months old. Additional data were collected on 48 daughters born in 1982 and 1983 (see 'data collection'). The study was restricted to female offspring because of the separate and differing social structures of cows and bulls, and to eliminate possible variation in development related to calf sex. The latter was suggested by preliminary findings in the present study, and has been documented in various ungulates (e.g., Duncan et al. 1984). Table 1 shows the 13 focal subjects, with birth dates and mothers' ages.

Adults were aged during roundups. Exact aging was possible for animals that retained the small numbered eartags inserted when they were calves or before all their teeth emerged. Ages of the few animals lacking eartags were estimated by tooth wear and horn length and curvature, using the methods described by Fuller (1959).

While some calves were seen during or soon after parturition, most birthdates were estimated by the appearance of the calf when first seen (e.g., size, coordination, curvature of legs, presence of umbilical cord) and by the last date on which the mother was seen prior to calving.

Among the subjects, all two- and three-year-old mothers were primiparous; the 4-year-old (Bump-Hump) had had one previous calf (pers. obs.). All older cows were multiparous. Five of the six older cows (all but Harp) bore a calf the previous year (1982), though their exact parity was not known; Harp nursed a yearling the previous year. One-horn and Nelly were also accompanied by (female) yearlings in 1982.

TABLE 1

FOCAL SUBJECTS

DAUGHTER	BIRTHDATE	MOTHER	MOTHER'S AGE
Vicky (VC)	4/20	Valerie (VA)	3
BB	4/20	CB	3
Chris (CS)	4/20	Crown (CR)	12
Holly (HO)	4/24	Harp (HP)	15
J	4/24	Judy (JD)	3
Nancy (NA)	5/1	Nelly (NE)	10
Heidi (HD)	5/1	1-Horn (IH)	8
Toby (TB)	5/1	Tess (TE)	3
UB	5/1	Uri (UR)	3
Lola (LA)	5/4	Lorn (LO)	17
Bonnie (BN)	5/27	Bump-Hump (BH)	4
CL	6/1	Cockeye (CO)	18
Reba (RB)	6/29	Orange-2 (RO2)	2

Field Techniques

Field work was conducted continuously during the 18 months from February, 1983, to August, 1984. A nine-month season of preliminary work was conducted from April to November, 1982. Follow-up observations were made in October, 1984, August, 1985, and July 1986.

I was able to recognize 180 individuals, primarily through natural variations in horn shape and length, hair growth (especially 'bangs' and 'beards'), body size, and coloration. Animals under two years of age were particularly difficult to recognize. Calves were identified soon after birth by variation in calf coat coloring and texture, differences in body size and length of horn buds, and by their mothers. Calves' coats began to change color after 1-2 months, resulting in variously mottled (though changing) patterns which facilitated recognition (see chapter 12). After their adult coats had grown in, many juveniles were marked with bleach, using a bow and blunt arrows, to aid identification. Roundups also afforded the opportunity for inserting colored plastic eartags in the ears of animals that were particularly difficult to recognize. Several animals were given such eartags prior to the beginning of field work, in January, 1982. This facilitated the process of learning individual identities.

Data Collection

Observations were made from a truck or on foot, depending on the location of the bison. When animals were found in an area inaccessible to vehicles, a closer approach was made on foot. Observation distances varied from 10m, when the herd could be observed from a vehicle, to 200m. Bison at Wind Cave are habituated to vehicles; at the close approach of the truck, the nearest animals show increased vigilance by looking frequently at the truck for 2-3 minutes. They then resume normal behavior and appear to take no further notice of the observers or the truck. Observers on foot have a greater effect, especially in areas near the middle of the park where contact with humans is uncommon. An observer can approach to 50m without greatly disturbing the bison provided she moves slowly and sits down as soon as the bison begin watching.

Subjects were observed through 10 X 50 binoculars and a 25X spotting scope. Data were recorded on audio tape and in notebooks. Mother-daughter dyads were observed in focal-animal samples (Altmann 1974) at frequent intervals (usually 1-4 days) from April through October, 1983, and from April to August, 1984. From November, 1983 to April, 1984, subjects were observed in ad lib samples at intervals of one to three weeks. Focal dyads were selected at random and observed until they could no longer be kept in sight. Since activity levels were generally low, up to three dyads could be observed simultaneously. During observation periods, I recorded the behaviors of each focal dyad and, at 2.5-minute intervals, the distance between mother and daughter and whether or not they followed each others' movements (see Measures). During rest periods, focal data on nursing interactions were supplemented with ad lib sampling. Observations ranged in duration from 0.3 to 7.5 h; brief observations were omitted from analyses because they usually occurred while the herd was moving so quickly as to preclude continuous focal sampling. Sampling periods were scattered throughout the daylight period. Observation hours (6-10 per day) alternated between dawn to mid-day and mid-day to dusk. Early observations after dark with a night vision scope indicated that night-time observations were impractical, particularly since individuals could not be identified. Nocturnal activity cycles appeared to be similar to those of the day.

Each of the 13 subjects was observed in focal samples for an average of 12-16 hours per month during months 1-7 and 15-16, except for two calves in months 6 and 7, and one calf in month 1. Data for nearly all subjects are not as abundant during the first, sixth, and seventh months as during the second, third, fourth, and fifth. During the first week post partum, several calves and their mothers were not observed. Therefore, for analyses of individual differences, week 1 was omitted from all records, particularly since the first week appears to differ greatly from succeeding weeks in most measures considered here (see chapter 3). Because of the frequent splitting and joining of bison groups, specific individuals occasionally disappeared for varying lengths of time. As a result, not all subjects were observed during every week. For analyses using weekly records, weeks have been combined to ensure that more than half the subjects (i.e., at least 7) are represented by each record.

Several analyses are based on a larger sample than the 13 focal dyads. In such cases data on other females born in 1982 and 1983 are included. Information on these animals is shown in appendix D; resulting sample sizes vary with measures and are provided in the methods sections of relevant chapters.

To clarify what follows, two terms require explanation:

a) *Month:* Offspring age was measured in terms of weeks (7 days, starting with birth) and lunar months (4 weeks). All references to 'months' of calf age specify lunar months. Thus the variability of calendar months (ranging from 28 to 31 days per month) was avoided.

b) *Herd:* Herds differ from groups in size. In references to social collectives, herds were defined operationally as 50 or more animals, while groups contained less than 50. The term is also used as 'the herd', or 'cow-juvenile herd', referring to the population of bison cows and juveniles within the park, all of which are part of the same social entity, although groups of changing composition often diverge and converge.

II. Measures of Mother-Daughter Relations

Activity Patterns and Proximity

Preliminary observations suggested that proximity of cows and calves varies with the type of activity. Therefore, the following data were collected: a) the percent of time cows and calves spent in various activities, b) the percent of time mothers and calves spent at various distances apart, and c) the percent of time spent within 10m of each other in each activity type. Analysis of activity patterns alone allows for examination of the extent to which the calf's activity is synchronized with the mother's, and how this changes with calf age.

A) ACTIVITY:

Scans on the activities of both mother and calf were taken at 2.5-minute intervals. Data were grouped in the following categories:

<u>Both Grazing</u> (activity of mother and calf synchronous): Mother and calf stand or move slowly with heads down, clipping, chewing, and swallowing grass and forbes. During the first week it was unclear whether a few calves were grazing or only going through the motions without really ingesting grass. Therefore any behavior that looked like grazing was counted as such.

<u>Mother Grazing, Calf Resting</u> (asynchronous activity): While mother shows grazing behavior, calf lies on the ground, either flat on one side or upright with legs folded under body

Mother Grazing, Calf Active But Not Grazing (activity synchronized in that both are active, but asynchronous in that mother grazes while calf does not): Mother shows grazing behavior while calf walks, stands, or plays.

Mother Resting, Calf Grazing (asynchronous activity): Mother stands motionless, with head at or slightly below the level of the shoulders, or lies on ground (flat or upright). Calf shows grazing behavior.

Both Walking (synchronous activity): Mothers and calves move in a faster and more directional manner than while grazing. While walking, heads are kept at the level of the shoulders, although they may occasionally nose the ground or bite off a mouthful of grass. Such behavior occurs during grazing periods (e.g., walking through the herd) as well as migrations, when all group members walk simultaneously.

Both Standing or Lying (synchronous activity): Mother and calf stand motionless with heads at or slightly below the level of the shoulders, or lie flat or upright on the ground.

Nursing: Mother stands or grazes while calf suckles (see below). This measure serves only as a source of comparison with other activity types; it is omitted from considerations of context-dependent proximity. A more precise measure of nursing time is provided below.

B) PROXIMITY

Distances between cow and calf were recorded at 2.5-minute intervals in 7 categories: <=1m, 2-5m, 6-10m, 11-20m, 21-40m, 41-100m, and >100m. Because patterns of change were similar in all categories (see chapter 3), proximity was analyzed in terms of an intermediate value: the percent of scans within 10m. This is a conservative estimate of the maximum distance within which mother and calf can monitor each others' behavior and are likely to be nearest neighbors.

Distances were estimated primarily by comparison with cow length. Previous training in distance-estimation, using pre-measured distances, also helped in collecting these data.

C) PROXIMITY IN RELATION TO ACTIVITY

From scans of activity and proximity I calculated the proportion of time when mother and calf were within 10m of each other in the following activity types:

While both graze

While mother grazes and calf rests

While mother rests and calf grazes

While mother grazes and calf is active but not grazing

While both walk

While both stand or lie down

Approaching and Leaving

These measures provide direct estimates of the relative roles of mother and calf in maintaining proximity, and suggest the extent to which cows and calves act independently of one another.

The following measures involve movements across borders between mother and calf of both 1m and 10m. For example, an approach involves a movement of one member of the dyad toward the other, across the designated boundary. By comparing data on movements across 1m and 10m boundaries, one may compare the roles of mother and calf in maintaining proximity at different distances.

Frequency/h: Calf approaches mother

Frequency/h: Mother approaches calf

Frequency/h: Calf leaves mother

Frequency/h: Mother leaves calf

$$\text{Percent approaching by calf (\%Ac)} = \frac{\text{approaches by calf}}{\text{approaches by calf + approaches by mother}} \times 100$$

$$\text{Percent leaving by calf (\%Lc)} = \frac{\text{leaves by calf}}{\text{leaves by calf + leaves by mother}} \times 100$$

%Ac-%Lc

The last of these measures (%Ac-%Lc) is a descriptive index developed by Hinde and Atkinson (1970), measuring the relative roles of mother and calf in maintaining proximity. Possible values range from 100 to -100; negative values reflect greater effort on the part of the mother in staying near the calf; positive values reflect the calf's greater role. Values of zero reflect equal contributions by both.

Orientation between Mother and Daughter During Movements

Since ungulate mothers do not carry their infants or restrain their movements, following behavior is the basic mechanism by which mothers and their young maintain proximity. When one member of the pair moves away from the other, the latter may or may not follow. Examination of the orientation of cows and calves in relation to each others' movements provides information on the relative responsibility of cow and calf in maintaining proximity regardless of their distance apart. For example, a calf that frequently follows her mother at a constant distance during movements might rarely be seen approaching her mother; by approach/leave measures she would therefore appear to make little effort at maintaining proximity. However, measures of orientation also estimate the total proportion of time when proximity is maintained, and the frequency with which each moves away from the other, indicating the extent to which the movements of cow and calf are dependent or independent of each other.

These measures may be closely related to activity patterns. For example, the percent of scans in which calves do not follow their mothers' movements might be correlated with time spent resting while mothers graze. Similarly, the percent of scans in which mothers and calves follow each other may be correlated with time spent in synchronous activities.

Scans at 2.5-min intervals were grouped in the following categories:

Following: Mother walks away, calf follows. Both move in the same direction, the calf behind or beside the mother. When it was unclear whether the follower's path of movement parallelled that of the leader, I waited until this could be discerned; if the follower's direction veered but was corrected within a few seconds, she was counted as following.

Leading: Calf walks away, mother follows. Both move in the same direction, mother behind calf (see 'following').

Not Following: Mother walks away to 10m or more; calf does not follow. The mother is active, the calf either active or resting.

Not Leading: Calf walks away to 10m or more; mother does not follow. The calf is active, the mother either active or resting.

Following + Leading: This is a combined measure, estimating total time during which proximity is maintained.

Not Following + Not Leading: This is a combined measure, estimating time during which proximity is not maintained.

Following + Not Following: This estimates the proportion of time in which the mother moves away from the calf.

Leading + Not Leading: This estimates the proportion of time in which the calf moves away from the mother.

Vocalization Between Mother and Calf

Mothers and calves sometimes call to each other by grunting, usually when they are more than 30m apart. Such behavior may supplement movements in maintaining proximity. For example, mothers might call to their calves in order to induce them to approach, rather than making the effort to do so themselves. In such cases the calves would appear to take responsibility for maintaining proximity, while in fact the mother also plays an important role. Calves may also control their mothers' behavior in this way.

There are a number of problems involved in an analysis of calling. Many calls may be inaudible to a distant observer, or the source of the sound may be difficult to identify. Moreover, mothers and calves may develop a method of signalling each other which does not involve sound and is undetected by the observer. For example, calves may learn to interpret their mothers' movements. The establishment of times for nursing bouts in some cases seemed to involve this type of communication. Therefore these data represent a partial record, reflecting primarily repeated calling which accompanies behavior such as looking or moving toward the partner. Measures of vocalization include:

Frequency/h: Calf calls Mother

Frequency/h: Mother calls Calf

Percent of all calling for which Mother (or Calf) is responsible

Nursing Interactions

Suckling calves stand reverse-parallel to their mothers, or behind and facing the same way, suckling between the mothers' rear legs. They often bunt (i.e., butt the udder) and switch teats while suckling; mothers either stand or graze. A problem arose in defining nursing bouts since nursing is often interrupted by calves' pauses. Preliminary analysis showed that intrabout pauses are distinguished from interbout intervals by their duration; distributions of intrabout pauses and interbout intervals form two distinct, widely separated populations. Based on this distinction, bouts were defined operationally as continuous periods of nursing behavior lasting longer than 5 seconds and separated by more than three minutes (Green 1986). Nursing terminology follows the recommendations of Cowie et al. (1951). Thus 'nursing' refers to the behavior of the mother, while 'suckling' refers to the behavior of the calf. Where neither member of the dyad is specified, 'nurse' is used.

Measures of nursing behavior include the following:

<u>Time spent nursing</u>:

Duration of nursing per bout (minutes)

Interbout interval (hours)

Nursing time (minutes/hour): mean bout duration/mean interbout interval

<u>Nursing conflict</u>:

Frequency of rejected suckling attempts per minute spent suckling: calf noses inguinal area; mother moves away or reacts aggressively.

Frequency of maternal aggression (e.g., horn threats, butting, kicking) per nursing minute.

Bout terminator:

Percent of bouts ended by calves: When calves end bouts, they stop suckling voluntarily and move away and/or change their activity, usually by lying down. In such cases mothers have not contributed to the termination, e.g., by moving. The behavior of calves at such times suggests that they are satiated. In contrast, when mothers end bouts, calves usually follow and repeatedly attempt to suckle.

Behavior during bouts:

Frequency of bout-interruptions caused by calves (i.e., calves pause while mothers stand quietly)

Relative and absolute frequencies of bout-interruptions caused by mothers (i.e., mothers move, causing the calf to interrupt its suckling)

Frequency of mothers' reactions, by moving or pivoting, immediately after calves bunt.

Percent of bout duration during which mothers graze

Non-Nursing Contact Interactions

Contact between mother and calf includes nosing, licking, and rubbing, performed by either member of the dyad. This combined measure involves the absolute and relative frequencies with which mothers and calves initiate such interactions:

Frequency per hour of mother-initiated contact interactions

Frequency per hour of calf-initiated interactions

Percent of contact initiated by mother

Measures of Long-Term Mother-Daughter Relations:

In order to describe long-term, or post-weaning interactions between mothers and daughters, the same measures of spatial relations were employed as for the pre-weaning period (as above). However, the post-weaning situation involves new variables as well. In contrast to earlier spatial relations, the most basic question of relations between yearling daughters and their mothers concerns whether or not they are in the same group. Assuming that this is the case, the next question involves their proximity. Because of substantial individual variation in these basic aspects of bond-longevity (see chapter 7), long-term relations were described primarily in terms of two variables: a) the extent to which mothers and daughters are present in the same group, and b) proximity between the two when in the same group. Most focal data were collected during two periods in the second year:

Months 15 and 16:

This represents an important period in long-term mother-daughter relations because it follows the birth of the mother's new calf. Most mothers and daughters separate during the final stages of the mother's pregnancy. After parturition, however, yearling daughters appear to resume associations with their mothers. In addition, this period occurs before the next rut; thus mother-daughter interactions are not affected by tending bulls. Measures of bond-longevity used in this period include:

Percent of days on which the mother is present in the daughter's group (% mother present).

Percent of time during which the mother and daughter are within 10m when in same group (proximity).

1.5 Years:

In order to determine to what extent mothers and their 1.5-year-old daughters were still associating, subjects were observed during the second October after their birth. The measure employed is a combination of *% mother present* and *proximity*. The reason for this new measure is that all cows and juveniles were together in the same herd for much of this time; therefore *% mother present* was insufficent. On days when a daughter was in the same group with her mother and within 10m of her during the first five minutes after initial identification, she was scored as being with her mother. The resulting measure, *percent of days with mothers*, consists of the percentage of days when daughters were with their mothers out of the total number of days seen.

PART II: PRE-WEANING INTERACTIONS

Chapter 3

PRE-WEANING SPATIAL RELATIONS BETWEEN MOTHERS AND CALVES

INTRODUCTION

PATTERNS OF CHANGE

One of the fundamental aspects of the interactions of mothers and young is their changing spatial relationship as offspring mature. What proportion of time do they spend close to each other? How is proximity maintained? Who is primarily responsible for maintaining proximity? These questions have been most thoroughly examined in studies of primates (e.g., Hinde 1971, 1974; Altmann 1980), which show substantial changes during the first few months in the time dyads spend in contact and at various distances, and the roles of mother and infant in contact-maintenance. For other mammals these questions have been addressed in a few studies, such as that of Taber and Thomas (1982) on southern right whales, and Crowell-Davis (1986) on Welsh ponies. The results of these investigations also show pronounced changes over the first few months. For example, Taber and Thomas (1982) found that, during the first three months, mothers and calves spend increasing amounts of time at a distance from each other, and approach and leave each other with increasing frequency.

The nature and extent of changes in pre-weaning spatial relations of mothers and offspring may differ in relation to social organization. For example, bonnet and pigtail macaques differ in social structure as well as in the spatial relations of mothers and infants (Rosenblum and Kaufman 1967; Kaufman and Rosenblum 1969; Rosenblum and Alpert 1977). Bonnet macaques are more gregarious than pigtails; while pigtail group members are generally dispersed, bonnets spend much of their time in close contact. The bonnet social system is less hierarchical, more placid, and based more on individual initiative than predefined roles, as compared with the pigtail system.

Correspondingly, bonnet infants show more spatial independence and take more responsibility for maintaining proximity with mothers. Their mothers also restrain and punish them less often.

In ungulates, gregariousness appears to be similarly associated with relatively loose, 'easy-going' mother-offspring relations, in which changes occur rather gradually. Associations with mothers and other group members are interspersed and potentially long-lived, allowing for the formation and maintenance of ties among group members. In contrast, less social species (or populations) show closer early relationships which end abruptly by the enforced dispersal of the offspring. Altmann (1958, 1960, 1963) compared the nature and longevity of mother-offspring relationships in relation to the social organizations of moose and elk. Moose live solitarily or in very small groups. The cow-calf relationship is closely synchronyzed and exists in isolation from conspecifics. Prior to the birth of the mother's next calf, she drives away her previous offspring. Their relationship ends abruptly and rather violently, given the offspring's reluctance to leave; the separation is permanent. Elk, in contrast, form relatively large herds; calves begin to associate with other herd members early in life. The cow-calf relationship is looser, in terms of spacing and coodination of movements, than that of moose. Parturient elk cows separate themselves from their previous offspring with little or no aggression; later their yearlings may resume relations with them. This comparison suggests that where adults are relatively gregarious, mother-young relations last longer but are looser in the sense that mothers and offspring spend more time apart and are less likely to synchronize their movements.

Geist (1967, 1971) describes differences in the social and developmental systems of moose and bighorn sheep in relation to the stability of their relative habitats. Like Altmann (1963), he notes that moose have close but short-lived relationships exclusively with mothers, and that this bond is broken abruptly and permanently after one year. He relates this forced dispersal to the instability of the habitat; islands of satisfactory habitat are too small and ephemeral to permit gregariousness. On the other hand, bighorn sheep habitat is relatively stable; here it is possible for daughters to inherit the home ranges of their mothers. The mother-offspring relationship is correspondingly loose and free of sudden changes. As in elk (Altmann 1963; Clutton-Brock et al.

1982), associations with other group members begin early in life; young females become integrated into the maternal group.

The hypothesis that gregariousness is associated with more gradual (and postponed) changes in maternal care is supported by studies of intraspecific variation in several ungulate species. Berger (1979c), in comparing weaning conflict in three different bighorn sheep populations, showed that weaning occurs most abruptly and earliest in the least gregarious population. Hirth (1977) found that, where white-tail does are more or less solitary, mothers drive away their previous offspring before the birth of the next fawn. In contrast, yearlings in more gregarious populations are not driven away.

HIDERS AND FOLLOWERS

Ungulate species differ dramatically in early mother-young spatial relations, and have been classified accordingly as 'hider' and 'follower' types (Lent 1974; Leuthold 1977; Walther 1965). In hider species, after a brief post-partum period, neonates leave their mothers, select a hiding place in tall vegetation, and lie down. These infants spend from 3 days to 3 months (Lent 1974) lying concealed at a distance from mothers. Contact with the mother is limited to nursing bouts, which are usually initiated by mothers' signalling their offspring to approach. In contrast, the young of follower species stay near their mothers early in life.

While hiders are protected from predators through concealment (Byers and Byers 1983), protection for follower infants appears to involve proximity to the mother and/or the social group (Lent 1974; Estes and Estes 1979). Crowell-Davis (1986) examined mechanisms of survival in one follower species, the Welsh pony. She found that, when the foal is sleeping and thus most vulnerable, the mother remains close to it. Moreover, mare-foal dyads maintain close proximity regardless of activity throughout the first four months.

While bison show some characteristics of followers, they do not fit well into the hider-follower dichotomy. Unlike hiders, bison calves do not leave their mothers when they lie down to rest, nor do they hide in vegetation. Rather, they spend much of their early life close to mothers and other herd members. On the other hand, bison differ from typical follower species. Ralls et al. (1986), in a study of hiders and followers in captivity, found that bison mothers and calves spend less time close to each other during the first week of life than do those of other follower species, e.g., wildebeest. They conclude that bison are weak followers.

This chapter describes spatial relations between bison mothers and daughters prior to weaning. Two questions are addressed:

1) To what extent do mothers and calves change during the pre-weaning period in (a) proximity and (b) relative contributions of each partner to contact-maintenance? Comparisons of developmental patterns in relation to social organization suggest that, since bison are gregarious, cows and calves should have relatively loose spatial relations in which changes are minimal.

2) Do bison cow-calf dyads show behaviors typical of follower species? If bison are followers, the means whereby their calves are protected should be similar to that of Welsh ponies (Crowell-Davis 1986): mothers should stay relatively close to their calves, particularly when the latter are resting. One might also expect that, as followers, bison calves spend relatively large amounts of time following their mothers' movements.

METHODS

In describing the spatial relations of bison cows and their calves, an important set of measures to be considered is the distance between mothers and offspring and the behaviors which result in distance changes. Hinde and Atkinson (1970) propose, as a measure of the relative contributions of mother and young to proximity-maintenance, the difference between the percent of leaving and approaching (e.g., across a 1-m boundary) for which the infant is responsible (%Ac-%Lc; see Chapter 2). This function emerged from studies of primates, and has been used in most recent investigations of mother-young spatial relations. However, for ungulates and other species where mother and offspring are usually at some distance from each other, such a measure provides limited information since it ignores proximity-maintaining behaviors such as following. Therefore I supplemented this measure by examining the orientations of mother and young relative to each other while moving. For example, how frequently does the offspring follow when the mother walks away; how frequently does it not follow? The same questions were asked about maternal orientation to the calf. Wilson (1974) used similar measures in her study of the common seal.

Such information should be particularly useful in distinguishing between hider and follower species. For example, in follower species, mothers should be less likely to walk away from offspring if the latter do not follow, as suggested by the findings of Crowell-Davis (1986). Thus the relative frequency with which offspring stay behind when their mothers move away should be greater for hiders than for followers.

In order to describe spatial relations between bison mothers and their calves, 13 cow-calf dyads were observed in focal-animal samples throughout the first seven lunar months of calves' lives. Measures of mother-daughter relations, as described in detail in Chapter 2, cover four areas: a) proximity, b) activity and its effects on proximity, c) approaching and leaving between mother and calf, and d) orientation between mother and calf during movements.

Data for each measure were averaged over all subjects for each week; due to small sample sizes, data for weeks 24 through 28 were pooled. Changes in measures were analyzed in regressions; percentages were analyzed as arcsine transformations. For all regressions, degrees of freedom are 1, 19. F values and probabilities are provided in the text.

In order to consider the extent to which mothers and calves maintain contact from a distance, relative and absolute frequencies of vocalization between mother and calf were also examined (see chapter 2). Because occurrences of this behavior were relatively rare, these data were not analyzed statistically; they are presented here for descriptive purposes only.

Data presented here were collected as part of a larger study on individual variation; in order to control for intersexual differences among calves, only female calves were included. However, that these data represent general patterns of development in bison is suggested by the fact that Crowell-Davis (1986), in examining similar measures of spatial relations between Welsh ponies and their foals, found no differences between male and female foals.

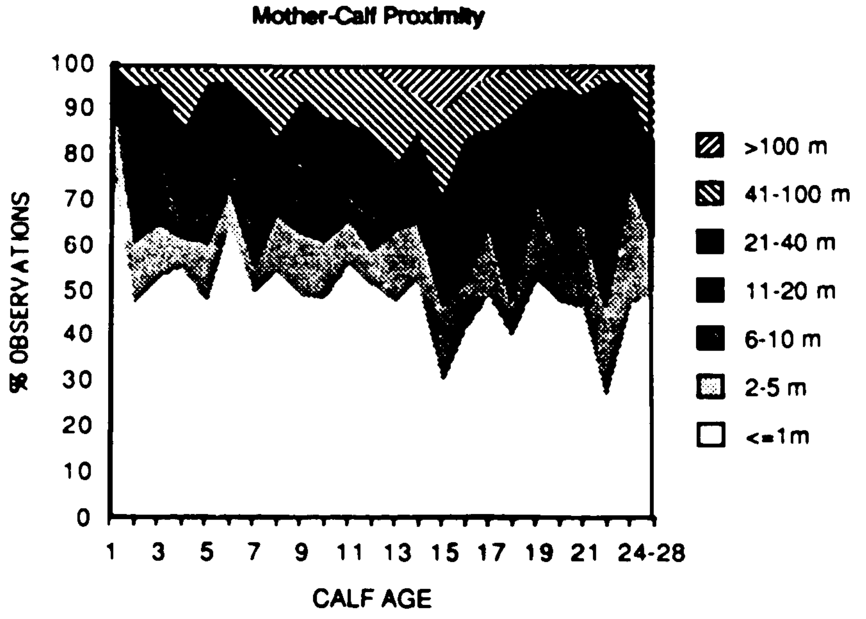


Figure 1: Mean percent of scans (at 2.5-minute intervals) when mothers and calves were within each of seven distances during the first 28 weeks. The distance between lines repesents percentages of time at different distances.

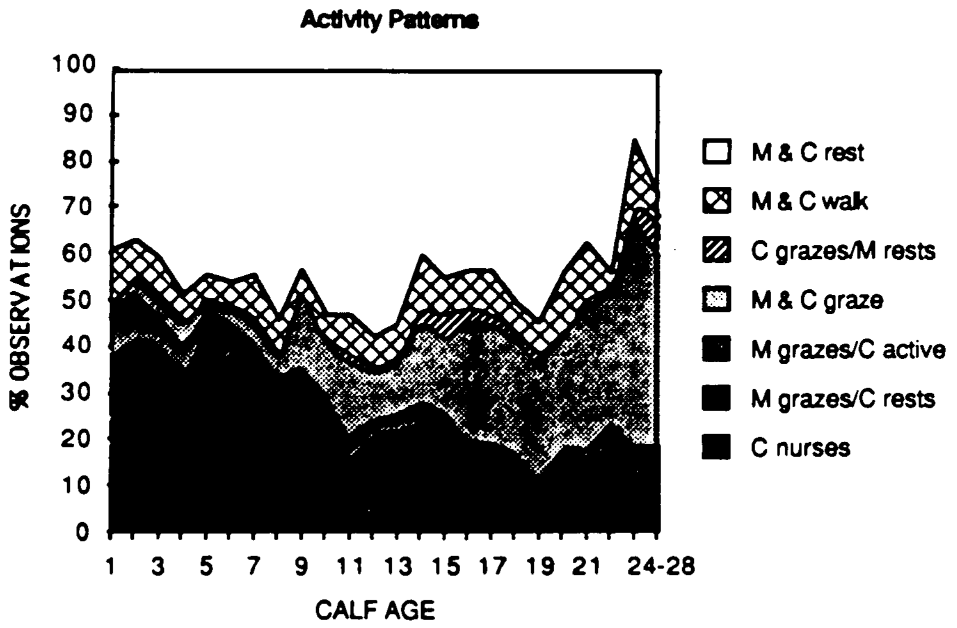


Figure 2: Mean percent of scans mothers (M) and calves (C) spend in different types of activity during the first 28 weeks.

RESULTS

Proximity of Mothers And Calves

Figure 1 shows the proportion of time mothers and calves spent at various distances from each other during the first seven months of calves' lives. Since the pattern of change is similar at all distances, the results are discussed in terms of an intermediate value: 10m.

The percent of time during which mothers and calves were within 10m of each other did not change over the first seven months (F=.002, p>.25). Only from week 1 to week 2 was there any real change: time spent within 10m decreased from 97 to 72% (95% confidence limits: 95-100% for week 1; 65-81% for week 2). After the first week proximity remained basically unchanged. In week 15, when many mothers were tended by bulls (chapter 5), mothers and calves were more often far apart; at this time they were within 10m only 56% of the time (95% confidence limits: 36-76%). Afterward, proximity returned to pre-tending levels.

These results indicate that bison mothers and calves spend relatively large amounts of time far apart even in the first month. By week 4, they are found at distances greater than 10m 34% of the time.

Activity Patterns of Mothers and Calves:

Developmental changes in activity patterns reflect a shift in the source of calves' nutrition as well as an increase in their behavioral synchrony with mothers. Over the first seven months, calves spent increasing proportions of time grazing (F=112, p<.001), and decreasing time resting (F=57.1, p<.001), while mothers grazed. These changes are shown in Figure 2. From the first to the seventh month, the time calves spent resting while their mothers grazed decreased from 45% to 17% (95% confidence limits: 38-53 in month 1; 5-28 in month 7). Meanwhile, the time calves spent grazing with their mothers increased from 3% to 45% (95% confidence interval: 2-5 in month 1; 26-64 in month 7). Nursing time also decreased during this period (F=31.4, p<.001). In month 1, calves spent 19% of their time suckling (confidence interval: 16-22), as opposed to 4% in month 7 (confidence interval: 0.2-8.3). Thus the primary source of nutrition shifts gradually from nursing to grazing, while the activity patterns of calves become increasingly like those of their mothers. This change in behavioral synchrony is reflected in the relative orientation of mothers and calves to each others' movements (see below). Rather surprisingly, however, it is not accompanied by reduced distances.

Variation in Proximity in Relation to Type of Activity

As shown by Figure 3, proximity appears to vary with the type of activity. Mothers and calves generally spend more time close together while their activities are synchronized than while they are not. This applies particularly to walking and resting; the average time within 10m in such activities throughout the first seven months is around 80%. When both graze, proximity is somewhat less, averaging around 70%. In contrast, mothers and calves spend the least time near each other when their activities differ: when mothers graze and calves rest, they spend less than 40 percent of their time within 10m in months 2 to 5.

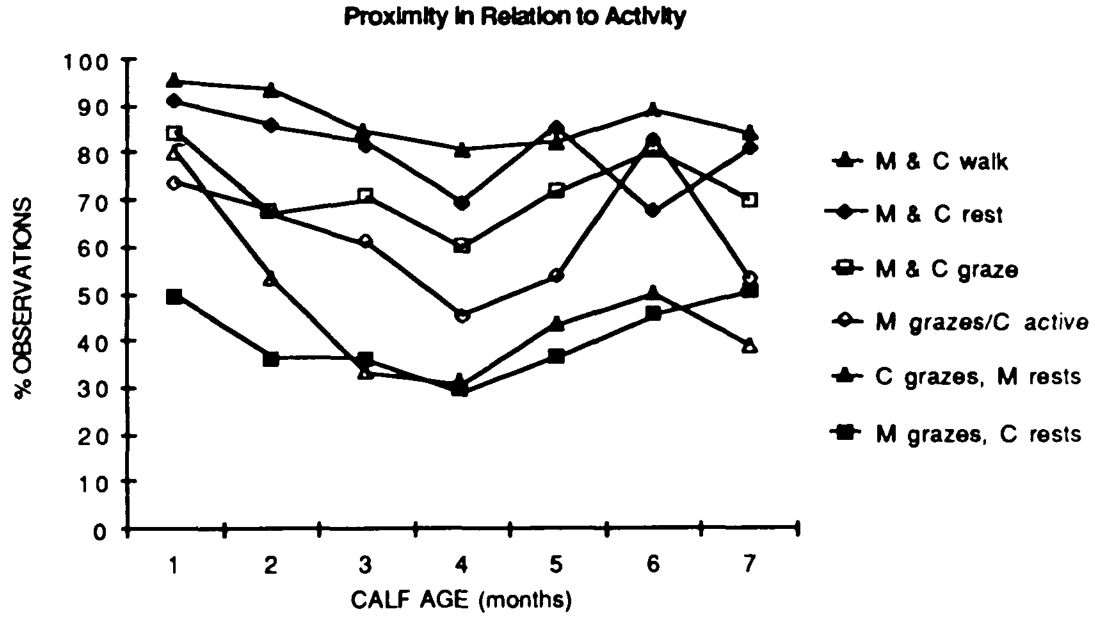
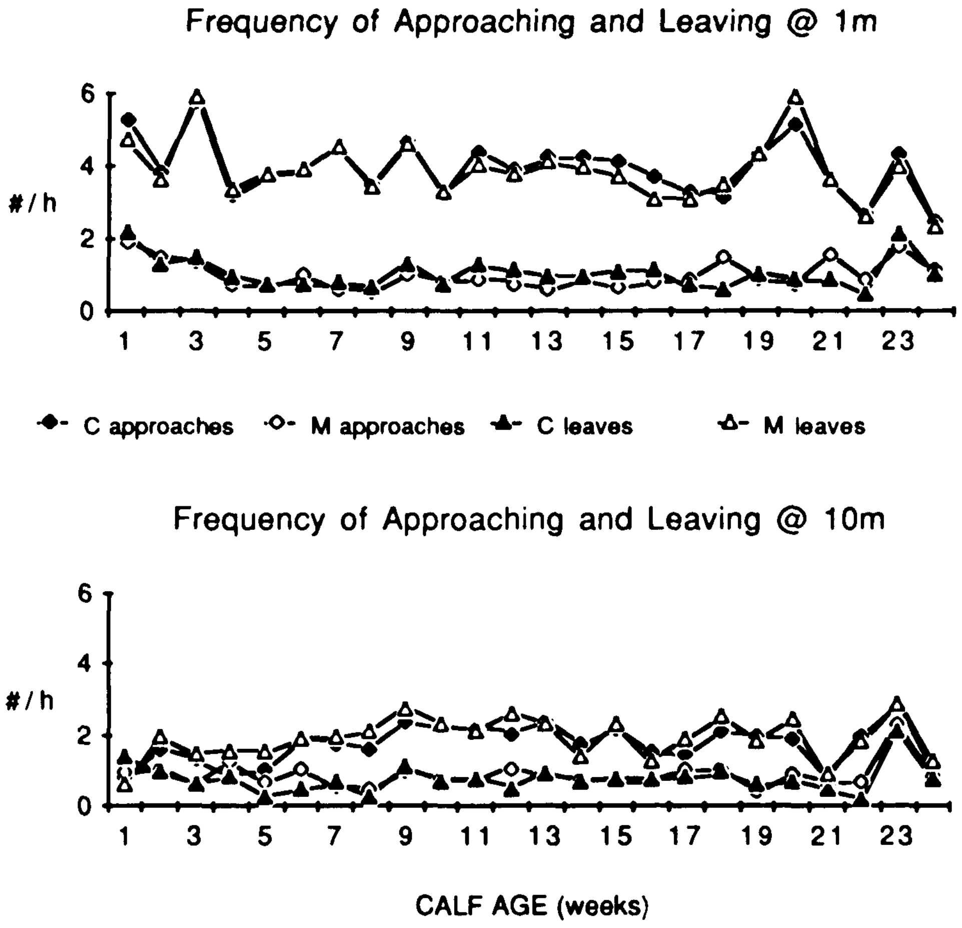

Proximity in Relation to Activity

Figure 3: Mean percent of time in each activity when mothers and calves are within 10m.



Figures 4 (top) and 5 (bottom): Mean frequencies per hour of approaching and leaving by mothers and calves at 1m (Figure 4) and at 10m (Figure 5). These graphs show the number of times mothers and calves move toward and away from each other, across boundaries between the two of 1 and 10m, respectively, over the first seven months. Week '24' represents data for weeks 24-28, pooled because of small sample sizes.

Approaching and Leaving Between Mother and Calf

Mothers and calves approached and left each other at more or less the same rates throughout the first seven months of the calves' lives (Figures 4-6). Regression analysis for the percent of approaching by calves over weeks 1 to 28, for example, results in F=4.02, p>.05. The pattern of developmental change is similar to that for proximity: after the first few weeks, no directional changes occur. Mothers and calves approached and left each other at 1m somewhat more often in the first three weeks than during the next three months (Figure 4). Calves' contributions to proximity-maintenance also increased somewhat during the first two months, while those of mothers decreased; this is indicated by increases in *%Ac-%Lc* (the difference between the percent of approaches and the percent of leaving by calves: Figure 6).

Calves assumed a greater role in the maintenance of proximity than did mothers. Throughout the first seven months, calves did 70-83% of the approaching and only 17-28% of the leaving across a 1m boundary. As a result, *%Ac-%Lc* is always positive (Figure 6). Moreover, the frequencies of approaches by calves were nearly identical to frequencies of leaving by mothers, suggesting that calves' approaches resulted from mothers' withdrawals (Figures 4 and 5).

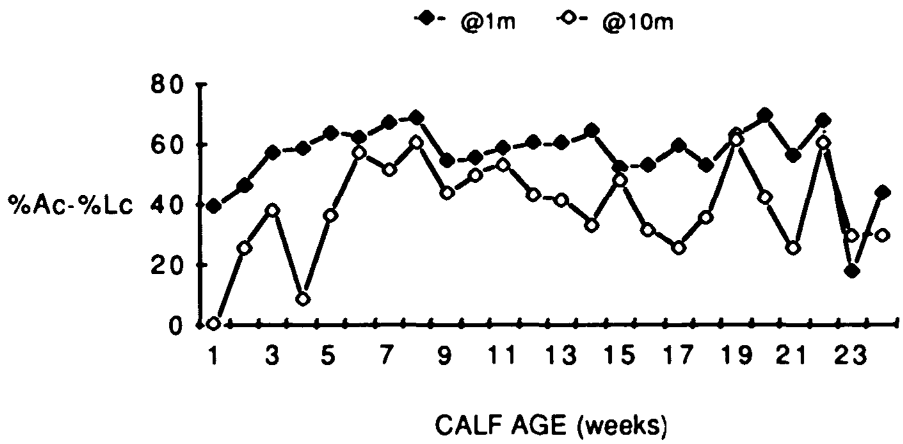


Figure 6. The difference between the percent of approaches and the percent of leaving for which calves are responsible over the first seven months of life (%Ac-%Lc). This measure, following Hinde and Atkinson (1970), reflects the relative contributions of mothers and calves in maintaining proximity. When it is positive (as it is here, through out the pre-weaning period), the calf is primarily responsible for contact-maintenance. Week '24' represents pooled data for weeks 24-28.

At 10m, the relative contributions of mothers and calves to proximity-maintenance was somewhat more equitable than at 1m (Figures 4 and 5). Mothers left and calves approached less often at the greater distance. Thus mothers took somewhat more responsibility for maintaining proximity at 10m than at 1m, particularly in the first month, and *%Ac-%Lc* is correspondingly lower

(Figure 6). Moreover, the lower frequencies of all approaching and leaving at 10m relative to 1m suggests that contact-maintenance activity occurs primarily within 10m (i.e., across a 1m rather than 10m boundary).

