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MOTHER-INFANT RELATIONS IN SEMI-CAPTIVE
ALASKAN MOOSE (*Alces alces gigas*).

University of Alaska, M.Sc., 1974
Zoology

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MOTHER-INFANT RELATIONS IN SEMI-CAPTIVE ALASKAN MOOSE
(*Alces alces gigas*)

A

THESIS

Presented to the Faculty of the
University of Alaska in partial fulfillment
of the Requirements
for the Degree of
MASTER OF SCIENCE

Stephen Frederick Stringham, B.S.
Fairbanks, Alaska
May 1974

MOTHER-INFANT RELATIONS IN SEMI-CAPTIVE ALASKAN MOOSE

(*Alces alces gigas*)

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INTRODUCTION

Infant moose (Alces alces ssp.) are dependent upon their mothers for protection and avoidance of predators and other dangers and from premature social contact. It is primarily the mother who insures that her calf will be in favorable conditions at appropriate periods of its development to obtain the nutrition, experience, and exercise of its faculties necessary for survival and eventual reproduction. Therefore, the study of mother-infant relations is crucial to our understanding of the social behavior, ecology, and management of moose.

There has been relatively little published on this topic. Altmann (1955, 1956, 1957a, 1957b, 1958, 1959, 1960, 1961, 1963) dealt with maternal care, social integration of calves, and group dynamics during the rutting season. These papers are primarily summaries of her findings. Knorre studied wild and domesticated moose over a period of 40 years; his major papers (1959, 1961) deal primarily with the moose domestication project in the U.S.S.R. These papers provide some information on mother-infant relations and on milk consumption. Information on wild calves has also been published by Denniston (1956), Espmark (1969), Dodds (1955), Geist (1959, 1963, 1966, 1971), Hatter (1945), Lent (1973), LeResche (1966, 1968), Markgren (1966, 1969), McMillan (1954), Mech (1966, 1970), Merrill

(1916), Peterson (1955), Seton (1929), Skuncke (1949), and a variety of others. Several workers have described tame calves, including Bierwirth (1954), Dodds (1959), Hediger (1955, 1964), Kellum (1941), Kramer (1963), Krott (1956), and Markgren (1966). Markgren's account is the most detailed. The literature is reviewed by Stringham (in press).

The most comprehensive integration of the literature on mother-infant relations in ungulates is by Lent (1973). I have emphasized some of the same aspects of behavior which he did in order to allow comparison between moose and other species on as many points as possible. Among the topics which have been excluded are: maternal aggressiveness and social distance, communication, the following response, and imprinting. Altmann (1958, 1963) presents some information on these subjects.

STUDY AREA

I conducted field work from mid-May through late August 1970 and mid-May to early August 1971 at the Moose Research Center on the Kenai Peninsula. The Center is operated jointly by the U.S. Bureau of Sport Fisheries and Wildlife (BSFW) and by the Alaska Department of Fish and Game (ADF&G). It is located on that portion of the peninsula which was burned extensively in 1947. The four one-mile-square enclosures contain representative vegetation, including both remnant stands of mixed birch _Betula papyrifera_, white spruce _Picea glauca_, and aspen _Populus tremuloides_, and regenerative stands of mixed birch and spruce. They also encompass some marshland that is frequented by moose during summer, surrounded by hillocks where the moose feed during winter, (LeResche and Davis, 1971). The vegetation of this pen is discussed and mapped in LeResche et al. (in press).

Most of my observations were made in the eastern half of Pen 4. This area and the contiguous region outside the pen are covered with dense stands of new growth and mature birch, spruce, and aspen, except for a few small bog-meadows and one large one. The large bog-meadow lies in the southeastern corner of the enclosure and extends several hundred meters eastward beyond the fence. Inside the enclosure, the meadow is interspersed with burnt and new growth spruce (P. mariana and P. glauca) and some birch which provides a moderate amount of cover. Outside the fence, the meadow offers little cover for moose. The enclosure contains one small lake and a few ponds. Free-ranging moose were also observed along timberline on the Kenai Peninsula from September 16 to 27, 1971.