Orientation Between Mother and Calf:

Measures of orientation reflect the relative frequencies with which mothers and calves either follow or fail to follow each others' movements during active periods. When one member of the dyad moves away to at least 10m, the other may move in the same direction, behind the first, in which case it is following. Alternatively, it may remain where it is, thus not following. When the calf is the one who moves away, the terms *leading* and *not leading* are used, while *following* and *not following* refer to the calf's behavior relative to the mother's movements (see chapter 2).

Figure 7 shows patterns of change in orientation between mothers and calves. The most abrupt changes in orientation occurred between the first and second weeks, when the time calves spent following mothers' movements decreased from 73% to 35% (95% confidence intervals: 73.1-73.6 in week 1; 34.4-34.6 in week 2). From the second week to the beginning of the third month (week 9), calves spent most of their time resting behind while mothers walked away to graze; by week 3, *not following* accounted for 59% of active time (confidence interval: 58.6-59.0). After the second month, calves spent increasing time following and leading mothers; the total time when they followed each other reached 76% by month 6 (confidence interval: 75.7-76.4). Time spent not following correspondingly decreased; by month 7 calves spent 18% of the time not following, 47% following; 16% leading and 19% not leading.

Over the first seven months, most of these measures changed significantly. Mothers and calves spent increasing amounts of time following each others' movements: the percent of time calves spent following (F=28.6, p<.001) and leading (F=30.9, p<.001) both increased, while time spent not following decreased (F=101.3, p<.001). The extent of change in *not leading* was not significant.

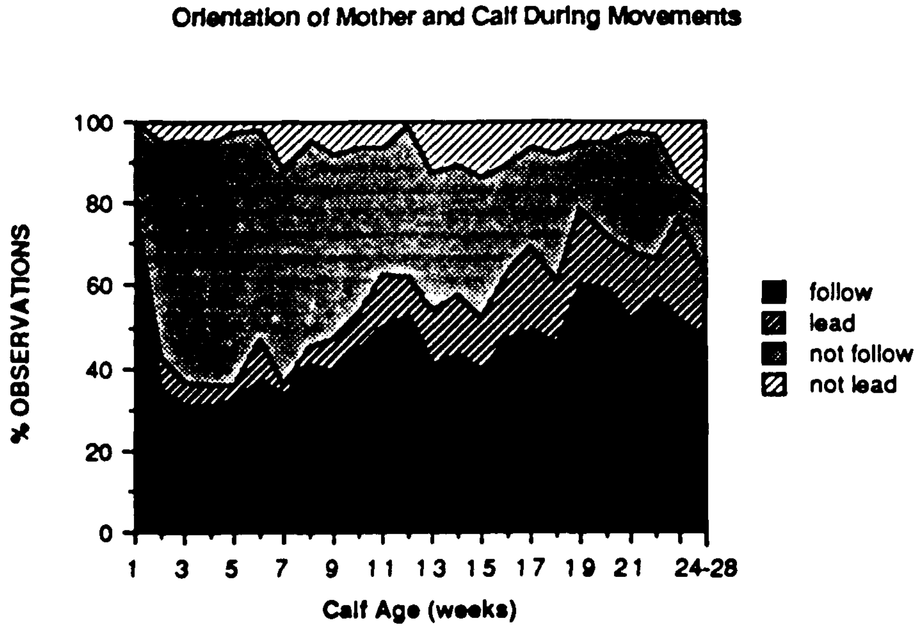


Figure 7: Mean percent of scans (at 2.5-minute intervals) during which mothers and calves orient in various ways to each others' movements, during the first seven lunar months of calves' lives. Distances between lines represent relative amounts of time during which: a) calves follow mothers' movements ('follow'), b) mothers follow calves' movements ('lead'), c) calves stay behind when mothers walk away ('not follow'), or d) mothers stay behind when calves walk away ('not lead').

Comparison of Figure 7 with Figure 2 (excluding resting time) shows that *not following* decreased with calf age in a pattern similar to that of *mother grazes/calf rests*, indicating that *not following* time was largely time when calves rested during grazing periods. At the same time, *following* and *leading* increased in a pattern similar to that of *mother and calf graze*. Thus, as calves grazed more with age, they followed and led their mothers more.

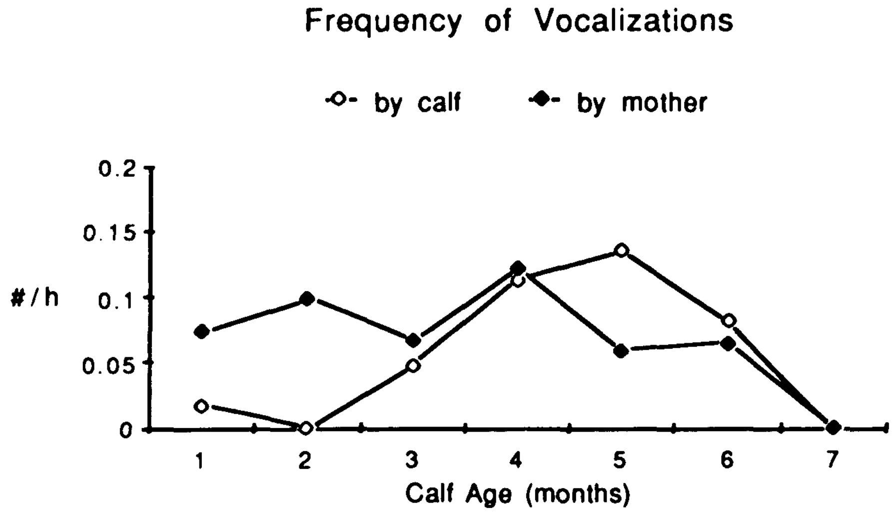


Figure 8: Mean frequencies per hour of vocalizations by mothers and calves over the first seven lunar months.

Vocalizations of Mothers and Calves:

Mothers and calves sometimes vocalize toward each other when far apart. This behavior may play a role in maintaining contact at a distance (see chapter 2); therefore patterns of change in such behavior are briefly described here.

Calling between mothers and calves occurred infrequently; during the first seven months mean frequencies were less than 1 vocalization in 10 hours (Figure 8). During the first two months nearly all vocalizations between mothers and calves were performed by mothers. Such behavior generally occurred while mothers tried to find their resting calves after having grazed some distance away (often >100m) for one or more hours. In such situations mothers often searched for 10 minutes, walking through the herd, nosing calves, looking around and grunting. When they were close enough that the calf became aware of them, the calf sometimes stood up and grunted toward the mother; more commonly the calf remained resting until the mother approached to within 10m. The calf then jumped up, raced to the mother and attempted to nurse.

The percent of calling by mothers decreased over the first seven months, from 80% in month 1 and 100% in month 2 to 44.4% in month 6. The change was due in large part to the increased calling by calves during months 3 to 6, parallelling changes in activity and in the relative time spent following mothers. Mothers did most, if not all of the calling until week 11; after week 12, calves called more than mothers in all weeks except 18. The period of increased calling by calves coincided with the weeks surrounding and including the time when mothers were tended by bulls.

DISCUSSION

These results support the prediction that, being gregarious, bison mothers and calves have relatively loose relationships in which changes are minimal. After the first week, the spatial relations of cows and their female calves change surprisingly little during the pre-weaning period. In contrast with other mammalian species (e.g., Welsh ponies: Crowell-Davis 1986), proximity and approaching/leaving show no directional change during the first seven months of calves lives. Activity and orientation measures show gradual changes as calves spend increasing proportions of time grazing with and following their mothers.

Mothers and calves spend large proportions of time at a distance, even when calves are quite young. During the first month, cows and calves were within 10m 76% of the time; by the second week of life this measure was already less than 80%. In contrast, Crowell-Davis (1986) showed that Welsh ponies and their foals spend around 97% of their time within 10m during the first month; time within 10m does not drop below 80% until week 18 or 19.

Bison cows make little effort at maintaining proximity with their calves. Even in the first month, mothers left often and approached relatively rarely, while calves took most of the responsibility for maintaining proximity. In most mammals, development involves a shift from mother to infant as the primary maintainer of proximity. For bison, no such shift occurs. Values of %Ac-%Lc (a measure for which decreasing values reflect greater efforts by mothers relative to calves at maintenance of proximity) were 50, 66, and 58 for the first 3 months, respectively, across a 1m boundary between cow and calf. At 10m these values were 28, 49, and 46. Comparable values for Welsh ponies are about 9, 23, and 25 at 5m, and -5, 22, and 7 at 10m (Crowell-Davis 1986). Domestic goats are a hider species in which mothers and kids spend much of their time at a distance during the first 2 months. For them, %Ac-%Lc at about 1m (1 mother-length) is close to zero during the first month (i.e., mothers and kids make equal efforts at maintaining proximity) and around 70 during the second and third (Lickliter 1984).

Bison cows seem to make little or no effort at protecting sleeping calves by staying nearby. In Welsh ponies, mothers are least likely to move away from foals when the latter are resting, apparently protecting foals more when they are most vulnerable (Crowell-Davis 1986). In contrast, grazing bison mothers spent more time at a distance from calves when the latter rested than when the calves were active.

These findings describe bison mother-young spatial relations as being relatively loose, asynchronous, unchanging, and maintained largely by calves. These results address the second question as well: Are bison followers? The results indicate that they are not. In follower species, mother and infant maintain "close and frequent contact" (Lent 1974, p.24). In contrast, bison cows and calves spend much of their time at a distance (i.e., 28% at >10m) as early as the second week of life. The fact that bison mothers and calves spend the least amount of time near each other while calves rest is further evidence that bison mother-calf spatial relations differ from those of typical followers. Rather than staying closer to offspring when they sleep, as Crowell-Davis (1986) found in a follower species, bison mothers often move away from calves at such times. Moreover, cows and calves spend only 33% of their active time following each others' movements in months 1 and 2. While similar data on other species are not available for comparison, one might expect that, in follower species, mothers and offspring spend much of their active time near each other and following each others' movements. Crowell-Davis' (1986) findings suggest that, as long as offspring are resting, 'follower' mothers do not walk away. The fact that bison mothers walk away so often during the first two months, and that calves so rarely follow them, provides further indications that bison are different from typical follower ungulates.

Hiding and following are essentially anti-predator strategies. In the absence of predators, might such behaviors wane? The work of Walther (1965) and Ralls et al. (1986) indicates that species-typical patterns of mother-offspring interaction are retained under varying degrees of captivity; in fact, Walther's original descriptions of the hider-follower dichotomy were based on studies in zoos.

If bison are neither hiders nor followers, how are bison calves protected from predators early in life when they spend much of their time sleeping? It may be that the presence of the herd allows for an unusual degree of independence between mothers and calves and plays a role in protection against predators. There is some evidence that calves become attached to the herd as well as to their mothers. For example, they often remain at rest far behind their grazing mothers for up to two hours when other herd members are resting nearby. Moreover, calves as young as a week of age race back and forth between the mother and the rest of the herd when the mother walks away from the herd (pers. obs). Even though calves always follow their mothers in the end, the situation seems to produce a great deal of conflict.

It may also be that the behavior of young calves includes some aspects of hiding. Their natal coat color is much lighter than that of older animals, and, at least to this observer, often matches the reddish color of the earth in many areas of Wind Cave National Park. Bison of all ages tend to select bare wallows as resting spots; when calves rest in such spots they sometimes seem to disappear.

These findings suggest that bison anti-predator behavior incorporates elements of both hiding and following, depending on the situation. Calves act much like hiders during grazing periods, but become followers when the herd begins to move. While the hider-follower dichotomy has limited utility in categorizing bison, it provides a basis for interpreting the spatial relations of mothers and calves.

Chapter 4

NURSING AND OTHER CONTACT INTERACTIONS IN RELATION TO MATERNAL AGE

INTRODUCTION

Differences in maternal behavior have been shown to affect the survival and reproductive success of offspring in various mammalian species (e.g., Reiter et al. 1981). Trivers (1974) hypothesized that young and old mothers should differ in maternal behavior since older mothers, who can expect fewer future offspring, incur a lower reproductive cost in caring for present offspring than do younger mothers. Therefore older mothers could increase their inclusive fitness by caring more for their present offspring.

While maternal behavior can take various forms, nursing is a particularly costly aspect. Blaxter (1971) calculated that, for many mammals, the caloric value of only 1-2 days' lactation is equal to that of the entire fetus. Studies of deer and domestic sheep show that lactating females lose weight even on highly nutritious diets, while functions such as hair growth are severely reduced (Moen 1973).

According to Trivers' (1974) hypothesis, older bison cows should spend more time nursing their calves, and allow their calves to end more nursing bouts, than should young cows. The latter prediction is based on the observation that, when calves end suckling bouts they appear to be satiated. In contrast, when mothers end bouts, calves follow and repeatedly attempt to continue suckling. Berger (1979c) describes similar observations in bighorn sheep. In a previous paper (Green 1986), preliminary findings confirmed that old and young bison mothers differ in these aspects of nursing behavior during the second and third months of their calves' lives. Older mothers nursed their calves longer at each bout and allowed their calves to end more bouts than did young mothers; nursing frequency did not differ between the two groups.

In the present study, old and young mothers are compared over most of the pre-weaning period in terms of nursing time and the percent of bouts ended by calves. At the same time, several other questions about maternal behavior in relation to age are examined:

a) Do old and young mothers differ in behavior during nursing bouts, for example in the frequency of bout-interruptions? Since interruptions decrease calves' suckling efficiency and therefore reduce the actual nursing time, young mothers should interrupt bouts more frequently. Similarly, expressions of parent-offspring conflict (Trivers 1974), such as rejected suckling attempts and maternal aggression, should occur more frequently between young cows and their calves.

b) Do old and young mothers differ in non-nursing interactions, such as the initiation of contact (e.g., nosing, licking, and rubbing) with calves? To the extent that such behavior involves maternal care, older mothers should initiate such interactions more frequently than young mothers.

c) If such differences exist, are they consistent throughout the pre-weaning period?

METHODS

In order to examine differences between old and young cows in nursing and other contact interactions with calves, and to determine the extent to which these measures change with calf age, individual data from months 1 through 5 were compared for the two groups. Data collected after month five were excluded because of differences in reproductive condition. All measures are listed with results in Table 2.

In the study group of 13 mother-daughter dyads, six multiparous cows formed the old group (aged eight through 18). Of the seven young cows, six were primiparous (five were three years old; one was two); the seventh was four years old and had borne one previous calf. Possible maternal differences related to offspring sex (e.g., Duncan et al. 1984) were eliminated since only female offspring were included in the sample.

Analysis of variance was performed, with months as repeated measures. Three comparisons were made:

1) Between subjects effects (maternal age), comparing old vs. young mothers in level of maternal care over months 1-5.

2) Within subjects effects (time), examining overall changes during the first five months.

3) Interactions between maternal age and time, determining whether old and young mothers differ in patterns of change over time.

Because of missing data points (one calf is not represented in month one, and two others are not represented for most measures in month five), sample size varies among analyses and is indicated with the results in Table 2. The SAS procedure GLM (SAS Institute 1985a, b) was used to perform the anovas.

RESULTS

Table 2 shows means and standard deviations for old and young mothers pooled over the first five months, together with sample sizes, F values and probabilities for each measure. Results of anovas are shown for age effects (differences between old and young mothers), time effects (changes over the first five months), and interactions between the two (differences between old and young mothers in patterns of change). Degrees of freedom differ for the two tests: for maternal age, df=1, N-2; for time, df = 4, 4 x (N-2). Measures included in the analysis are listed with results.

NURSING INTERACTIONS

Of the eleven measures of nursing behavior tested, six showed significant differences between old and young mothers ($p<.05$). Older cows spent more time nursing their calves (bout duration/interbout interval), as illustrated by Figure 9, which shows group means and standard errors for nursing time in minutes/hour. As shown in Figure 10, calves of older mothers made fewer suckling attempts that were rejected. Calves of older mothers also ended more bouts and spent more time pausing during bouts while their mothers continued to stand. Young mothers were responsible for a higher proportion of bout interruptions.

Intervals between nursing bouts were, on the average, quite similar between young and old mothers. This finding, when compared with the substantial difference in nursing bout duration, indicates that differences in nursing time are due to longer bouts rather than increased nursing frequency.

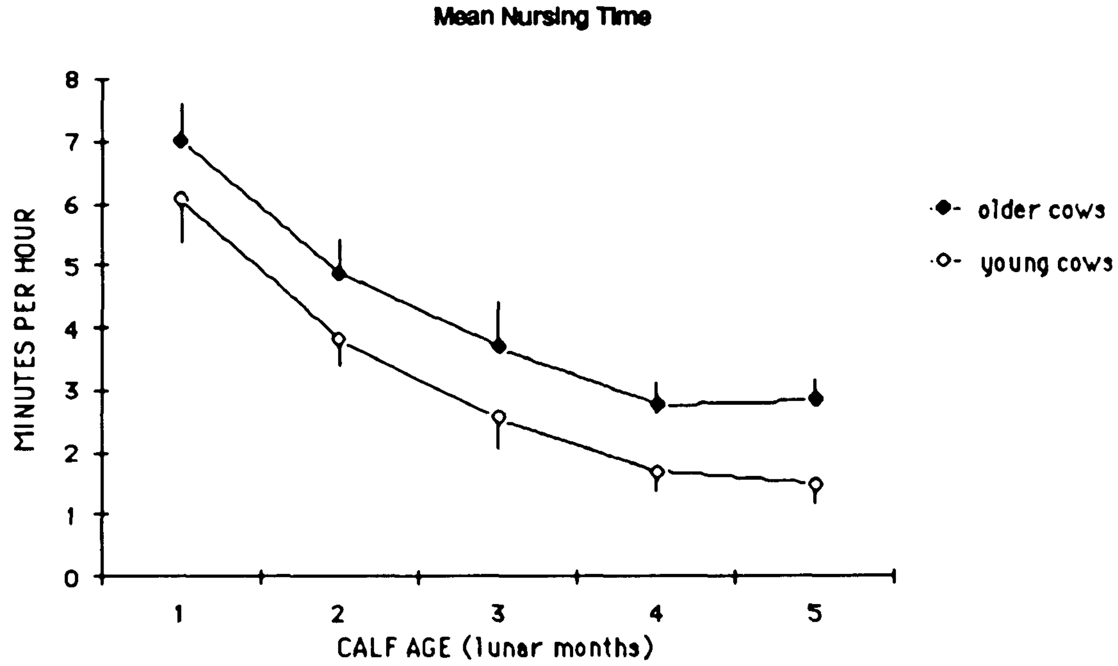

Mean Nursing Time

Figure 9: Mean number of minutes per hour spent nursing (bout duration/interbout interval) for old and young mothers over months 1 to 5. Vertical lines indicate one standard error.

CONTACT INTERACTIONS

Contrary to expectations, older mothers did not contact calves more frequently than young mothers. In fact, the results show just the opposite effect: young mothers initiate more contact interactions (Figure 11). This difference was most pronounced in terms of relative frequencies: young mothers initiated higher proportions of all nosing, licking, and rubbing interactions with their calves. Conversely, calves of older cows initiated higher proportions of contact interactions with their mothers than did calves of young mothers.

TABLE 2

NURSING AND OTHER CONTACT INTERACTIONS: (a) OLD VS YOUNG MOTHERS; (b) CHANGES WITH CALF AGE

	(Mean and SD for months 1-5 pooled)					(a)		(b)	
	Older Mothers		Young Mothers			Old vs. Young Cows		Change w/ Calf Age	
Measure	X	SD	X	SD	N	F(Age)	P	F(Time)	P
Nursing Interactions:									
Mean duration of suckling/bout (minutes)	9.61	1.49	6.34	1.07	11	44.80	<.001	1.97	.134
Mean interbout interval (hours)	2.63	0.40	2.60	0.55	10	0.12	.733	13.57	<.001
Mean nursing time: duration/interval (min/h)	4.15	0.98	3.18	0.61	10	8.22	.021	18.67	<.001
Rejected suckling attempts/nursing minute	0.17	0.08	0.41	0.17	11	9.77	.012	3.38	.020
Maternal aggression/nursing minute	0.06	0.05	0.17	0.17	11	3.57	.091	2.24	.145
Percent of bouts ended by calf	52.02	17.53	17.11	5.79	12	5.70	.038	5.03	.002
Bout-interruptions by mother/bout	21.58	15.09	28.83	18.38	11	0.24	.634	4.06	.033
Bout-interruptions by calf/bout	21.12	10.78	10.09	7.21	11	4.31	.068	4.34	.006
Duration of bout-interruptions by calf (sec)	19.93	13.74	7.63	5.60	11	5.85	.039	1.36	.280
Percent of bout-interruptions by mother	39.01	6.86	82.77	3.10	11	9.95	.012	0.29	.835
Mother's reactions to calf's bunting/bout	0.13	0.15	0.53	0.34	11	4.12	.073	1.04	.375
Contact Interactions:									
Frequency/h: interactions initiated by mother	0.10	0.07	0.25	0.12	12	4.90	.051	5.09	.005
Frequency/h: interactions initiated by calf	0.68	0.15	0.51	0.12	12	3.87	.078	4.03	.029
Percent of contact initiated by mother	7.80	3.24	23.33	1.87	11	7.04	.026	3.19	.029

Table 2 shows results of analysis of variance with months 1-5 as repeated measures.
Young cows are 2-4 years old; older cows are 8-18.

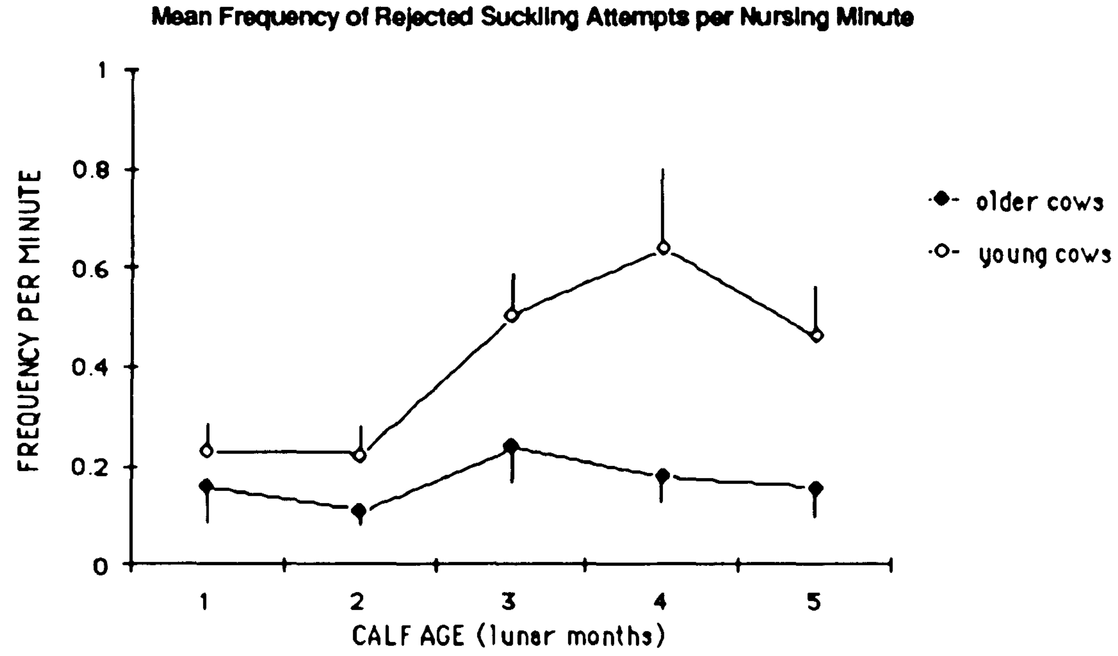


Figure 10: Mean frequencies of rejected suckling attempts per minute spent nursing, for old and young mothers. One standard error is indicated.

PATTERNS OF CHANGE

Old and young mothers differ in patterns of developmental change in only one measure. The frequency of rejected suckling attempts increased over the first five months for offspring of young cows, but not for those of older mothers (F=2.84, p=.038, df=4, 36; see Figure 10).

In all other measures the pattern of change was similar for the two groups. Of the eleven measures of nursing behavior, only six show significant changes during the first five months. The amount of time spent nursing (Figure 9) decreased as a result of increased interbout interval length. The fact that nursing bout duration did not change significantly indicates that, while calves suckled less often as they matured, suckling time per bout changed little. The percent of bouts ended by calves decreased during this period, as did the frequencies of bout-interruptions by both mothers and calves. The increasing frequency of rejected suckling attempts reflects primarily young mothers, as discussed above. Maternal aggression did not change in frequency during this period, nor did the duration of calves' bout-interruptions and the percent of interruptions caused by mothers.

Mothers initiated contact with decreasing frequency over the first five months (Figure 11), as did calves. However, the percent of interactions initiated by mothers also decreased, indicating that the frequency with which mothers initiate contact decreased more rapidly than did that of calves.

These results indicate that patterns of developmental change are generally similar for calves of old and young mothers. Secondly, calves show little or no change during the first five months in several aspects of nursing behavior.

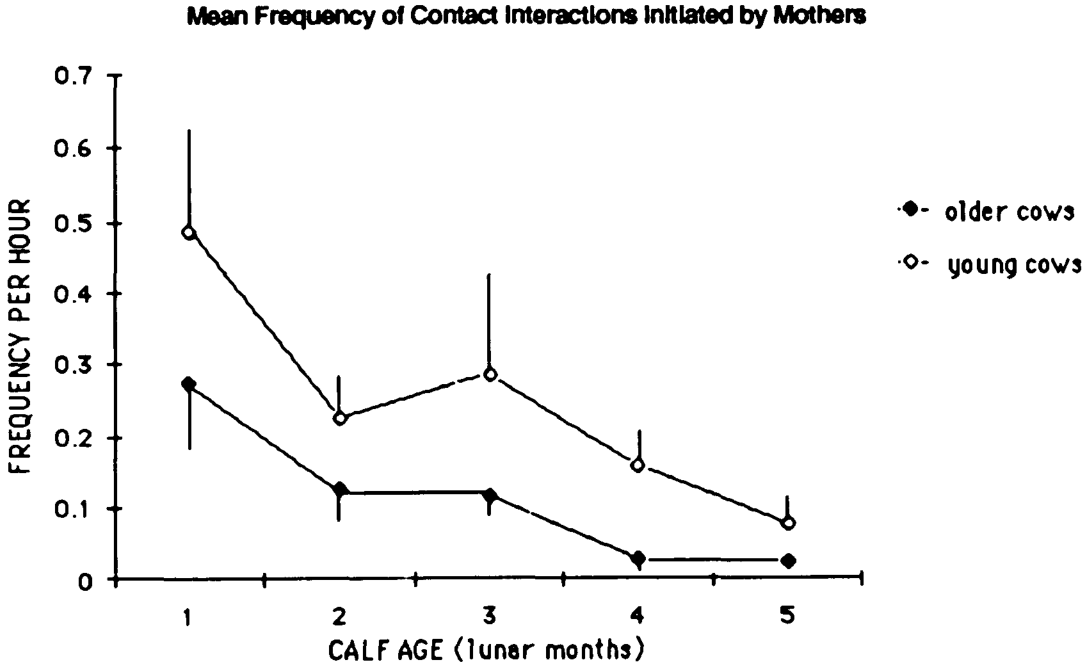


Figure 11: Mean frequency per hour of contact interactions (e.g., licking, rubbing) initiated by old and young mothers, over months 1 to 5. One standard error is indicated.

DISCUSSION

Comparisons of maternal behavior in old and young mothers reveal significant differences in both nursing and contact interactions. However, results differ for the two categories: while older mothers nurse their calves more and behave more patiently during nursing bouts, young cows initiate more contact interactions.

The findings that older bison cows spend more time nursing their calves, allow their calves to end more bouts, and behave more 'patiently' during nursing bouts support the prediction from Trivers' (1974) hypothesis, that older mothers care more for present offspring. Such age-related differences in maternal behavior are likely to be associated with differences in milk production. In domestic cattle, which are among the closest relatives of bison, milk production increases with age until the fourth or fifth lactation, while milk composition and flow rate do not change significantly (Bath et al. 1978; Dodd 1957; Johansson and Claesson 1957). If milk production follows a similar pattern in bison, and the amount of time spent nursing is correlated with the amount of milk produced (as suggested by Martin 1984), older bison cows provide their calves with more milk than do young cows.

The probability that young mothers produce less milk would in part explain their more apparent discomfort and conflict with calves over nursing. Young cows were frequently observed to pivot restlessly when their calves bunted during nursing bouts. While the difference in bunting reactions between old and young cows was not significant ($P=.07$), this may be due to high variability.

While some of the findings described above support the hypothesis that older mothers invest more in present offspring than do young mothers, others suggest that age-related differences in bison maternal behavior are in fact more complex and may involve contrasting strategies of investment by old and young mothers. That young mothers initiate more contact interactions with calves, in particular, appears to contradict the prediction that older mothers provide more maternal care. Although such behavior incurs a lower cost than nursing, it nevertheless uses energy and takes time away from grazing and resting. Assuming that it benefits calves, initiating contact may be a cost-effective form of maternal care.

Young mothers may compensate for maternal deficiencies such as inferior milk production, as primate mothers and infants adjust their behavior in relation to each others' handicaps (Meier 1984). For example, longer periods of maternal care could benefit the offspring of young cows, particularly under adverse conditions. The relatively high frequencies with which young cows contact their calves may help to strengthen and prolong the mother-young bond. This possibility is supported by the fact that young mothers have longer associations with their daughters than do older cows (chapter 12); this difference has been found in other species as well (e.g., zebu cattle: Reinhardt and Reinhardt 1981; red deer: Clutton-Brock et al. 1982).

The fact that young cows initiate contact frequently suggests that they pay more attention to their calves. Edwards and Broom (1982) suggest that calves may present a more novel stimulus for inexperienced cows early in the mother-young relationship. These researchers found that the post-partum behavior of primiparous dairy cows is more affected by the presence of neonates than is that of multiparous cows. Inexperienced mothers remain focused on the calf for longer periods, taking longer to resume normal activities. That this behavior is due in part to fear of the calf is suggested by the fact that primiparae often meet their calves' approaches with lowered head, as if to ward off an attack. Perhaps, after this initial period of contact with the calf, young cows retain this interest in their calves but without the element of fear.

Chapter 5

MATERNAL EXPERIENCE AND THE EFFECTS OF TENDING ON RELATIONS WITH DAUGHTERS

INTRODUCTION

Differences in maternal experience can influence mother-offspring relations in diverse ways. Reiter et al. (1981) found that older, more experienced northern elephant seal mothers were much more successful than primiparae at rearing pups within the mayhem of the rookery. The harems in which parturition and pre-weaning development take place constitute such crowded and complex social environments as seriously to impair the chances of a pup's surviving; pre-weaning mortality ranges from 13 to 40% on Año Nuevo Island. Pup survival depends to a large extent on its mother's ability to control the situation. Older females are larger, more aggressive and dominant, and occupy central positions in the harem, away from fighting bulls and crowding females on the periphery. They also arrive and establish their positions earlier, enhancing their ability to defend them; thus their early-born pups fare better for a number of reasons.

For bison, the activity of bulls during the breeding season creates a complex and hazardous social environment, similar in some ways to that of the elephant seal rookery. During July and August, bison bulls join the cow-juvenile herd for the rut. Bulls spend much of their time fighting, roaring, stirring up dust, and racing through the herd, chasing cows and each other; the normally peaceful herd is transformed into a battle ground.

Bulls circulate frequently through the herd, testing cows' urine to determine reproductive status. As cows approach estrus they are increasingly attended to by bulls, or "tended" (see Lott 1981). Tending usually lasts for a few days or a week. During this time one or more bulls drive the estrous cow as far away from the herd as they can; the cow and her consort spend much of this time standing close together on the edge of the herd.

Tending appears to affect mother-calf relations in many ways. Since the bull impedes a cow's normal movements, she is unable to maintain proximity with her calf. The calf is often driven away by the bull, or at least discouraged from assocating with her mother. The cow's efforts to stay with the herd are also impeded; the calf, in following the herd, must often walk away from the mother. Thus calves behave more independently during this period. Nursing bouts become difficult when one or more large bulls are standing close behind or beside the cow; at the slightest movement by a tending bull, the cow bolts away. Some cows become extremely nervous under these conditions, pivoting and running frequently during nursing bouts, so that their calves are able to suckle very little for the duration of tending.

While no calf mortality resulted from rutting activity during the course of the present study (broken legs were the worst physical damage), the rut appears to disrupt the mother-calf relationship. In particular, developmental patterns of maternal and filial behavior may be altered when the mother is tended. Maternal experience could be of particular advantage in the complex social environment of the rut. It may be that inexperienced cows are more easily frightened by tending bulls and therefore unable to sustain previous levels of maternal care.

Mother-daughter relations during tending are examined here for the purpose of testing the hypothesis that maternal experience mitigates the effects of tending on relations with calves. This hypothesis predicts that during tending, proximity, coordination of movements, and synchrony of activities decrease more for primiparous than for experienced mothers and their calves. The frequency of approaching and leaving between young mothers and their calves may be more severely reduced, and their relative contributions to maintenance of proximity altered. Young mothers should also reduce nursing time during tending more than older mothers; as a result, the former may show increased conflict with calves over nursing.

METHODS

Mother-daughter relations during tending were compared with those before and after tending, in order to determine how the presence of tending bulls affects mother-daughter relations and whether or not effects differ for experienced and inexperienced mothers.

SUBJECTS: Of the 13 mothers in the study, nine were extensively tended (all except one of which (CR) calved the following year). The other four mothers (the three oldest and the youngest) were tended very briefly or not at all and so were excluded from this analysis. The three older and the six young cows formed two groups, representing experienced and inexperienced mothers; all of the young cows were primiparous except one cow with one previous calf. Cows in the older group were all multiparous and ranged in age from eight to 12 years. Since individual calves' ages were somewhat different when their mothers were tended (cows were tended when their calves were four or five months old), these three periods represent slightly varying maturational stages.

MEASURES: In order to compare tending and non-tending periods in experienced and inexperienced cows, several categories of mother-young relations were examined. These include:

a) Spatial Relations: What effect does tending have on the percent of time mothers and their calves spend within 10m and following each others' movements? Do calves leave mothers more during tending?

b) Activity Patterns: Is nursing time reduced during tending? Do mothers and calves spend more time in asynchronous activities (i.e., when one member of the dyad grazes while other rests)?

c) Vocalizations: Do mothers and calves call to each other more often during tending?

d) Nursing Conflict: Do mothers show more aggression toward calves while tended?

DATA ANALYSIS: Data collected during the week when mothers were tended were compared with data pooled over the previous month and the month after tending. Pooling over these two months provides a relatively long period representing 'normal' relations, and minimizes developmental and seasonal changes. Data for experienced and inexperienced mothers were compared in analysis of variance with time periods (i.e., tending, non-tending) as repeated measures. Tests of interaction between time periods and maternal age determine whether experienced and inexperienced mothers differ in the effects of tending on relations with calves.

The SAS procedure GLM was used for the analyses (SAS Institute 1985a, b). Percentages were subjected to arcsine transformations prior to analysis to normalize distributions.

RESULTS

Table 3 shows means and standard deviations for experienced and inexperienced mothers in all measures, for tending and non-tending periods. Results of analysis of variance (F values and probabilities) are shown for interactions between time periods and maternal age. Significant interactions indicate that mothers of the two groups are differently affected by tending. Sample size is the same for all tests; degrees of freedom are 1, 7. Figures 12 to 16 show group means before, during, and after tending for five measures. The months before and after tending, as shown in these graphs, comprise the intervals over which data were pooled to represent the non-tending period.

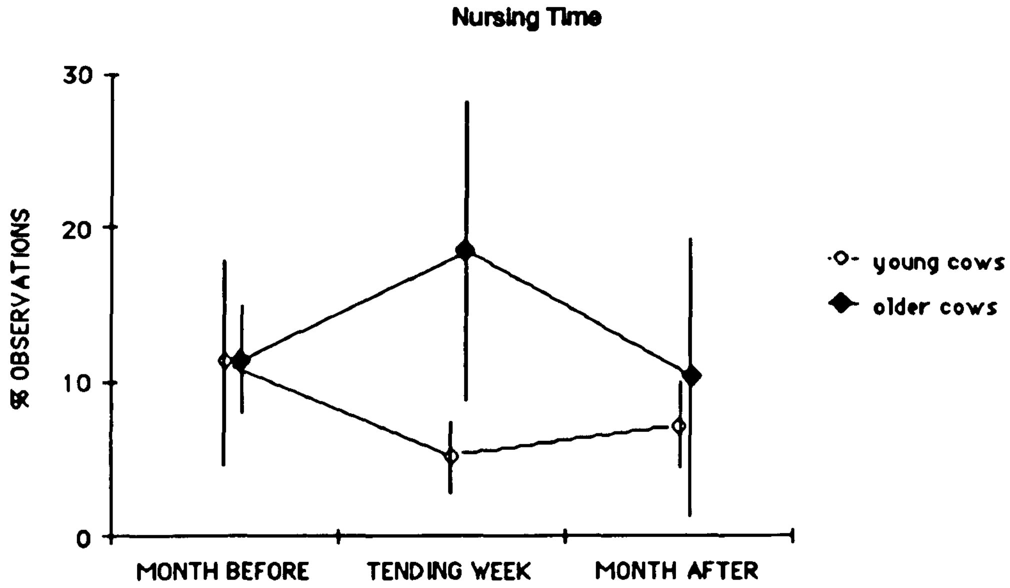


Figure 12: Mean percent of scans, with 95% confidence intervals, when mothers nursed their calves. Older mothers (N=3) are compared with young mothers (N=6) in the week when the mother was tended and the months before and after.

TABLE 3

MATERNAL EXPERIENCE IN RELATION TO THE EFFECTS OF TENDING ON INTERACTIONS WITH CALVES:

	Older Mothers N = 3				**Young Mothers** N = 6				**Anova Results** (Time x Age)	
	Tending		No Tending		Tending		No Tending			
Measure	X	SD	X	SD	X	SD	X	SD	F	P
% time within 10m	65.4	20.4	32.5	4.9	46.9	18.0	38.9	4.1	3.63	0.099
% grazing time w/in 10m	66.7	36.8	44.5	13.8	36.1	20.5	70.1	12.3	4.39	0.074
% time following and leading	57.1	17.8	56.8	6.2	37.2	5.6	70.1	6.1	9.43	0.018
Total approaches & leaves	8.9	6.3	9.8	2.4	6.8	1.8	11.1	2.4	0.99	0.353
% leaving by calves	10.6	12.4	17.8	2.9	31.6	9.7	20.5	1.9	1.20	0.309
% time in asynchronous activities	22.8	11.6	27.3	7.6	40.4	7.5	21.9	4.4	9.55	0.018
% time nursing	18.0	8.6	10.7	4.0	4.8	2.9	8.7	5.6	7.74	0.027
Maternal aggression/suckling attempt	0.2	0.2	0.2	0.2	0.3	0.3	0.5	0.5	0.82	0.395
Calling/h by mother and calf	0.8	1.1	0.1	0.1	0.3	0.2	0.2	0.1	1.17	0.315

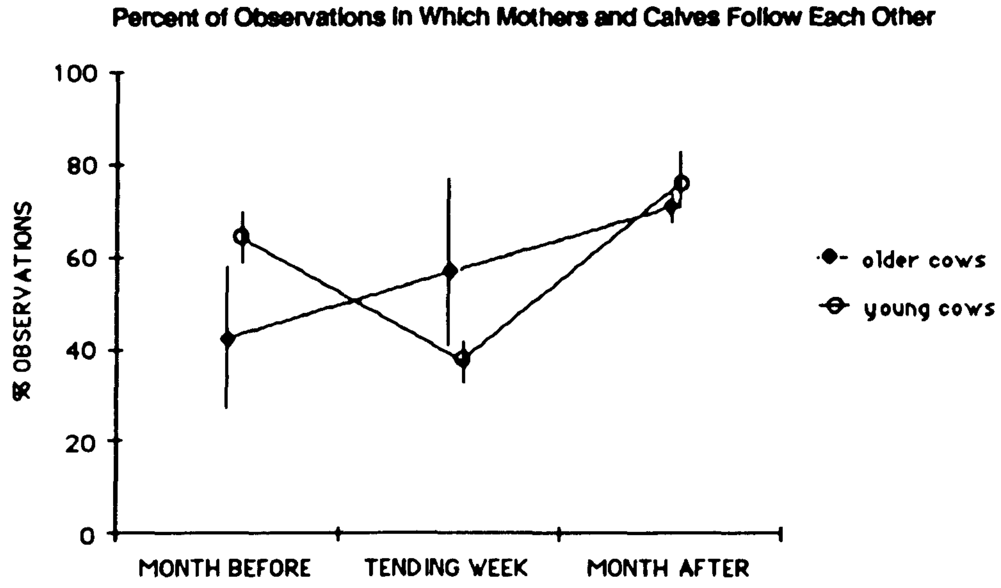


Figure 13. Mean percent of scans (at 2.5-minute intervals) with 95% confidence intervals, during which calves followed or led their mothers. Means for young mothers and their calves are compared with those for old cows and their calves for the week when the mother was tended and the months before and after.

The effects of tending on mother-calf relations differ for experienced and inexperienced mothers in several ways. As predicted, young mothers spent less time nursing their calves in the presence of tending bulls (Figure 12). In contrast, older cows and their calves actually nursed more than usual. During the week of tending, calves of young cows were observed suckling in less than 5% of samples, on the average, as opposed to 18% for calves of older cows. In spite of the extreme difference in nursing time, conflict with calves over nursing did not increase for young mothers; the frequency of maternal aggression remained more or less constant for both groups.

Comparisons of young and old mothers in changes in spatial relations during tending suggest that maternal experience helps to maintain normal synchrony of movements and activity between mother and calf. The proportion of samples in which young mothers and their calves followed each others' movements dropped sharply in the presence of tending bulls. For experienced mothers, the change is quite different. Figure 13 shows that normal developmental increases in the time when mothers and calves follow each other are not interrupted by tending for older cows as they are for young mothers. The percent of samples in which the activities of mother and calf are asynchronous normally decreases during this time as calves graze increasingly often with their mothers (chapter 3). As shown in Figure 14, older mothers and their calves showed relatively uninterrupted developmental changes in activity patterns, while the activities of young cows and their calves became dramatically less synchronized during tending. Old and young mothers show opposite patterns of change in proximity during grazing periods, although the difference is somewhat less than significant. While the percent of scans in which older cows grazed within 10m of their calves increased during tending from 45 to 67%, tended young cows spent only half as much time as usual grazing near their calves. Measures of approaching and leaving between mother and calf did not show different patterns of change for the two groups.

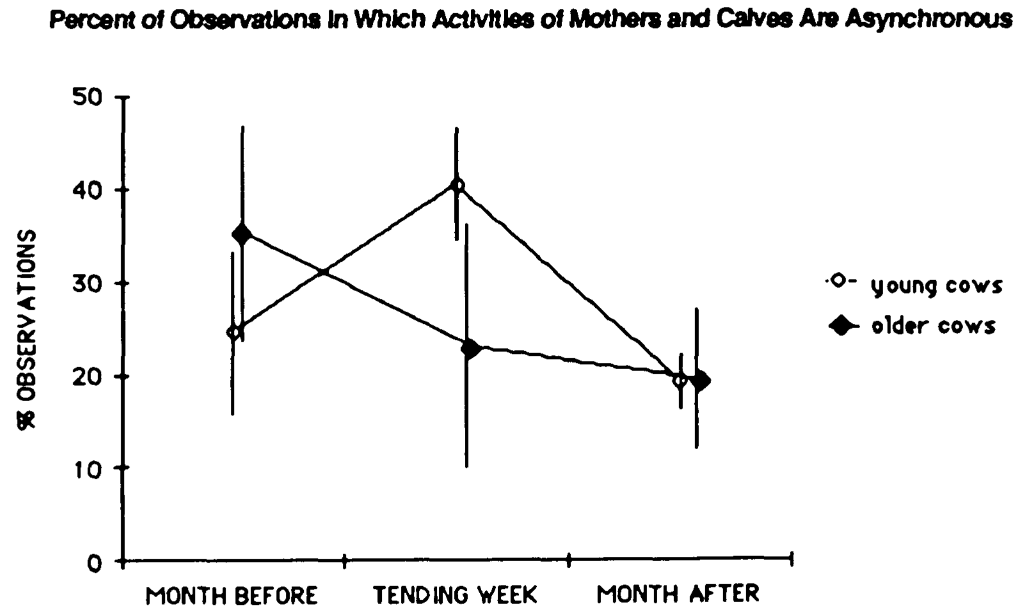


Figure 14: Mean percent of scans, with 95% confidence intervals, during which one member of the cow-calf dyad grazed while the other rested.

VOCALIZATIONS

Maternal experience might allow mothers as well as their calves to compensate for the interference in spatial relations caused by tending bulls. One likely method would be for both members of the dyad to call to each other more frequently when forced apart by bulls. However, while older mothers and their calves appear to increase the frequency of vocalizations during tending more than young cows and their calves, as shown in Figures 15 and 16, the differerences are not significant. Because of the high variability, more data are needed to address this question.

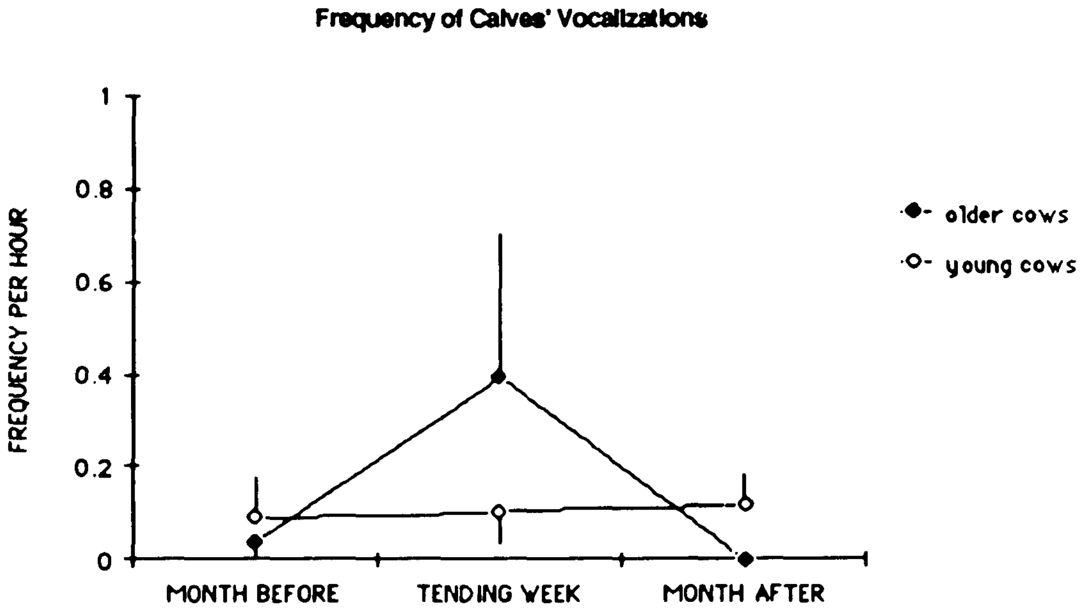


Figure 15: Mean frequency per hour, ± SE, of calves' vocalizations toward mothers. Calves of old and young mothers are compared in the week when the mother was tended and the months before and after.

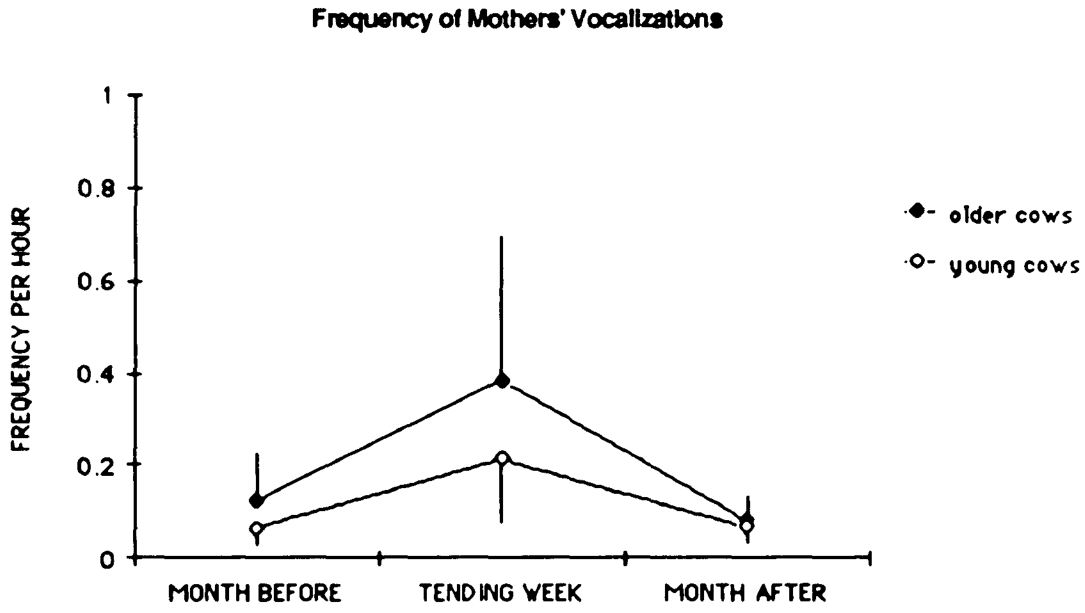


Figure 16: Mean frequency per hour, ± SE, of old and young mothers' vocalizations toward calves during the week of tending versus the months before and after.

DISCUSSION

Comparisons of old and young mothers show that, in several ways, the effects of tending on relations with calves depend on maternal experience: for young mothers and their calves, nursing time decreases during tending, activity and movements become less synchronized, and mother and calf spend somewhat less time grazing close together. In contrast, older mothers and their calves show either no change or a change in the opposite direction. These results, while based on a limited sample, suggest that older mothers are better able to maintain previous levels of nursing care during tending, and to synchronize their activity and movements with those of their calves in spite of interference. Older cows have been tended more often than young cows, particularly since even non-reproductive cows (appendix A) are tended (pers. obs). That older cows have had more experience with bulls is likely to enhance their ability to continue relations with calves during tending.

Several aspects of mother-young interactions do not differ between old and young cows as predicted. Changes in patterns of approaching and leaving between mother and calf are not significantly influenced by maternal experience. The frequency of maternal aggression, which is generally higher where nursing time is less (chapter 4), does not increase for young cows and their calves during tending; in fact, it decreases somewhat. It may be that the presence of tending bulls has an inhibiting effect on mothers and their calves. Frequencies of vocalization between mothers and calves, which might help to compensate for the interference of bulls, do not differ significantly between young and old mothers; larger samples may shed more light on this issue.

The finding that older cows nurse their calves more during tending than before or after is rather difficult to interpret. Older cows may produce more milk while tended, or release it more slowly. They may also be impeded from moving away from the calf by the bull's presence. On the other hand, they might stand longer for nursing bouts during tending as a way of compensating for the impediments to mother-calf relations caused by bulls. Their calves may also suckle longer as a pacifier during stressful situations.

Previous experience with bulls may help mothers to minimize disruptions of relations with calves in various ways. Tending could be dangerous for cows who do not respond correctly to bulls' signals. If older cows have more control over the situation, they may somehow compensate for the unavoidable interruptions of normal relations with their calves, for example by spending more time nursing. That at least some older cows and their calves vocalize more during tending (Figures 15 and 16) suggests that they may try to compensate for the bulls' obstructions to maintenance of contact. It is unclear, however, why calves of young mothers do not seem to increase their calling at all, particularly since their mothers do so to some extent.

Spatial relations during tending may be determined largely by the behavior of calves, particularly since mothers' movements are blocked by bulls. The offspring of older mothers may be better prepared for the problems encountered during tending and therefore able to contribute to the solutions. When their mothers are not being tended, daughters of older cows are generally more independent and take more control over spatial relations than do those of young mothers (chapter 11).

The function of the mother-offspring relationship is put to the test in stressful situations such as occur in elephant seal rookeries (Reiter et al. 1981). For bison, parallel situations may exist when the herd is under seige from predators or when bulls join the herd for the rut. Such conditions increase the potential for disruption of spatial relations between mothers and calves.

PART III: LONG-TERM RELATIONS

Chapter 6

WEANING IN BISON: A REDEFINITION OF THE MOTHER-DAUGHTER RELATIONSHIP?

INTRODUCTION

Weaning constitutes a major aspect of development, with profound implications for the mother-offspring relationship. In some species the bond ends when weaning is complete (e.g., woodchucks: Barash 1974; common seals: Wilson 1974; northern elephant seals: Reiter et al. 1981). Where mothers continue to associate with their young beyond the period of physical dependence (e.g., cattle: Reinhardt and Reinhardt 1981; red deer: Clutton-Brock et al. 1982; African elephants: Moss and Poole 1983), weaning may result in only subtle changes in non-nursing aspects of the relationship.

Patterns of change in maternal care are related to aspects of social organization. For example, Altmann (1963) points out that moose cows, which are essentially solitary, drive their calves away suddenly and violently, while in the gregarious elk, no such abrupt change occurs. Similarly, more gradual, less punitive weaning is associated with increased gregariousness (Rosenblum and Kaufman 1967; McGuire and Novak 1984). This relationship has been described within, as well as between species. For example, bighorn lambs are weaned later and less abruptly in more gregarious populations (Berger 1979a, c). Since bison cows are extremely gregarious in open habitats, one might expect that weaning would occur relatively late and at a gradual pace.

Weaning is defined as the cessation of nursing (Counsilman and Lim 1985). However, as Martin (1984) points out, exclusive use of this definition may obstruct rather than aid its description. One problem is that weaning is not a point in time but rather a complex process, sometimes beginning long before the end of nursing. It involves not only a change in the amount of milk transferred, but also the occurrence of behaviors reflecting conflict between mother and offspring (Trivers 1974). Moreover, the end of the nursing period is difficult to determine without constant observation of subjects. Therefore, arbitrary endpoints (e.g., low levels of successful nursing attempts: Berger 1979c) are often used as operational definitions. Martin (1984, p. 1258) proposes, as an alternative definition of weaning, "the phase of parental care during which the rate of parental investment...drops most sharply." His model describes parental care as increasing initially, reaching some maximal level, and then decreasing rapidly to zero or a low level (Figure 17); weaning is viewed as the period of rapid decrease in parental care.

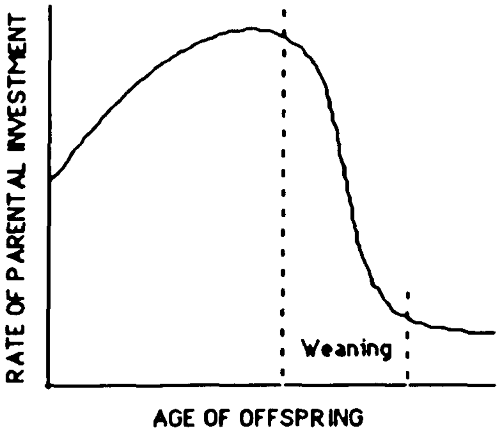


Figure 17: A model of weaning, adapted from Martin (1984). The period of weaning is the time when parental investment decreases most rapidly (between dotted lines).

While the age at which nursing ends does not in itself constitute weaning, it is nevertheless an important element and is necessary to a complete description of the process. Moreover, it is a significant period of transition which must be identified before post-weaning changes in mother-offspring relations can be described (see chapter 7).

One factor which may influence the duration of the nursing period is the mother's subsequent reproductive status (appendix A). In many ungulate species, females may or may not give birth every year (e.g., bison: McHugh 1958; elk or red deer (*Cervus elaphus*): Altmann 1963; Clutton-Brock et al. 1982). When the mother does not reproduce, she generally continues to nurse her yearling. Thus individual dyads vary in the duration of the exclusive mother-young relationship. This variation may have significant long-term effects on offspring as well as immediate effects on the longevity of the relationship. As Clutton-Brock et al. (1982) point out, this delayed weaning may be advantageous in that the yearling's growth rate is increased with little cost to the mother's future reproductive potential. These researchers found that the dominance status of red deer hinds whose mothers had not calved in the subsequent year ('barren' mothers) was higher than that of other hinds.

In this section, two aspects of weaning among female bison are described:

1) THE WEANING PROCESS: How does maternal care change in bison? Is there a period of rapid decrease? Based on Martin's model, one would expect average nursing time (as the major currency of maternal care) to increase initially to a maximum level, then decrease rather abruptly to zero or to a very low level. Meanwhile behaviors reflecting conflict should show opposite patterns, being negligible when maternal care is increasing and maximally frequent during the period of rapid decrease in nursing time. In order to test these predictions, the pattern of change in maternal care during the first seven months is examined graphically and compared with Martin's (1984) model.

2) THE END OF THE NURSING PERIOD: Differences in the reproductive conditions of mothers observed in this study during the year after subjects' birth provided an opportunity to examine durations of nursing periods in two types of mothers: those that calved the following year and those that did not. In this section, daughters' age at the end of weaning is estimated for each group. This information on the end of the nursing period, together with that on earlier stages, permits a more thorough comparison between the weaning process in bison and Martin's (1984) model.

I. THE WEANING PROCESS

METHODS

Subjects included 13 female calves and their mothers in a free-ranging herd at Wind Cave National Park. Data were collected in focal animal samples during 1983, throughout the first seven lunar months of calves' lives.

Since lactation constitutes one of the most important and costly aspect of maternal investment (Blaxter 1971), maternal care was estimated as mean nursing time (minutes per hour) for each week. Estimated nursing time is calculated as mean nursing bout duration (min) / mean interbout interval (h). Conflict between mothers and calves over the extent of maternal care was examined in order to determine whether such behavior occurs during a concentated 'weaning' period which coincides with a period of decreasing nursing time. Conflict was estimated as mean frequency of rejected suckling attempts and maternal aggression per minute spent nursing. Rejected suckling attempts involve calves' nosing the mothers' inguinal area and mothers' moving away or reacting aggressively. Maternal aggression includes all instances of mothers threatening their calves with horn swings and/or kicking and butting them.

The nature and timing of weaning depends to some extent upon infants' ability to obtain and utilize adult food types. In order to consider this factor, changes in nursing time were compared with changes in the percent of scans (at 2.5-minute intervals) in which calves grazed.

RESULTS

Figure 18 shows changes in nursing time over the first seven months. Since the end of nursing does not occur until sometime between the eighth and the twelfth months (see below), the data shown represent only about the first two thirds of the nursing period. This graph shows that maternal care, as estimated by average time spent nursing, decreases in a relatively gradual and steady fashion during the first three months; the largest drops in nursing time occur in the first five weeks. Subsequent ad-lib observations suggest that no abrupt changes take place after the seventh month. If a period of rapidly decreasing nursing time exists, it would have to be the first five weeks. However, since calves continue to nurse for up to 40 weeks beyond that, this decrease characterizes the early nursing period, rather than weaning.

Behaviors reflecting conflict over nursing occur infrequently and change relatively little during the first seven months. For most of this period, the frequency of rejected suckling attempts is less than two acts in 10 minutes of nursing (Figure 19), while fewer than one act of maternal aggression occurs in 20 nursing minutes (Figure 20). During the first 15 weeks, rejected suckling attempts increase in frequency as nursing time decreases. The frequency of maternal aggression, on the other hand, remains quite low during the first two months, when nearly all decreases in nursing time occur; this suggests that maternal aggression plays little or no role in decreased nursing. Both maternal aggression and suckling rejections are more frequent during weeks nine to 15 than at other times. This period of relative conflict might be viewed as a time of weaning; however, there is little or no simultaneous decrease in maternal care, as measured by nursing time.

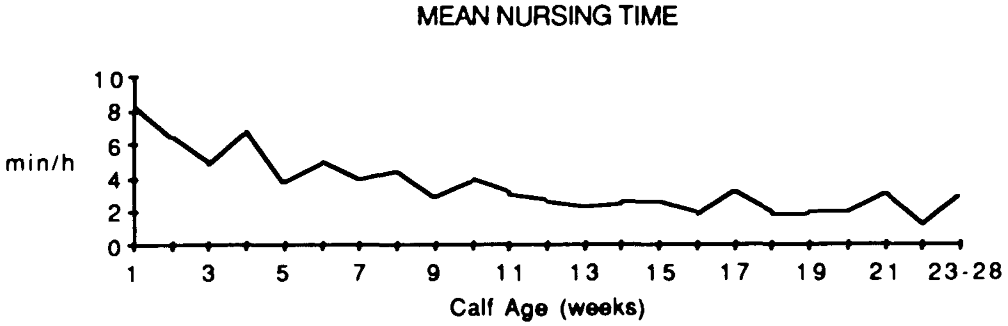


Figure 18: Changes in nursing time (minutes per hour), averaged over all thirteen subjects, during the first seven lunar months of life. Data for weeks 23-28 are pooled because of low sample sizes for each week.

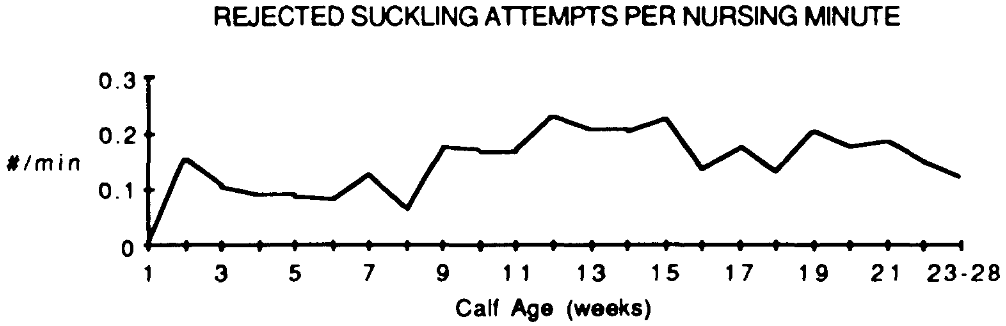


Figure 19: Changes with calf age in mean frequency of rejected suckling attempts per minute spent nursing.

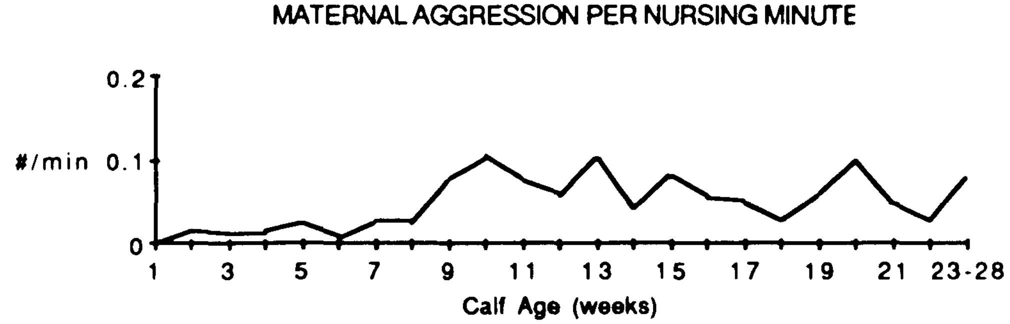


Figure 20: Changes with calf age in mean frequency of aggressive acts by mothers per minute spent nursing.

The pattern of change in maternal care varies substantially among individuals; such variation is obscured by the overall patterns shown above. For older cows in particular, expressions of conflict occur almost entirely during a period of a few weeks, around the third month of the calf's life. Subsequently, nursing time is established at a lower level; conflict between mother and calf largely ends at this point, as if an understanding has been reached. For some young cows and their calves, conflict begins around the second or third month and intensifies erratically thereafter. Still other mothers are extremely tolerant of their calves suckling attempts, showing little or no conflict with calves until the end of the nursing period.

Early decreases in nursing time are accompanied by increases in the percent of samples in which calves graze. Calves appear to begin grazing around the end of the first week of life. During the first five weeks, when nursing time decreases most abruptly, grazing time increases but remains relatively low; calves spend less than 10 percent of their time grazing at this stage. During the first four months, the percent of time calves spend grazing increases to around 40%; no further changes occur during the next three months (see also chapter 3). Thus the period of decreased nursing time coincides largely with that of increased time spent grazing.

II. THE END OF THE NURSING PERIOD

METHODS

Among the 13 mothers in this study, five did not calve in 1984. These included the four oldest mothers as well as the youngest (a 2-year-old cow); the two oldest cows died without calving again. Mothers that calved in 1984 are referred to as 'pregnant'; those that did not, as 'barren.'

In order to estimate the age at which nursing ceased, subjects were observed as frequently and as long as possible in ad-lib samples. However, the only way to be sure that a calf has stopped nursing is to observe it at every moment of the day and night. Moreover, the end of the nursing period proved to be quite difficult to observe. Cows wean their calves gradually; nursing bouts grow shorter and less frequent until they are never observed. Since bison are mobile and gregarious, individuals frequently move out of sight for a few minutes (i.e., long enough for a brief nursing bout) during observation periods.

Problems of spotting increasingly brief and rare events are exacerbated by many factors, particularly that weaning occurs in winter, when: a) group sizes decrease, lowering the chances of finding specific individuals, b) bison are less approachable and must be observed at great distances, c) bison are more mobile, increasing difficulties of locating and following groups, d) snow is deep; there is no access to bison wintering grounds by vehicle, and e) sub-zero temperatures prevent extended observations. Moreover, the scarcity of observed behaviors reflecting weaning conflict suggests that weaning is effected rather subtlely.

Because of the difficulties described above, limited data on late nursing behavior were supplemented with another estimate of the time when nursing ends. The best indication that weaning is completed is the fact that mother and calf are in separate groups. Nursing dyads are always in the same group; in contrast, after nursing ends, daughters may be found in groups separate from their mothers. Therefore, in order to estimate weaning age, information on the last observed nursing activity was compared with the earliest date on which mothers and daughters were seen in separate groups. Although the first time a separation is observed may be some time after nursing has ceased, this approach brackets a time period within which weaning is completed.

RESULTS

Pregnant Cows

Nursing behavior near the point of its cessation was observed for three of the eight pregnant mothers (Table 4). The end of nursing was confirmed for one of these calves (HD) by the fact that, soon after the observed nursing behavior occurred, mother and calf began frequenting separate groups. The other two (VC and J) were observed nursing as late as the end of the eleventh month. While neither was absent from her mother's group until around the middle of the thirteenth month, the sightings of such late nursing activity indicates that their weaning was not complete before month 12. Details of these cases are provided below:

HD, whose mother had been unusually tolerant during nursing bouts, was weaned early, apparently by the middle of the ninth month. Near the end of month 8 she was seen attempting to nurse repeatedly (seven or more times); all attempts were rejected. Previously, even single rejected nursing attempts had been extremely rare for this dyad. As early as the tenth, and possibly ninth, month, this calf completely stopped associating with her mother, spending nearly all her time in groups separate from the mother. For her, separation took place three or more months earlier than for other calves.

VC and J were weaned later, around the twelfth month; both are daughters of primiparous (3-year-old) cows. Each was seen nursing near the end of the eleventh month, with little accompanying conflict. One (VC) was also seen attempting to nurse once on three separate occasions during her twelfth month; the intensity of conflict shown in these interactions did not appear greater than in those of her first few months.

For the remaining five daughters of pregnant cows, no nursing behavior was observed after month 8, yet none were seen in groups separate from their mothers before month 12; three were not seen apart from their mothers until month 13 or later. It is impossible to determine how long before that time they were weaned. Information on weaning dates for calves of pregnant cows is summarized in Table 4; ages are shown in lunar months.

TABLE 4
PREGNANT MOTHERS:
ESTIMATED AGE OF DAUGHTERS AT END OF WEANING

NAME:	AGE AT LAST OBSERVED NURSING	AGE AT FIRST ABSENCE FROM MOTHER'S GROUP	ESTIMATED AGE AT WEANING
HD	mid month 8	early month 10	month 9
VC	end month11	mid month 13	month 12
J	end month11	mid month 13	month 12
NA	end month 8	mid month 12	month 9-11
BB	end month 7	beginning month 12	month 8-11
TB	early month 8	early month 13	month 8-12
UB	mid month 8	end month 12	month 9-12
BN	end month 7	(after month 16)	(after month 7)

Barren Cows:

The five barren cows continued to nurse their daughters well into the second year of life. Only one of these was weaned (i.e., observed in groups separate from her mother) before the end of the field season in August, 1984. This yearling (CS), the largest of all her peers, was 17.5 months old when she stopped nursing. Her mother was being tended at the time; the yearling repeatedly walked away from the mother, while the mother, followed by her consort, repeatedly followed the yearling. When next seen, six days later, they were in separate groups and remained so for the next 15 days, even though they had several opportunities to relocate each other. The yearling's behavior was so independent that her weaning appeared to be voluntary, although interference from the tending bull may have contributed to the process. Her mother had made unusual efforts at staying with her during the previous few weeks. Little more than one week before the weaning, the mother became extremely agitated when the yearling failed to stay with the mother's group as it began moving away; she ran back and forth and grunted constantly for twenty minutes until she found her daughter.

For the other four daughters of barren cows, it appeared that the nursing period had not yet ended in mid-October, 1984, when they were about 1.5 years old. During brief observations three of these yearlings (HO, CL, and LA, aged 20, 19, and 19.5 months, respectively) were observed suckling. RB (aged 17.5 months) and her mother, though not observed nursing, stayed as close together as they always had. For these mother-daughter dyads, relations appeared to change rather little over the first 1.5 years.

Barren vs. Pregnant Cows:

The age at which daughters stop suckling differs substantially in relation to the mother's reproductive status in the subsequent year. Among pregnant mothers, nursing ended when daughters were between 9 and 12 lunar months of age. Nursing continued much longer for barren mothers; the earliest age at which any in this group stopped nursing was 17.5 months, while three of the five were still suckling at 19-20 months. Figure 21 shows estimated changes in nursing time during the nursing period for each group.

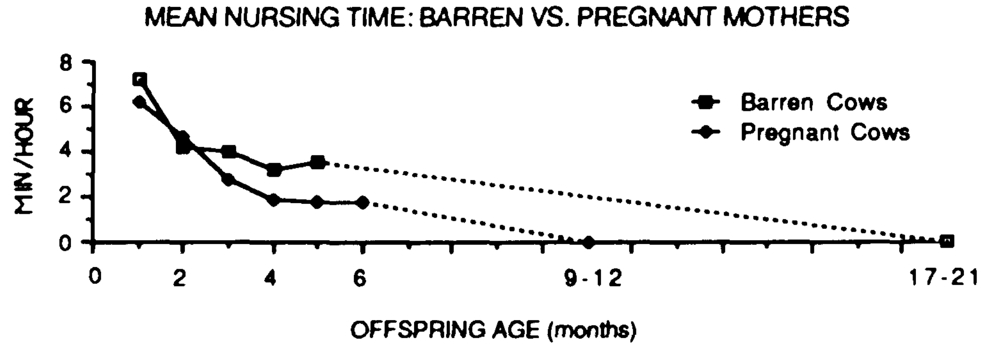


Figure 21: Average nursing time (minutes per hour) throughout the nursing period (measured in lunar months) for barren and pregnant cows and their daughters. Dotted lines represent periods during which nursing activity was observed but not quantified. The end of the nursing period is indicated at the midpoint of the range shown by members of each group.

DISCUSSION

Patterns of change in nursing time and conflict among bison mothers and calves do not follow Martin's (1984) model of weaning as a period of rapidly decreasing maternal care. In contrast, nursing care decreases gradually during the first three months and then continues at a lower and relatively unchanging level for at least four more months. Calves spend gradually increasing proportions of time grazing as nursing time decreases. Conflict between cow and calf is infrequent and does not reflect a concentrated 'weaning' period, as suggested by the model. The latter point is emphasized by the fact that the frequency of maternal aggression shows no significant change over the first five months, as demonstrated in chapter 5. Moreover, both maternal aggression and rejected suckling attempts decrease somewhat after week 15, while nursing continues. This suggests that by the fifth month conflict between mothers and calves has been largely resolved. Rather than ending the cow-calf bond, conflict of this nature may serve to redefine the relationship at a lower level of physical dependency.

Individual dyads differ greatly in the age at which weaning is completed. Barren mothers nurse their daughters about twice as long as pregnant cows. Even among the pregnant mothers, one calf stopped suckling in month 9, while two others continued until month 12. It is interesting that the latter two were daughters of primiparous cows, while the mother of the former was eight years old. This suggests that primiparous mothers nurse their offspring over longer periods than older cows, as has been found in other species (e.g., horses: Duncan et al. 1984).

The nursing period in bison appears to be quite long, even for pregnant mothers. Female calves do not appear physically disadvantaged by being orphaned at six months; for example, their dominance status seems little affected. Moreover, forced separation of calves from mothers at five or six months is the normal management practice for some herds (e.g., Custer State Park, South Dakota). While calves do not appear to be harmed by this, the nursing period may last twice this long under natural conditions. Moreover, bison cows nurse their calves for four to eight months after the conception of the next calf. In other species, such as red deer (Clutton-Brock et al. 1982), nursing ends in the same month as conception. In contrast, bison mothers invest in present and future offspring simultaneously.

Long-term nursing, even during the second year, may involve substantial transfer of milk. This possibility is supported by the fact that daughters of barren cows weigh significantly more as yearlings (chapter 12; see also Clutton-Brock et al. 1982).

The fact that bison mothers nurse their calves longer than is physically necessary, and do so while producing a new offspring, suggests that prolonged nursing may have a social bonding function. For example, even when little milk is exchanged, periodic nursing bouts may strengthen attachments, resulting in long-term relationships with daughters. That longer periods of nursing result in more persistent mother-daughter associations is suggested by several facts. First, of the three dyads for whom weaning dates could be identified, the two primiparous cows nursed their calves about three months longer than the older cow. Second, young cows associate longer with their daughters than do older mothers (chapter 12); this has been found in other species as well (e.g., zebu cattle: Reinhardt and Reinhardt 1981; red deer: Clutton-Brock et al. 1982).

Martin's (1984) model suggests that weaning is a process through which mothers end relationships with their young. These results, as illustrated by Figures 18-21, indicate that a different model is needed for gregarious species like bison. In a physical sense, weaning is essentially the transition from complete dependence on the mother for nutrition to complete independence. However, weaning also involves a non-nutritive, social aspect. For bison, the last few months of nursing may be of greater social than physical significance. Figure 22 compares changes over the first seven months in nursing time (as reported in section I) with those in the percent of time when mothers and daughters attempt to maintain contact with each other during movements (as described in chapter 3).

Figure 22 shows that, after the second week of life, contact-maintenance increases in frequency as nursing time decreases. While nutritive care and dependency wane, other aspects of the relationship become increasingly important; the latter are represented here by spatial coordination during movements. In contrast to implications of the model, the decreasing nursing care which reflects weaning is not accompanied by deterioration of the relationship. This suggests that, for gregarious species, weaning results in a redefinition of, rather than an end to, the mother-daughter relationship. Post-weaning relations are described in the following two chapters.

Changes in Nursing Time and Contact-Maintenance

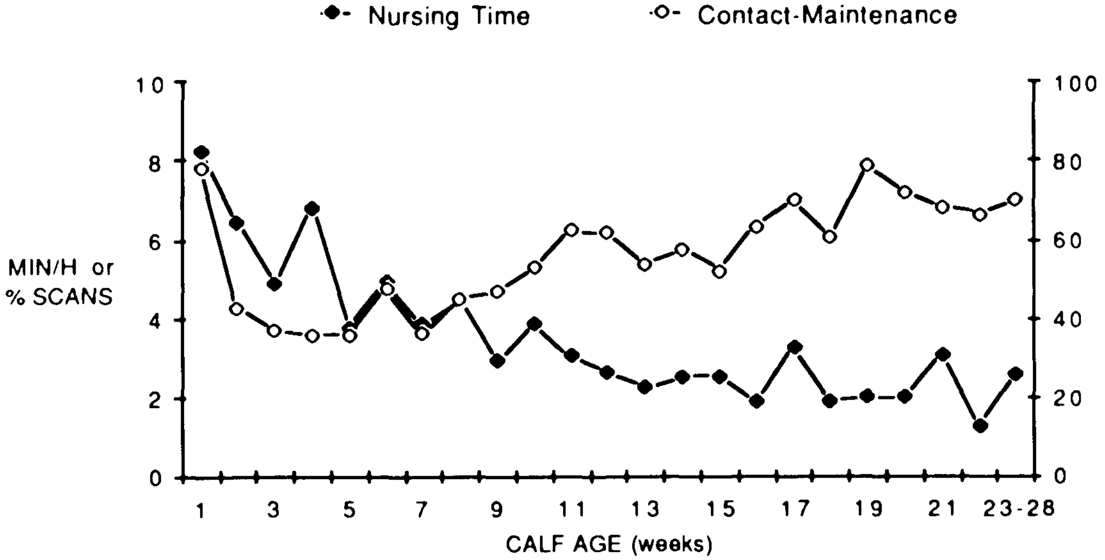


Figure 22: Comparison of changes with calf age in nursing time and the synchrony of movements between mother and daughter. Filled markers show mean nursing time (minutes per hour) during the first 28 weeks, or 7 lunar months. Open markers show the mean percent of scans (at 2.5-minute intervals) when mothers and daughters follow each others' movements. The Y-axis at left shows minutes/hour; that on the right shows percentages of scans.

Chapter 7

DO BISON DAUGHTERS HAVE LONG-TERM ASSOCIATIONS WITH MOTHERS?

INTRODUCTION

Of the events which affect mother-offspring relations, weaning and the birth of the mother's next infant appear to exert the strongest influence. In some species weaning constitutes the end of the relationship (e.g., woodchucks: Barash 1974; seals: Bartholomew 1959; Wilson 1974; Reiter et al. 1981). Where mother-young associations continue past weaning, the prolonged association may reflect non-nutritive dependency. For example, M. Altmann (1958, 1960, 1963) found that moose calves are weaned in the fall, yet they remain with their mothers until driven away before the birth of the next calf in spring. This post-weaning association with the mother is necessary for the calf's survival; orphaned calves rarely survive the winter. Altmann (1963, p. 249) lists several aspects of post-weaning maternal care, including "choice of feeding and shelter places, safety and flight decisions, and later the selection and timing of winter grouping in river drainages." Hirth (1977, 1985), in his study of white-tailed deer, found that fawns were more or less weaned by 10 weeks of age (around the end of August), yet their associations with mothers continued until the birth of the next fawn, and sometimes resumed afterward. It may be that, like moose calves, they need their mothers' continued presence for survival.

The birth of the mother's next offspring appears to be a critical point in her relations with previous young; in many species contact-maintenance is interrupted at this time (Horwich et al. 1977). By now the previous offspring is presumably physically independent (although for a few species this is not the case, e.g. chimpanzees: Pusey 1983). Where bonds with mothers extend past this point, they may have little or no effect on offspring survival. In ungulates, long-term relations with mothers are generally limited to daughters. In many species mother-daughter relations are resumed after the mother's parturition and may persist beyond the birth of the daughter's offsprings; stable matrilineal groups have been identified in red deer (Clutton-Brock et al. 1982), hartebeest (Gosling 1969) and African elephants (Moss and Poole 1983). Mother-daughter associations of several years' duration have been described in many ungulate species, including zebu cattle (Reinhardt and Reinhardt 1981), water buffalo (Tulloch 1978), cape buffalo (Sinclair 1977), zebra (Klingel 1967), black-tailed deer (Dasmann and Taber 1956), reindeer (Espmark 1971), feral goats (Rudge 1970), mouflon (Pfeffer 1967), and domestic sheep and goats (Collias 1956).

Comparisons among species suggest that the longevity of the mother-daughter association is related to the gregariousness of the species (Jarman 1974; Estes 1974; Horwich et al. 1977). Even within a species, daughters appear to associate longer with mothers where average group size is larger (Hirth 1977). Thus one might expect that, in a species as gregarious as bison, mother-daughter relations persist beyond weaning and the birth of the mother's next calf.

The existence of long-term relationships between mothers and daughters has not been documented in bison. Lott and Minta (1983) followed three marked female calves in a herd on Catalina Island. They found that daughters stopped associating with their mothers soon after weaning. This suggests that mother-daughter relations end with nursing. On the other hand, in the Wind Cave herd, several pieces of evidence lend support for the prediction that bonds with mothers persist. These include the findings that weaning is very gradual and that nursing extends beyond the period of physical necessity (chapter 6).

In order to determine whether or not mothers and daughters stop associating when nursing ceases and/or the mother's next calf is born, three approaches are employed in the following sections.

1) Changes in post-weaning spatial associations between mothers and daughters are described in terms of the percent of days when both were present in the same groups.

2) Weaned and unweaned daughters of the same age are compared in spatial relations with their mothers. Proximity and behaviors used in its maintenance are examined for pregnant and barren mothers and their daughters, from the early stages of pregnancy until 2-3 months after the

birth of the new calf. If the relationship ends with nursing, the spatial relations of pregnant and barren mothers should differ significantly.

3) The question is addressed: Do weaned daughters associate more with their mothers than with other cows? To this end, the percent of days on which daughters were seen in the same groups with their mothers is compared with the time they were in groups with other, randomly-chosen cows, during the second and third years of life. If daughters do not have long-term associations with mothers, they should spend as much time with other cows as with their mothers.