Most of the adults in Pens 2 and 4 had been tagged previously by ADF&G personnel, and their ages had been determined by tooth section analysis. Few yearlings and no calves were tagged during the study period. Calves were rarely identifiable except when seen with their tagged mothers. Yearlings changed appearance so rapidly that only those seen fairly often could be reliably identified. Particularly prior to mid-July 1971, the rate of change in natural markings (face structure; pelage; size, shape and coloration of the vulval patch and bell) in each of the three female yearlings was too great to permit individual recognition from one semi-weekly observation period to the next.

Data on the populations in Pens 2 and 4 are provided in Table 1. Further details are given by LeResche and Davis (1971). During the investigation, each moose was referred to by a letter-number code. However, these designations are easily confused by one not familiar with them; so for the purposes of presentation, the moose have

Table 1. Populations of Moose within the 2.6km^2 (1 mi^2) Study Enclosures

Date	Pen No.	Bulls	Yearlings	Cows	Calves	Total
VI/14/71	2	4	3	9	9	25
II/1/70	4	2	0	11	5	18
VI/14/71	4	3	3♀♀ 2♂♂	8	6	22

(after: LeResche and Davis, 1971)

been given names. The letter-number designations, names and personal history information are given in Table 2.

Attention was focused on the cows Mary Ann and Amazon and their calves in Pen 4 during May through August, 1970 and 1971. Prudence, Olga, and their calves were watched occasionally. Observations were also carried out on Carie, Wanda, and Suzanna in Pen 2, during the first two weeks after each gave birth in 1971. Suzanna had twins; all of the others had singlets. Considerable time was also spent with the two calves I reared, Boltar and Taunga. Boltar was less than 24 hours old when deserted by his mother due to human disturbance. When he died four weeks later, he showed signs of malnutrition (LeResche, _viva voce_) and had been scouring badly since he was a few days old. Taunga also scoured, but, once I began boiling his milk, this ceased. Taunga was probably less than two weeks old when captured on June 8, 1970 (estimated by LeResche, _viva voce_). He died the following December, apparently due to malnutrition; the marrow of his femur was red and jelly-like.

Table 2. Individual Identification and Life-History Data

Pen No.	Name and ID Numbers	ADF&G of Cow	Age of Cow in 1971 (years)	Name and Sex of Calf		Date of Birth of Calf	
2	Carie	R-70-7	8	Twister	?	May 28-29	1971
		04245					
	Suzanna	untagged	4(?)	Darkness	?	May 21-22	1971
				Lightning	?		
	Wanda	#52 cow	4	Willey	?	June 4-7	1971
	Belta	R-70-4	4	Boltar*	♂	May 23	1970
4	Mary Ann	R-70-1	7	Roxy	♀	May 26-28	1970
		08742		Rolly	♂	June 1-3	1971
	Amazon	R-70-3	3	Arnold	♂	May 21-22	1970
		09515		Alfe	♀	May 31	1971
	Olga	#22 cow	6	Olivia	♀	Before Aug.	1969
		08746		Oliver	♂	May 17-19	1971
	Prudence	#36 cow	8	Prucilla	♀		1970
		09869					

Table 2. (Cont'd)

Pen No.	Name and ADF&G ID Numbers of Cow	Age of Cow in 1971 (years)	Name and Sex of Calf	Date of Birth of Calf
	free untagged	?	Taunga* ♂	May 24 to June 1 1970

*hand reared

(data on cows from ADF&G records; LeResche et al., 1971)

METHODS

Observation technique was largely determined by the type of habitat that the moose were using. Both inside and outside the enclosures, the vegetation was sufficiently dense that moose were rarely visible from distances greater than 50 to 100 m. Long distance observations were possible only when the moose were traveling along the fences or were in the large bog-meadow or the birch-spruce regrowth patches immediately surrounding it. In 1970 the cow-calf pairs I was observing avoided open areas (at least during the day), forcing me to follow at close range. To minimize adverse effects, I usually discontinued following whenever the moose became disturbed. Thus, during 1970, observer influences were often a problem, and observation could rarely be maintained for more than 4 hr at a time. However, during summer 1971, the moose could be found in relatively open areas far more often, allowing me to make the bulk of my observations unnoticed from 50 to 250 m. Observer influences were rarely a problem, and observations could be maintained for much longer periods than in 1970. Moose could usually be followed from time of sighting until dusk. On a few occasions they were followed during the hours of darkness. When possible, their activities were monitored for several days in succession; but problems in visibility hampered attempts to keep continuous records of many types of behavior, such as suckling and elimination.