I. Post-Weaning Changes in Associations of Mothers and Daughters

This section describes changes in mother-daughter spatial relations between the end of weaning and month 17, which is about three lunar months after the birth of the mother's new calf.

METHODS

As a result of weaning, one aspect of proximity between mother and calf is in nearly all cases changed: the two are no longer always in the same group. Thus a new measure of spatial relations is introduced: the number of days when mothers and calves are both present in the same group as a function of the total number of days both were observed (% M present). The measures of spatial relations used previously (chapter 3) are, in most cases, only applicable when mothers and daughters are in the same groups. It should be noted that, for example, while a yearling might be reported to spend 75% of the time within 10m of her mother when the two are in the same group, she may be present in her mother's herd only 25% of the days observed. When it was unclear whether two animals were in the same group, e.g., when group members spread out over large areas, animals separated by gaps of at least 200m were considered to be in distinct groups.

Of the 13 focal dyads, only the eight in which mothers calved in the next year were considered in this analysis. Variation due to differences in the mother's subsequent reproductive condition was thereby eliminated.

RESULTS

CHANGES IN MOTHER-DAUGHTER ASSOCIATIONS IN RELATION TO MOTHER'S NEXT CALVING

Sometime after weaning was completed, most daughters of pregnant cows began to spend at least some of their time in groups separate from their mothers (Figure 23). Through the eleventh month, all except one dyad were always observed in the same group. In their twelfth month, 4 of the 8 pregnant mothers were in groups separate from daughters at least some of the time time; these dyads were in the same groups 0, 12, 30, and 50 percent of the time, respectively. As the time of the mothers' parturition approached, calves associated markedly less with their mothers. Some, like HD, were never seen with their mothers. This trend was most extreme in month 13, the month before parturition, when all but one daughter (BN) spent some time in groups separate from the mother. On the average, daughters of pregnant cows spent 29% of their time in the same groups as their mothers in this month (range: 3 to 85%). In contrast, daughters of barren cows were always in the same groups with mothers throughout this period.

All pregnant mothers calved when their yearlings were fourteen months old (i.e., during the month following their first birthdays). Month 14 represents a period of transition, since mothers calved in various parts of the month. In this month, daughters spend slightly more time in their mothers' groups ($\bar{X}$=42%).

After the birth of the mother's new calf, most daughters appear to associate more with their mothers. Immediately after parturition, many mothers and yearlings are in separate groups and require several days or even weeks before their groups join and reunion is possible. If this were not the case, the average value for time spent in the mothers' groups in month 14 would probably be higher. Increased post-calving association is suggested by the fact that most daughters become more directed toward their mothers, and resume patterns of proximity-maintenance similar to those of the pre-separation period. In month 15 and 16, daughters spend an average of 76% of their time in the same groups as their mothers.

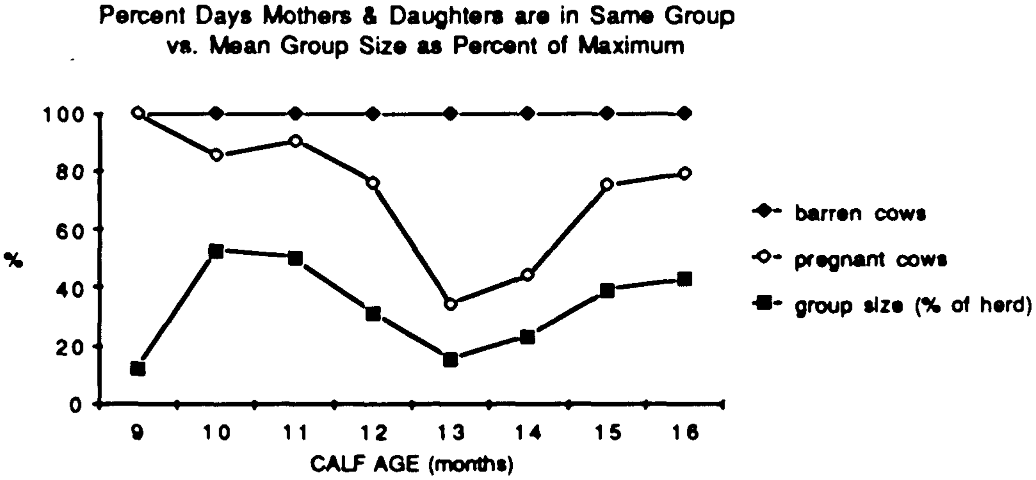


Figure 23: Mean percent of days when daughters are in the same groups with mothers, for barren and pregnant mothers, in comparison with average group size. The latter is expressed as the percent of maximum herd size (i.e., the total number of cows and juveniles in the park). The abscissa shows calf

age in lunar months from late weaning through post-calving. Mothers' new calves were born in month 14. Average group size, as a percent of total herd size, is plotted against the age of a calf born at the midpoint of the calving season. For example, month nine shows average group size during the 4-week period when the calf is nine months old.

PERCENT OF DAYS MOTHER IS PRESENT IN RELATION TO INCREASED GROUP SIZE

During the months between the end of weaning and the post-calving period, major changes occur in the average size of cow-juvenile groups. For much of the winter, groups are often small; in early spring they increase in size. In late March and April, as calving time approaches, cows become more likely to leave the herd. Older cows sometimes spend a few days or weeks in solitude or join small bull groups prior to calving. Even yearlings may be seen in groups of around 10 (as when one cow-calf dyad, followed by a group of yearlings, splits off from the herd for a few days). When calves are born, mothers and neonates generally spend a few days alone. In May, after most calves have been born, cows and juveniles reassemble into much larger groups. As the summer rut approaches all begin to form one large herd.

Changes in group size affect the frequency with which yearling daughters are present in their mothers' groups. As group size increases, so does the probability that mothers and their yearling daughters will both be in the same group, regardless of their tendencies to maintain proximity. Figure 23 compares the average value of *% M present* for all daughters of pregnant cows for months 9 through 17 with average group size expressed as a proportion of maximum herd size. This graph shows that changes in average group size are similar to those in *% M present* for daughters of parturient cows. Thus daughters may appear to associate more with mothers after calving in part, at least, because of this increased probability.

CONCLUSIONS

During the 2-4 months between the end of weaning and the birth of the mother's next calf, most pregnant mothers and their daughters spend increasing amounts of time in separate groups. Some dyads stop associating altogether. However, this period of relative disassociation appears to be temporary; after the birth of the mother's next calf, daughters spend more time in the same groups with their mothers. This may reflect preferential association between yearlings and their mothers; on the other hand, it may result from increasing group size.

These findings raise the question: Do mothers with new calves and their yearling daughters associate with each other by chance or by active maintenance of proximity? Evidence of the latter would indicate the persistence of mother-daughter bonds. This question is examined in the following two sections.

II. Spatial Relations in Months 6 to 16: Pregnant vs. Barren Mothers

Pregnant cows wean their previous offspring during the winter following their birth, while barren cows continue to nurse theirs well into the second year; for the latter group, the nursing period may last twice as long as for the former (chapter 6). Comparisons of mother-daughter relations in the two groups when weaning is complete for pregnant but not barren mothers should provide information on the extent to which spatial relations depend on nursing. If the relationship ends when nursing ceases, patterns of spatial relations between the two groups should be significantly different. Pregnant mothers and their daughters should permanently stop maintaining proximity. As a result, they should spend less time close together than should barren mothers and their daughters. Differences between the two groups should also be apparent in terms of contact-maintenance behaviors, such as approaching and following each other. These aspects of spatial relations when mothers and daughters are in the same groups are examined below.

METHODS

Subjects formed two groups of mother-daughter dyads: those in which mothers calved again in the subsequent year (pregnant cows: N=8) and those in which they did not (barren cows: N=5). The two groups were compared in months 6 to 16, from the early stages of pregnancy until 2-3 lunar months after the birth of the mother's new calf.

In order to test predictions of the hypothesis that the relationship ends with nursing, pregnant and barren mother-daughter dyads were compared in six measures of spatial relations (see also chapter 2): the percent of scans (at 2.5-minute intervals) in which mothers and daughters were within 10m, the percent of scans in which mothers and daughters follow each others' movements, the percent of approaches at 10m made by daughters, the percent of leaving at 10m by daughters, and the frequencies of daughters' approaching mothers and mothers' approaching daughters at 10m. If relations end with weaning, barren mothers and their daughters should spend more time within 10m, follow each others' movements more, and approach each other more often than pregnant mothers and their daughters. Relative frequencies with which mothers and daughters approach and leave each other should also differ; barren mothers should make greater efforts at staying near daughters than should parturient mothers.

For the first four measures, individual values were tested in analysis of variance with time periods as repeated measures, in order to compare groups as well as the patterns of change shown by the two groups. The SAS procedure GLM was used for this analysis (SAS Institute 1985a, b). Data began with month six, soon after mothers began to differ in reproductive condition. Repeated measures include pooled values for each individual for months 6-7, 10-11, 12-13, 14, and 15-16; by grouping months within time periods, missing values were eliminated. To compare groups in the last two measures, individual rates of approaching per hour by each member of the dyad were averaged over months 6 to 16. These values were tested in one-way analysis of variance. Percentages were subjected to arcsine transformations prior to analysis in order to normalize distributions.

RESULTS

DIFFERENCES BETWEEN PREGNANT AND BARREN MOTHERS

Of the six measures of spatial relations tested over months 6 to 16, pregnant and barren groups differ only in proximity: pregnant mothers spend a lower proportion of time within 10m of their daughters than do barren mothers ($F=6.01$, $df=1,11$; $p=.032$). This measure also shows significant interaction between reproductive condition and time periods ($F=4.03$, $df=4, 8$; $p=.0445$); pregnant and barren groups differ not only in the amount of time in proximity but also in the rate of change in this measure. Pregnant cows, unlike barren ones, spend decreasing amounts of time near their daughters. Figure 24 compares group means from months 1 to 16 for the percent of time when mothers and daughters are within 10m.

Contact-maintenance behaviors do not differ between the two groups. Pregnant and barren mothers and their daughters follow and approach each other with similar frequencies. Moreover, daughters in the two groups do not differ in the percent of approaching or leaving for which they are responsible. Figure 25 shows the percent of time when daughters of both groups follow mothers during the first 16 months. Mean frequencies per hour of approaches by daughters in months 6 to 16, ± standard errors, are 1.75 ± 0.37 for barren, and 1.77 ± 0.33 for pregnant mothers (F=.002, d.f.=1,11). Barren mothers approached daughters at an average rate of 1.23/hour ± 0.17, while pregnant mothers approached 0.88 ± 0.20 times per hour (F=1.43, d.f.=1,11).

Percent of Time when Mothers and Daughters are within 10m

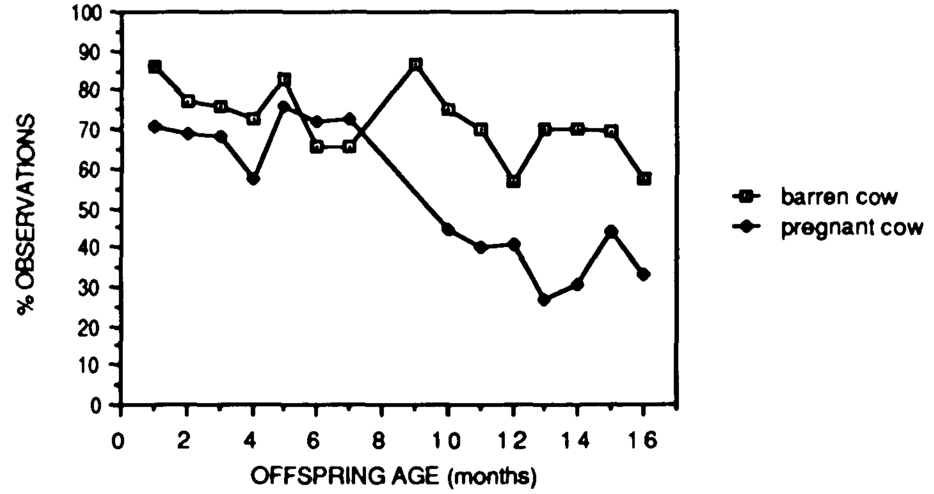


Figure 24: Mean percent of scans (at 2.5-minute intervals) when mothers and daughters are within 10m of each other from lunar months 1 to 16. Subjects are grouped according to maternal reproductive status: the 8 cows who bore new calves are termed 'pregnant'; the 5 that did not are 'barren'. New calves were born in month 14.

MONTHS 6 TO 16: EFFECTS OF TIME AND PARTURITION

Mothers and daughters of both groups spend decreasing proportions of time within 10m during this period (F=7.67, df=4,44; p=.0001: see Figure 24). Time when daughters follow and lead mothers also decreases (F=5.13, df=4,44; p=.002). The latter measure, having increased steadily during the first nine months (chapter 3), abruptly changes direction and decreases from month 9 to 16.

Approaching and leaving measures show few directional changes with time (see also chapter 3). Daughters' leaving changes somewhat over months 6 to 16: the proportion of leaving for which daughters are responsible increases somewhat over this period (F=2.54, df=4,44; p=.053).

As parturition approaches, spatial relations between pregnant mothers and their yearling daughters appear to undergo dramatic but short-lived changes. During the month before the birth of the mother's new calf, frequencies of approaching and leaving by mothers and daughters increase sharply, as do distances between the two. The latter effect is illustrated in Figure 24 by the decrease in percent of time within 10m in month 13.

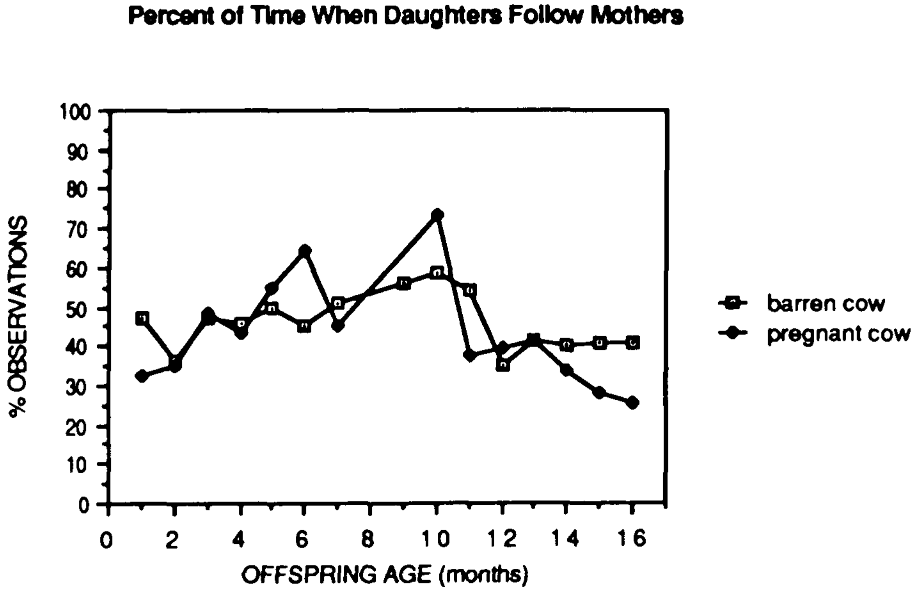


Figure 25: Mean percent of scans during which daughters of pregnant and barren mothers follow their mothers' movements during the first 16 lunar months.

CONCLUSIONS

Comparisons of long-term mother-daughter relations between pregnant and barren mothers reveal that pregnant mothers and their daughters spend less time near each other around the end of the daughter's first year. Thus the end of weaning and the birth of the mother's next calf affect the proximity of mothers and daughters. However, this is the only significant difference. The two groups do not differ in any of the five behaviors mediating spatial relations which were included in the analysis. Mothers and daughters follow and approach each other with similar frequencies, regardless of the mother's reproductive state. Daughters in both groups were also responsible for similar proportions of approaching and leaving. These results suggest that relations with mothers do not end with weaning. Rather, as suggested by previous findings (chapter 6), the relationship appears to be redefined. This issue is addressed more directly in the next section.

III. Do Weaned Daughters Continue to Associate with their Mothers?

This section addresses the question: Do weaned daughters associate more frequently with their mothers than with other cows?

METHODS

In order to determine whether or not daughters associate preferentially with mothers in their second and third years, the percent of days on which they were in the same groups with mothers was compared with the percent of days on which they were in the same groups with other cows. Subjects included eighteen yearling and twelve two-year-old daughters of cows with new calves; thus variation related to differences in the mother's reproductive status was eliminated. A parturient cow other than the mother was chosen at random for each subject.

Data were collected between May and July, 1984. Because most cows had already calved, effects of calving on mother-daughter relations were minimized. Moreover, the period of data collection preceded the rut, thus eliminating the effects of tending bulls on associations among cows. At three-day intervals during this period, group composition data were examined to determine the relative frequencies with which daughters were in the same groups with mothers and with unrelated cows. Arcsine transformations of percent associations were compared in one-way anovas.

RESULTS

Daughters spend significantly more time in groups with their mothers than with other cows. The relative frequency of association with mothers is even greater in the third year of life than in the second. For the 18 yearlings, mean percent of days spent in groups with their mothers, ± SE, was 74±1.5, as opposed to 40.2±1.3 with other cows (F=17.5, df=1,34, p<.001). The 12 two-year-olds spent 83±0.8 percent of their time in groups with mothers, while associating with other cows with the same frequency as did yearlings (40.7 ± 0.6) (F=33.2, df=1,22, p<.001). The results indicate that weaned daughters continue associate with their mothers at least until sexual maturity, around the third year.

INDIVIDUAL VARIATION IN POST-WEANING RELATIONS WITH MOTHERS

While most bison daughters associate with their mothers for several years, as demonstrated by the above results, individuals vary substantially in post-weaning relations (see Figure 26). For example, two yearlings of parturient mothers, BN and NA, represent the greatest possible extremes in this respect. BN was never observed in a group separate from her mother up to the end of the field season in mid-August, 1984, when she was 17 months old. Moreover, she and her mother maintained relatively close spatial relations when observed in October, 1984 (at 19 months), in August, 1985 (at 2 years and 4 months), and in July, 1986 (at 3 years and 3 months). Her older sister (Her mother's first calf) also remained continuously in close association with her mother until she was killed at 2.5 years. In contrast, NA completely stopped associating with her mother soon after weaning. She spent less than 10% of her time in the same group with her mother in months 13 and 14, and only slightly more than 20% in months 15, 16, and 17. She was observed to stay within 10m of ner mother for less than five minutes on only 2 occasions between her twelfth and eighteenth months (i.e., until the end of the field season), and was never observed near her mother at later dates.

The relations of other daughters with their parturient mothers were less extreme than the two described above, yet showed unique patterns. For example, BB spent all of her time with her mother up to the end of her twelfth month and after the birth of her younger brother in month 14; indeed, she maintained close proximity even during her mother's next tending. In month 13 and 14, in contrast, she was almost never seen with her mother; during this period she maintained close proximity with a different cow and calf. Another daughter, HD, separated from her mother unusually early, in her ninth month, and remained so for nearly five months. After the birth of her mother's new calf, however, she rejoined her mother and thereafter spent 97% her time in her mothers' groups.

VARIATION IN PRE-CALVING SEPARATION

While most mothers and daughters go through a period of relative separation before and during the birth of the next calf, some do not. One cow, BH, was accompanied by her older daughter through two successive parturitions. In 1983, when BN (her second daughter) was born, her first daughter (BHC) remained within a few meters; BH showed no aggression toward her, even when she approached and nosed the calf. The three stayed in a secluded area apart from the herd until about an hour after the birth, when the herd left the area. BH and BN did not move; BHC slowly left her mother and followed the herd. Five days later BH and BN rejoined the herd and BHC. In 1984 BHC (now two years old) again stayed near her mother during the birth of the new calf; BN stayed with the herd, out of sight of her mother and apparently unaware of the birth until her mother and sister returned to the herd later that day.

Post-Calving Proximity of Mothers and Daughters

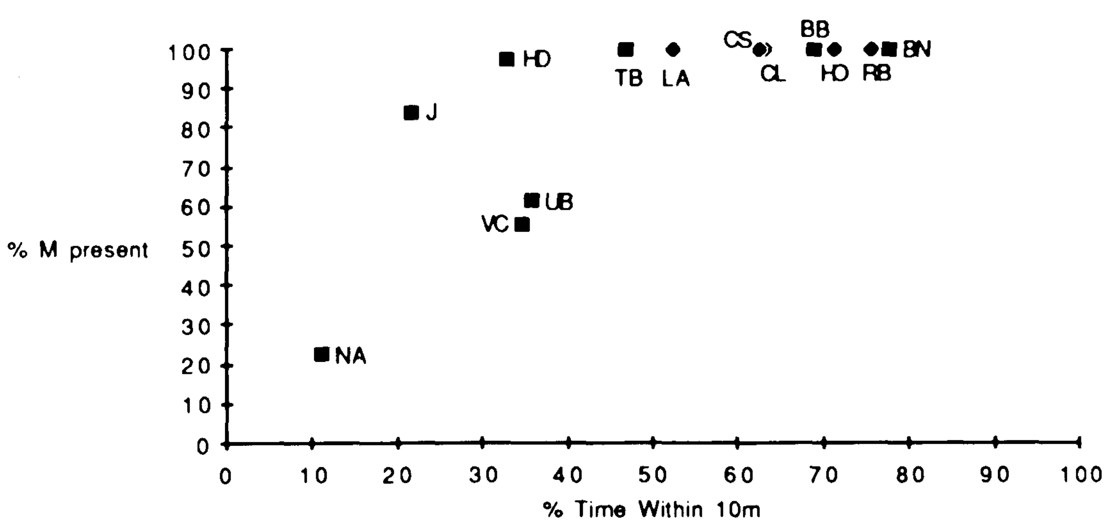


Figure 26: Individual variation in two measures of spatial relations in months 15 and 16: percent of days when mother and daughter are in the same group (% M present), and the percent of time within 10m of each other when they are in the same group. Squares represent daughters of mothers with new calves; diamonds represent daughters of barren mothers.

DISCUSSION

Individual bison daughters vary widely in long-term relations with mothers. Nevertheless, daughters spend significantly more time with mothers than with other cows in the second and third year of life. Moreover, results of previous sections show that, while mother-daughter associations are looser after weaning and the birth of the mother's next calf, behavioral aspects of their spatial relations are more or less unchanged. These findings indicate that many bison daughters continue to associate with mothers until sexual maturity, and possibly beyond.

These results differ from those of Lott and Minta's (1983) study of associations in a herd on Catalina Island. This may be interpreted in several ways. Populations in contrasting habitats may show differences in the longevity of mother-offspring bonds. Catalina Island constitutes a relatively closed habitat, being broken up into steep ridges and rather narrow canyons (Lott and Minta 1983). Wind Cave, in contrast, is composed of open grassland and rolling hills. In bison, as in other species, group size decreases in more closed habitats (Shackleton 1968; Van Vuren 1983; Rutberg 1984). As in white-tailed deer (Hirth 1977), bison daughters may associate longer with mothers in open than in closed habitats. Moreover, the extensive individual variation found in the present study suggests that the three dyads observed in Lott and Minta's study may not constitute a sufficient population to address questions of long-term association.

That mother-daughter associations continue beyond weaning and the birth of the mother's next calf is partially obscured by short-lived changes in the relationship, such as the abrupt separation of most dyads before the birth of the mother's next calf. In addition, some daughters form 'substitute' associations with other cow-calf dyads while separated from the mother. In such cases, the yearling follows the substitute cow consistently, much as she would her own mother, until the mother's new calf is born. These temporary alliances with other cows may explain the fact that two-year-old daughters spend more time with mothers than do yearlings. Only yearlings form such alliances, which sometimes persist even after parturition. While daughters follow substitute mothers, they appear to have completely stopped associating with their mothers.

Chapter 8

THE MOTHER'S ROLE IN MAINTAINING LONG-TERM RELATIONS

INTRODUCTION

Mother-daughter associations of several years' duration have been described in many ungulate species, including zebu cattle (Reinhardt and Reinhardt 1981), water buffalo (Tulloch 1978), and cape buffalo (Sinclair 1977). Stable matrilineal groups have been identified in red deer (Clutton-Brock et al. 1982), hartebeest (Gosling 1969) and African elephants (Moss and Poole 1983). In American bison, associations between mothers and daughters have been shown to persist into the third year of daughters' lives (chapter 7; but see Lott and Minta 1983). However, the longevity of bison mother-daughter associations varies widely among dyads.

Why do bison mothers and daughters continue to associate after weaning? Do mothers as well as daughters benefit from continued association? That the relationship may confer a direct advantage on daughters is demonstrated by Clutton-Brock et al. (1982): red deer daughters are more likely to be threatened and displaced from food sources by unrelated hinds than by mothers. Thus, for young, low-ranking hinds, association with mothers reduces feeding interference as well as the risk of injury.

When mother-daughter associations persist beyond weaning, one or both members of the dyad presumably benefit. If the daughter gains an advantage while the mother does not, one would expect the mother merely to tolerate the daughter's efforts at maintaining proximity, if the cost is low. On the other hand, if the mother benefits directly from the association, she should contribute to its maintenance.

This chapter addresses the questions: As daughters mature, how do mothers' and daughters' roles in maintaining proximity change? Do behavioral dynamics associated with bond-longevity reflect the efforts of daughters, mothers, or both?

METHODS

The extent to which mothers contribute to long-term relations with daughters was examined in two ways: 1) Changes in behavioral measures of spatial relations from months 1-5 to months 15-16 were described graphically for individual mother-daughter dyads. This allows the comparison of changes in maternal versus filial behavior between the period prior to weaning and that following the birth of the mother's next calf. 2) The same changes in spatial relations from months 1-5 to months 15-16 were tested for correlations with measures of longevity of individual mother-daughter bonds. Thus maternal and filial efforts at contact-maintenance were compared with the longevity of the association.

SUBJECTS

Bison cows sometimes alternate years in reproduction, continuing to nurse their previous offspring well into its second year. In such cases mother-daughter relations during the second year include nursing interactions, which are likely to affect maintenance of proximity (chapters 6 and 7). Therefore, of 13 mother-daughter dyads observed in 1983 and 1984, only the eight in which mothers calved the next year were included.

MEASURES AND DATA ANALYSIS

The measures used for this analysis are of two types (see also chapter 2):

1) Changes in Spatial Relations from Pre-Weaning to Post-Calving

Changes are calculated by subtracting individual means for months 1-5 from those for months 15-16. Measures include: a) orientation, or the percent of scans at 2.5-minute intervals when daughters *follow, lead, do not follow,* and *do not lead* mothers, while one or both are moving. The proportion of time when *mothers walk away from daughters* is estimated as the percent of scans when daughters follow and do not follow mothers' movements. The total proportion of time when *daughters walk away from mothers* is estimated as the percent of scans when daughters lead and do not lead mothers (i.e., mothers follow and do not follow daughters' movements). b) The relative roles of mothers and daughters in maintaining proximity are measured as well in terms of the relative and absolute frequencies of *approaching* and *leaving* by mothers and daughters across a 1m boundary between the two.

2) Measures of Bond-Longevity:

Bond-longevity is measured during two periods in daughters' second year: a) In months 15-16, dyads are evaluated in terms of the percent of days when mother and daughter are present in the same group (% M present), and the percent of scans at 2.5-minute intervals when mother and daughter are within 10m (%10). b) At 1.5 years of age, a combination of the above two measures was used (see chapter 2): the percent of days when mother and daughter are in the same groups and within 10m of each other during the first five minutes after identification (% with M).

Changes in measures of spatial relations were compared with scores on measures of bond-longevity in Spearman-rank correlation tests. Sample size is eight for all tests; all tests are two-tailed. Correlation coeficients are shown in the text with asterisks to indicate the level of significance (*= .05, **= .01; ***= .001).

RESULTS

CHANGES IN SPATIAL RELATIONS FROM PRE-WEANING TO POST-CALVING

Figures 27-30 show changes in four measures of spatial relations: the difference between months 1-5 and months 15-16 in the percent of scans when daughters walk away and when mothers walk away, and the relative frequencies of daughters' approaching and leaving. For all dyads, the primary change in spatial relations between the pre-weaning and post-calving periods is increased filial independence and increased maternal efforts at proximity-maintenance. Daughters spend increasing proportions of time walking away from mothers (Figure 27), while mothers spend decreasing amounts of time walking away from daughters (Figure 28). Similarly, the percent of approaching for which daughters are responsible decreases (Figure 29), while the percent of leaving increases (Figure 30). The changes illustrated by these graphs indicate that, after weaning, the responsibility for maintaining proximity shifts away from the daughter and toward the mother.

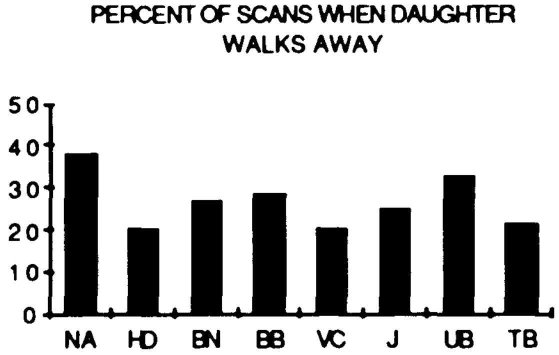

PERCENT OF SCANS WHEN DAUGHTER WALKS AWAY

Figure 27: Changes (months 1-5 subtracted from months 15-16) in the percent of scans when daughters walk away from mothers (i.e., *leading + not leading*). Abbreviations of the names of daughters are shown along the abscissa.

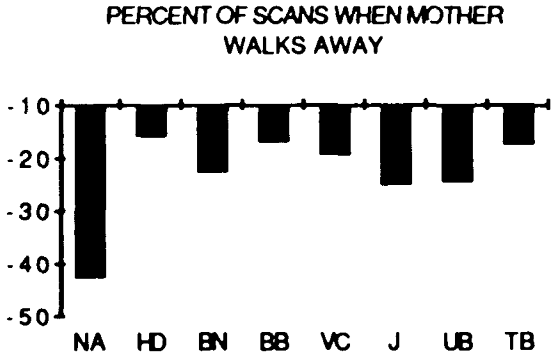

PERCENT OF SCANS WHEN MOTHER WALKS AWAY

Figure 28: Changes in the percent of scans when mothers walk away from daughters (i.e., *following + not following*).

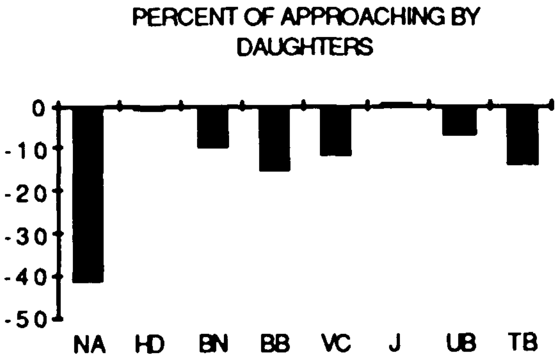

PERCENT OF APPROACHING BY DAUGHTERS

Figure 29: Changes in the percent of all approaches between mother and daughter (across a 1m boundary) for which daughters are responible.

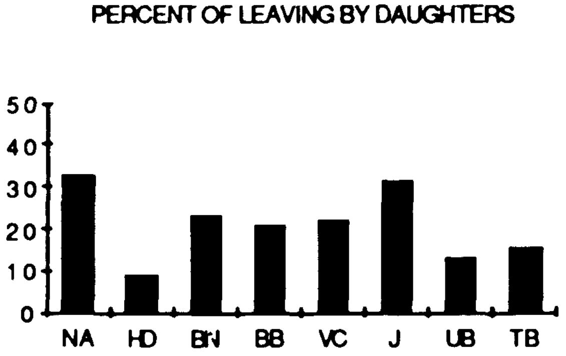


Figure 30: Changes in the percent of all leaving between mother and daughter for which daughters are responsible.

COMPARISONS OF CHANGES IN SPATIAL RELATIONS WITH BOND-LONGEVITY

Results of correlations between changes in contact-maintenance and measures of bond-longevity show that long-lasting mother-daughter bonds are related primarily to increases in maternal efforts at maintenance of proximity. Measures of bond-longevity show close positive correlation with increases in the proportion of time when mothers follow daughters' movements (leading). Correlation coefficients for *leading* versus *% M present* and *%10*, respectively, are: $r_s = .91^{**}$ and $.93^{***}$. Since *leading* either increases or stays the same for all dyads, this finding indicates that the greater the (positive) increase, the longer bonds with mothers persist. Conversely, increased proportions of time when daughters walk away and mothers do not follow (*not leading*) are negatively correlated with all three measures of bond-longevity. All dyads show an increase in this measure; those with the greatest increases associate least often in the second year. Correlation coefficients for *% M present, % 10,* and *% with M*, respectively, are: $r_s = -.88^{**}$, $-.88^{**}$, and $-.74^{*}$.

Change in the proportion of time when daughters follow mothers' movements is positively correlated with one measure of bond-longevity, *% M present* ($r_s = .76^{*}$). Since all daughters spent decreasing proportion of time following, the smaller the (negative) change, the longer bonds last. Changes in time when daughters do not follow mothers' movements are not significantly related to bond-longevity, nor are changes in the absolute and relative frequency of mothers' and daughters' approaching and leaving.

The most conspicuous change in orientation between mothers and daughters from months 1-5 to 15-16 is that the proportion of time when daughters walk away from mothers increases (Figure 26), while the time when mothers walk away decreases (Figure 27). The former is more closely correlated with bond-longevity. Within this category, however, the two alternate types of orientation (*leading, not leading*; i.e., the mother follows, the mother does not follow) are related in opposite ways to bond-longevity: increases in *not leading* (mother does not follow) are negatively associated with bond-longevity, while increases in *leading* (mother follows) are positively correlated.

DISCUSSION

These results indicate that bison mothers contribute significantly to long-term maintenance of bonds with yearling daughters, even after the birth of their next calves. Moreover, their efforts appear largely to determine whether or not associations continue. The duration of mother-daughter relations is correlated primarily with increasing maternal contact-maintenance at a time when daughters are increasingly independent. While daughters may also expend energy in leading their mothers, e.g., by monitoring their behavior, the frequency with which mothers follow their daughters' movements appears to be the primary mechanism in long-term contact maintenance.

From months 1-5 to months 15-16, daughters spend increasing amounts of time walking away from mothers, while mothers spend decreasing amounts of time walking away from daughters; daughters are responsible for increased proportions of leaving and decreased proportions of approaching. These changes do not simply reflect changes in nursing status. While relative frequencies of approaching and leaving may be affected by the absence of nursing in months 15-16, *following/not following* are not. The latter measures are recorded in continuous scans during movements, when subjects are grazing or walking (chapter 2), and therefore are not likely to reflect nursing-related spatial transitions.

Various advantages to offspring of prolonged association with mothers have previously been described. For example, Altmann (1963) states that the winter survival of moose calves depends upon post-weaning maternal guidance. In bison, associations last longer for young mothers and their daughters than for older mothers (chapter 11); this difference exists in red deer as well (Clutton-Brock et al. 1982). Daughters of young cows may derive particular benefit from long-term association with mothers. They may need to compensate for physical disadvantages early in life. For example, young mothers spend less time nursing their calves and probably produce less milk (chapter 4). Their daughters may increase their post-weaning growth rates by associating more closely with their mothers, as suggested by the findings of Clutton-Brock et al. (1982; see above).

That bison mothers make the major contribution to maintaining proximity with their weaned daughters suggests that mothers benefit directly from the associations. The question of maternal benefit from long-term relations with offspring has received little attention. In bison, young mothers may be more likely to benefit than older mothers. Young cows, like their offspring, might compensate for deficiencies, such as their social positions within the herd, by continuing to associate with daughters. Since young cows are generally subordinate to older cows (Rutberg 1983; chapter 13), the proximity of grown or juvenile daughters may aid in dominance interactions. Moreover, young cows appear to be less likely to lead other herd members than do older cows (McHugh 1958). This suggests that they must expend more energy in staying with the herd and, therefore, avoiding predation. The presence of loyal followers could reduce the amount of vigilance necessary to stay with the herd and to spot predators. Since the former have more enduring bonds with daughters (chapter 11), the results described here suggest that young mothers benefit more than older mothers from long-term relations with daughters.

PART IV: VARIATION AMONG DYADS

Chapter 9

PATTERNS OF VARIATION IN MOTHER-DAUGHTER RELATIONS

INTRODUCTION

Interindividual variation in animal behavior is often regarded as an impediment to research, particularly in field studies. Under field conditions it is rarely possible to control for variation such as the experience of the subjects. However, as Slater (1981) points out, even when tight control is possible, so as virtually to eliminate individual differences, the results may be applicable only to one genetic strain or microenvironment. This point helps to underscore the fact that individual variation is an integral part of the behavior of natural populations and is therefore an important area of study in itself.

The developmental environment has profound effects on individual social behavior, as demonstrated by social deprivation and foster rearing experiments such as those of Harlow and Harlow (1965) and Gilbert (1974). By rearing subjects under social conditions that differ grossly from normal, these experiments produce individuals whose social behavior is beyond the range of normal interindividual variation. Thus extreme variations in social behavior can result from extreme modifications of the early social environment.

Studies of naturally-occurring individual variation, such as J. Altmann's (1978, 1980) observations of free-ranging yellow baboons, reveal that even subtle differences in early social experience are linked to observable differences in social behavior. Altmann showed that socially high-ranking mothers behave in a more tolerant manner toward their infants, while low-ranking mothers more frequently restrict their infants' movements. Infants of dominant females subsequently spend more time away from their mothers during the first six months and achieve spatial independence at an earlier age.

Differences among relationships present a particularly complex problem. Relationships consist of repeated interactions over time; thus, each interaction may affect subsequent ones (Hinde

1983). Variations in mother-offspring relationships may result from behavioral adjustments between members of the dyad (Meier 1984). If the behavior of one differs from the norm, particularly in a way that could threaten the relationship, the other might be expected to change its behavior in some compensatory way. Thus individual infants may adjust to unusual aspects of their early social environments (e.g., normal variation in maternal behavior) by performing certain behaviors at an unusual frequency. For example, Meier (1984) describes ways in which rhesus infants compensate for the behavioral deficiencies of their isolate-reared mothers. Such mothers frequently perform behaviors such as rocking, tumbling, pacing, and self-biting which could interfere with the formation of bonds with neonates. The activity and vocalizations of vaginally-born infants reduce the frequencies of these activities; in contrast, the depressed behavior of surgically-delivered infants does not. Similarly, mothers may compensate for infant incapacitation (Rumbaugh 1965, on squirrel monkeys).

Relationships may also differ as a result of variation in the larger social environment. Wolfheim et al. (1970) showed that the relations of solitary mother-infant pigtail macaque dyads differed from those within a social group. Solitary dyads spent less time close together; such mothers also showed more aggression toward their infants.

Analysis of variation in interaction patterns may identify behavioral polymorphisms related to bond-stability. For example, Bekoff (1974, 1977; see also Fox 1972) found that dominant coyote pups are least successful in soliciting play with littermates. He suggests that these pups consequently do not form strong social bonds and are most likely to disperse. Similarly, Armitage (1982, 1986; see also Svendsen and Armitage 1973, Nowicki and Armitage 1979) compared individual differences in the social behavior of yellow-bellied marmots with their dispersal patterns. Through factor analysis, they identified several classes of individuals, based on differences in their responses to a mirror image. These classes (e.g., 'sociability', 'avoidance') were related to subjects' tendencies to form groups or live as isolates under natural conditions.

Bison provide an excellent opportunity to examine relationships between early and long-term variation in interactions between mothers and offspring. Several aspects of individual variation in bison mother-daughter relations have been described (chapters 4-7, 9-15). For example, individual relationships vary in duration. Most bonds persist into the third year; a few dyads, however, end their associations at weaning (chapter 7). Proximate mechanisms contributing to bond-longevity might be identified within patterns of individual variation in early mother-daughter relations. It may be that individual dyads vary in consistent ways across many aspects of their interactions, so that certain categories of relationships can be identified, some of which last longer than others. Thus the members of some dyads may be more likely to form long-term bonds with others.

One variable which may affect the closeness or longevity of mother-daughter bonds is the frequency of early maternal aggression. In the present study, mothers rarely threatened, kicked, or butted their calves during the first three weeks postpartum. Such acts stand out conspicuously from the usually tolerant early maternal behavior. Only six out of 13 mothers were ever seen acting aggressively toward calves during this period. For five of the six, rates of aggressive acts during the first three weeks were low, ranging from .05 to 0.33 acts per bout; moreover, these cows used only threats (head and foot movements), never touching the calf. The sixth cow (NE), however, not only showed more aggression than the others (0.9 acts per bout) during the first three weeks, but also kicked and butted the calf on several occasions. The disparity in this behavior evokes the question of what effect, if any, such early interactions may have on long-term mother-daughter relations. One hypothsis is that such aggression disrupts the bond between mother and calf, resulting in an early end to the relationship. Alternatively, it might increase the calf's dependence on the mother, as has been reported for macaque infants (Kaufman and Rosenblum 1969).

In this chapter, patterns of variation in mother-daughter interactions are examined. The first section addresses the question: Can categories of relationships be identified? The second considers the question: What aspects of pre-weaning mother-daughter relations are correlated with bond-longevity?

METHODS

MEASURES OF MOTHER-DAUGHTER RELATIONS

Pre-Weaning Relations: Measures of pre-weaning mother-daughter interactions were examined in an effort to identify categories of relationships and to compare variation in early interactions with that in bond-longevity. Data collected in focal-animal samples were pooled for each dyad over the first five months of calves' lives. Most measures changed relatively little during this period (chapter 3). Pooling resulted in extensive individual records, based on 66-104 hours of observation per individual. Data collected after month 5 were omitted because of differences in the reproductive condition of mothers.

Measures of pre-weaning relations (see chapter 2 for details) include:

nursing time (minutes/hour)
frequency of maternal aggression per nursing bout
% scans (at 2.5-minute intervals) when both calves and mothers graze
% scans when mothers graze and calves rest
% scans when calves graze and mothers rest
% scans when mother and calf are within 10m
% scans when calves follow mothers' movements
% scans when calves do not follow mothers' movements
% scans when mothers follow calves' movements
% scans when mothers do not follow calves' movements
frequency/h of mother's approaching calves
frequency/h of mother's leaving calves
frequency/h of calves' leaving mothers
frequency/h of mother's vocalizations toward calves
frequency/h of calves' vocalizations toward mothers
frequency/h of calf-initiated contact with mothers

In addition, so as to consider the effects of very early maternal aggression on the longevity of associations with daughters, the frequency of maternal aggression per nursing bout during the first three weeks of calves' lives was included in the data set for the second principal component analysis (see below).

Bond-Longevity: After daughters are weaned, they are not always in the same groups with their mothers. The most basic measure of their post-weaning relations with mothers is whether or not they are in the same group. When this is the case, measures of their early spatial relations can be applied; in particular, proximity was determined. Thus bond-longevity was measured as: a) the percent of days on which the mother was present in the same group (*percent mother present*), and b) the percent of scans (at 2.5-minute intervals) in which mother and daughter were within 10m. These data were collected during two periods in the daughters' second year: months 15 and 16, and at 1.5 years.

Months 15 and 16 represent an important period in long-term mother-daughter relations, since it follows the birth of the mother's new calf. By this time, most yearling daughters have resumed spatial relations with their mothers (see chapter 7). This period also precedes the mother's next tending during the rut, so that there is no interference from bulls.

In order to determine whether mothers and daughters were still together after about 1.5 years, a combination of the above two measures was used. This new measure was used since observations were limited to a period when all cows and juveniles were usually in the same herd, so that *percent mother present* was insufficent. At that time, I recorded the percentage of days on which daughters were in the same groups with their mothers and within 10m of them during the first 5 minutes after identification (*% with mother*).

DATA ANALYSIS

In order to answer the questions listed above, two analytic techniques were used: principal component analysis (PCA) and correlation coefficients. The first of the three questions above was examined through PCA (section I), the second through PCA and correlations (section II).

PCA: Principal component analysis was used to identify behavioral continua along which to characterize dyads in terms of multiple variables, thus describing categories of relationships. PCA yields a new set of orthogonal variables from the original set; each is an axis which accounts for the maximal variation among individuals in the original data. Each dyad is ranked along each axis (for example, see Figure 25). While there are as many principal components as original variables, the first few generally account for most of the variance (Frey and Pimental 1978; Neff and Marcus 1980). The SAS procedure PRINCOMP (SAS Institute 1985a, b) was used for this analysis.

The first PCA (section I: Pre-Weaning Relations) included the 16 behavioral measures listed above, representing mother-daughter relations during months 1-5. In order to consider the relative importani of non-behavioral measures in patterns of variation in early interactions, maternal age and the week of calves' birth were also included in the data set. Calculations of the last two measures are described in chapters 2 and 12.

In the second PCA (section II: Pre-Weaning Relations and Bond-Longevity), the three measures of bond-longevity were added to measures of pre-weaning relations (i.e., the same 16 behavioral variables for months 1-5 plus maternal age and birth week) and the frequency of maternal aggression per nursing bout in weeks 1-3. The purpose here was to determine whether patterns of variation in bond-longevity are similar to those in pre-weaning relations.

Correlations: In section II, measures of pre-weaning and long-term mother-daughter relations were also tested for correlations. This facilitated interpretation of PCA results by identifying the aspects of the early relationship most closely related to the duration of the bond. Both Pearson product-moment and Spearman rank correlation coefficients were calculated, depending on whether or not variates were normally distributed. The former test was employed for arcsine transformations of percentages, while the latter was generally used for behavioral rates. All tests are two-tailed. The SAS procedure CORR (SAS Institute 1985a, b) was used for these analyses.

SAMPLE SIZE

Comparisons of pre-weaning measures are based on 13 mother-daughter dyads. Since maternal reproductive condition during the year after a daughter's birth affects long-term relations (chapters 6 and 7), tests involving bond-longevity are based on the eight dyads in which mothers had new calves.

RESULTS

I. PATTERNS OF VARIATION IN PRE-WEANING MOTHER-DAUGHTER RELATIONS

Results of the first principal component analysis describe patterns of variation in pre-weaning mother-daughter relations. The first seven components in this analysis together account for 95% of the total variance. While interpretations of the first two are unambiguous, components 3-7 have no clear behavioral meaning. Therefore, only the first two components, accounting for 58% of the variance, are described here. The measures most strongly weighted on each component describe a continuum of qualities of mother-calf interactions. Positive and negative weightings describe opposite extremes of the vector.

FIRST PRINCIPAL COMPONENT: FILIAL/MATERNAL INDEPENDENCE

The first principal component accounts for 35% of the variance. This axis is primarily a measure of filial and maternal independence. The positive end reflects calves who frequently walk away from their mothers; the latter may or may not follow their calves' movements. These calves control spatial relations in the dyad to a large extent; they also spend much of their time at a distance from their mothers.

The negative end of the axis represents mothers who walk away frequently and whose calves tend to follow their movements. Such dyads spend more time close to each other as a result of the calves' efforts at maintaining proximity. Here, the relationship is largely controlled by the mother.

Secondarily, this axis describes maternal nursing tolerance and intolerance. Independent calves have relatively tolerant mothers, while independent mothers tend to be intolerant. Maternal age also plays a role on this continuum: more independent calves have older, more tolerant mothers. In contrast, young mothers are more independent. The 10 dominant measures on the first principal component, i.e., those with the highest loadings, are listed in Table 5.

TABLE 5

PRE-WEANING MOTHER-DAUGHTER RELATIONS

DOMINANT MEASURES ON THE FIRST PRINCIPAL COMPONENT:

Filial/Maternal Independence

	MEASURE	LOADING
POSITIVE:	% scans when calves walk away and mothers do not follow	0.36
	% scans when calves walk away and mothers follow	0.29
	Frequency/h of calves' leaving mothers	0.25
	Frequency/h of calves' vocalizations	0.24
	Nursing time (minutes/hour)	0.22
	Maternal age	0.22
NEGATIVE:	% scans when mothers walk away and calves follow	-0.37
	% scans when mother and calf are within 10m	-0.32
	Frequency/h of mother's leaving calves	-0.30
	Frequency of maternal aggression per nursing bout	-0.24

SECOND PRINCIPAL COMPONENT: SYNCHRONY BETWEEN MOTHERS AND DAUGHTERS

The second principal component, which accounts for 23% of the variance, essentially measures synchrony of activity and movements between mothers and calves. The positive end reflects calves who frequently graze with their mothers, while the negative end represents calves who tend to rest while mothers graze. The positive end reflects later-born calves and relatively close, coordinated relations in which calves often initiate movements; their mothers are responsive and follow their initiatives. Such calves are relatively active and seem to work together with their mothers in determining movements.

TABLE 6

PRE-WEANING MOTHER-DAUGHTER RELATIONS:

DOMINANT MEASURES ON THE SECOND PRINCIPAL COMPONENT:

Behavioral Synchrony between Mothers and Calves

	MEASURE	LOADING
POSITIVE:	Calves' time of birth	0.37
	% scans when calves walk away and mothers follow	0.33
	% scans when both calves and mothers graze	0.31
	Frequency/h of calves' leaving mothers	0.29
	% scans when mother and calf are within 10m	0.28
NEGATIVE:	% scans when mothers walk away and calves do not follow	-0.43
	Frequency/h of mother's vocalizations	-0.30
	% scans when mothers graze and calves rest	-0.29

The negative end of the axis reflects earlier-born calves with looser, less coordinated associations with their mothers. Such calves appear rather 'lazy', spending less time following their mothers' movements and grazing with their mothers. Correspondingly, their mothers call to them more frequently. Dominant measures and their loadings on the second component are listed in Table 6.

It is interesting to note that on this axis proximity is at the same end as calves' leaving and leading their mothers. As shown in chapter 10, proximity is correlated with calves' efforts at spatial relations but not with those of mothers. The fact that the percent of time mothers and calves spend within 10m is at the positive end suggests that, in the type of relationship described by the positive end of this axis, both mother and calf maintain proximity.

INDIVIDUAL RANKINGS

In Figure 31, scores for each dyad on the first and second principal components are plotted. Relative positions of individuals along the first component (represented by the abscissa) indicate that subjects form three groups. This suggests that three distinct categories of mother-daughter relations exist, as described by this axis. In the most positive group (LA, CL, TB, and HD), calves are more independent than others, while mothers are more tolerant. Three of the four mothers are also older (i.e., 8, 17, and 18 years old). In the most negative group (RB, BN, and BB), mothers are unusually independent and intolerant; calves maintain close proximity. All three of these mothers are young (i.e., 3-4 years old). The relations of dyads in the middle are intermediate in these respects.

Along the second principal component (represented by the ordinate), some grouping of subjects occurs, particularly RB, LA, and CL (late-born calves) on one end and CS (early-born) at the other. However, clustering is less distinct on this axis.

Categories of Mother-Daughter Relationships

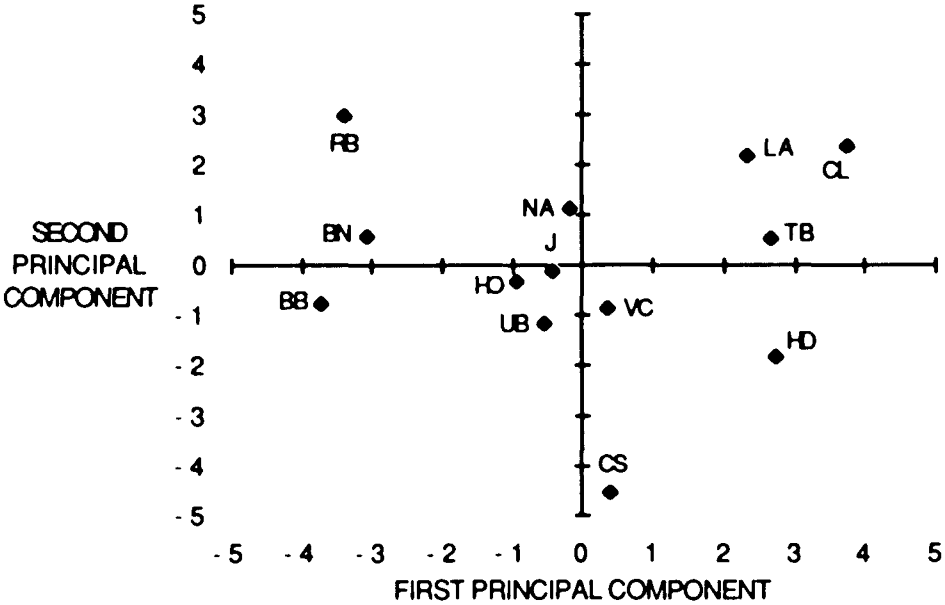


Figure 31: Scores of dyads (indicated by abbreviated names of daughters) are plotted for the first versus the second principal components. Each component describes a continuum of relationships based on 16 measures of pre-weaning interactions; individual scores indicate the position of each dyad along that continuum. Relative positions of dyads along the first principal component (abscissa) indicate that individual dyads form three groups. Dyads in the group on the right have positive scores; those on the left, negative scores. The qualities associated with this component are described in the text.

II. EARLY MOTHER-DAUGHTER RELATIONS AND BOND-LONGEVITY

In this section, variation in pre-weaning mother-daughter relations is compared with that of bond-longevity. The following question is addressed: a) Are certain types of mother-daughter relationships more enduring than others? and b) What aspects of early relations are related to bond-longevity? The first question is addressed through principal component analysis; the second through correlations, as described above.

Principal Component Analysis

The first two principal components from this analysis, accounting for 61% of the total variance, are compared with those of the first analysis.

FIRST PRINCIPAL COMPONENT

Like the first axis of the previous analysis, this component reflects filial and maternal independence. One measure of bond-longevity is included with this set: proximity of mother and daughter in months 15-16. This suggests that independent, intolerant mothers and dependent calves have the most persistent relationships. Dominant measures and their loadings on this axis are listed in Table 7.

This component is nearly identical to the first axis in the analysis of pre-weaning relations alone. The only difference in month 1-5 measures is that 'not following' is included here (at the positive end), but not in the previous analysis. The similarity between this component and that of the previous analysis, in spite of the differences in data sets, reinforces the possibility that this continuum points to basic differences in the way the social unit operates.

TABLE 7

EARLY AND LONG-TERM MOTHER-DAUGHTER RELATIONS:

DOMINANT MEASURES ON THE FIRST PRINCIPAL COMPONENT

	MEASURE	LOADING
POSITIVE:		
months 1-5:	% scans when calf walks away & mother follows	0.32
	% scans when calf walks away & mother does not follow	0.27
	% scans when mother walks away & calf does not follow	0.27
	Nursing time (minutes/hour)	0.25
NEGATIVE:		
months 1-5:	% scans when mother walks away & calf follows	-0.32
	% scans within 10m of mother	-0.32
	Frequency of maternal aggression per nursing bout	-0.29
	Frequency of leaving by mother	-0.26
months 15-16:	% scans within 10m of mother	-0.26

SECOND PRINCIPAL COMPONENT

The second axis is dominated by new measures (i.e., those used only in the second analysis) to the extent that it bears little resemblance to its counterpart in the first analysis. On this axis, bond-longevity is negatively associated with early maternal aggression, maternal age and nursing time. Mother-daughter relationships are shorter where mothers are older, act aggressively toward calves early in the relationship, and spend much of their time nursing. Conversely, bonds last longer where the activities of mothers and daughters are often asynchronous (i.e., when one member of the pair rests and the other grazes) and the calves frequently initiate interactions (vocalizations and contact) with mothers. Dominant measures and their loadings are listed in Table 8.

TABLE 8

EARLY AND LONG-TERM MOTHER-DAUGHTER RELATIONS:

DOMINANT MEASURES ON THE SECOND PRINCIPAL COMPONENT

		MEASURE	LOADING
POSITIVE:	months 1-5:	% scans when calf grazes and mother rests	0.31
		Frequency of calf's initiating contact with mother	0.31
		% scans when mother grazes and calf rests	0.27
		Frequency of calf's vocalization	0.26
	months 15-16:	% days mother present	0.39
		% scans within 10m of mother	0.26
	1.5 years	% days with mother	0.31
NEGATIVE:	weeks 1-3:	Frequency of maternal aggression per nursing bout	-0.40
	months 1-5:	Minutes/hour spent nursing	-0.25
		Maternal Age	-0.25

Correlations

The three variables which measure the longevity of the mother-daughter bond, as listed above, are: percent of days mother present and percent of time within 10m in months 15-16, and percent of days with the mother at 1.5 years. Measures of mother-daughter relations during the pre-weaning period which are correlated with one or more of these measures are listed in Table 9, with correlation coefficients and associated probabilities. The type of correlation coefficient employed (Pearson or Spearman) is also indicated.

TABLE 9

EARLY CORRELATES OF BOND-LONGEVITY

	<u>MEASURE</u>	*r*	*p*	<u>Test</u>
	POSITIVE:			
months 1-5:	% nursing-bout interruptions caused by mothers	.74	.036	P
	Frequency of calves' approaching mothers at 10m	.71	.050	S
	% calf-grazing/mother-resting time within 10m	.71	.050	P
	Frequency of maternal aggression per nursing bout	.69	.057	S
	NEGATIVE:			
months 1-5:	% scans when calves walk away and mothers follow	-.76	.028	P
	Nursing time (minutes/hour)	-.77	.027	S
weeks 1-3:	Frequency of maternal aggression per nursing bout	-.90	.002	S

P = Pearson product-moment correlation coefficient

S = Spearman rank correlation coefficient

PERSISTENT BONDS: Patterns of early interactions correlated with bond-longevity are similar to those suggested by the first principal component. Daughters who associate longest with their mothers are those whose mothers spend the least amount of time nursing and are relatively aggressive toward calves during the first five months. On the other hand, these cows show the least aggression during the first three weeks (Figure 32). Such mothers are restless during nursing bouts, causing most of the bout interruptions. These calves rarely lead movements (i.e., they rarely walk away and/or, when they do, their mothers rarely follow). They approach their mothers often and spend the most time near their mothers during the type of activity in which distance to the mother is exclusively controlled by the calf (i.e., calf grazing/mother resting).

Maternal Aggression during the First Three Weeks vs. the Longevity of the Mother-Daughter Bond

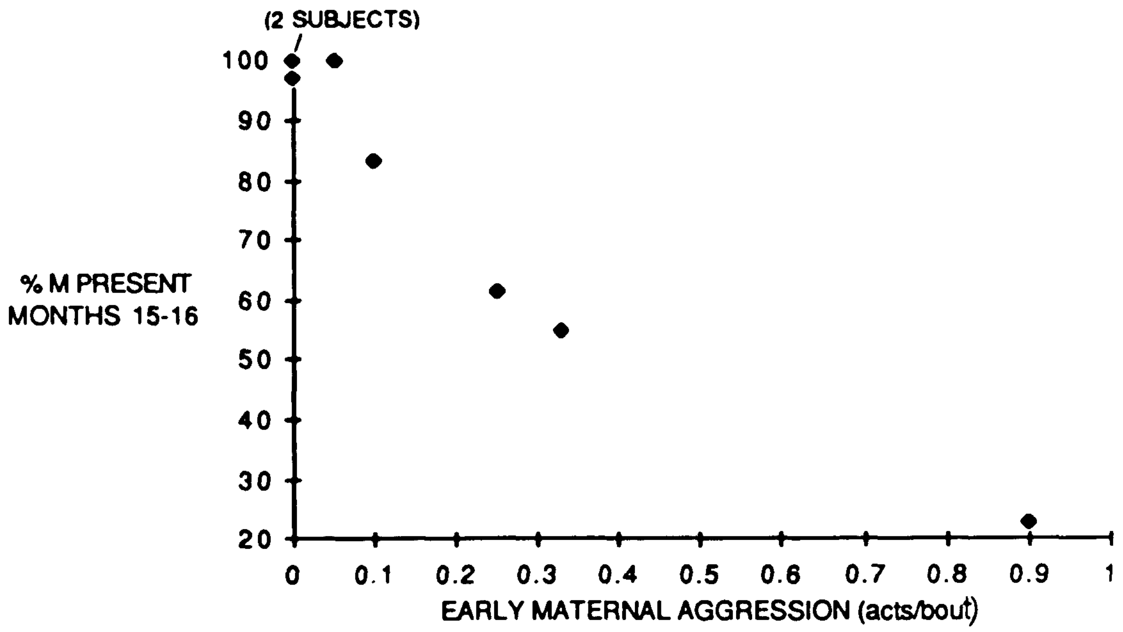


Figure 32: The frequency of mothers' aggressive acts per nursing bout during the first three weeks of calves' lives, as compared with the percent of days on which mothers and daughters were present in the same groups in months 15 and 16. Data shown are for eight dyads in which the mother had a new calf at the time of the latter measurement.

SHORT-LIVED BONDS: Daughters that have the shortest bonds with mothers spend the most time nursing during the pre-weaning period; their mothers' nursing tolerance is also reflected in that they interrupt nursing bouts less often than do their calves. Their mothers show relatively little aggression during the first five months; however, they are unusually aggressive during the first three weeks (Figure 32). These daughters are relatively independent, often leading and rarely approaching their mothers. They spend the least time near their mothers when distance is under their control (i.e., while they graze and mothers rest).

DISCUSSION

These results demonstrate that bison mother-daughter relationships are polymorphic, and that certain classes of associations last longer than others. Predominant classes are characterized by spatial independence shown by mothers and daughters, and by maternal nursing tolerance. In one type of dyad, mothers frequently walk away from their their calves, who follow them closely. Such mothers show little or no aggression toward their calves in the first three weeks, but frequently threaten, kick, and butt them during the rest of the pre-weaning period. These relationships tend to persist longer than others. In contrast, daughters develop independence earlier when mothers provide extensive, uninterrupted nursing time and are most likely to follow calves' movements. Maternal age appears to be an important variable in interactions; young mothers are generally represented by the first type of relationship, associating longer with daughters than older mothers (see chapter 11).

Relationships differ among dyads in consistent patterns across many behavioral variables. This polymorphism suggests that dyads adopt different patterns of mother-offspring interaction. For example, the results suggest that some dyads need a longer, more intensive period of association than others. Daughters who are less independent early in life associate longer with their mothers.

The longevity of mother-daughter bonds appears to be related to the question of who controls early interactions. Where the bond persists, relationships are controlled primarily by mothers. Conversely, daughters who exert most control have the shortest bonds with mothers. Control by mothers is indicated by such measures as the frequency of maternal aggression, percent of bout-interruptions by mothers, calves' following mothers, and mothers' leaving. Control by calves is reflected in the percent of time spent walking away from mothers (particularly when the mother follows) and the percent of bout-interruptions by calves.

The results of principal component analysis differ from those of correlation coefficients in a few respects. PCA suggests that bond-longevity is related to maternal as well as filial dependence; however, only the latter is actually correlated with bond-longevity. Moreover, the second principal component suggests that calves who frequently take initiative in interactions with mothers associate longer with mothers, but this is not born out by correlations. Despite the differences, however, the pictures which emerge from the two analyses are very similar. This fact further strengthens the possibility that the patterns described reflect basic variables in bison mother-daughter relations.

Chapter 10

FILIAL INDEPENDENCE AND RELATED MATERNAL QUALITIES

INTRODUCTION

Many studies refer to the 'development of independence' as if independence were the goal of development or the inevitable outcome of the parent-offspring relationship. In some ways this must be true, particularly with respect to nutritional independence. However, the extent to which development gives rise to social independence varies among species, populations, and individuals. In relatively solitary species, the mother-young bond ends completely; where adults are more gregarious, however, offspring may continue to associate with mothers while becoming integrated into the social group. For example, M. Altmann (1963) contrasts the abrupt and permanent end of the mother-calf relationship in the solitary moose with the gradually changing mother-offspring bond in the gregarious elk. Even where differences in social stucture are more subtle, developing animals may vary in degree of independence from their mothers. For example, mother-infant interactions have been compared in relation to the contrasting social structures of two closely related primate species, bonnet and pigtail macaques (Rosenblum and Kaufman 1967; Kaufman and Rosenblum 1969; Rosenblum and Alpert 1977). Members of bonnet macaque groups spend much of their time in close contact; in the pigtail macaque, group members are generally dispersed. The bonnet social system is less hierarchical, more placid, and based more on individual initiative than predefined roles. Bonnet mothers restrain, retrieve, and punish their infants less often. Correspondingly, bonnet infants show more spatial independence and take more initiative in interactions with mothers than do pigtail infants.

Within a species, individual offspring may become spatially independent of their mothers at different rates and/or to a different extent due to variation in the early environment. For example, Jensen et al. (1967) found that the timing of independence varies with the quality of the environment. Pigtail macaque mother-infant dyads housed alone in 'privation' environments spend more time close together than do those in complex settings; the latter direct more of their behavior toward the surroundings. Naturally-occurring variations in mother-young relationships and corresponding contrasts in infant independence are described by J. Altmann (1978, 1980; see also White and Hinde 1975; French 1981). She found that socially high-ranking yellow baboon mothers behave in a more tolerant, unrestrictive manner toward their infants, while low-ranking mothers frequently restrict their infants' movements. Infants of dominant females subsequently spend more time away from their mothers during the first six months and achieve independence at an earlier age.

Few studies examine the relative contributions of mother and offspring to individual variation in dyadic interactions. One exception is Hinde and Spencer-Booth (1967a, 1971), who examined correlations among measures of rhesus mother-infant spatial relations and contact interactions. The results provided a detailed description of patterns of individual variation, clarifying the roles of mothers and infants. They found that differences among mothers accounted for most variation in early interactions, while those among infants became increasingly prevalent with age. Their findings suggest ways in which mothers and offspring influence each others' behavior. For example, infants who were rejected more took more responsibility for maintenance of proximity with their mothers.

Meier (1984) considers mutual adjustments between mother and young in greater detail. He describes development as a 'dialog' between mother and offspring, in which each compensates for the other's deficiencies. As a result, species-specific developmental goals are achieved in spite of substantial individual variation, in the sense of von Bertalanffy's (1968) 'equifinality'. For example, Meier (1984) describes ways in which rhesus infants compensate for the behavioral deficiencies of their isolate-reared mothers. Such mothers frequently perform behaviors such as rocking, tumbling, pacing and self-biting which could interfere with the formation of bonds with neonates. The activity and vocalizations of vaginally-born infants reduce the frequencies of these activities; in contrast, the depressed behavior of surgically-delivered infants does not. Similarly, when squirrel monkey infants are incapacitated, their mothers alter their behavior in order to compensate for the infant's inability to hold on and to move into a suckling position (Rumbaugh 1965).

The findings described above suggest that development of independence is affected by behavioral differences among mothers. Maternal behavior may vary in relation to such factors as age, size, social status, and previous experience, thus creating different developmental microenvironments for offspring. Moreover, individual variation among mothers may be in part the product of behavioral differences between their infants. In a previous paper (chapter 9), individual differences in the spatial independence of bison calves and their mothers were found to account for much of the variation in mother-daughter relations. Moreover, calves who behaved most independently early in life had the shortest bonds with mothers. These results suggest that bison daughters differ widely in spatial independence in relation to the behavior of their mothers, and that early differences affect the longevity of the bond.

Among bison cows, various aspects of social behavior vary in relation to age. Rutberg (1983) demonstrated that dominance rank increases with age; older cows also appear more often to act as group leaders (McHugh 1958). Moreover, maternal behavior differs between old and young cows. Older mothers spend more time nursing their calves and allow them to end more bouts; young mothers reject more suckling attempts and interrupt more bouts (Green 1986, chapter 4). On the other hand, young cows initiate more contacts with their calves and form more enduring bonds with daughters (chapters 4, 11). In view of these age-related differences in the behavior of bison cows, one might expect calves of old and young cows to differ in the development of independence.

This chapter describes behavior associated with filial independence in bison calves and addresses the question: What maternal qualities tend to enhance the development of independence in bison calves? For example, based on the findings of Altmann (1978, 1980), calves may behave more independently when their mothers make little effort to maintain contact with them. The findings of Hinde and Spencer-Boothe (1967, 1971) suggest that filial independence may be greater where mothers infrequently reject their calves' suckling attempts.

METHODS

SUBJECTS

Thirteen mother-daughter dyads in a free-ranging herd at Wind Cave National Park were observed in 1983. The mothers ranged in age from 2 to 18 years. Only female calves were included in the sample so as to eliminate possible variation resulting from differences in offspring sex; such variation has been reported in many species (e.g., Duncan et al. 1984).

DEFINITIONS

Spatial Relations: Independent vs. Dependent Behavior

Measures of spatial relations between mothers and calves involve two types of movements: those that increase and those that decrease distance. Maternal and filial independence involve distance-increasing behaviors, while dependent behaviors are those that tend to decrease distances. In order to measure spatial relations, data were collected on three aspects of maternal and filial behavior:

1) approaching and leaving

2) following or not following each others' movements

3) activity patterns: filial independence is indicated by the frequency with which calves initiate grazing activity while their mothers continue to rest.

The first and second categories differ in that approaching and leaving quantify events and are defined by a specific boundary between mother and calf. In contrast, *following* and *not following* are behavioral states, recorded in scans at 2.5-minute intervals, which measure the orientation of mothers and calves in relation to each others' movements, regardless of their distance apart. The latter measures are particularly useful when the herd is grazing and/or walking. At such times, contact-maintenance frequently entails maintaining a certain distance rather than moving closer. The following categories are used to measure spatial relations between mothers and calves:

Filial Independence:

Calves walk away from mothers to 10m or more; mothers do or do not not follow (% of scans)

Calves leave mothers (i.e., move from <=1m to >1m; relative and absolute frequencies)

Calves graze while mothers rest (percent of scans)

Maternal Independence:

Mothers walk away from calves to 10m or more, while calves do or do not follow (% of scans)

Mothers leave calves (i.e., move from <=1m to >1m; relative and absolute frequencies)

Filial Dependence:

Calves approach mothers (i.e., move from >1m to <=1m; relative and absolute frequencies)

Calves follow when mothers move away to 10m or more (percent of scans)

Difference between the percent of all approaches between mother and calf for which calf is responsible and the percent of all leaving for which calf is responsible (%Ac-%Lc). This function, following Hinde and Atkinson (1970), measures the calf's contribution to maintenance of proximity, relative to that of the mother; higher values indicate greater efforts by calves.

Maternal Dependence:

Mothers approach calves (i.e., move from >1m to <=1m; relative and absolute frequencies)

Mothers follow when calves move away to 10m or more (percent of scans)

Nursing Interactions: Maternal Tolerance vs. Intolerance

Nursing interactions are controlled largely by mothers; therefore aspects of nursing considered here are limited to maternal behavior. Correlations among measures of nursing behavior (described in appendix B) show that these variables form two groups, or ends of a continuum, described by maternal tolerance and intolerance. Within each group, measures are positively correlated; between groups, measures are negatively correlated. Components of these two behavioral classes are listed below, with abbreviations used in Table 12:

Maternal Tolerance

Nursing time: mean bout duration/mean interbout interval (minutes/hour) (MIN/H)

Percent of bouts ended by calf (i.e., calf stops suckling voluntarily and moves away, while mother continues to stand quietly) (%CEN)

Frequency/nursing bout of calf's interruptions (pauses) while mother stands quietly (CPS)

Maternal Intolerance

Frequency of rejected suckling attempts per nursing minute (RSA)

Frequency of maternal aggression (e.g., horn threats, kicking) per nursing minute (MAR)

Percent of bout-interruptions caused by mothers (%MINT)

Contact and Vocalization

In addition to spatial and nursing interactions, mother-daughter relations involve non-nursing contact (nosing, rubbing, and licking) and vocalization by mothers and calves. Consideration of maternal and filial roles in initiating these interactions may complement information on spatial and nursing interactions. It seems likely that vocalization is related to spatial relations, since it provides a mechanism for maintaining contact from a distance. Contact interactions may be related to nursing, particularly those initiated by calves: calves appear to perform such behaviors in conjunction with suckling attempts. The function of contact initiated by mothers is unclear.

DATA COLLECTION AND ANALYSIS

Data were collected in focal-animal sampling, as described in chapter 2; measures of mother-daughter relations used here are also described. Where measures are based on scans (as noted below), values are calculated as the percent of scans at 2.5-minute intervals. All data were pooled for each dyad over the first five months of calves' lives.

Pearson product-moment correlation coefficients were calculated for arcsine transformations of all percentages. Spearman rank correlation coefficients were calculated for behavioral rates. All tests are two-tailed. The SAS procedure CORR was used for these analyses (SAS Institute, 1985a, b). All comparisons are based on a sample of 13 dyads.

RESULTS

Filial Independence: Associated Calf Behavior

CONTACT INTERACTIONS

Independent daughters frequently initiate contact with their mothers. As shown in Table 10, the frequency of calf-initiating contact is positively correlated with the relative and absolute frequencies with which calves leave their mothers ($p=.017$ and .016, respectively) and the percent of scans in which calves walk away ($p=.021$). Conversely, dependent daughters rarely initiate contact with mothers. This is underscored by the findings that the frequency of calf-initiating contact is negatively correlated with calves' efforts at maintenance of proximity (%Ac-%Lc: $p=.021$) and with the percent of scans in which calves follow mothers' movements ($p=.036$).

VOCALIZATION

Independent daughters vocalize frequently. Table 11 shows correlation coefficients for comparisons of spatial relations with the percent of vocalization performed by calves. These results indicate that calves who call more leave more (frequency of leaving: $p<.001$; percent of leaving: $p=.011$; percent of scans in which calves walk away: $p=.018$). They also spend more time grazing while their mothers rest (the only activity which reflects calf independence: $p=.029$). Dependent calves, who *infrequently leave their mothers and graze while their mothers rest,* correspondingly vocalize rarely. This is emphasized by the fact that the percent of vocalizations by calves is negatively correlated with calves' efforts at maintenance of proximity (%Ac-%Lc: $p=.012$).

Absolute frequencies of vocalization by calves are less closely related to spatial relations, possibly because of low frequencies and high variability (in a few dyads, calves were never heard vocalizing). However, the frequency of calves' calling is positively correlated with the frequency of calves' leaving ($r_S=.664$, $p=.013$), the percent of time spent grazing while mothers rest ($r_S=.643$, $p=.018$), and the frequency of mothers' approaches ($r_S=.617$, $p=.024$; see below).

TABLE 10
CALF-INITIATED CONTACT WITH MOTHERS VERSUS SPATIAL INDEPENDENCE

		Acts per hour:
Filial Independence:	Percent of leaving by calf	.650 *
	Frequency/hour of leaving by calf	.652 *
	Percent scans in which calf walks away	.771 **
Filial Dependence:	% approaching by calf - % leaving by calf (%Ac-%Lc)	-.630 *
	Percent scans in which calf follows mother	-.583 *

Table 10 shows Spearman rank correlation coefficients for comparisons of spatial relations with the frequency of contact interactions (e.g., nosing, rubbing) initiated by calves. Significance levels are indicated by * ($p<.05$), ** ($p<.01$), and *** ($p<.001$). All tests are two-tailed and based on a sample of 13 mother-daughter dyads. Data are pooled for each dyad over months 1 to 5.

TABLE 11
RELATIVE FREQUENCY OF VOCALIZATION BY MOTHER AND CALF AS COMPARED WITH SPATIAL INDEPENDENCE

		% Calling by Calf
Filial Independence:	Percent of leaving by calf	.740 **
	Frequency/hour of calf's leaving	.810 ***
	Percent scans in which calf walks away	.640 *
	Percent scans when calf grazes & mother rests	.600 *
Filial Dependence:	% approaching by calf - % leaving by calf (%Ac-%Lc)	-.674 *
Maternal Independence:	Frequency/hour of mother's leaving	-.600 *
Maternal Dependence:	Frequency/hour of mother's approaches	.620 *
	Percent scans in which mother follows calf	.670 *

Table 11 shows correlation coefficients for comparisons between measures of spatial relations and the percent of vocalization between mother and calf for which the calf was responsible
For behavioral rates and %Ac-%Lc, Spearman rank correlation coefficients are shown; for arcsine transformations of percentages, Pearson product-moment coefficients were calculated.
Significance levels are indicated by * ($P < .05$), ** ($P < .01$), and *** ($P < .001$).
All tests are two-tailed and based on a sample of 13 mother-daughter dyads.
Data are pooled for each dyad over the first five months of calves' lives.

PROXIMITY

Proximity between mothers and calves is determined largely by calves; the more dependently daughters behave, the more time they spend near their mothers. The percent of scans in which mothers and daughters are within 10m of each other is closely related to the percent of scans in which daughters follow their mothers' movements ($r=.914$, $p<.001$). The percent of time within 10m is also positively correlated with the percent of approaching by calves ($r=.616$, $p=.025$). The fact that these two measures are the only aspects of spatial relations significantly related to proximity emphasizes the role of the calf in maintaining close spatial relations with the mother.

Filial Independence: Associated Maternal Behavior

SPATIAL RELATIONS

Filial and maternal independence are negatively related. Table 12 shows correlation coefficients for comparisons of filial and maternal behavior. These results show that the more one member of the dyad acts independently of the other, the less does the other. Relative and absolute frequencies of leaving by mothers are negatively correlated with the percent of scans in which calves walk away ($p<.001$ for both tests). Similarly, the relative and absolute frequencies of leaving by calves are negatively correlated with the percent of scans in which mothers walk away ($p<.001$ for both tests; see Figure 33). Moreover, the time calves spend grazing while mothers rest is negatively correlated with the percent of leaving by mothers ($p=.025$).

The relationship between maternal and filial behavior is even more complex; as one member walks away more, the other not only walks away less but also approaches more. Filial independence is positively related to maternal dependence, and vice-versa. For example, Table 12 shows that the percent of approaches by mothers is positively correlated with the percent of scans in which calves walk away ($p=.007$), while the percent of approaches by calves is positively correlated with the percent of scans in which mothers walk away ($p=.007$).

TABLE 12
CORRELATIONS AMONG MEASURES OF SPATIAL RELATIONS: FILIAL VERSUS MATERNAL INDEPENDENCE AND DEPENDENCE

		Filial Independence:			
		Leaving by Calf		% scans	% scans
		Percent	Frequency	Calf walks away	C grazes/M rests
Maternal Independence:	Percent of leaving by mother	-	-	-.948***	-.614*
	Frequency of leaving by mother	-	-.662*	-.810***	-.343 ns
	% scans mother walks away	-.948***	-.836***	-	-.486 ns
Maternal Dependence:	Percent of approaching by mother	.757**	.749**	.710**	.229 ns
	Frequency of approaching by mother	.495 ns	.592*	.372 ns	.212 ns
	% scans mother follows calf	.915***	.723**	-	.388 ns

		Filial Dependence:		
		Approaching by Calf		
		Percent	Frequency	%Ac-%Lc
Maternal Independence:	Percent of leaving by mother	.757**	.623*	-
	Frequency of leaving by mother	.813***	.961***	.775**
	% scans mother walks away	.710**	.690**	.863***

Table 12 shows correlation coefficients for comparisons of independent measures reflecting filial independence and maternal independence or dependence (see text).

For comparisons involving behavioral rates and %Ac-%Lc, Spearman rank correlation coefficients are shown.

Those involving arcsine transformations of percentages employ Pearson product-moment correlation coeficients.

*, **, and *** indicate significance levels of .05, .01, and .001, respectively. All tests are two-tailed and based on a sample of 13 mother-daughter dyads. Data are pooled for each dyad over the first five months of calves' lives.

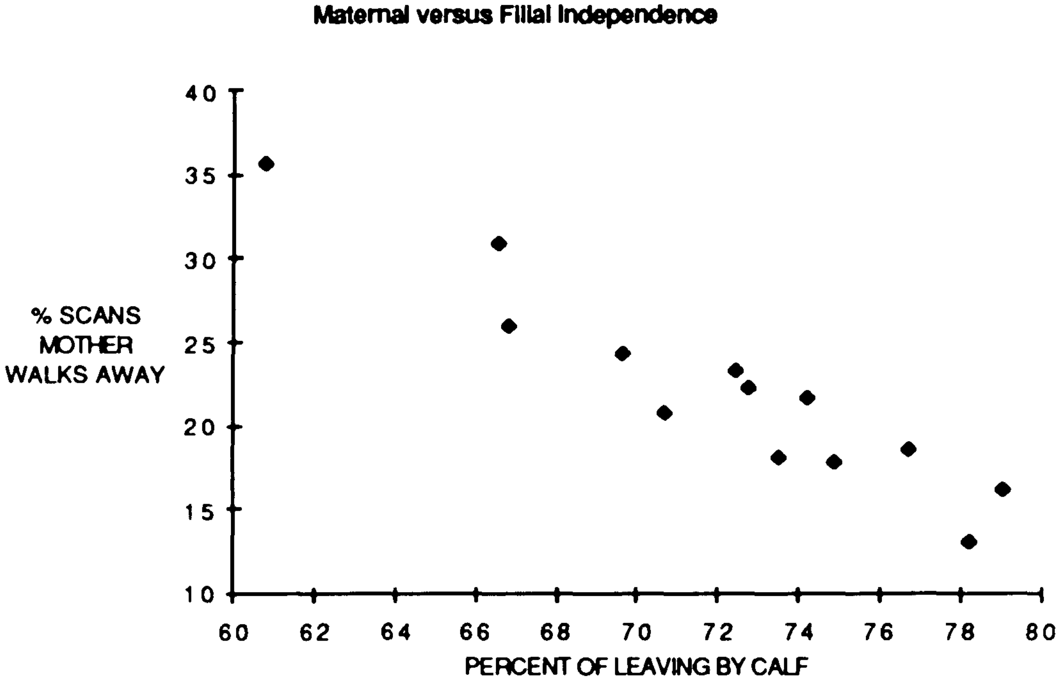


Figure 33: Maternal independence, measured by the percent of scans in which mothers walk away from calves, as compared with filial independence, measured by the percent of leaving by calves. Data are pooled for each dyad over months 1-5. See methods for explanations of measures.