As they became increasingly accustomed to me, my proximity disturbed them less and less. This also facilitated observations. For instance, in spring 1970, the cows had usually fled with their infants if they detected me even 100 m away. On two occasions, I was attacked when I came within 20 m of cows with newborn calves. But in spring 1971, I was often able to watch very young infants and their mothers from within 30 to 50 m without eliciting flight or attack.

As is typical in field studies of animal behavior, my assessment of when a moose was disturbed was largely intuitive. Nevertheless, there was an obvious need to attempt to establish what facets of moose behavior gave rise to my impressions. To the extent that it was possible to analyze this within the time available, and without making extensive film records, this basis is discussed below. It is, of course, only a first step.

If a moose continued feeding or resting as I approached it, and did not look up towards me or swivel its ears in my direction, I assumed that I had not been detected. The reliability of this judgement was supported by their behavior if I broke a branch, yelled, or attracted their attention in some other way. They usually looked up abruptly and often ran at least a few paces before stopping and looking back at me. As the moose became increasingly habituated to me, their responses became more subtle. As an undisturbed moose fed, it usually seemed to wander aimlessly in an area several body-lengths in radius, for up to an hour or more. After I had been detected, especially if I attempted to move closer, the moose still seemed to wander aimlessly; but instead of remaining in a small area, it drifted away from me. If I persisted in trying to follow, an increasing proportion of its time was spent moving away from me, and less on movements towards or tangential to me. Furthermore, it moved faster, took fewer bites between steps, and defecated, urinated and performed "comfort activities" (see Geist 1963) more often. (It was uncommon to see an undisturbed moose defecate <u>or</u> urinate more than once per hour -- usually less often. But on one occasion when I followed Amazon for over an hour, during the last half-hour or so, she defecated three times. She also showed the other manifestations of disturbance described.) In addition, the movements of the moose being followed became more abrupt, and it seemed more sensitive to other sources disturbance. When I nevertheless continued to follow, flight became more accentuated and feeding more intermittent. Eventually, if I persisted, the moose ceased feeding and walked or trotted away. The more subtle responses, which one might call manifestations of mild disturbance, were strongly reminiscent of "nervous" behavior by humans. More intense responses were often reminiscent of "anxiety" or "fright".

Social interactions between the moose frequently occurred so rapidly and lasted so briefly that without filming them, it was not possible to analyze more than a few characteristics of the events. Because of the need to concentrate on particular facets, such as ear orientations, head height and vocalizations, I was faced with the choice of either saying nothing about other features, or merely giving my overall impression of them. In most instances I said nothing, because the overall pattern was not familiar, and hence could not be named. But on those occasions that I recognized the pattern, I indicated this by use of the corresponding term. There are obvious dangers in using words like "nervous", "frightened", "threat", "submissive" and "dominant", without describing the exact features of behavior which they refer to. Yet, under these circumstances, these dangers were outweighed by the advantages of the more complete record which they allowed. Even vague information can be valuable, so long as it is accurate.

During 1970, field observations were made on an irregular schedule; but in 1971, Mary Ann and Amazon were observed during alternate weeks, beginning with the first week postpartum. Observations were made with 7 x 35 X binoculars and a 20X spotting scope. Cameras employed were a 35-mm SLR and a 16-mm cine. A pocket tape recorder was used for taking notes.

PARTURITION AND RELATED BEHAVIOR

Events associated with the birth of ungulates have received considerable attention in the literature (see Lent 1973). Mothers of most species, as is typical for mammals (Ewer 1968), seclude themselves before giving birth.

Results

Maternal Seclusion

In considering maternal seclusion, a distinction should be made between association of a cow and her yearling or other moose, and simple physical proximity of individuals. Two moose are "associated" when they travel, feed, and rest together; synchrony in their activities is typical. Amazon was last seen associated with other moose twelve days before she bore Alfe; but she was seen feeding within 50 m of four different individuals four days before calving. Mary Ann was last seen associated with her yearling, Roxy, six to eight days before bearing Rolly. Suzanna was last seen in association with her yearling two days before Lightning and Darkness were born. Since observations were sporadic, however, interactions may have occurred even closer to parturition.