PROXIMITY

In contrast to the positive relationship between proximity and calves' efforts at contact-maintenance, mothers' efforts are either unrelated or negatively related to proximity. For example, the relative and absolute frequencies with which mothers approach calves are negatively correlated with the percent of scans in which the two are within 10m (percent of approaches: $r = -.616$, $p = .025$; *frequency*: $r_s = -.634$, $p = .020$). Since maternal approaches are also correlated with filial independence, the implication is that, where mothers attempt to maintain proximity, calves frequently increase distances by walking away.

VOCALIZATION

Mothers of frequently-vocalizing calves are relatively dependent. Such mothers follow their calves' initiatives, take much responsibility for contact-maintenance, and leave their calves infrequently. As demonstrated by the results in Table 11, the more calves vocalize, the more frequently their mothers approach (p=.024), follow their movements (p=.012), and the less often their mothers leave (p=.025).

Conversely, mothers who do most of the vocalizing are relatively independent spatially and have dependent calves. This is indicated by the results shown in Table 11, when considered from the mother's point of view. Comparisons involving the percent of calling by mothers result in the same correlation coefficients, except that signs are reversed. Mothers who call more are less likely to approach and follow their calves. Their calves walk away infrequently, and rarely graze while their mothers rest.

NURSING INTERACTIONS

Filial independence increases with maternal nursing tolerance; mothers of independent calves spend more time nursing and show more patience during bouts. In contrast, independent mothers are frequently intolerant. Their dependent calves receive the least nursing care. The results in Table 13 show, for example, that mothers who spend more time nursing (MIN/H) are more likely to follow their calves (p=.034) and less likely to leave them (p=.044). The percent of nursing bouts ended by calves (%CEN) and the frequency of calves' pauses during bouts (CPS) are both positively correlated with the percent of scans during movements in which calves are walking away from mothers (p=.007 and p<.001, respectively). The latter relationship is illustrated by Figure 34. Both measures are negatively correlated with the frequency of calves' approaches (p=.002, p=.035) and the frequency of mothers' leaving (p<.001 for both tests; see Figure 35). These findings indicate that independent calves end more bouts than dependent calves, and pause more often during bouts while their mothers stand patiently. On the other hand, independent mothers rarely allow their calves to pause or end bouts.

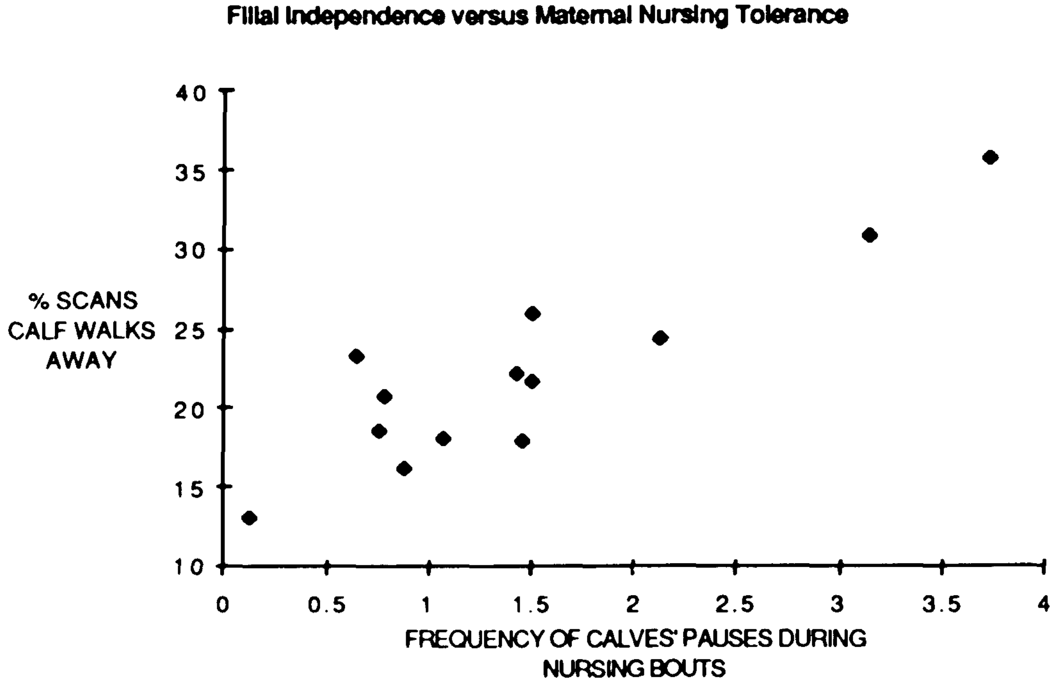


Figure 34: Filial independence, measured by the percent of samples in which calves walk away from their mothers, as compared with maternal nursing tolerance, measured as the frequency with which calves pause, interrupting nursing bouts, while their mothers continue to stand.

In contrast, the frequencies of rejected suckling attempts (RSA) and maternal aggression (MAR) are positively correlated with calves' approaches ($p=.002$ and $p<.001$, respectively) and mothers' leaving ($p=.011$, $p=.007$). These results suggest that independent mothers show more aggression toward their calves and reject more of their calves' suckling attempts, while their calves are relatively dependent. Other measures of nursing behavior show similar patterns in comparison with spatial relations.

TABLE 13
NURSING BEHAVIOR VERSUS SPATIAL INDEPENDENCE AND DEPENDENCE

		Maternal Tolerance			**Maternal Intolerance**		
	Measure of Spatial Relations:	MIN/H	%CEN	CPS	RSA	MAR	%MINT
Filial Independence:	Percent of leaving by calf	.435 ns	.712**	.834***	-.398 ns	-.440 ns	-.535 ns
	Frequency/hour of leaving by calf	.244 ns	.425 ns	.591*	-.240 ns	-.407 ns	-.379 ns
	Percent scans when calf walks away	.510 ns	.704**	.898***	-.473 ns	-.519 ns	-.680*
Maternal Dependence:	Percent scans when mother follows calf	.593*	.692**	.918***	-.430 ns	-.449 ns	-.679*
	Percent of approaching by mother	.488 ns	.700**	.710**	-.510 ns	-.601*	-.514 ns
Filial Dependence:	Frequency/hour of approaching by calf	-.657*	-.783**	-.720**	.764**	.861***	.641*
	Percent of approaching by calf	-.488 ns	-.700**	-.710**	.510 ns	.601*	.514 ns
	%Ac-%Lc	-.471 ns	-.749**	-.842***	.469 ns	.500 ns	.562*
	Percent scans when calf follows mother	-.449 ns	-.649*	-.556*	.651*	.463 ns	.494 ns
Maternal Independence:	Frequency/hour of leaving by mother	-.564*	-.848***	-.810***	.681*	.708**	.673*
	Percent scans when mother walks away	-.510 ns	-.704**	-.898***	.473 ns	.519 ns	.680*

Table 13 shows correlation coefficients for comparisons between measures of spatial relations and those of nursing behavior.
Measures of nursing interactions describe two extremes of maternal behavior: tolerance and intolerance (see text and Appendix B).
For comparisons involving behavioral rates and %Ac-%Lc, Spearman rank correlation coeficients are shown;
Pearson product-moment correlations are calculated for tests involving arcsine transformations of percentages.
All tests are two-tailed and based on a sample of 13 mother-daughter dyads. Data are pooled over months 1-5.
Significance levels of .05, .01, and .001 are indicated by *, **, and ***, respectively.

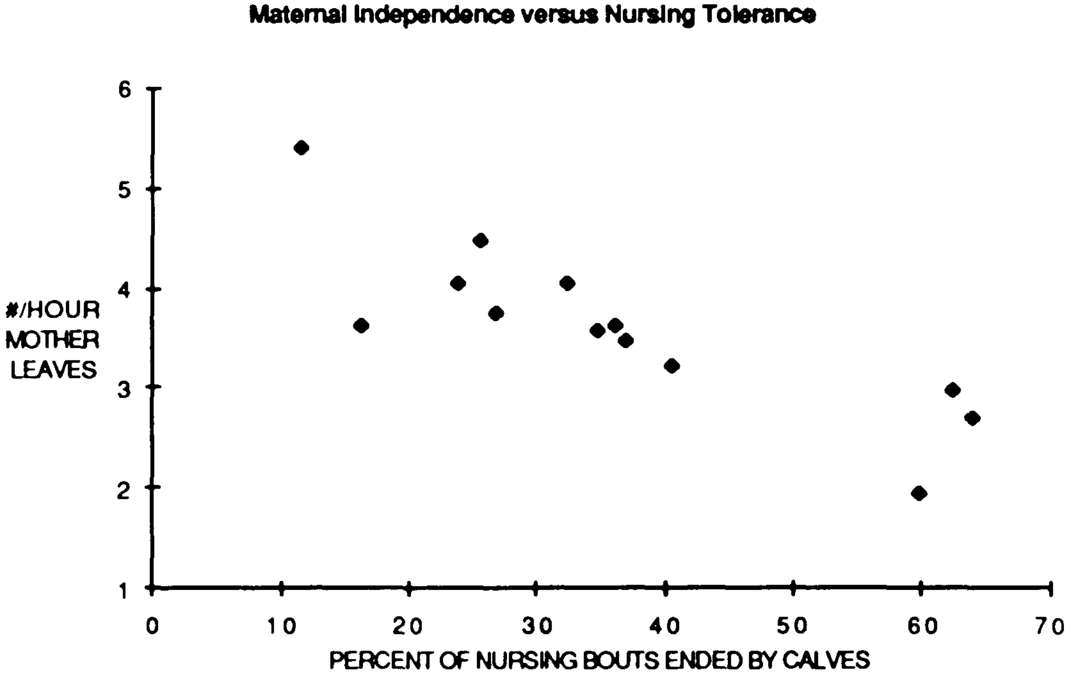


Figure 35: Maternal independence, measured by the frequency per hour with which mothers leave calves, as compared with maternal nursing tolerance, measured by the percent of nursing bouts which are ended by calves while mothers continue to stand quietly.

DISCUSSION

Patterns of individual variation in maternal and filial behavior reveal a distinct continuum. At opposite ends are independent mothers and independent calves; these two types are never found in the same dyad. Diverse aspects of mother-offspring interactions are included in this continuum, being correlated with maternal and filial independence. The results demonstrate that filial independence varies substantially in relation to maternal behavior. Calves are most independent when mothers frequently approach and follow calves' movements, walk away infrequently, and behave patiently during nursing bouts. When mothers show opposite behavior patterns, calves are less independent and make great efforts at maintaining proximity.

While patterns of interaction are clear, the issue of who controls whom is not. Mothers could be expected to affect the behavior of calves to a large extent; they are likely to dominante nursing interactions in particular. However, maternal behavior may also be affected by that of the calf. For example, some calves may exert control over their mothers' behavior by frequently walking away and vocalizing toward the mother. The results indicate that the mothers of such calves make greater efforts at maintaining proximity than other mothers; they may do so as a result of their calves' behavior.

Independent calves appear to show more initiative than their dependent peers, as evidenced by the findings that they vocalize more and initiate more contact interactions with their mothers. These findings indicate that, rather than not maintaining contact with their mothers, they do so differently from more dependent calves. Independent calves appear to tolerate greater distances from their mothers and exert more control over mother-offspring relations. Frequent vocalization probably helps in both respects, by allowing calves to maintain contact without approaching their mothers. Similarly, independent mothers appear to use vocalization rather than approaching or following as an alternate method of maintaining contact with their calves.

These results support the hypothesis, based on the results of Hinde and Spencer-Boothe (1967a, 1971), that mothers' rejections (i.e., of suckling attempts) discourage filial independence. However, the findings of Altmann (1978, 1980; see also White and Hinde 1975), that baboon offspring develop independence earlier when mothers make fewer efforts at contact-maintenance, have no parallel in bison. In fact, the opposite relationship is revealed; maternal efforts at maintaining proximity appear to enhance filial independence. Several differences between baboons and bison may contribute to this disparity. For example, the ability of primate mothers to grasp their infants affects spatial relations. Secondly, maternal efforts at proximity-maintenance and the restriction of infants' movements occur primarily among primate mothers of low dominance rank (White and Hinde 1975; Altmann 1978, 1980; French 1981). Thus in baboons the development of independence is intimately associated with the rank of the mother and the extent to which freedom of movement may incur danger. While the offspring of dominant cows tend to be more independent (chapter 14), dominance relations do not appear to play such an important role in bison development. A third difference lies in the fact that baboon infants depend on their mothers for food to a greater extent than do bison calves. Subordinate baboon mothers, for whom foraging is impeded by displacements, may need to restrict their infants' movements to reduce the latters' nutritional needs (Altmann 1980). That such infants develop independence later appears to be related to numerous factors, only one of which is the mothers' contact-maintenance behavior.

The patterns of individual variation described here demonstrate that bison mother-daughter relations are polymorphic. Mothers and calves complement each others' behavior, resulting in a diversity of relationships. Under the prevailing conditions during this study, the mother-young bond appeared to function equally well in its various forms; all daughters survived long past weaning. Under adverse conditions, however, some types of relationships might prove more viable than others.

Chapter 11

EFFECTS OF VARIATION IN FILIAL AND MATERNAL AGE ON MOTHER-DAUGHTER RELATIONS

I. Offspring Birth Order

INTRODUCTION

Bison calves are born over a period of several months. As a result, within each age class individuals differ in age and size. Moreover, differences in the time of birth are associated with changes in the physical and social environment. One of the most important changes for developing calves is the fact that the number and size of other calves in the herd increases, affecting the nature and frequency of potential interactions with peers. Calves born late have mostly older, larger, and more experienced peers with which to interact. As a result, such animals may be weaker and socially less competent (as in squirrel monkeys: Baldwin 1969). Differences in the availability of peers may also affect relations with mothers; Hinde and Spencer-Boothe (1967b) demonstrate that the presence of peers causes rhesus infants to spend less time with their mothers.

Calves born at different times may also be affected by the fact that average group size increases during the calving season. Between the beginning of the calving season in April and the onset of the rut in mid July, mean group size increased from 29 to 79 in 1984. During the rut (in July and August), all females and juveniles were usually together (185 animals in 1984) and joined by large numbers of bulls. Thus late-born calves start life in a larger, more complex social group. Moreover, as group size increases, so does the frequency of rutting activity; late-born calves are confronted earlier in life with the disruptions and potential hazards caused by rutting bulls. In natural bison herds the increased dangers for a later-born calf, particularly of losing its mother, may be substantial.

Because these differences in their social environment, late-born calves may be at a substantial disadvantage as compared with earlier-born calves. This disadvantage may be increased by changes in the physical environment during the calving season. For example, late-born red deer calves are less likely than others to survive the winter (Clutton-Brock et al. 1982; Guinness et al. 1978). The findings of Guinness et al. (1971) indicate that milk yields of red deer hinds decline in late summer; among hinds prevented from conceiving until late in the season, only one in six produced enough milk to rear her calf. Moreover, even when red deer are reared with ample forage, late-born calves weigh significantly less than early-born during the fall after their birth (Blaxter et al. 1974, cited by Clutton-Brock et al. 1982). In the present study, late-born female bison were found to be subordinate to those born earlier during their first 3 years (as in pronghorns: Byers 1986), and to weigh less as yearlings (chapter 13). Thus the time of a calf's birth may have persistent effects on growth and related aspects of development.

Developing animals, when confronted with sub-optimal conditions, may 'settle for less' by modifying ontogenetic goals in relation to the environment (Bateson 1976). In a similar way, late-born calves and their mothers might compensate for disadvantages by adopting a strategy of interaction uniquely suited to their situation and thus different from those of other dyads. There are several forms which such compensation could take. For example, late-born calves and their mothers might stay closer together than other dyads. In order to do so, they should show higher frequencies of contact-maintaining behavior and/or lower frequencies of distance-increasing behavior. Secondly, late-born calves may mature faster; if so, they should spend more time grazing and less time resting than other calves. In addition, such dyads might compensate by prolonging their association.

In order to test these predictions, differences in mother-daughter interactions are compared with offspring birth order.

METHODS

Measures of pre- and post-weaning mother-daughter relations, as described in chapter 2, were compared with birth dates of offspring in Spearman rank correlations. Measures of pre-weaning relations include: proximity (percent of scans within 10m), efforts of mothers and calves at contact-maintenance (frequency of approaches, percent of scans following each other), distance-increasing behaviors (frequency of leaving, percent of scans walking away or not following), activity patterns (percent of time when calves graze or rest while their mothers graze), and nursing interactions (nursing time, measures of maternal 'patience' during bouts). Pre-weaning relations were described for two time periods: a) the first three weeks of life (nursing behavior only), and b) the first five months, over which period data are pooled for each dyad.

The longevity of post-weaning associations was measured: a) during months 15-16, as the percent of days when mother and daughter are in the same groups, and as the percent of scans when the two are within 10m, and b) at 1.5 years of age, as the percent of days on which daughters are in the same groups with mothers and within 10m of them during the first five minutes after identification (*% with mother*).

Calves' birth dates were estimated by week, starting from the birth of the first calf of the year. For calves whose births were witnessed, birth dates were known exactly. In other cases, birth dates were estimated by comparison with known-age calves, in terms of the appearance of the calf when first seen (e.g., size, coordination, presence of the umbilical cord) and by the last date on which the mother was seen prior to the birth.

Sample size varies among periods of data collection. In weeks 1-3, data were collected on 12 subjects; in months 1-5, 13 subjects. Comparisons involving bond-longevity include only dyads in which the mother has a new calf in order to avoid differences due to maternal reproductive condition (see chapter 7). Since only eight of the 13 study dyads met this condition, supplementary data from other known dyads in 1983 and 1984 were used for these comparisons.

Samples vary for the latter tests and are indicated with the results. Tests of spatial relations and activity patterns are one-tailed, based on predictions above; all other tests are two-tailed.

RESULTS

In 1983, birth dates ranged from late April to early July. The 13 subjects were born in weeks 3 through 13; three were born in week 3, two in week 4, four in week 5, and one each in weeks 6, 8, 9, and 13.

PRE-WEANING INTERACTIONS

In the first three weeks of life, mothers of later-born calves show more nursing tolerance than those of early-born calves. Late mothers spend less time grazing during bouts (r_S=.-664, p=.009), and interrupt bouts less often (percent of interruptions caused by mothers: r_S=-.584, p=.023). Later-born calves also pause more often during bouts (r_S=.627, p=.015). On the other hand, late-born calves do not differ from those born earlier in time spent suckling or in the percent of bouts which they terminate.

Proximity-maintaining behaviors during the first five months are closely related to offspring birth order. The movements of late-born calves and their mothers are highly synchronized. Late-born calves spend more time than others leading their mothers (r_S=.585, p=.018) and less time staying behind (not following) when mothers move away (r_S=-.630, p=.011). Mothers leave their late-born calves infrequently (r_S=-.553, p=.025); their calves also approach them infrequently (r_S=-.707, p=.004), probably as a result of mothers' infrequent withdrawals. However, the percent of time spent within 10m is not correlated with birth order.

Contrary to predictions, activity patterns do not differ for early- and late-born calves. The latter do not spend more time grazing, nor do they spend less time resting while their mothers graze.

Measures of nursing behavior during months 1-5 are less closely related to birth order than during the first three weeks. One measure, the frequency of maternal aggression, is significantly correlated: mothers of late-born calves threaten, kick, and butt their calves less than other mothers (r_S=-.512, p=.037).

These results indicate that late-born calves and their mothers differ from other dyads primarily in that their movements are more synchronized; late mothers also show somewhat more nursing patience, particularly during the first three weeks.

BOND-LONGEVITY

In contrast to predictions, the duration of mother-daughter relationships do not increase significantly with time of birth. In fact, rather than associating longer with mothers, late-born daughters stop associating with them somewhat earlier than other daughters (birth order vs. % *with mother* at 1.5 years: $r_S=-.327$, N=33, $p<.05$, two-tailed). Thus lateborn offspring do not appear to compensate by associating longer with mothers.

DISCUSSION

These results support the hypothesis that late-born calves and their mothers compensate for disadvantages by maintaining contact more frequently and showing lower frequencies of distance-increasing behavior than other dyads. Late-born calves and their mothers synchronyze their movements more often. Such mothers are less likely than others to leave their calves, and more likely to follow their calves' movements. Moreover, late-born calves rarely stay behind when their mothers walk away. These findings suggest that increased synchrony of movements enhances the ability of late-born calves and their mothers to maintain their relationship in the face of frequent interruptions and hazards within the rutting herd.

The question of whether later-born calves and their mothers stay closer together than others requires further consideration. In contrast to predictions, proximity is not significantly correlated with birth order. However, when compared in a one-way anova, early- and late- born calves show near-significant differences in the percent of time spent within 10m of their mothers. Calves born in weeks 3-5 were within 10m of their mothers in 62.5% of scans, as opposed to 72.0% for those born in weeks 6-13 (F=4.77, p=.051, df=1,11). Examination of the data suggests that effects of birth order are confounded by those of maternal age. While late-born calves of young mothers stayed unusually close to their mothers, those of old mothers did not (also see below).

Tests of the prediction that late-born calves compensate by maturing faster, i.e., by adopting adult behavior patterns earlier, yield equivocal results. The findings that late calves do not spend more time grazing, nor do they spend less time resting while their mothers graze, seem to present contradictory evidence. On the other hand, this prediction is supported by the fact that, contrary to expectations, late-born daughters have somewhat shorter associations with their mothers than do those born earlier. The finding that late calves are unlikely to remain resting behind when their mothers walk away may also lend support; however, this might reflect other factors, such as rutting activity. Evidence concerning physical maturation also tends to support the prediction: late-born calves lose their natal coats at an earlier age than those born earlier (chapter 12).

Late mothers behave more tolerantly during early nursing bouts. If, as for red deer (Guinness et al., 1971), bison milk yields decline during the summer, one could expect such dyads to show more conflict over nursing than other dyads, since late-born calves should receive less milk. It is interesting, then, that in fact they show less nursing conflict. This finding is consistent with the compensation hypothesis.

A different but complementary hypothesis is that the interactions of late-born calves with mothers are related to their interactions with peers. In chapter 13, birth order is shown to be closely correlated with offspring dominance: early-born daughters are dominant to later-born ones. This finding suggests that age differences among offspring have a great impact on peer relations, perhaps even more so than on mother-daughter relations. However, the fact that late-born calves are subordinate to their peers may be reciprocally related to their close relations with mothers. In the first place, pressures (e.g., from rutting activity) to stay close to their mothers and avoid separation may cause them to spend less time interacting with peers. At the same time, the fact that they are younger and smaller than their peers may put them at a disadvantage in social competition, as in squirrel monkeys (Baldwin 1969). The synchronyzed relations of late calves and their mothers may be in part a consequence of calves' low social status; such calves may prefer to be with their mothers rather than with other herd members.

II. Maternal Age

INTRODUCTION

In a previous paper (Green 1986; chapter 4), nursing behavior was found to differ between old and young bison cows, supporting the hypothesis that parental care increases with the age of the parent, while conflict with offspring decreases (Trivers 1974). Older mothers spend more time nursing their calves, allow their calves to end more bouts, reject fewer suckling attempts, and interrupt bouts less often. It is likely that milk production also increases with age, as in domestic cows (Bath et al. 1978; Dodd 1957; Johansson and Claesson 1957); young mothers behave as if they have less milk to give, and experience more discomfort in giving it.

Young bison mothers appear to be at a disadvantage relative to older mothers in other ways as well. For example, they are generally subordinate to older cows (Rutberg 1983; chapter 13). Low social status may aggravate problems of milk-production since young cows and their calves are frequently displaced from food sources. Rutberg (1984, 1986a) found that foraging efficiency is lower for low-ranking bison cows, and that the difference increases as cows spend more time searching, as when food is sparsely distributed. At Wind Cave, displacements are particularly frequent at natural mineral licks where bison gather to lick or chew the earth. The small area of these licks limits the number of animals that gain access. The relatively intense competition suggests that real advantages accrue to those who win; displaced animals are prevented from obtaining minerals during the limited time which the herd spends in the area. Low-ranking mothers and their calves may either stay behind the herd, increasing the risk of predation, or do without. It may be that young, subordinate mothers are less able to nourish their calves because of the difficulties they encounter in obtaining their own nutrients.

The ways in which young mothers interact with their offspring might serve to compensate for their disadvantages. For example, Altmann (1978, 1980) found that subordinate baboon mothers are more restrictive of their infants' movements than are dominant mothers; infants of the former develop spatial independence at a correspondingly more advanced age. She suggests that low-ranking mothers maximize their potential maternal care by staying close to their infants and controlling their movements. They may compensate for frequent displacements from food sources by reducing the activity level and corresponding nutritional needs of their infants.

Previous findings revealed that young bison cows make greater efforts than older mothers in non-nursing interactions with calves: they initiate more non-aggressive contact (chapter 4). This suggests that age-related differences in maternal behavior involve more than just nursing, and that differences in the extent of parental investment between young and old cows may not be as clear-cut as would be expected on the basis of Trivers' (1974) hypothesis.

In order to compensate for nutritional deficiencies, young mothers and their calves may employ strategies of early and long-term relations different from those used by older mothers and their offspring. Like subordinate baboon dyads, young cows and their calves may maintain particularly close relations; the offspring may also develop independence at a later age. If this is the case, young mothers and their calves should show higher frequencies of contact-maintenance behaviors and spend more time close together early in calves' lives. Moreover, post-weaning associations should last longer for young than for older cows and their daughters.

In this section, maternal age is compared with early and long-term spatial relations in order to examine the hypothesis that young mothers and their daughters compensate for disadvantages by interacting differently from older mothers and their offspring.

METHODS

Subjects include 13 mothers, aged 2 to 18 years, and their female calves (born in 1983). Ages of mothers were determined primarily through park ear tags inserted during their first year of life (see chapter 2 for a more detailed description). The fact that all calves were of the same sex eliminated the possibility of individual variation in relation to offspring sex. Moreover, tests of bond-longevity among bison mother and offspring must be limited to daughters, since sons do not usually associate with their mothers after weaning.

The following measures of mother-daughter spatial relations (see chapter 2), pooled over the first five months for each dyad, were compared with maternal age in Spearman rank correlations:

1) In order to describe overall proximity between mother and calf, I measured the percent of scans at 2.5-minute intervals during which mother and calf were within 10m. Secondly, proximity was recorded specifically at times when both mother and calf grazed. The latter measure is particularly likely to reflect filial independence because it includes only those times during which both are active and thus have a greater chance of becoming separated.

2) To examine the extent to which members of dyads coordinate their movements or behave independently of each other, the percent of scans were measured: a) when calves and mothers follow each others' movements, and b) when one walks away and the other does not follow.

3) The contributions of mothers and calves to proximity-maintenance were evaluated in terms of the relative and absolute frequencies of approaching by each, across a boundary of 1m.

4) In order to describe long-term differences in the development of independence, the longevity of the mother-young relationship was measured in the offspring's second year (i.e., post weaning), following the same methods as in section I.

Sample size is 13 for all comparisons of maternal age with measures of early mother-daughter relations (i.e., during months 1-5). For tests of bond-longevity, only cows who calved again the next year were included. Since only eight of the 13 dyads fell into this category, supplemental data on yearlings in 1982 and 1983 were used. Sample sizes for such tests vary and are indicated with the results. All tests are one-tailed, based on the predictions above.

RESULTS

Young mothers and their calves stay closer together while grazing and coordinate their movements more than do older cows and their calves. Maternal age is negatively correlated with the percent of time when mothers and calves graze within 10m of each other (r_s=-.486, p=.046) and the percent of time when calves follow their mothers' movements (r_S=-.492, p=.044). Calves of young mothers are also less likely to walk away from their mothers when the latter do not follow (r_S=.552, p=.025). These results suggest that it is the calves of young mothers who are primarily responsible for maintaining closer proximity when both are grazing.

While all significant associations tend to support the predictions, a number of measures tested do not vary significantly with the ages of mothers. In particular, overall proximity and approaching are not correlated with maternal age

As predicted, young mothers have longer associations with their daughters than do older cows: the percent of time daughters spend with mothers at 1.5 years of age is negatively correlated with the age of the mother (r_S =-.459, N=33; p<.01). Figure 36 compares this measure among mothers of three age groups.

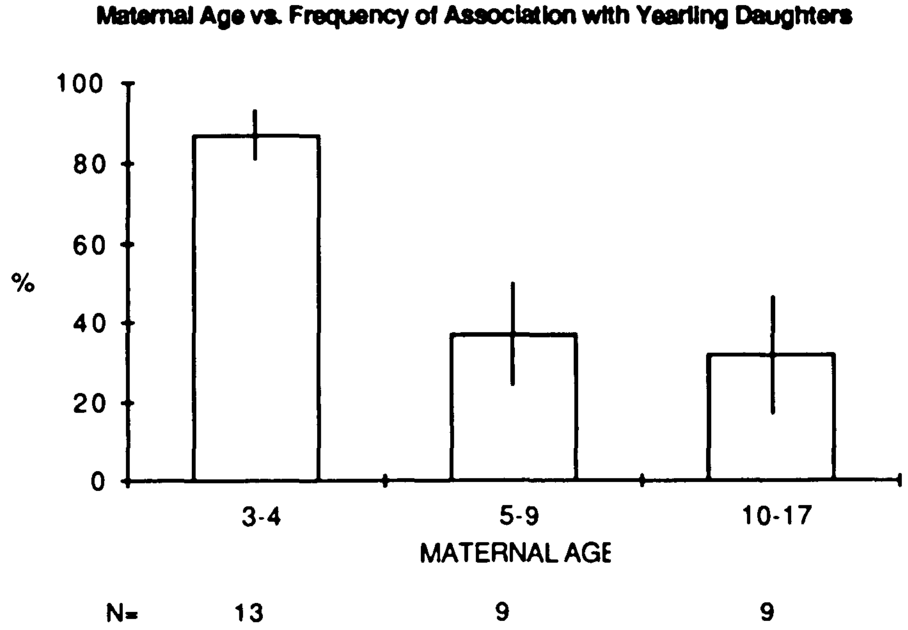


Figure 36: Mean percent (± SE) of the days when mothers of three age-groups were seen in the same groups with their daughters and within 10m of them during the first five minutes after identification. Data were collected in October of 1983 and 1984, when daughters were about 1.5 years of age.

DISCUSSION

The results suggest that young bison mothers and their daughters more frequently synchronize their movements and graze close together than do older mother-calf dyads. The behavior of calves is primarily responsible for the difference; those of young mothers behave less independently. Several of the measures tested are not significantly correlated with maternal age. These include overall proximity and the relative and absolute frequency of approaching by mothers and calves. That these negative results do not contradict the positive is indicated by the fact that somewhat different aspects of spatial relations are reflected in each case. Proximity during active periods alone, relative to that in all activities, provides a better reflection of the degree of behavioral coordination between mother and calf. The former measure is limited to those times when both are active (as are other herd members) and therefore more likely to become separated. Approaching involves decreases in distance from >1 to <=1m. The fact that measures of approaching are not significantly associated with maternal age indicates that relative contributions of mothers and calves to such decreases in distance do not vary with the age of mothers, nor does the absolute frequency of such distance changes. In contrast, the proportion of time calves spend responding to their mothers' movements by following is significantly greater for calves of young mothers, while those of older cows spend more time walking away from their mothers. The latter results show that the relative contributions of mothers and calves to *maintaining* proximity, though not decreasing it, vary in relation to maternal age.

It appears that young bison mothers and their daughters differ from older mother-calf dyads not only in nursing and contact interactions, as previously described, but also in spatial relations. The results suggest that daughters of young cows develop spatial independence later than those of older mothers. This possibility is further supported by the fact that young mothers and their daughters continue to spend more time together than other dyads during the daughters' second year of life. Studies of red deer (Clutton-Brock et al. 1982) and zebu cattle (Reinhardt and Reinhardt 1981) suggest that the same relationship between maternal age and filial independence exists in other ungulate species as well; young mothers associate longer with their daughters than do older mothers.

These findings suggest that, as in baboons (Altmann 1980), young, subordinate bison mothers and their calves stay closer together than other dyads. In this case, however, it is the offspring, rather than the mothers, who are primarily responsible for the effect. It may be that young mothers train their calves to maintain close proximity. For example, by not following when the calf walks away, a mother may discourage filial independence.

MATERNAL AGE AND OFFSPRING BIRTH ORDER

Maternal age and offspring birth order are two variables which, though not associated with each other, substantially affect mother-daughter relations. Each variable appears to be associated with a different range of social and physical factors, wherein dyads at one end may have an advantage over those at the other. For both mothers and daughters, to be older than one's peers seems to confer an advantage. Young mothers and late-born calves, together with their partners, behave as if to compensate for their disadvantage. In both types of dyads, mothers and daughters maintain closer, more coordinated relations. If the mother is young, the calf takes a major responsibility in this effort. Where calves are late-born, it is the mother.

Dyads in which the mother is young and the daughter late-born should be particularly disadvantaged. Perhaps this is why, between 1982 and 1986, only older cows gave birth very late (i.e., after July). The latest-born calf of a primiparous cow during this five-year period was a subject of the present study. In this case the mother calved at an unusually early age (two years); the calf was born in early July (birth week 13). A description of this relationship reveals that, in such a 'high-risk' dyad (Meier 1984), the behaviors used by both members to compensate for potentially life-threatening problems are basically the same as those reported above; here, however, they are more pronounced. This pair stayed closer together than any other dyad during the first five months. The calf spent the least time resting while her mother grazed, and the most time following when her mother walked away. This mother nursed her calf longer at each bout than any of the other six young cows (aged 3-4; all primiparous except one), and showed the least maternal aggression. She also initiated more contact with her calf than all other mothers except one. In the year following this calf's birth, the mother did not calve; she was the only barren cow under 12 years of age. She continued to nurse and maintain close relations with her first offspring for at least 1.5 years.

Chapter 12

PHYSICAL VERSUS SOCIAL DEVELOPMENT

INTRODUCTION

Maternal care may affect offspring growth and survival in various ways. For example, growth rates increase with nursing bout duration and frequency in domestic sheep (Ewbank 1967) and red deer (Clutton-Brock et al. 1982). The survival of elephant seal pups depends to a large extent on the amount of milk provided by the mother (Reiter et al. 1981). Other aspects of maternal behavior are also related to the physical condition of offspring. Studies of elephant seals provide examples of maternal behaviors which enhance pup survival. Successful mothers are most likely to respond rapidly to their newborn pups, stay close to them, and defend them aggressively (Reiter et al. 1981; McCann 1982). In addition to the mother's contribution, offspring growth might be influenced as well by the specific ways in which mothers and their young interact.

Individual charateristics of mothers and young, such as maternal age, social rank, and offspring birth order, may also affect offspring growth and survival. For example, primiparous domestic cows produce less milk than older cows (Dodd 1957). Red deer calves born late in the year are less likely than others to survive; their mothers may be unable to produce enough milk due to seasonal changes in forage availability (Guinness et al. 1971). The fact that socially low-ranking mothers produce fewer offspring (e.g., primates: Chapais and Schulman 1983) may be related to decreased foraging efficiency as a result of displacements (Altmann 1980; Rutberg 1984, 1986a).

Another factor which may affect offspring growth is the mother's reproductive status during the year following the offspring's birth. Red deer mothers who are subsequently barren often nurse their previous offspring over much longer periods than do those who reproduce the next year; daughters of the former have significantly higher dominance ranks (Clutton-Brock et al. 1982).

This chapter examines the question: Are variations in bison physical development related to individual differences in (a) the mother-offspring relationship, and (b) physical and social variables of mothers and daughters, including age, dominance, and subsequent maternal reproductive status? Two estimates of physical development are examined: 1) offspring size (as defined below), and 2) the duration of the natal coat. Offspring survival is not considered, since mortality among cows and juveniles is quite low in the Wind Cave herd. Natural predators no longer exist, and the herd is maintained below carrying capacity through culling.

I. Offspring Size

Evidence from various mammalian species suggests that size is related to survival and reproduction. Among red deer hinds, weight and body condition are closely related to fertility (Mitchell and Brown 1974, cited by Clutton-Brock et al. 1982). For developing animals, size is associated with survival. Among red deer calves, birth weight is correlated with summer survival (Guinness et al. 1978; Clutton-Brock 1982). In elephant seals, pup size and weight increase with maternal age, size, and weaning success; pups that survive are generally the heaviest (McCann 1982; Reiter et al. 1981).

Variations in offspring size are related to differences in behavioral and physical characteristics of the mother. One could predict that bison mothers who provide more maternal care raise larger offspring. For example, offspring size may increase with nursing time. Since maternal age is closely related to nursing behavior in bison (chapter 4), offspring size might also vary with the age of mothers. Moreover, since bison mother-daughter dyads vary substantially in the closeness and synchrony of their spatial relations (chapters 9, 10), one might expect offspring size to vary with spatial relations.

METHODS

MEASURES

The size of daughters was measured in three ways: weight and horn length at 1.5 years of age, and relative calf size, as estimated visually when calves stood together on flat ground. Weight and horn length were measured during fall roundups. Weights were collected on female yearlings of two age classes (i.e., in 1983 and 1984); horn lengths are available for 1983 yearlings only. Methods of measuring age and birth order are described in chapters 2 and 11; those of calculating dominance are described in chapter 13.

Data on mother-daughter interactions were pooled for each calf over the first five months of life. These include the following measures:

Maternal Nursing Care:

Nursing time (minutes/hour)

Percent of bouts ended by calves

Frequency of maternal aggression per nursing minute

Frequency of rejected suckling attempts per nursing minute

Percent of bout-interruptions by mothers.

Spatial Relations:

1) Proximity: the percent of scans at 2.5-minute intervals in which mothers and calves are within 10m of each other

2) Synchrony of activity and movements: the percent of scans in which mothers and calves:

   do or do not follow each others' movements

   graze together

   do not graze together (i.e., one grazes while the other rests)

3) Approaching and leaving between mother and calf across a 1m boundary (frequency/hour; percent of total approaching)

DATA ANALYSIS

Individual scores on size measures were tested in Spearman rank correlations against all measures of mother-daughter relations and other characteristics of mothers and offspring. In order to determine whether maternal reproductive status affects offspring size, the weights at 1.5 years of age for daughters of barren and parturient mothers were compared in a one-way analysis of variance; sufficient data were not available to compare horn length with relative calf size. Sample size varies among measures and is listed with the results. All tests are two-tailed.

RESULTS

Yearling weight varied from 167 to 337 kg; horn length, from 17.8 to 25.4 cm. Associations of these variables and relative calf size (abbreviated below as RCS) with other characteristics of mothers, daughters, and their interactions, are described below.

MOTHER-DAUGHTER RELATIONS:

In contrast to predictions, nursing time is not significantly correlated with the size of daughters, nor are other aspects of maternal nursing behavior. Spatial relations between mothers and calves, however, vary consistently in relation to offspring size. Larger daughters spend less time than others near their mothers (RCS: r_S=-.555, N=13, p=.049). Their mothers leave them more often (weight: r_S=.603, N=12, p=.038). The relative lack of synchrony between larger daughters and their mothers is also indicated by the fact that they spend little time following each others' movements (RCS: r_S=-.637, N=13, p=.019). Moreover, larger offspring spend more time than others resting behind when their mothers go off to graze (weight: r_S=.582, N=12, p=.047; relative calf size: r_S=.815, N=13, p<.001).

MATERNAL CHARACTERISTICS:

Yearling weight differs substantially, depending on the mother's subsequent reproductive condition. Daughters of barren cows (mean weight ± SE = 311±15 kg, N=6) were significantly heavier than those whose mothers calved again (mean weight = 260 ±12 kg, N=34; F=6.56; d.f.=1,38; $p<.025$). Subsequent maternal reproductive status also appears to be related to the age at which daughters begin calving, although data were insufficient to determine this statistically. During the two years of the study, only two females calved at two years of age; the mothers of both were barren during the year after their birth. Mean age at first calving was 3.2 years for the 27 daughters of 'parturient' mothers. In contrast, the 6 daughters of barren cows first calved, on the average, at 2.6 years.

Comparisons of yearling weight, horn length, and relative calf size with maternal age, size and dominance indicate that the latter variables are not significantly associated with the offspring size.