Birth Sites

Identification of birth sites was inferential in all cases, based on the very limited locomotory capabilities of the calves and the fact that none was seen to have moved more than 5 m from where first spotted until at least a few days postpartum. Thus, by "birth site" I am referring to the area up to 5 m in radius around the spot where each calf was first seen. In five of the ten instances, the calves were still very unsteady on their feet when found, and in two cases, their coats were still moist from birth fluids. They had great difficulty walking and went only a few meters in any direction except when prompted to flee by their mothers in response to disturbance by the observer. The cows did this by vocalizing and leading their calves or by nudging them from behind.

In 1970 Mary Ann and an untagged cow in Pen 3 both gave birth in extremely dense stands of immature birch. When bedded down, they were not visible from 3 m away. The same was true of Mary Ann and Wanda in 1971 (see Table 3). In contrast, in 1971 Amazon calved in a stand of mature birch and aspen where windfall and sparse bushes provided moderately dense screening (Fig. 1). She could be seen without binoculars from over 50 m away due to her brightly colored ear flags and collar. Cover and screening at three

Fig. 1. Birth site in moderately dense cover: Amazon with Alfe on the day of his birth, 1971.

other birth sites were intermediate between these densities. But two sites were found where there was essentially no cover; these were both in the 5-m wide cleared swath flanking the fence around Pen 4 (Fig. 2).

Postpartum Interactions

Once an ungulate calf is born, a period of intensive reciprocal stimulation begins between it and its dam, which is probably essential for eliciting and orienting its activities (e.g., suckling), arousing maternal behavior, and establishing the reciprocal bond with its mother (Lent 1973) According to Skuncke (1949), Knorre (1959), and Altmann (1958, 1963), licking begins immediately after the young are born. The youngest calves that I saw were already a few hours old. By that stage, all licking by their mothers was sporadic, and concentrated on their heads, backs and rumps. However, four of them also showed extensive lick marks on their flanks, necks and shoulders. Two of these infants were still moist.

Discussion

Maternal Seclusion

The tendency of parturient cows to avoid other moose has also been reported by other investigators. In Wyoming, moose cows become increasingly aggressive even towards their own yearlings as parturition approaches. About 10

Fig. 2. Birth site with essentially no immediate cover: untagged cow outside Pen 4, 1970.

to 15 days before the new calves are born, cows chase their yearlings to a distance of up to 100 yards (90 m) (Altmann 1958, 1960, 1963). After its new sibling is born, the yearling may or may not rejoin its dam. Geist (1963, 1971) and LeResche (1966) give data on cow-yearling disassociation. This will be discussed later.

Birth Sites

Altmann (1958, 1963) mentioned three characteristics which were typical of birth sites in Wyoming: secluded shelter, available browse, and proximity to a source of water. Markgren (1969) found no indication that the sites themselves had to offer water and forage. The 15 (inferred) sites he examined did not all feature shelter, forage, and water. The most consistent feature was seclusion (screening?) from the surrounding terrain; this was found at 10 (67%) of the sites.

Peterson (1955) pointed out that many cows give birth on peninsulas and islands in lakes and rivers; he suggested that these sites may be preferred for the seclusion they offer. He based this on his own observations and those of Seton (1929), Clark (1936), and Cowan (1946). Klein (*viva voce*) has pointed out that on the Kenai Peninsula many cows give birth on islands, spots seldom frequented by wolves, bear, or other predators. Knorre (1961) reported that cows give birth on river margins where they can drink without venturing far from their calves.

In all eight of the cases where a Kenai cow calved in cover, she fed on the plants available at the immediate site. In no case did I find water within 75 m, although there may have been small snow-melt puddles hidden in the brush.

It appears as though birth sites in clearings are uncommon, if not rare. Not only do the above-mentioned investigators emphasize cover, but the Alaska Department of Fish & Game personnel that I have talked with have indicated that this was characteristic of all (inferred) sites they have found. I suspect that the two instances when Kenai cows calved in the cleared margins outside Pen 4, resulted from the typical reactions of local moose when confronted with a fence. They walked back and forth along several hundred meters of fence for hours, occasionally pushing against it as though wanting to cross. Moose within the enclosures paced this way even after more than 2 years of captivity. The fences around Pen 4 had been erected the previous summer (1969). Perhaps in preceding years these cows gave birth in areas now within the enclosure. There does seem to be some preference for calving areas. In 1971, Mary Ann and Amazon both calved within 100 m of their 1970 calving sites. Markgren (1969:196) reported a general belief among Scandinavian hunters that a cow will return to the same spot to calve several years in succession. Although pointing out the problem of proving that it is the same cow year after year, he stated that some of his observations also suggested repeated use of birth sites by individual cows.

Parturition

I saw no births. The only records that I have found are by Knorre (1959; summarized and translated into English by Markgren, 1969), with reference to domesticated moose in Russia. Skuncke (1949) observed at least one birth at the Skansen Zoo in Stockholm. Labor begins over one hour before delivery and strainings are obvious. The cows may alternately get up and lay down, but the calves are born while they are bedded. Delivery lasts 3 to 15 min. Afterwards, the cows continue resting for one to two hours and first nurse their young in this position. According to Fraser (1968), alternate standing and lying, and strainings have also been reported for other ungulates; acute restlessness is considered to be an indication of pain. Skuncke and Knorre have both indicated that cows seldom consume the afterbirth, but Markgren reported many observations of this.

PROTECTION OF THE YOUNG

Cervids utilize three fundamental strategies in protecting their infants from predators: flight, defense, and concealment. The relative importance of each varies with the age of the fawn, and from one species to the next. One of the most complex and important mechanisms employed by many species in the concealment of their infants is periodic, prolonged isolation between the does and fawns. This has been named "Abliegen" by Walther (1964, 1965) and may be translated as "lying-apart". (A fawn does not necessarily remain lying at all times while its mother is away.) Does leave their fawns in hiding and feed and rest at a distance from them throughout the day and perhaps throughout the night. Nursing and grooming occur during the brief, infrequent contact periods. For example, white-tailed Odocoileus virginiana deer mothers may venture up to one mile from their young (White et al. 1972) and visit them only two or three times during the 24-hr day (Jackson et al. 1972). This pattern of separations, and thus the "hiding phase" (by definition), begins when the mother or infant first leaves the birth site and ends when the fawn regularly accompanies her during her daily activity (Lent 1973). Among white-tailed deer the hiding phase may last up to several weeks (Severinghaus and Cheatum 1956). Exposure is also minimized by the fact that mothers and young normally do not communicate while separated (communication becomes more common towards the end of the hiding phase) (Lent, 1973).

Those ungulate species exhibiting lying-apart have been called "Ablieger Typ" by Walther (1964, 1965) and "hiders" by Lent (1973). Most of those which do not, have been called "Nachfolger Typ" or "followers"; young of these species begin accompanying their mothers regularly as soon as they leave the birth site. Prolonged separations are unusual. Thus, Lent characterized the hider vs. follower dichotomy by contrasting the normal spacing between mothers and infants of the two types, during the first weeks postpartum. In general, it has been possible to distinguish whether a given species is hider or follower on the basis of this spacing.

Results

Spacing Between Infant Moose and their Dams

I never saw a cow venture more than 5 m from her calf on the first day or two postpartum. During the next week or so, they continued to remain within about 10 m most of the time, but they were occasionally separated from the young by 40 m or more for over an hour (Table 3). These wider separations occurred after the calves had bedded down. They are termed "periods of isolation", to

Table 3. Cow-Calf Isolation as a Function of the Calf's Age During the First Two Weeks Postpartum

Names of Cows	Carie	Mary Ann		Suzanna				
Names of Calves	Twister	Rolly		Lightning and Darkness				
Ages of Calves (days)	1	2 or 3	3 or 4	2	5	8	10	13
Maximum Spacing Seen (meters)	5	40	40	5	75 -100	75	40	80
No. Hours of Observations	12.5	11.5	16	0.75	14.5	8.5	5	5
% of Time Cow and Young Were Isolated From Each Other	0	5	28	0	10	17	10	45
No. Times Isolated	0	1	2	0	3	2	1	1
Ratio: Times Isolated/ Hours of Observation*	0	0.09	0.12	0	0.21	0.24	0.20	0.20

*(note the almost constant ratio for Suzanna and her calves for more than one week)

distinguish them from instances when a cow and calf were briefly separated by more than a few meters while still interacting with one another. For instance, a cow often walked several meters from her calf after interrupting nursing. Her calf sometimes followed her and tried to resume suckling. When, on the otherhand, the calf bedded down, and the cow continued moving away from it as she fed, this was the beginning of a period of isolation. Isolation ended when the dam returned to her calf and aroused it, or when she came near and it approached her. When the calves were a few days old, they followed or approached their mothers when separated by up to 5 or 10 m; by age one week they did so when separated by up to 20 m. Beyond those distances they did not approach even when they obviously desired contact, as manisfested by their bleating. I have observed this vocalization on well over a hundred other occasions when its function likewise seemed to be to elicit care and/or approach by or to the mother. Bleating is the juvenile form of grunting, which also solicits approach.