OFFSPRING BIRTH ORDER AND DOMINANCE:

Earlier-born daughters are larger, heavier, and have longer horns than those born later; all three measures of size are negatively correlated with birth order (weight: $r_s=-.488$, N=41, $p<.01$; relative calf size: $r_s=-.839$, N=13, $p<.001$; horn length: $r_s=-.842$, N=13, $p<.001$). Moreover, larger daughters are dominant to smaller ones: all three measures are positively correlated with offspring dominance value and rank, as shown below:

	DOMINANCE VALUE	RANK
WEIGHT	$r_s=.462$, N=41, $p<.01$	$r_s=.437$, N=41, $p<.01$
RELATIVE CALF SIZE	$r_s=.638$, N=13, $p=.020$	$r_s=.802$, N=13, $p<.001$
HORN LENGTH	$r_s=.680$, N=13, $p=.012$	$r_s=.877$, N=13, $p<.001$

DISCUSSION

The results do not support the prediction that offspring size is enhanced by more extensive nursing care early in life. In contrast, however, offspring weight differs significantly, depending on the duration of the nursing period. When mothers do not calve in the year following daughters' birth, and therefore prolong the period of nursing and other maternal care, daughters weigh substantially more as yearlings, and may also reproduce earlier.

That offspring size does not differ in relation to the extent of early nursing care may be due to the relatively stress-free environment inhabited by the study population. Robbins and Moen (1975) found that white-tailed deer fawns which were bottle-fed on lower quantities of milk showed the same growth rates as those fed more milk. The former appeared to compensate by consuming more of the available horse pellets and hay. This suggests that variation in growth rate is less dependent upon milk intake when developing animals can obtain ample nutrients in other ways.

The results indicate that size is related to social relations with both mothers and peers. Larger daughters are more independent of their mothers and higher-ranking among peers. Large calves and their mothers synchronize their movements less and spend less time close together than do other dyads. Larger daughters are also born earlier in the year, develop higher social status, and may calve earlier, than smaller daughters.

Large size appears to confer an advantage in interactions with peers. However, it may be merely a by-product of the head start afforded by early birth (see chapter 11). Calves born earlier become larger than, and dominant to, those born later. They spend less time with their mothers and, perhaps, more time with peers. In contrast, later-born calves remain smaller and subordinate. Such calves and their mothers stay closer together and coordinate their movements to a greater extent.

II. Duration of the Natal Coat

INTRODUCTION

In various mammalian species the coat color of infants differs from that of adults. For example, in baboons, infants are much darker than adults for the first six months of life (Altmann 1980). In bison, calves' coats are conspicuously lighter than those of adults until around three months of age. Because its duration coincides with the period of greatest physical dependency, the natal coat has been hypothesized to elicit maternal care (Poirier 1977). If this is the case, maternal care should decrease when calves moult. Such a finding would indicate that bison cows perceive and respond to the difference in coat coloration. However, this prediction is difficult to test since the relationship between maternal care and coat color is obscured by other changes, such as declining milk production, which may occur simultaneously.

Therefore, functions of the natal coat are examined here in terms of individual variation in the age of calves at moulting. If the natal coat elicits maternal care, care should decrease when calves change color. According to this hypothesis, later-moulting calves should receive more total maternal care during the pre-weaning period.

METHODS

In order to test this prediction, ages of calves at moulting were compared with individual variation in the quality of maternal nursing care throughout the first five months of life (i.e., until 3 weeks after the last calf moulted).

Moulting was defined operationally as the time when calves' coats had undergone about 90% of the change from the natal rust to the dark brown of adults. Since the change usually occurs in patches, this was the age (in weeks) when all but small spots on the body were dark brown, i.e., when the calf's general appearance was of solid brown. Data on moulting age were collected for 23 female calves born in 1983. All subjects were born during a 13-week period between late April and early July. Since in 1983 no calves were born after July, the possibility of the moult being delayed due to cold weather was eliminated.

Measures of maternal nursing care used in this analysis are the same as those in section I. As in the previous analysis, data were pooled for each calf over the first five months of life. Moulting age was compared in Spearman rank correlations with these measures. Sample sizes are indicated with results. Tests concerning maternal care are one-tailed, based on the prediction; all others are two-tailed.

RESULTS

Calf age at 90% color change varied from 10 to 17 weeks. Comparisons of moulting age with nursing interactions indicates that the age at which calves lose their natal coats does not differ in relation to maternal care. Of the measures of maternal behavior examined, only one is significantly associated with natal coat duration: mothers of later-moulting calves interrupt nursing bouts less often (r_s=.557, N=13, p=.024). These results generally do not support the hypothesis that the natal coat elicits maternal care.

Several interesting associations of the duration of the natal coat were revealed during the course of the study. For example, moulting age is significantly related to offspring birth order and maternal dominance. Earlier-born calves retain their natal coats longer, as do those of dominant mothers. The duration of the natal coat is negatively correlated with birth order (r_s=-.413, N=23, p=.025), and positively correlated with maternal dominance value (r_s=.659, N=13, p=.007). However, moulting age does not vary significantly with maternal age and size. Moreover, daughters who retain their natal coats longer appear to grow faster and reproduce earlier. The age at which calves change color is positively correlated with yearling weight (r_s=.567, N=17, p<.02). It is also negatively related to the age at which daughters begin calving (r_s=-.494, N=16, p<.05); daughters that moult later begin reproducing earlier. On the other hand, moulting age is not correlated with offspring dominance.

DISCUSSION

The hypothesis that late-moulting calves receive more maternal care is not supported by the results. Moulting age appears to be associated with offspring birth order and maternal dominance; calves of more dominant cows, and those born earlier in the season, retain their natal coats longer. Moreover, late moulting daughters weigh more at 1.5 years and reproduce earlier, on the average.

The results suggest that the duration of the natal coat, while not correlated directly with maternal care, is in some ways associated with benefits to offspring. This possibity is supported by the findings that late-moulting daughters weigh more and calve somewhat earlier. In addition, the fact that their mothers are higher-ranking quite possibly confers some benefit. For example, the calves of dominant cows have priority of access to mineral licks when in proximity to their mothers (see chapter 11). Their early mineral intake is probably superior to that of other calves.

The finding that earlier-born calves moult later suggests that such calves may also benefit from seasonal changes. The findings of Guinness et al. (1971), that late-calving red deer hinds produce less milk, suggests that forage quality may change during the calving season. If so, early-born calves could have a nutritional advantage over those born later, even without nursing more. Their mothers' milk as well as their own grazing may be of superior quality to that available later.

It may also be that late-born calves moult at an earlier age because of the approach of autumn and the growth of the winter coat. The fact that calves born at the end of the summer retain their natal coats throughout the winter (i.e., for around eight months) suggests that there is a cutoff time, after which the normal moulting at 3-4 months of age is precluded.

The natal coat might also provide camouflage. This possibility is suggested by the fact that, to this observer, at least, bison calves are similar in color to the earth, particularly in areas frequented by the Wind Cave herd. Since calves spend much of the time resting in bare wallows, they sometimes seem to disappear. Calves often rest far from their grazing mothers (chapter 3); their coats may allow them some degree of crypsis during the period of development when they spend the most time resting.

Chapter 13

DOMINANCE RELATIONS AMONG ADULT AND JUVENILE BISON COWS AS COMPARED WITH AGE, SIZE, AND REPRODUCTION

INTRODUCTION

AGE VERSUS SIZE

Dominance relations vary with environmental and social conditions (Rowell 1967; Gartlan 1968). The individual characteristics with which dominance is associated differ between and within taxa. In many primate species, offspring acquire their mothers' dominance ranks (Sade 1967; Berman 1983a, b; Samuels et al. 1987). Dominance among female ungulates often changes with age (e.g., bison: Rutberg 1983; red deer: Clutton-Brock et al.1982; Hall 1983; reindeer: Espmark 1964; highland ponies and cows: Clutton-Brock et al. 1976). On the other hand, for some female and many male ungulates, dominance is related to body size (e.g., bison cows: Lott and Galland 1987; dairy cows: Reinhardt and Reinhardt 1975; feral mares: Berger 1977; red deer stags: Clutton-Brock et al. 1982) and/or horn size (e.g., bighorn rams: Geist 1971; young bison bulls: Rothstein, in prep.).

Among bison cows, the qualities with which dominance is associated may depend on the potential for individual recognition among herd members. Lott and Galland (1987) found that, on Catalina Island, dominance increases with weight. In contrast, Rutberg (1983) found no such association in a Montana herd; rather, dominance is strongly correlated with age. As Lott and Galland (1987) point out, this disagreement suggests that dominance is primarily age-related where herds are relatively small, cohesive, and utilize largely open habitats (e.g., the Montana herd). Such cows are likely to interact repeatedly, reinforcing dominance relations established early in life, when members of different age-classes differ greatly in size. In contrast, lack of previous contact between individuals should favor dominance hierarchies based on qualities related to fighting ability, such as body size (Lott and Galland 1987; Rutberg 1983). This hypothesis is supported by Thouless and Guinness' (1986) finding that older red deer hinds are dominant within their home ranges, but not outside.

The objective of this study is to examine relationships of age and body size with dominance relations among two groups of bison cows:

1) Mature cows, aged 3-19 years: The study herd is relatively small and cohesive; home ranges of all cows appear to overlap completely. The habitat consists of open grasslands and rolling hills. Because herd members appear to have ample opportunity for repeated interactions throughout life, dominance relations should be based on age rather than body size, as in the Montana herd studied by Rutberg (1983, 1986a).

2) Juveniles born in the same year: Within a juvenile cohort, individuals differ in age by as little as a few days or weeks, and size differences are equally subtle. Calves interact initially as strangers among themselves. If dominance among strangers is related to body size, as suggested above, early dominance relations should be associated primarily with size differences. Body size should continue to be related to dominance during the first few years if peers grow at the same rate.

REPRODUCTION

Effects of dominance among females on fitness have been examined primarily in primates, where dominant matrilines have been found to produce more surviving offspring than subordinate families (e.g., Chapais and Schulman 1983; Sade et al. 1976). Of the few studies which have addressed this question in ungulates, results are equivocal. Eccles and Shackleton (1986) found that dominance among bighorn ewes was not associated with forage quality, seasonal weight changes, nor with lambing success in a particular year. However, as these researchers point out, long-term studies may be necessary in order evaluate the effects of dominance. Thus the findings of Clutton-Brock et al. (1986), reflecting about fifteen years of research, reveal that the lifetime reproductive success of dominant red deer hinds is significantly greater than that of subordinates. Dominant hinds calve more frequently, and do so earlier in the year; their calves are also heavier and survive to maturity more often than do those of subordinate hinds.

This study examines the relationship between dominance and reproductive success among bison cows. The finding of Rutberg (1984, 1986a), that dominant bison cows graze more efficiently than subordinates, suggests that high rank could enhance fitness. Preliminary observations for the present study offer tentative support for this prediction. At Wind Cave National Park, displacements among bison cows occur with dramatic frequency at natural mineral licks. Bison gather at these depressions in the ground to lick or chew the earth. The small area of the licks limits the number of animals that gain access; often a few holes, into which only one or two adults can fit, are preferred. Displacements occur almost constantly among animals around such holes. The intense competition seen here suggests that real advantages accrue to those who win; displaced animals are prevented from obtaining minerals during the limited time which the herd spends in the area. Low-ranking cows may either stay behind the herd, increasing the risk of predation, or do without.

METHODS

SUBJECTS AND DATA COLLECTION: Subjects were members of a free-ranging bison herd, including around 200 cows and juveniles, at Wind Cave National Park, South Dakota. The herd utilized primarily grassland areas, which comprise 80% of the park's 70 square km area. Data were collected during 1983 and 1984 in focal-animal and ad lib samples. Focal animals included 13 females born in 1983 and their mothers. Supplemental ad-lib sampling included juveniles born in 1982 and 1983, and parturient cows (aged 3-19 years). Adult cows were limited to 29 seen interacting with at least 8 other cows (table 14). The 46 juveniles were between 6 months and 2 years of age during the study. Data for the two juvenile age-classes (21 females born in 1982 and 25 born in 1983) were considered separately for calculations of dominance measures, but for comparisons of dominance measures with age, weight, and reproduction, data for all juveniles were analyzed together. Tables 18-20, in appendix D, show data for all subjects on dominance, age, body size, and reproduction.

ESTIMATES OF DOMINANCE: Following McHugh (1958) and Rutberg (1983), dominance interactions among cows were characterized as hasty withdrawals by subordinates from threats (e.g., head tosses or horn swings) or approaches by dominants. Interactions were summarized in matrices of frequencies with which each animal displaced and was displaced by each other animal. Three separate dominance matrices were constructed: one each for juveniles born in 1983 (table 15), juveniles born in 1982 (table 16), and cows who were parturient by 1983 (table 14). The best order of dominance rank was determined by minimizing the number of entries below the diagonal (Brown 1975). Ranks were reversed so that dominance increases with the magnitude of the score; thus positive correlations indicate that dominant animals score higher on other measures. Because of numerous departures from linearity in hierarchies and the absence of interactions between some individuals, a second measure of dominance was used as well. Dominance value (DV) measures an animal's tendency to dominate social partners, regardless of their relative positions in the hierarchy. Following Beilharz and Mylrea (1963), DV is calculated as the arcsine transformation of the ratio of animals dominated to the total number of social partners.

MEASUREMENT OF AGE AND SIZE: For cows, age was measured in years. Most were aged by means of eartags inserted during roundups when they were calves, or before all their teeth had grown in. Ages of the few animals lacking eartags were estimated by tooth wear and horn growth (Fuller 1959). For each of the two juvenile age classes, more precise age differences reflect the range in calving dates over a period of three to six months. Age within each peer group was measured in weeks beginning with the first calf of the year. Age differences within each cohort are generally referred to below in a relative sense, as birth order.

Size was measured as body weight and horn length for juveniles. Both measurements were made at fall roundups, when subjects were around 1.5 years of age. Among cows, size differences were estimated primarily in terms of weight. Cows were weighed each year for three years (1984-86). Weights were correlated between years ($p<.01$); since more cows were weighed in 1984, data from that year were used in analyses. Since many older cows have broken horns, relative horn length among adults was estimated as the number of intact horns (0=2 broken horns, 1=1broken horn, 2=none).

MEASUREMENT OF REPRODUCTIVE SUCCESS: For juveniles, relative reproductive success was estimated as the age at first parturition (N=37). Fertility was calculated for adult cows as the percent of years during which each cow calved over a five-year period (1982-1986). Because fertility decreases after age 10 (appendix A), only cows who were between 3 and 10 years of age throughout this period were included (N=21). Offspring mortality rates were not considered since they are extremely low (e.g., of 153 live births during a 3-year period, one calf died); the study herd is free of natural predators and maintained below carrying capacity.

DATA ANALYSIS: Measures of dominance were compared with individual scores on measures of size, age, and reproduction in Spearman rank correlations. Pearson product-moment correlation coefficients were calculated for comparisons between two percentages; in such cases, both variables were first subjected to arsine transformations. Sample sizes vary among measures and are provided with the results. All tests are two-tailed.

Table 14: DOMINANCE INTERACTIONS AMONG ADULT COWS

		Loser																													Total
		KA	CR	MM	SB	LE	CU	RH	TN	LO	CO	HP	EM	FH	BU	NE	IH	ET	FR	VH	BH	SD	CB	RO	BM	JD	TE	VA	UR	R02	Wins
	KA	-	4	1	1	1	1	2		1	1		1	1		2	1										1		1		19
	• CR		-	1	1	2		1	1	1	1	1	1	1			3					1	1		1	2				1	20
	MM		1	-	2									1			1														5
	SB				-			1		2				1			2	1			1		1								9
	LE					-		2		2	1	1					3				1				1						11
	CU						-	1		4	1					1										1		1			9
	RH							-		14							1	1		1		3						1			21
	TN								-	1	1		2														1			1	6
	• LO						1			-	1	3			1				1		4					2					13
	• CO										-	1			1					1	3					1	2				9
	• HP							1				-	2	3		3								1		3		2	2		17
	EM			1		1							-						1		1						1		2	1	8
Winner	FH							1				1		-			2		1		1		1				1				8
	BU														-	1	2				2		2				1		2		10
	• NE									1						-	2		1	2	4		2	2					2	2	18
	• IH			2					1								-	2	1		1		3			1	2			2	15
	ET																1	-			1	2	1					1	1		7
	FR																		-		2			1			3				6
	VH																			-	1				5			4	1	1	12
	• BH												1								-		2	1							4
	SD																					-	2			1		1			4
	• CB	1																					-			2	1	1	2		7
	RO																				1			-							1
	BM																								-	1	2		1	1	5
	• JD																									-	1	3			4
	• TE																				1			1			-				2
	• VA																					3				1		-	2		6
	• UR																		1					1					-		2
	• R02																													-	0
	Total Loss	1	5	5	4	4	2	9	2	26	6	7	7	7	2	7	18	4	6	4	24	9	15	7	7	15	16	14	16	9	

• Focal subjects (mothers)

TABLE 15: DOMINANCE INTERACTIONS AMONG YOUNG FEMALES BORN IN 1983

		Loser																									Total
		RZ	VC	SO	CS	TU	EL	AN	J	MG	PN	CA	NA	BB	HO	HD	UB	TB	WL	RK	CL	LA	GA	RB	BUC	BN	Wins
	RZ	-	1	2	2					1	2		2	4		9		3			1						27
	• VC		-	3	2		3		7		4	1	2	1	2	2	5	5		3	2		2				44
	SO		1	-	2				5	1	2	3	3		1	3		11			1				2	1	36
	• CS	1			-	2	2	5	1			2		2	1	2		4				2					24
	TU				3	-		1	5		3			1	5	5	6	1			1		1		1	3	36
	EL						-	1		1						2	3				1					1	9
	AN		1					-	3				3	2		2	3				2		1				17
	• J	2		1		1			-		12		5	11	2		2	5	3	5			2		1	2	54
	MG				6					-	1		2	1	3	7		4								3	27
	PN										-		3	4			2	4		3	3		5				24
	CA											-	12			1			1			1	1	1	4		21
	• NA					1				1			-	6	4	2		4		5			1	4	2	3	33
Winner	• BB				1					1	1			-	3		1	4	1	1			1				14
	• HO					1					1		1		-	1		3									7
	• HD											1	4			-	2		1	4	1		1	1		2	17
	• UB									1	1						-	3	7		2		2		2	2	20
	• TB																	-		2	2					1	5
	WL								3									1	-		1	3			1	1	10
	RK												1			2	1			-	1				1		6
	• CL								2				2								-	1	1	1	1		8
	• LA														1		1					-		5			7
	GA														2								-			2	4
	• RB																				1			-		1	2
	BUC																								-		0
	• BN																									-	0
	Total Losses	3	3	6	16	5	5	7	26	6	27	7	40	32	24	38	26	52	13	23	19	7	18	12	15	22	

• Focal subjects

TABLE 16: DOMINANCE INTERACTIONS AMONG YOUNG FEMALES BORN IN 1982

		Loser																					Total
		C1	FC	UC	C2	BHC	DT	DC	SHC	CW	CT	WOC	LEC	LOC	IHC	CC	TG	SC	MC	OL	YC	WH	Wins
	C1	-		3				2		1				1		1			1				9
	FC		-		4		2	1		4	3		2	2	7			2		1	1		29
	UC			-	2	1		1		1		1			2	3		2			4		17
	C2				-	1	5		4		2	1	1	1	2			1				1	19
	BHC			1		-			3		10	1	2	2	1	1		3			2		26
	DT						-	2		1	2			2	1						1	1	10
	DC				3			-	1	3				1	5	1		1		1	5	1	22
	SHC					1			-		1					1							3
	CW									-	5	1		1	5		2						14
	CT										-	1	2	1	3	1	1	2			2	1	14
Winner	WOC			2				1				-	1	1		2	1	3		2	1		14
	LEC												-	2	1			1		1			5
	LOC											2		-	2	5	1		2		2	4	18
	IHC							1							-		2				2		5
	CC									1				1		-		2	1		1		6
	TG												1				-	1	1				3
	SC																	-	2				2
	MC													3					-				3
	OL																			-	2		2
	YC																				-	6	6
	WH													1								-	1
	Total Losses	0	0	6	9	3	7	8	8	11	23	7	9	19	29	15	7	18	7	5	23	14	

RESULTS

Dominance interactions appear to be more frequent among adult than juvenile cows; for the 13 focal dyads, mothers were engaged in about 0.3 interactions per hour, as opposed to 0.1 for daughters. Tables 14, 15, and 16 show the outcomes of dominance interactions of adult cows and two juvenile age-classes, respectively. Departures from linearity, including triangles and reversals, are numerous in all three hierarchies. For example, among 1983-born juveniles, 10.6% of the 452 matrix entries fall below the diagonal. The oldest cows seemed to be hardest to position in the adult hierarchy; while some were dominant to other older, high-ranking cows, they were occasionally displaced by young, generally subordinate cows. It appeared that their rank was decreasing during the period of the study, as senescence approached. The fact that data were collected over a two-year period may have accentuated such changes; this may also explain the relative absence of linearity in comparison with Rutberg's (1983, 1986a) data. On the other hand, reversals and triangles were also fairly common among the youngest, lowest-ranking adult cows.

The two measures of dominance, rank and dominance value, are closely correlated (juveniles: $r_S=.885$, N=46, $p<.001$, adults: $r_S=.786$, N=29, $p<.001$). In spite of the different aspects of dominance relations reflected, the two measures result in similar hierarchies.

AGE

Dominance among females increases with age, both within and between age classes, regardless of the magnitude of age differences. Among 29 adult cows, age (in years) is positively correlated with both dominance measures (dominance rank: $r_S=.792$, $p<.001$; dominance value: $r_S=.765$, $p<.001$). For the 13 focal mothers, age accounted for 88% of the variance in maternal dominance rank ($r_S=.938$) and 67% of the variance in dominance value ($r_S=.820$).

For juvenile females, dominance is related to birth order. Early-born daughters are dominant to those born later (dominance rank: $r_S=-.631$, N=46, $p<.001$; dominance value: $r_S=-.574$, N=46, $p<.01$; see Figure 37). Among the 13 focal subjects, birth order explained 79% of the variance in dominance rank ($r_S=-.889$) and 55% of the variance in dominance value ($r_S=-.741$).

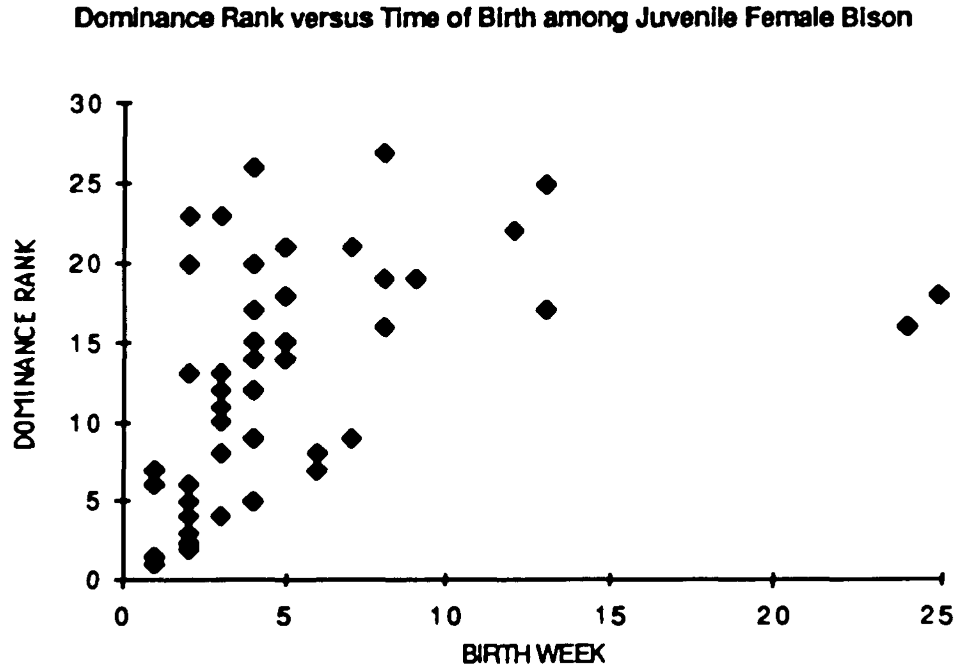


Figure 37: Dominance rank versus birth week for juvenile females. As shown here, the highest rank is #1. Dominance interactions were observed in 1983 and 1984, when subjects were between 6 months and 2 years of age. A separate hierarchy was calculated for each of two age classes; therefore more than one animal have the same rank. Birth weeks begin with the birth of the first calf of the year (in mid to late April). Nearly all daughters were born within the first 13 weeks (by the beginning of July); in 1982, however, two were born in September (i.e., weeks 24 and 25).

WEIGHT AND HORN LENGTH

Dominance among adult cows is quite unrelated to weight (e.g., dominance value vs. weight: r_S=.007, N=32). Horn length is also uncorrelated with dominance; many older, higher-ranking cows have broken horns. In contrast, dominance among juveniles increases with weight and horn length. For weight (N=41) vs. dominance value, r_S=.462, $p<.01$; rank: r_S=.437, $p<.01$. Horn length (N=20) shows closer correlations: for rank: r_S=.682, $p<.01$; dominance value, r_S=.594, $p<.01$.

REPRODUCTION

Among mature cows, reproductive success appears to be associated with some aspects of social status. Among cows in their prime (between 3 and 10 years old), those with higher dominance values produced more calves over a five-year period (r=.495, N=20, $p<.05$). However, dominance rank was not significantly correlated with fertility. These results suggest that reproductive success is related to the frequency with which cows win dominance interactions, but not with their relative ranks.

Comparisons of dominance among juveniles and the age at first calving suggest that dominant females tend to begin calving earlier than subordinates (dominance value: r_S=.-.388, N=37, $p<.05$; dominance rank: r_S=.-.327, N=37, $p<.05$). While correlation coeficients are low, the significant associations suggest that dominant juveniles are more likely to begin calving at 2 years, and subordinates to wait until they are 4.

DISCUSSION

These results suggest that dominance among bison cows confers a reproductive advantage. Comparisons of dominance with age and body size support the prediction that, where individuals recognize each other, dominance relations among members of different age classes are based on age rather than size. Thus findings for adult cows agree with those of Rutberg (1983). In contrast, dominance relations among juveniles within an age class are related not only to subtle differences in age, but also to aspects of body size, i.e., horn length and weight. Similarly, Beilharz and Mylrea (1963) found correlations between chest girth and dominance in yearling dairy heifers.

The fact that body size is associated with dominance among young animals but not among adults may be explained by the hypothesis that lack of previous contact between individuals favors dominance hierarchies based on size (Thouless and Guinness 1986; Lott and Galland 1987). Early size differences may play a role in establishing dominance relations. Dominance relations develop when animals are young, probably during the earliest interactions of calves. The relationship between birth order and social status suggests that age differences of as little as a few days can determine relative ranks. During the first week of life, calves born one day apart differ in size, coordination, and, perhaps, social experience. Baldwin's (1969) description of development in squirrel monkeys suggests the existence of similar relationships between birth order, size, and strength on the one hand, and dominance on the other.

Dominance relations of juveniles and adults also differ because of variation in the extent to which body size changes with age (see appendix C; see also Berger and Peacock, in prep.). Dominance develops while age and size are related; once individual relationships have been established, changes in relative size appear to have little effect on social status. Early-born bison daughters are larger as calves than those born later, weigh more as yearlings, and have longer horns (chapter 11). In contrast, weight does not increase with age for cows over three years old (appendix C; Lott and Galland 1987), and older cows often have broken horns.

Chapter 14

EFFECTS OF MATERNAL DOMINANCE ON RELATIONS WITH DAUGHTERS

INTRODUCTION

Associations between female dominance and reproductive success have been found in a number of mammalian species (e.g., elephant seals: Christensen and Le Boeuf 1978; primates: see Chapais and Schulman 1983 for a review; red deer: Clutton-Brock et al. 1986; bison: chapter 13). A related question which has received little attention is whether the maternal behavior of dominant mothers differs from that of subordinate mothers in such a way as to enhance the well-being of offspring. For example, within the crowded and rather dangerous elephant seal rookeries, the maternal behavior of high-ranking cows increases their reproductive success in several ways: relative to low-ranking cows, they obtain better parturition sites, protect their pups more effectively, and provide them with more milk (Reiter et al. 1981; McCann 1982). Dominance-related differences in maternal behavior have also been described in several primate species. Dominant mothers spend less time near their infants, initiate contact less often, and restrict their infants' movements less than subordinant mothers (Altmann 1978, 1980; Hinde and Spencer-Boothe 1971; White and Hinde 1975; French 1981). The behavior of dominant mothers may be influenced by the fact that their infants are more likely to be protected by other relatives (Berman 1983a, b), while subordinate mothers may restrict their infants' movements due to their fear of other group members (Altmann 1980; White and Hinde 1975). Altmann (1978, 1980) shows that the 'laissez-faire' behavior of dominant mothers is associated with earlier spatial independence in their infants. The offspring of dominant mothers also play more, probably due to their mothers' more relaxed attutudes toward their withdrawals and the presence of play partners (Gard and Meier 1977; French 1981). In light of the fact that most primate offspring acquire their mothers' ranks, these results suggest that the maternal behavior of dominant mothers helps their offspring acquire high ranks.

Long-term mother-offspring associations may also be influenced by maternal dominance. Fairbanks and McGuire (1985) examined interactions between 1-to 3-year-old vervet monkeys and their mothers. They found that daughters of dominant mothers spent more time near their mothers, approached their mothers more, and were more often aided by their mothers in dominance interactions. Clutton-Brock et al. (1982) report that dominant red deer hinds associate more with their adult daughters than do subordinate mothers. They found, moreover, that young hinds are protected from threats of other deer by the proximity of their mothers. Since dominant mothers afford greater protection than subordinate ones, these results suggest that, as in vervet monkeys, dominant red deer hinds protect their daughters more often than do subordinate mothers.

The purpose of this section is to compare maternal behavior and dominance among bison cows, and to consider ways in which the maternal behavior of dominant cows might result in advantages to their offspring, such as earlier independence and higher social status. Based on the findings described above, dominant bison cows should nurse their calves more than subordinate mothers. The spatial relations of dominant cows and their calves may encourage early filial independence; for example, dominant mothers may maintain proximity to daughters less often than other mothers. Finally, long-term associations with daughters should be more frequent for dominant than for subordinate mothers; daughters of the former might benefit from their mothers' protection.

METHODS

In order to test these predictions, interactions between mothers and daughters were compared with maternal dominance.

SUBJECTS: 13 mothers and their female calves (born in 1983) were observed during most of the first two years of the daughters' lives. For tests of long-term associations and maternal versus filial dominance, only mothers who calved again the next year were included; thus variation due to maternal reproductive condition was avoided. Since only eight of the 13 dyads fell into this category, supplemental data on yearlings in 1982 and 1983 were used. Sample sizes for such tests vary and are indicated with the results.

The fact that all offspring were female eliminated the possibility of individual variation in relation to offspring sex. Moreover, tests of bond-longevity among bison mother and offspring must be limited to daughters, since sons do not usually associate with their mothers after weaning.

DOMINANCE: In chapter 13, dominance interactions are described and data are summarized. Outcomes of dominance interactions are shown in table 14 for focal mothers and other cows, and in table 15 for focal daughters and their age-mates. To avoid ambiguity in relative status among cows resulting from missing data or departures from linearity, relative dominance was estimated in terms of dominance values; these were calculated as in chapter 13.

MOTHER-DAUGHTER RELATIONS: Data on pre-weaning interactions were pooled over the first five lunar months for each dyad. Measures used to evaluate maternal behavior include:

a) Nursing Behavior: Time spent nursing (mean bout duration and interbout interval). This was supplemented with aspects of the mother's behavior during bouts, in order to estimate the extent to which mothers discouraged their calves from nursing: the percent of bouts ended by calves, percent of bout-interruptions caused by mothers, and mean frequencies of rejected suckling attempts and maternal aggression.

b) Contact-Initiation: The frequency of non-nursing, non-aggressive contact interactions (e.g., nosing, rubbing) initiated by mothers and by daughters.

c) Proximity: The percent of scans at 2.5-minute intervals when mother and calf are within 10m, during all types of non-nursing activity, and during grazing periods.

d) Approaching: The frequency per hour with which mothers and daughters approach each other.

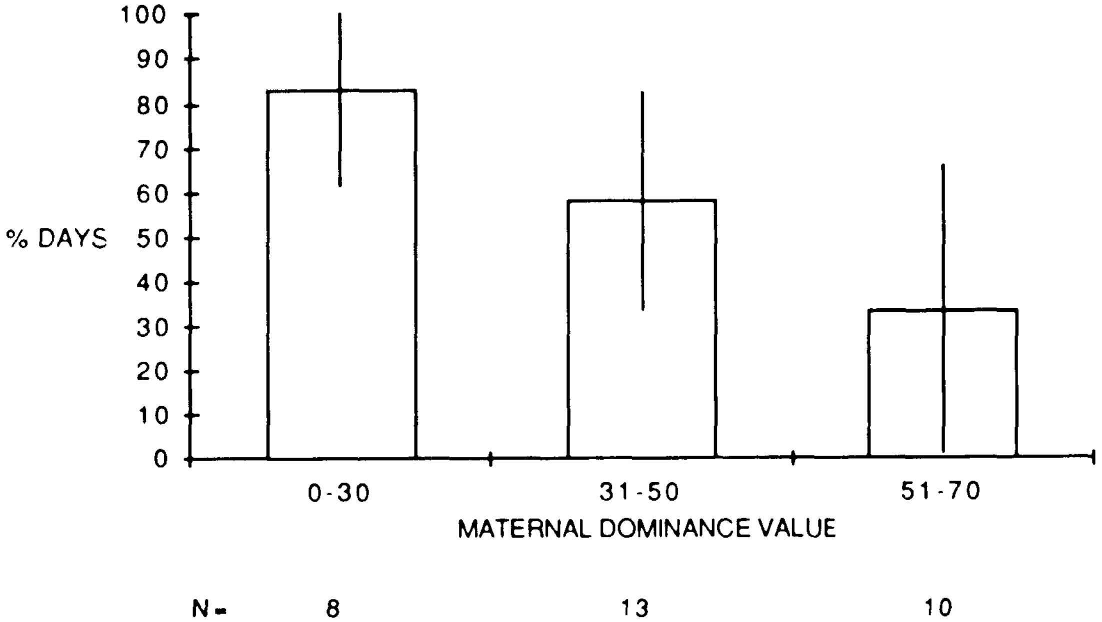
e) Following: The percent of scans at 2.5-minute intervals when mother and/or calf follow each others' movements. Following occurs when, after one walks away to 10m or more, the other moves in the same direction, behind the first.

The longevity of mother-daughter associations was estimated when daughters were about 1.5 years old. This measure entailed the percent of days when mother and daughter were in the same group and within 10m during the first five minutes after identification.

ANALYSIS: Maternal dominance values were compared with individual scores on all measures of mother-daughter relations, as well as with filial dominance values. Spearman rank correlation coeficients were calculated for comparisons involving behavioral rates. Pearson product-moment correlation coeficients were calculated for comparisons involving arcsine transformations of percentages. All tests are one-tailed, except where otherwise noted.

RESULTS

Comparisons of maternal dominance value with measures of nursing behavior suggest that dominant bison cows provide their calves with more nursing care than do subordinate mothers. Dominant mothers spend more time per bout nursing their calves: maternal dominance increases with bout duration (r_S=.602, p=.015). Estimated nursing time (mean bout duration/mean interbout interval) shows near-significant correlation with maternal dominance during the first month alone (r_S=.467, p=.054), but not during months 1-5 together. Thus early differences in nursing time appear to be more closely related to maternal dominance than are differences during succeeding months. That nursing care increases with mothers' status is further indicated by comparisons involving their behavior during nursing bouts. Dominant mothers interrupt bouts less often than do subordinate cows: maternal dominance decreases with the percent of bout-interruptions caused by mothers (r=-.566, p=.022). Dominant mothers also reject fewer of their calves suckling attempts (r_S=-.489, p=.045), and, during the first month, show less aggression toward calves (r_S=-.623, p=.015).



Maternal Dominance vs. Frequency of Association With Yearling Daughters

Figure 38: Mean percent of days (with 95% confidence limits) when mothers and their yearling daughters were seen in the same groups and within 10m of each other during the first five minutes after identification, as compared with maternal dominance. Mothers are grouped according to low, intermediate, and high dominance value; this measure is calculated as the arcsine transformation of the ratio of animals dominanted to the total number of social partners. Data on the percent association of mothers and daughters were collected in October of 1983 and 1984, when daughters were about 1.5 years of age.

Comparisons of maternal dominance and proximity-maintenance with offspring provide support for the predictions above. Results suggest that spatial relations between dominant mothers and their calves are not as closely synchronized as are those of subordinate cows and their offspring. The former dyads graze at larger distances; maternal dominance decreases with the percent of grazing time when mothers and calves are within 10m ($r=-.616$, $p=.013$). Dominant mothers and their calves also follow each other less frequently: dominance value decreases with the percent of time mothers and calves spend following each others' movements ($r=-.539$, $p=.029$). Moreover, dominant mothers rarely initiate contact with their calves; the frequency of mothers' initiation of contact is negatively correlated with dominance value ($r_s=-.720$, $p=.003$). Frequencies of mothers' approaching calves, however, do not support the predictions; subordinate mothers do not approach their calves more often than dominant mothers.

Examination of long-term mother-daughter relations indicates that, contrary to predictions, dominant mothers do not have longer associations with their daughters than subordinate cows. In fact, just the opposite is the case: dominant mothers associate least often with their yearling daughters ($r=-.911$, $N=8$, $p=.002$, two-tailed; including supplemental data: $r=-.491$, $N=31$, $p<.01$; see Figure 38). This suggests that daughters of dominant mothers do not benefit from the latters' protection.

Comparison of maternal and filial dominance suggests that daughters of dominant mothers tend to be dominant themselves; the dominance values of mothers and daughters are positively correlated ($r=.404$, $N=28$, $p<.05$).

DISCUSSION

Dominant mothers, relative to subordinates, provide more nursing care and have less closely synchronized spatial relations with their calves. The results suggest that, as predicted, the maternal behavior of dominant mothers enhances filial independence. This prediction is also supported by the finding that, contrary to expectations, dominant cows have shorter associations with their daughters than do subordinate mothers. Assuming that early independence is beneficial, daughters of dominant mothers thus appear to be at an advantage. That daughters of dominant mothers are at an advantage is suggested as well by the finding that they tend to achieve higher status among peers.

That subordinate, rather than dominant, mothers associate longer with their daughters argues against the hypothesis that long-term associations are important for the protection of daughters from threats of conspecifics, based on the findings of Clutton-Brock et al. (1982; see above). Rather, long-term associations may benefit subordinate mothers as well as their relatively subordinate daughters. Fairbanks and McGuire (1985) found that low-ranking vervet mothers were more often supported in dominance interactions by their juvenile offspring than were high-ranking mothers. While bison are unlikely to cooperate in dominance interactions in the same way as vervet monkeys, the dominance of mother and daughter may somehow be enhanced by their proximity and coordinated behavior (chapters 7 and 8). An alternate explanation, proposed earlier, is that, if young, subordinate cows must spend more energy in staying with the herd and watching for predators, they may be aided by close associations with subadult offspring.

In bison, dominance among cows is positively correlated with age (Rutberg 1983; chapter 13). Many of the same measures of mother-daughter relations are related to both factors. Thus it is difficult to separate the effects of these variables on relationships with young. For example, nursing behavior could be more closely related to age than dominance. This is suggested by the findings that, in domestic cattle milk production increases with age (Dodd 1957), but not with dominance (Collis 1976). However, the latter point may be an artifact of management procedures (Collis 1976). Moreover, in the present study, when maternal age was held constant, dominance value was positively correlated with nursing time during the first month. Rutberg's (1984, 1986a) finding, that dominant cows forage more efficiently than subordinates, also suggests that milk production is linked to dominance.

Chapter 15

DEVELOPMENT OF DOMINANCE

INTRODUCTION

How does the mother-young relationship affect offspring dominance? In many primate species (e.g., rhesus monkeys: Berman 1983b), offspring acquire the ranks of their mothers. Several mechanisms appear to contribute to this system. For example, offspring may learn the mother's rank by observing her interactions with other group members (Altmann 1980) or through maternal intervention in their own encounters (Cheney 1977). Altmann (1980) suggests that an infant's exposure to its mother's fear during dominance interactions is of major importance in the establishment of the infant's rank. Moreover, infants' ranks may be influenced by the protection of other relatives in addition to the mother; dominant infants have larger and more cohesive families (Berman 1983a, b).

Little is known about how female ungulates acquire dominance. In red deer, young hinds are protected from the threats of conspecifics through proximity to their mothers and other relatives (Clutton-Brock et al. 1982). The dominance ranks of daughters are related to those of mothers in red deer (Clutton-Brock et al. 1986) and in bison (chapter 14). These findings suggest that at least some aspects of the development of dominance in female ungulates are similar to those described for primates.