During this stage of development, Kenai calves usually bedded down within a meter or two, and never over 5 m, from where their mothers were resting or had last rested with them. The one pair of twins observed, Lightning and Darkness, likewise rested within a few meters of one another. Not only did mothers and young usually rest at the birth sites for several days, but in some cases they repeatedly bedded at other sites for longer than one day. Twice, on different days, Olga and Oliver returned to a spot (probably the birth site) after fleeing over 100 m from it in response to disturbance by the observer.

All Kenai calves more than two weeks old left the bed site when obviously desiring contact rather than waiting until their dams returned. When a calf of this age was resting, its mother usually remained within 30 to 50 m, but sometimes ventured 100 to 200 m away, and rarely went over 400 m for as long as 4 hr. The calf usually joined its mother soon after arising. On two occasions, I saw a calf approach its mother from over 75 m away, although she could not have been visible to it. When a cow bedded down, it was usually within several meters of her infant. (Matanuska Valley cows also normally rested with their young, although they occasionally bedded in the open, 10 to 20 m from the calves; LeResche 1966.) When a Kenai cow and calf were both active, they usually ranged within 10 to 20 m of one another, only rarely going over 50 m apart.

Discussion

Seton (1929) and Peterson (1955) have also reported separations between cows and calves less than two weeks old. Dodds (1955), LeResche (1966) and Dunn (*viva voce*) have reported them for older calves. But it is debatable whether these, or the separations I observed were instances of lying-apart. Altmann (1958, 1963), Geist (1966), Espmark (1969, pers. comm.) and Peek (viva voce) have found no evidence of lying-apart by moose in Wyoming, British Columbia, Sweden or Montana, respectively.

The mere fact that a mother and her young are not together at all times can not be construed as evidence of lying-apart. Theoretically, lying-apart should be distinguishable by the facts that isolation is maintained for long periods by the behavior of both mothers and infants, and that this isolation helps to conceal the infants. Even after hider young regularly accompany their dams during the day, separations may occur -- albeit for much shorter periods, in general. Even if a dam gets up before her fawn does, and moves away from it as she feeds, it may arise and join her on its own initiative. Only during the hiding phase is concealment the major determinant of spacing between hider mothers and young (Lent viva voce). Seton, Peterson and Dodds do not provide sufficient information to allow one to distinguish the nature of the separations they observed between infant moose and their mothers. LeResche and Dunn do, however.

The prolonged separations observed by LeResche (1966) in the Matanuska Valley of Alaska and by Dunn (viva voce) in Baxter Park, Maine, were for calves more than a week or two old (LeResche did not begin observations until mid-June; most calves in Alaska are born in late May or early June). These separations occurred when the cows fed in lakes or large open meadows. They apparently resulted from the differences in response to clearings and to deep water by cows versus their young.

In the Matanuska Valley, moose of all ages tend to avoid open areas much of the time. When they approach or pass lakes or open meadows, they move along or just within the perimeter of brush and trees. Avoidance is most pronounced for cows with calves and for lone calves (LeResche 1966). It seems to be greatest for neonates and to decrease with maturity. During their first two weeks of life, Lightning and Darkness did not approach their mother when she was in clearings (Lent 1973); yet I saw older calves enter equivalent areas on their own initiative without obvious hesitation. When cows feed in lakes, their infants usually remain on shore, hidden in or near cover (Altmann 1963). This is supported by the observations of Denniston (1956), LeResche (1966), and Geist (*viva voce*). The calves seen by LeResche also remained in cover when their mothers fed in large open meadows. When a Matanuska cow left cover to feed in a lake or in the open bog-meadow encompassing it, her calf sometimes accompanied her for a few minutes before returning to cover and bedding down. Calves sometimes arose and fed before their mothers rejoined them and periodically, but briefly, visited the dams in the open. Visits became more frequent as the calves matured. By late August, they occurred at least once per half hour. Although calves sometimes tried to suckle during the visits, they were unsuccessful. Matanuska cows permitted suckling and rested with their calves only after rejoining them in cover. Similar observations have been made by Dunn (*viva voce*) in Baxter State Park. Calves were occasionally seen along the shore or in the shallows of a 60-acre (24-ha) pond as early as mid-June. By early July, they too visited their mothers in deep water for several minutes at a time before returning to the shallows or to shore.

According to Altmann (1958, 1963), these are the only circumstances under which Shiras cows were isolated from their young. In cover, Shiras calves normally accompanied the dams, as was also true of the Kenai young. (Since there were no large lakes or open meadows in Pen 4, I have no data on behavior in these habitats.) One would assume that accompanyment in cover was typical for the Matanuska Valley and Baxter Park cow-calf pairs too, although neither LeResche (1966) nor Dunn (*viva voce*) have data on this. The Matanuska moose were not visible to LeResche when deep in cover, and Dunn did not collect this sort of information on the Baxter Park animals. The fact that calves do not accompany their mothers feeding in lakes is probably due to their preference for cover and aversion to deep water. The spacing thus maintained between mothers and young is definitely not lying-apart.

I have shown that separations between Kenai cows and their young occur at all stages of calf development. But there is no indication that they significantly helped to conceal the young at any stage. The only phase when calves did not join their mothers whenever they obviously desired contact, was during the first two weeks postpartum. This is the only phase when one might say that isolation was maintained. The reason for this maintenance is unexplained. Two hypotheses are offered: The observations suggest that this may have been related to the distance separating mothers and young. Lent (1973) proposed that motivation to approach may be distance-dependent for the infants of most ungulate species. On the otherhand, inhibition of approach by the calves, beyond these observed distances, may have been due to inability to see the mother in the distance because of intervening foliage. The apparent distance-dependency may have been an artifact of the small number of observations. Further investigation is necessary before conclusions can be drawn.

Although during this stage, Kenai calves remained at rest sites until rejoined by their dams, their behavior differed from the typical hider pattern in a number of respects. Cows always rested with their infants and usually fed nearby. Periods of isolation were relatively short and infrequent. When the cows did leave, their infants often bleated for them, which would have revealed the locations of the infants to any predator in the vicinity. White et al. (1972) stated that when white-tailed deer fawns were being tagged, their bleating attracted coyotes. (After age two weeks, Kenai calves normally accompanied their mothers feeding and frequently initiated reunions on those occasions that their mothers wandered away grazing while they rested.)

Thus, although separations do occur between moose cows and their infants, there is no evidence that these are products of a mechanism for concealing them. Rather, in some instances, separation may increase exposure, instead of minimizing it. This small body of observations is not sufficient to justify concluding that moose, as a species, do not exhibit lying-apart. But the burden of proof is on whoever proposes that they do. Ideally, he should show that calves are less susceptible to predation when separated from their dams, than when associating with them.

Protection of Calves that are Associated With Their Mothers

According to Mech (1966, 1970), once a moose calf is discovered by a wolf (*Canis lupus*), it is essentially helpless unless it is defended by its mother, regardless of whether it flees. He has seen 12 encounters between wolves and cows with calves. In four instances, the cow-calf pair stood at bay when they discovered the wolves nearby. The cow stood behind her calf, protecting it from the rear, the usual point of attack. None of these calves was killed. On a few occasions I have seen a calf stand under its mother, or try to, while she was threatening me with her head low, ears back and mane erected. In each case, the calf was aware of me and acted "frightened". Murie (1944) described how a cow in Mount McKinley National Park successfully defended her newborn calf against two huskies. In the eight other wolf encounters that Mech observed, the cow-calf pairs fled. During flight too, a cow usually remained behind her calf. So long as the calf was with its mother, it was relatively safe; but, if it became separated from her, as happened in three instances, it quickly fell prey. During my own observations on the Kenai Peninsula, calves usually followed their mothers when they fled from me or from aircraft. On those occasions that they ran ahead of their mothers, they seemed to be especially frightened and perhaps were panic-stricken. In these instances, the calves typically became separated from their mothers by more than 10 m. If a calf reacted in that same way to wolves, it would probably be killed, judging from what Mech reported.