In bison, the order in which calves are born is closely correlated with their dominance ranks (chapter 13). Similar relationships exist in pronghorn antelope (Byers 1986) and in squirrel monkeys (Baldwin 1969). Why are early-born animals dominant to those born later? Baldwin (1969) attributes this to the fact that late-born young have only larger and more experienced peers to play with; thus they are likely to be dominated in interactions with peers. This appears to be the case in bison as well; the close relationship between birth order and dominance suggests that age differences of as little as a few days are accompanied by differences in rank.

Mother-young relations may also differ for early- and late-born calves; these differences may be an important factor in the development of offspring rank. For example, dominant daughters, being born earlier in the year, may receive more milk early in life. This is suggested by the finding of Guinness et al. (1971), that in red deer, milk yields decrease in the late summer; when hinds were prevented from conceiving until late in the season, only one in six had enough milk to rear her calf. This suggests that later-born calves are at a large disadvantage, not only in terms of peer relations, but also early nutrition. Indeed, late-born red deer calves are less likely to survive than other calves (Guinness et al. 1978; Clutton-Brock et al. 1982). Late-born bison calves appear to have additional problems in that they are born during or close to the rut, when the normally peaceful herd is transformed into a battle ground by bulls. The normal relations of mothers and calves are frequently interrupted (chapter 5). Late-born daughters and their mothers, perhaps to compensate, synchronyze their movements more than earlier-born calves and their mothers (chapter 11). This suggests that the patterns of spatial relations between bison mothers and calves differ between high- and low-ranking offspring, and that these differences may be similar to those described for baboons. Dominant baboon infants spend more time at a distance from their mothers and develop independence earlier; subordinate mothers are more restrictive of their infants' movements, probably as a result of greater potential danger from other group members (Altmann 1978, 1980).

This section examines associations of offspring dominance with early and long-term interactions with mothers, in order to identify aspects of the mother-young relationship which may play a role in the development of dominance. For example, dominant daughters may suckle more early in life, and show correspondingly less conflict with mothers over nursing time. Moreover, as in baboons, they may develop independence earlier than lower-ranking daughters.

METHODS

In order to test these predictions, measures of mother-offspring relations were compared in Spearman rank correlations with the dominance of daughters in relation to other females born during the same year. Comparisons involving nursing time and filial independence are one-tailed, based on the predictions above.

SUBJECTS

Thirteen mothers and their female calves born in 1983 were observed during most of the first two years of the daughters' lives. The fact that all offspring were of the same sex eliminated the possibility of individual variation in relation to offspring sex. In order to consider the extent to which subsequent maternal reproductive condition is related to filial dominance, tests of post-weaning relations were performed on all subjects (N=13) as well as on a smaller subset of this group (N=8) including only mothers who calved again the next year.

MEASURES

Dominance: Dominance interactions were observed when subjects were between 6 months and 2 years of age. Such interactions are described in chapter 13, as are methods of calculating two measures of dominance: rank and dominance value. Rank was employed in this analysis because of its sensitivity to the relative positions of peers within the hierarchy; dominance value was omitted in an effort to reduce redundancy. Correlations between rank and dominance value are extremely close; for the 13 subjects, $r_S=.976$, $p<.001$. Table 15 (chapter 13) shows dominance interactions among the subjects and their peers. Ranks are reversed in the results, so that dominance increases with the magnitude of the score; thus positive correlations indicate that dominant animals score higher on other measures.

Mother-Daughter Relations: While pre-weaning relations between mothers and calves were estimated primarily over the first five months, nursing interactions during the first three weeks were examined as well, so as to consider the relationship between early nursing behavior and offspring dominance.

Measures of pre-weaning relations are as follows (see chapter 2):

1) Weeks 1-3: Nursing time (min/h), estimated as mean bout duration/mean interbout interval.

2) Months 1 to 5: Data for each dyad were pooled over the first five lunar months, excluding the first week of life. Measures include:

a) Nursing Behavior: Time spent nursing (mean bout duration/mean interbout interval). In order to estimate nursing conflict as well as the extent to which mothers discouraged their calves from nursing, these data were supplemented with aspects of the mother's behavior during bouts: the percent of bouts ended by calves, percent of bout-interruptions caused by mothers, and mean frequencies of rejected suckling attempts and maternal aggression.

c) Vocalization: In order to estimate long-distance contact-maintenance, the frequency with which mothers and calves vocalized toward each other were examined.

d) Proximity: The percent of scans (at 2.5-minute intervals) when mother and calf are within 10m, during all types of non-nursing activity, and during grazing periods.

e) Approaching: The frequency per hour with which mothers and daughters approach each other across a 1m boundary.

f) Following/Not Following: The percent of scans (at 2.5-minute intervals) when mother and/or calf do or do not follow each others' movements. Following occurs when, after one walks away to 10m or more, the other moves in the same direction, behind the first. Not following is scored when one remains behind after the other has moved away to 10m or more.

3) Post-weaning relations were measured during the second year of daughters' lives, in months 15 and 16. This period included the time after the mother' next calf had been born and before the mother was tended again; thus outside constraints on maternal relations with yearling daughters were minimized. Measures (b), (c), and (d) include only time when mother and daughter were both present in the same groups; these measures are the same as those used during the first five months.

a) Group Membership: The percent of days when mother and daughter were in the same group.

b) Proximity in all activity types

c) Approaching

d) Following/Not Following

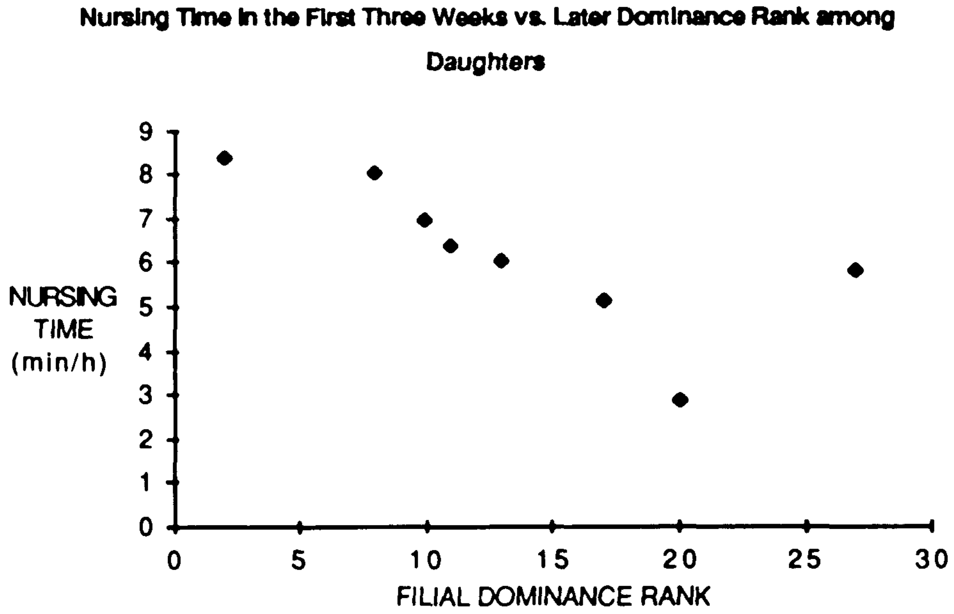


Figure 39: Estimated nursing time (mean nursing bout duration/mean interbout interval, in minutes/hour) during the first three weeks of calves' lives, as compared with the dominance ranks of daughters as yearlings. 27 female yearlings were included in the hierarchy (see table 15, chapter 13). Data shown here are for focal dyads in which mothers calved again during the year after the subjects were born.

RESULTS

NURSING TIME DURING THE FIRST THREE WEEKS:

Filial dominance rank is closely related to early nursing behavior. When mothers spend more time nursing during the first three weeks, daughters are more likely to become dominant: time spent nursing (minutes/hour) is positively correlated with dominance rank ($r_S = .793$, $p = .001$). Among the eight focal dyads in which mothers gave birth the following year ($r_S = .929$), 86.3% of the variance in yearling dominance rank is explained by nursing time during the first month of life (see Figure 39).

NURSING AND SPATIAL INTERACTIONS DURING MONTHS 1 TO 5

In contrast with the first three weeks, filial dominance is not significantly related to nursing time during the first five months (r_S=.167 ns), nor is it correlated with the behavior of mothers and calves during nursing bouts.

Comparisons between dominance among daughters and their pre-weaning spatial relations with mothers suggest that high social status is related to early independence. Higher-ranking daughters are more likely to remain behind when their mothers walk away: the percent of time when daughters do not follow mothers' movements is positively correlated with dominance rank (r_S=.631, p=.011). Dominant daughters spend correspondingly less time than others resting within 10m of their grazing mothers (r_S=-.522, p=.034). That their mothers vocalize more frequently than other mothers (r_S=.595, p=.031) may be related to the first two findings.

Several measures of pre-weaning spatial relations are not significantly related to filial dominance. In particular, proximity in all types of activity, and the frequencies with which mothers and calves approach each other, do not differ for high- and low-ranking daughters.

POST-WEANING SPATIAL RELATIONS

Because of the relationship between bond-longevity and the mother's reproductive status during the year after the offspring's birth (chapter 6), the following results are based on samples limited to mothers with new calves (N=8).

As predicted, subordinate daughters have longer-lasting associations with their mothers. During Months 15 and 16, dominant yearlings spend less time than subordinates in the same groups with their mothers (r_S=-.805, p=.008). When mothers and daughters are in the same group, dominant yearlings spend less time near their mothers: the percent of time within 10m is negatively correlated with filial dominance: r_S=-.667, p=.036. That high-ranking daughters become independent of their mothers earlier is further indicated by the fact that some of the behaviors involved in mothers' and daughters' efforts at maintaining proximity during the second year are related to filial dominance. Subordinate daughters and their mothers spend more time following each others' movements than do other dyads: dominance rank is negatively correlated with the percent of time mothers spend following daughters (r_s=-.810, p=.008) and daughters spend following mothers (r_s=-.762, p=.014).

The above associations are significant for all focal dyads (N=13) as well as those in which the mother had a new calf (N=8). This suggests that the mother's reproductive status has little effect on yearling dominance rank. Social status appears to be established during the first few months, before mothers differ in reproductive condition. Subsequent reversals in the dominance status of daughters of barren as opposed to pregnant cows occurred rarely if at all.

DISCUSSION

EARLY NURSING CARE: The results indicate that early nursing care is closely related to filial status. Dominance increases with nursing time during the first few weeks; however, nursing behavior throughout the first five months does not differ for high- and low-ranking daughters. This suggests that nursing time very early in life is a particularly important factor in offspring dominance.

Comparisons of this finding with those of previous sections suggest that early nursing time is directly related to offspring dominance, rather than contributing through another variable, such as weight. Nursing time is correlated with offspring dominance, but not with any of the variables associated with the latter factor. Nursing behavior is not correlated with offspring size, weight, or horn length (chapter 12), all of which are related to filial dominance (chapter 13). Moreover, birth order is not significantly correlated with nursing time (chapter 11), thus weakening the hypothesis that early-born bison daughters become dominant because they receive more milk (based on the findings of Guinness et al. 1971).

FILIAL INDEPENDENCE: As suggested by Altmann's (1978, 1980) observations of baboons, high-ranking bison daughters appear to develop independence earlier than subordinates. While comparisons of pre-weaning spatial relations with filial dominance yield equivocal results, stronger evidence from post-weaning relations reinforces the possibility that subordinate daughters and their mothers more frequently follow each others' movements, stay closer together, and maintain the association longer. While the frequency of approaches does not vary in relation to dominance, this measure reflects decreased distance rather than synchrony of movements and the maintenance of proximity (see chapter 11).

Subordinate, later-born calves may compensate to some extent for their apparent disadvantages by relatively close, synchronized mother-daughter relations, and by prolonged associations with mothers after weaning. Low-ranking daughters may receive different types, rather than smaller quantities, of maternal care. This possibility is supported by the fact that both subordinate daughters and their mothers make greater long-term efforts at maintaining proximity (see also chapter 8).

Dominance relations among juveniles may also be reciprocally related to their spatial relations with mothers. For example, late-born calves are subordinate to those born earlier (chapter 13) and have closer, more synchronized relations with mothers (chapter 11). Their subordinate status may be interrelated with the closeness of their relations with mothers. In the first place, problems associated with late birth, such as interruptions of mother-calf relations due to rutting activities, may necessitate their staying close to their mothers to avoid separation. This may cause them to spend relatively little time interacting with peers. At the same time, the fact that they are the youngest of all calves puts them at a disadvantage in social competition (as in squirrel monkeys: Baldwin 1969). Thus the relatively close, synchronyzed relations of late calves and their mothers may result in part from the calves' low status among peers; such calves may prefer to be with their mothers rather than other herd members.

Chapter 16

SUMMARY

CHAPTER 3: PRE-WEANING SPATIAL RELATIONS BETWEEN MOTHERS AND CALVES

The early spatial relations of bison mothers and daughters are largely unsynchronized. Even in the second week of life, cows and calves follow each others' movements infrequently and are often at a distance; calves take most of the responsibility for maintaining proximity. That mothers do not protect their sleeping calves is suggested by the fact that they spend more time at a distance when calves rest than when the latter are active. Spatial relations change minimally during the first seven months. These results suggest that bison are neither hiders nor followers, but incorporate aspects of both anti-predator strategies.

CHAPTER 4: NURSING AND OTHER CONTACT INTERACTIONS IN RELATION TO MATERNAL AGE

Older bison cows, relative to young cows, spend more time nursing their calves, allow their calves to end more bouts, and behave more patiently during nursing bouts. These results support the hypothesis that older mothers care more for present offspring. However, the finding that young mothers initiate more non-aggressive, non-nursing contact with calves suggests that age-related differences in bison maternal behavior are in fact more complex and may involve contrasting strategies of parental investment by old and young mothers.

CHAPTER 5: MATERNAL EXPERIENCE AND THE EFFECTS OF TENDING ON RELATIONS WITH DAUGHTERS

The effects of tending on various aspects of mother-young relations depend on maternal experience. For young mothers and their calves, nursing time decreases during tending, activity and movements become less synchronized, and mother and calf spend somewhat less time grazing close together. In contrast, older mothers and their calves show either no change or a change in the opposite direction. These results suggest that experience helps mothers and their calves to maintain normal relations during tending.

CHAPTER 6: WEANING IN BISON: A REDEFINITION OF THE MOTHER-DAUGHTER RELATIONSHIP?

Patterns of change in nursing time do not conform to a model of weaning as a period of rapidly decreasing maternal care. Rather, nursing care decreases gradually during the first three months and then continues at a lower and relatively unchanging level for at least four more months. Conflict between cows and calves is infrequent and does not reflect a concentrated 'weaning' period, as suggested by the model. Calves gradually increase their grazing time as nursing time decreases. The age at which daughters stop suckling depends on the mother's reproductive status in the subsequent year. For daughters of pregnant mothers, nursing ended between 9 and 12 lunar months of age, as compared with 17.5 to more than 20 months for those of barren mothers. These results suggest that, in gregarious species, weaning does not signal the end of the relationship, but rather its redefinition.

CHAPTER 7: DO BISON DAUGHTERS HAVE LONG-TERM ASSOCIATIONS WITH MOTHERS?

Post-weaning associations vary widely among dyads. Between the end of weaning and the birth of the mother's next calf, most pregnant mothers and their daughters spend increasing amounts of time in separate groups. However, this period of separation generally ends after the birth of the mother's next calf. Comparisons of the long-term relations of pregnant and barren mothers with daughters show that weaned daughters and their mothers spend less time close together, but do not differ in behavioral aspects of spatial relations. Subjects associated with their mothers significantly more often than with other cows in the second and third year of life. These results indicate that, for most bison daughters, relations with mothers do not end with weaning.

CHAPTER 8: THE MOTHER'S ROLE IN MAINTAINING LONG-TERM RELATIONS

Bison mothers contribute substantially to the maintenance of long-term bonds with daughters, even after the birth of their next calves; their efforts appear largely to determine whether or not the associations continue. These results suggest that mothers benefit directly from long-term associations.

CHAPTER 9: PATTERNS OF VARIATION IN MOTHER-DAUGHTER RELATIONS

Principal component analyses indicate that bison mother-daughter relationships are polymorphic, and that certain types of relationships last longer than others. Predominant classes are characterized by spatial independence, e.g., the frequencies with which mothers and calves walk away from each other, and by maternal nursing tolerance. Daughters appear to develop independence earlier when mothers provide more extensive, uninterrupted nursing time, more often follow calves' movements, and most frequently threaten and kick their calves in the first few weeks of life.

CHAPTER 10: FILIAL INDEPENDENCE AND RELATED MATERNAL QUALITIES

Correlations among measures of maternal and filial behavior describe a continuum of dyadic interaction. At opposite ends are independent mothers and independent calves; these two types are never found in the same dyad. Calves are most independent when mothers frequently maintain proximity and behave patiently during nursing bouts. When mothers show opposite behavior patterns, calves make great efforts at maintaining proximity. Independent calves appear to maintain contact in part by controlling their mothers' behavior. These results demonstrate that filial independence and dependence varies substantially in relation to maternal behavior.

CHAPTER 11: EFFECTS OF VARIATION IN FILIAL AND MATERNAL AGE ON MOTHER-DAUGHTER RELATIONS

Late-born calves and their mothers synchronize movements more than do the members of other dyads. Late mothers are less likely to leave their calves, and more likely to follow their calves' movements; when they walk away, their calves rarely stay behind. Such mothers also show more nursing tolerance than other mothers. Similarly, young mothers, relative to older cows, have somewhat closer, more synchronized spatial relations with their calves. Young mothers and their daughters continue to spend more time together in the daughters' second year of life. Young mothers and late-born calves, together with their partners, behave as if to compensate for disadvantages such as inferior milk yields and low social status.

CHAPTER 12: PHYSICAL VERSUS SOCIAL DEVELOPMENT

Larger daughters are born earlier in the year, develop higher social status, and may calve earlier, than smaller daughters. In contrast to predictions, offspring size is little related to early maternal care and close spatial relations; in fact, large daughters and their mothers spend less time close together than other dyads, and behave more independently of each other. On the other hand, the prolonged maternal care given by mothers who do not calve in the year following a daughter's birth results in greater offspring size and, possibly, earlier reproduction. A second measure of offspring physical condition, the duration of the natal coat, shows similar correlations. Calves who retain their natal coats longer are born earlier, weigh more as yearlings, have higher-ranking mothers, and may reproduce earlier, but do not receive more maternal care.

CHAPTER 13: DOMINANCE RELATIONS AMONG ADULT AND JUVENILE BISON COWS AS COMPARED WITH AGE, SIZE, AND REPRODUCTION

Dominance is correlated with age but not body size among bison cows of varying age classes. In contrast, dominance among juveniles within an age class is related not only to subtle differences in age, but also to aspects of body size (i.e., horn length and weight). These results support the hypothesis that the outcomes of initial dominance interactions are determined primarily by size differences; once individual relationships have been established, changes in relative size have little effect on social status. Thus, where individuals recognize each other, dominance relations are based on age rather than size. The results suggest, moreover, that dominance among bison cows confers a reproductive advantage.

CHAPTER 14: EFFECTS OF MATERNAL DOMINANCE ON RELATIONS WITH DAUGHTERS

Dominant mothers provide their calves with more nursing care than do subordinates. Their daughters develop independence earlier than others; where the mother is dominant, early spatial relations are less synchronized and the bond ends earlier. That daughters of dominant mothers are at an advantage is indicated by the finding that they tend to be dominant among peers.

CHAPTER 15: DEVELOPMENT OF DOMINANCE

Daughters who receive more early nursing care become dominant among peers. High-ranking daughters are more independent of their mothers than are subordinates, as indicated by pre- and post-weaning spatial relations. Low-ranking daughters and their mothers follow each others' movements more often and stay closer together. That dominant daughters develop independence earlier is emphasized by the finding that their associations with mothers end earlier.

Appendix A

REPRODUCTION AND MORTALITY

I. Factors Affecting Reproduction Among Cows

AGE

First Calving: Most cows calve for the first time at 3 years of age. Out of 86 cows whose time of first calving was known between 1982 and 1986, 4 cows (5%) had their first calves at age 2, 68 cows (79%) at age 3, and 14 cows (16%) at age 4.

Last Calving: During the five years between 1982 and 1986, 10 cows were considered to be post-reproductive. Of these, six died naturally (see Mortality, below), one was killed at an advanced age (21) after not having calved in several years, and three are still alive. The latter three have passed the maximum age at which other cows have stopped calving (i.e., 18 years); moreover, they have produced no calves for the last two or three years. These 10 cows produced their last calves at the following ages: two at 16, two at 17, five at 18, and one at 19 years. (The last calves of the three living cows were born at 18, 18, and 19 years). Most cows die within two or three years after the birth of their last calf. One cow died early in her seventeenth year after producing calves during each of the four previous years. Another produced her last calf at 17 and remained active though barren for the next four years.

Non-Reproductive Cows: A few cows never reproduced between 1982 and 1986. Of 74 cows known for at least 3 years while they were three or more years old, 5 never calved. Many such cows were larger than the average cow, and behaved rather differently. They were frequently seen near each other, or with other barren cows, often at the edge of the herd. One non-reproductive cow spent much of the year in small groups of bulls, completely separate from other cows and juveniles.

INCIDENTS OF NON-CALVING AMONG NORMALLY REPRODUCTIVE COWS

Those cows which are not post-reproductive, nulliparous (up to age 4) or "non-reproductive" (as described above) are here referred to as 'reproductive'; most mature cows are included in this category. Each year, some of these cows failed to calve. In 1982, 22% of the reproductive cows did not calve; in 1983, 4%; in 1984, 12%; in 1985, 13%, and in 1986, 38% were barren (see Figure A1). An unusually high proportion of cows failed to calve in 1986, possibly as a result of unusually dry conditions in the previous year.

Do incidents of calving failure reflect a dimorphic reproductive strategy or a widespread, infrequent phenomenon? The limited data presented here lend some support to the former possibility. Of the 69 cows who were reproductive in three or more years, only 48% (33 cows) calved every year. Eight cows were barren in two (N=6) or three (N=2) out of five years. Alternating patterns of reproduction were apparent during the five-year period for six of these eight, representing 9% of reproductive cows. On the other hand, the fact that calving failures were so much more common in 1986 than in 1983-85 suggests that ecological conditions play an important role in determining whether or not all cows reproduce.

If calving failure is caused by poor physical condition, one would expect very young and old cows to be barren more frequently. This prediction is supported by results of the present study. Data on reproduction in 1982-1986 indicate that very young parous cows are more likely not to calve: all four cows who began calving at two years of age failed to calve the following year. Those who start calving at 3, in contrast, do not show a greater than average incidence of calving failure the following year. Similarly, cows from 10 to 17 years of age failed to calve significantly more often than did those of less than 10 years (those over 17 were omitted since nearly all non-calving ocurred among post-reproductive cows). Figure A1 shows the rates of calving failure in each year for cows under 10 as compared with those 10 or over. During the four-year period from 1982 through 1985, the rate of calving failure was 29% for cows 10 or older and 8% for those under 10. (X^2 = 16.2, df=1, $p<.001$). When 1986 is included, the difference is somewhat smaller (28% for cows >=10 and 16% for those <10 years; X^2 = 4.4, df=1, $p<.05$; see below). These results indicate that whether or not a cow calves in a given year is related to her age, and, probably, physical condition. They also suggest that the end of reproduction is a gradual rather than abrupt phenomenon.

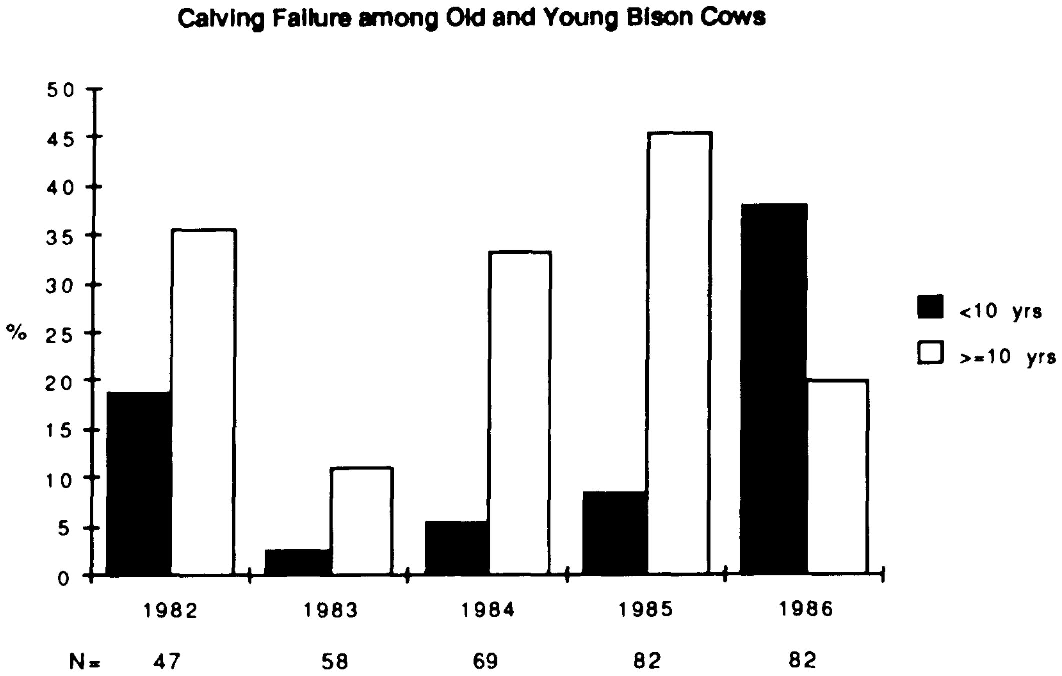


Figure A1: The percent of 'reproductive' cows (see text) that failed to calve in each of two age classes, during 1982 through 1986.

In 1986, the relationship between age and fertility was reversed (see Figure A1). In that year, an unusually large number of cows (38%) did not calve. Out of 29 barren cows, one was 10 years old, and one was over 10; the rate of calving failure among cows under 10 was about twice that of older cows (39% vs. 20%). While the proportion of the herd represented by older cows had decreased since 1982, it was not different from that in 1985 (i.e., about 12%). It appears that the conditions which lowered the calving rate in 1986 did so only for younger cows. For example, of the 16 four-year-olds in 1986, only five calved, and four of these were the cows that had delayed their first reproduction until their fourth year. Only one from this age class calved in both 1985 and 1986. In contrast, older cows actually produced more calves under these conditions: Nine out of 11 cows 10 years and older calved in 1986.

OFFSPRING BIRTH DATE

The time of a calf's birth may play a role in determining whether or not the mother calves again the next year. The normal period between successive calves appears to be slightly more than a year; for13 cows, parturition in 1984 occurred between 53 and 55 weeks after the previous calving. Therefore mothers of late-born calves are likely to calve even later the next year. Results of the present study suggest that late calving is related to calving failure in the next year. In 1982-1986 , 17 calves were born after August 15. In 12 of these cases, the mother did not calve in the subsequent year. Thus 71% of late births were followed by calving failure.

Cows who calve late may skip a year to avoid possible disadvantages associated with late calving (see chapter 11). For example, one cow calved in September in three consecutive years, and then failed to calve in the fourth. Subsequently, she calved during the spring birth peak for at least two years.

OFFSPRING SEX

Previous research has suggested a relationship between alternate-year reproduction and offpring sex. Rutberg (1986) reports that bison cows who were previously barren are more likely to have male calves. Data from the present study do not support this thesis: of 28 cows calving after a year's respite, 14 produced female and 14 male calves. Since the rationale is that such cows are in better physical condition than those that have just raised a calf and are therefore more likely to produce a successful son, one might also consider cows who postpone their first calving until the fourth year. However, these data also fail to confirm Rutberg's results: six out of nine such cows produced female calves.

If offspring sex affects calving rates, perhaps the subsequent rather than the previous year is more critical. In other words, mothers of sons may be more likely to be barren in the year following the son's birth. Assuming that male calves need more care than females, the process of nuturing a son might decrease the mother's condition ablility to reproduce the next year. Moreover, maternal care over a longer period might add significantly to the young bull's mating success. Data on female yearlings show that those nursed in their second year (i.e., when mothers are barren) weigh significantly more than other yearlings (chapter 12); sons may also benefit from long-term maternal care. Results of the present study provide tentative support for this hypothesis: of 53 calves produced by subsequently barren cows, 59% were male.

OFFSPRING SEX AND MATERNAL AGE

If, as these data suggest, calving rates are related to both maternal age and offspring sex, maternal age and offspring sex may also be interrelated. Data from 1982-1986 suggest that such a relationship exists. Specifically, very old cows bore a predominance of female calves: 9 out of the 10 last calves produced during this period were female. This suggests that cows are more likely to bear female calves when in poor physical condition.

II. Mortality

In the absense of predation, old age and calving appear to be the major natural causes of death among bison cows. Between 1982 and 1986, six older cows died naturally; these were aged 21, 21, 19, 19, 19, and 17. During the same period, five younger females died naturally. Two cows, aged 11 and two years, disappeared during the calving peak; the two-year-old had been found to be pregnant during the roundup five months earlier. Thus they appear to have died while calving. An unknown cow and newborn calf were also found dead in the spring of 1982. For three other females, aged 3 years, one year, and one month, respectively, the causes of death were not identified, although the calf appeared weakened by disease. Calf mortality was clearly rare: of 153 live births in three years, one calf died from natural causes. During the same period, however, at least five still births occurred.

Appendix B

NURSING INTERACTIONS: MATERNAL TOLERANCE AND INTOLERANCE

Comparisons among measures of nursing interactions between 13 cows and their female calves indicate the presence of a continuum, the extremes of which may be described as maternal tolerance and intolerance. Within each group (i.e., at each end of the continuum), measures are positively correlated; between groups, they are negatively correlated. Components of these two behavioral extremes are listed below. Table B1 shows correlation coefficients; measures are described in chapter 2.

MATERNAL TOLERANCE

- Nursing time: minutes/hour (MIN/H)
- Nursing bout duration: minutes (NDUR)
- Percent of bouts ended by calves (%CEN)
- Frequency of calves' interruptions (pauses) per nursing bout (CPS)

MATERNAL INTOLERANCE

- Frequency of rejected suckling attempts per nursing minute (RSA)
- Frequency of maternal aggression per nursing minute (MAR)
- Percent of bout-interruptions caused by mothers (%MINT)

TABLE B1
CORRELATIONS AMONG MEASURES OF NURSING BEHAVIOR*

		%CEN	CPS	RSA	MAR	%MINT
Maternal 'Tolerance'	NDUR	.587 *	.669 *	-.697 * *	-.598 *	-.466 ns
	MIN/H	.779 * *	.696 * *	-.732 * *	-.609 *	-.697 * *
	%CEN		.861 * * *	-.828 * * *	-.648 *	-.741 * *
	CPS			-.707 * *	-.566 *	-.840 * * *
Maternal 'Intolerance'	RSA				.774 * *	.734 * *
	MAR					.576 *
	%MINT					.

* For behavioral rates, Spearman rank correlation coefficients are shown; for arcsine transformations of percentages, Pearson product-moment coefficients.
Significance levels are indicated by * (p<.05), ** (p<.01), and *** (p<.001).
All tests are two-tailed and based on a sample of 13 mother-daughter dyads.
Data are pooled for each dyad over the first five months of calves' lives.

Appendix C

AGE VERSUS WEIGHT IN FEMALE BISON

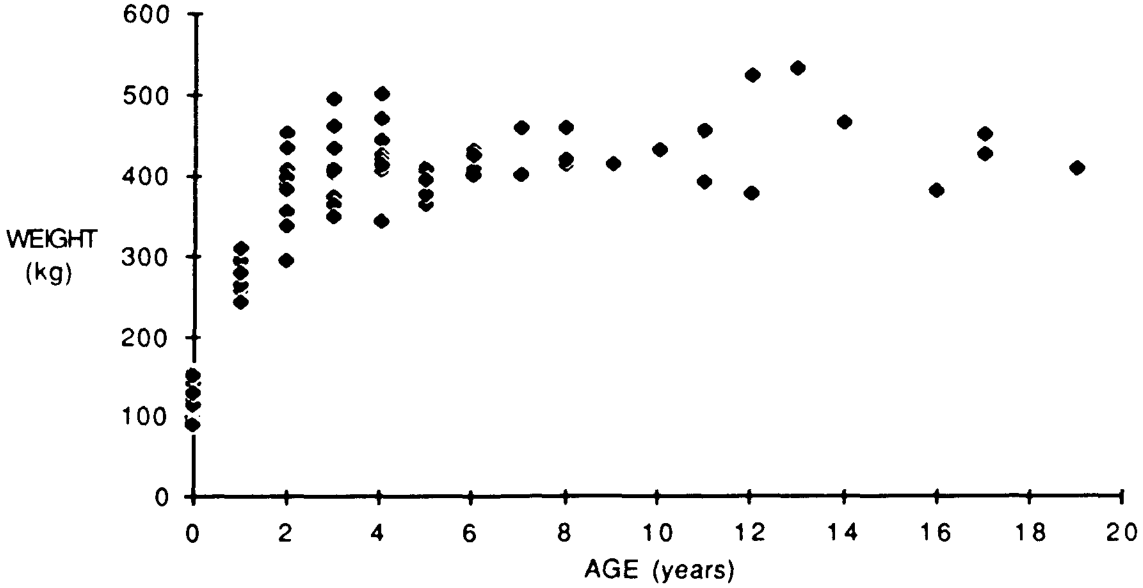


Figure C1: A comparison of weights of female bison representing all ages, from the calf stage (age=0) to 19 years of age. Weights were measured during fall roundups. The pattern suggests that weight increases dramatically with age during the first three years, but changes little thereafter.

CORRELATIONS AMONG ADULT COWS:

For cows aged 4-19, size and age are not significantly correlated (r=.190, N=38). When three-year-old cows are included, however, size increases with age (r=.410, N=57, p<.01, although age differences account for only 17% of the variance in weight.

TABLE D1: DOMINANCE, AGE, WEIGHT, AND FERTILITY IN ADULT COWS

Cow:	Rank	DV	Age	Weight (kg)	Fertility (%)	Cow:	DV	Age	Weight (kg)	Fertility (%)
KA	1	67.2	11	523	100	RT	49.1	11	377	60
CR	2	73.2	12	534	75	SN	60.0	10	393	40
MM	3	39.2	7	439	80	HT	65.9	7	419	100
SB	4	54.9	16	418	60	WC	45.0	7	425	100
LE	5	51.7	14	466	100	IS	60.0	6	402	100
CI	6	56.8	18	-	-	WT	63.4	6	427	80
RH	7	45.0	10	457	80	AM	60.0	5	395	100
TN	8	54.7	5	401	100	OM	57.7	5	400	100
LO	9	46.2	17	-	-	RM	60.0	5	439	80
CO	10	43.3	18	-	-	ST	63.4	4	414	100
HP	11	54.7	15	382	25	WM	45.0	4	-	100
EM	12	47.3	17	400	60	YM	0.0	4	420	60
FH	13	51.7	10	459	80	PE	35.3	4	380	100
BU	14	62.0	17	-	-	RS	54.7	4	377	100
NE	15	56.8	10	443	100	BR	50.8	4	397	100
IH	16	45.0	8	411	100	GN	60.0	3	343	67
ET	17	54.7	4	436	60	LR	0.0	3	377	100
FR	18	43.3	3	-	-	AB	90.0	3	503	100
VH	19	43.1	4	425	100	T1	45.0	3	395	100
BH	20	29.4	4	411	80					
SD	21	30.0	4	411	60					
CB	22	28.9	3	448	100					
RO	23	20.7	3	418	100					
BM	24	41.8	5	430	80					
JD	25	30.0	3	427	75					
TE	26	23.4	3	395	50					
VA	27	27.3	3	439	75					
UR	28	25.2	3	450	75					
RO2	29	15.5	2	380	-					

Notes: Dominance ranks, dominance values (DV), ages, weights, and fertility are shown for all cows who were parturient as of 1983.
Cows included in the dominance hierarchy (i.e., those on left, for whom ranks were estimated) were observed interacting with at least 8 other cows; all others were omitted from the hierarchy.
Dominance interactions were observed in 1983 and 1984 (see 'Methods', chapter 13, for explanation of dominance value).
Ages shown are for 1983; weights shown were measured in 1984.
Fertility is measured as the percent of years, from 1982 to 1986, in which cows had calves.
In most cases the maximum is 5 calves; for younger cows, however, the maximum is 3 (N=4) or 4 (N=6).

TABLE D2: FEMALES BORN IN 1983

Name	Rank	Dominance Value (DV)	Birth Week	Weight (kg)**	Age at 1st Calving	Mother's Age	Mother's Rank	Mother's DV	Mother's Weight (kg)	Mother had 1984 calf?
RZ	1	65.9	1	298	-	11	3	49.1	377	yes
VC	2	65.9	2	308	3	3	33	27.3	422	yes
SO	3	64.4	2	292	-	4	-	63.4	411	yes
CS	4	54.8	2	-	-	12	1	73.3	534	no
TU	5	61.0	2	257	3	16	2	54.8	425	yes
EL	6	60.0	1	295	-	4	37	54.8	398	yes
AN	7	58.5	6	265	3	5	19	60.0	402	yes
J	8	56.5	3	-	3	3	32	30.0	427	yes
MG	9	49.1	7	245	4	7	8	39.2	459	yes
PN	10	41.4	3	264	3	4	26	35.2	366	yes
CA	11	49.8	5	280	3	18	9	56.8	-	(M died)
NA	12	43.9	4	309	3	10	10	56.8	453	yes
BB	13	46.5	3	-	3	3	31	28.9	445	yes
HO	14	35.2	3	308	2	15	5	54.8	382	no
HD	15	40.9	4	299	3	8	16	45.0	414	yes
UB	16	40.5	4	315	-	3	34	25.3	473	yes
TB	17	28.1	4	264	4	3	28	23.4	427	yes
WL	18	47.6	5	255	3	4	32	45.0	-	yes
RK	19	40.2	2	-	-	4	23	54.8	377	yes
CL	20	34.2	9	282	3	18	13	43.5	-	no
LA	21	45.0	5	-	-	17	11	46.4	-	no
GA	22	22.2	12	205	-	5	-	-	-	(M died)
RB	23	32.3	13	261	3	2	35	15.5	374	no
BUC	24	0.0	4	245	4	17	-	61.9	-	(M died)
BN	25	0.0	8	218	4	4	29	29.4	411	yes
Q	- *	45.0	8	239	3	5	24	57.7	408	yes
RA	- *	35.2	3	-	-	5	12	60.0	432	yes

* Data on Q ans RA were insufficient to determine rank

Subjects for whom no ages at first calving are shown either died or were unidentified

** Weights were measured at 1.5 years of age

TABLE D3: FEMALES BORN IN 1982

Name	Rank	Dominance Value (DV)	Birth Week	Weight (kg)*	Horn Length (cm)*	Age at 1st Calving	Mother's Age	Mother's Rank	Mother's DV	Mother's Weight (kg)	Mother had 1983 calf?
C1	1	90.0	1	321	25.4	2	18	-	-	409	no
FC	2	90.0	2	266	25.4	3	3	18	43.1	-	yes
UC	3	60.0	4	193	22.9	3	16	14	61.9	-	yes
C2	4	57.7	2	252	22.9	4	9	6	51.6	432	yes
BHC	5	62.4	3	227	22.9	-	3	29	29.4	409	yes
DT	6	61.9	2	301	21.6	2	6	21	49.1	-	yes
DC	7	52.2	6	286	22.9	3	3	30	30.0	420	no
SHC	8	45.0	1	307	24.8	3	9	-	-	-	(M died)
CW	9	42.4	4	248	24.1	-	6	17	45.0	414	yes
CT	10	50.8	3	227	22.9	3	4	20	43.1	409	yes
WOC	11	52.2	3	230	21.6	3	13	15	60.0	-	yes
LEC	12	39.2	3	236	19.1	3	13	4	51.6	467	yes
LOC	13	36.3	4	227	17.8	3	16	11	46.4	-	yes
IHC	14	28.7	2	286	22.9	4	7	16	45.0	414	yes
CC	15	38.4	5	241	19.1	4	17	13	43.5	-	yes
TG	16	37.8	24	180	20.3	3	5	22	63.4	425	yes
SC	17	17.6	7	168	20.3	3	3	-	-	-	(M died)
MC	18	22.2	13	159	20.3	3	6	8	39.2	459	yes
OL	19	26.6	25	-	-	4	16	7	54.8	451	no
YC	20	16.8	8	164	20.3	3	3	36	0.0	415	yes
WH	21	22.2	2	180	22.9	3	3	32	45.0	-	yes

* Weight and horn length measured at 1.5 years of age

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