Moose cows are also able to defend their infants from black bear (Ursus americanus) and sometimes against brown bear/grizzlies (U. arctos). Conley (1956) reported a case where a cow moose attacked a black bear that was carrying off her calf and wounded it before an observer shot the predator. Geist (1963) also described an encounter with a black bear. LeResche (1966) concluded that, although predation by bears does occur in the Matanuska Valley of Alaska, it is:

> probably an important mortality factor only in very young calves. Calves more than a month old seem capable of escaping bears under ordinary circumstances [at least when accompanied by their mothers], and probably fall prey only in unusual situations of surprise or harsh environmental conditions. . . . The demonstrated ability of a brown bear to take a young calf even though it is closely protected, as well as the much greater fear shown by moose at the presence of a brown bear, suggests that they are a more important predator on moose than the black bear, although the latter are much more numerous.

Protection of Lone Calves

Thus, when a calf is alone, its primary defense against predators must be concealment. The accentuated tendency of young to avoid open areas has already been mentioned. Another mechanism for minimizing exposure is "freezing". When Alaskan infants are pursued by humans during tagging activities, they sometimes drop to the ground and lay motionless (LeResche, *viva voce*). However, this appears to be much less common for moose than for typical hiders. During many years of tagging, Wyoming Game Commission biologist Jim Straley saw only one instance of the "prone response" (term used by Lent 1973). "The youngster had traveled a long ways and was obviously very tired" (Van Wormer 1972:56). When cows resting with neonates are disturbed, they too typically freeze.

It is a common notion that the coloration of fawns of some hider species serves to camouflage them from predators. But it is uncertain whether this is also true for moose. So far as I know (see Flerov 1954:168, 174), moose infants are greyish- or reddish-brown in color throughout the range of the species. Under the conditions that I observed them and in color and black-and-white photographs I took, this did not appear to my eyes to provide better camouflage than the coloration of adults. James Peek (_viva voce_) reports that both cows and calves are highly conspicuous in the open sagebrush habitat of Montana.

Some hider species protect their infants from olfactory detection through maternal consumption of the afterbirth and the neonate's feces and urine; furthermore, the infants are so nearly odorless that predators cannot detect them by scent alone (Lent 1973). In contrast, although some moose cows do consume their afterbirth, this is not typical (see earlier). Markgren (1969 and _viva voce_) has found both afterbirth and neonatal feces at birth sites. Although I watched carefully on many occasions, I saw no indication that cows consumed either feces or urine.

Since cow-calf pairs normally remain at the birth site for at least a few days (Altmann 1958, 1963; see earlier), odors must accumulate there. Moose calves are commonly thought to be odorless (Mech 1970), but I know of no evidence to support this. Boltar and Taunga both had a mild odor which, to me, resembled a blend of the odor of milk and of the scent that was typical of adults and yearlings that I encountered at close range. But this was milder than the scent of the older moose; I could detect it only when within about half a meter of them. (On the few occasions that I was within 10 or 15 m of an infant, I was too concerned about its dam's reaction to notice whether I could smell it.) Furthermore, Markgren (1966) reported that calves he reared had an odor reminiscent of formic acid ($HCOOH$), associated with a greasy secretion which apparently came from sebaceous glands in the skin; this odor diminished as the calves matured. It is debatable whether the grooming that wild calves receive from their mothers could reduce these odors below detectability by predators (see Pinter 1964 and Raesfeld et al. 1965). It is also questionable whether hand-rearing could have induced such odors and that they would not develop for wild calves.

Considering that moose dams usually feed and rest near their infants, that the infants may habitually rest within a few meters of one another at the birth site or at some other location, the tendency of the young to vocalize when separated from their mothers, their lack of cryptic coloration, the poor development of the prone response (at least in Wyoming), and the fact that odors are not minimized: it seems that they are much less well adapted for concealment than are typical hider young. In view of the defenselessness of calves when alone, one must also conclude that they are not well adapted for <u>isolation</u> from their dams, which further argues against the occurrence of lying-apart. Moose definitely are not "hiders"; nor can they be judged as "followers" since separations do occur between cows and infants, and because they do not depend primarily on flight for protection. Rather, they fall into a third class which I will call "defenders" or "Verteidiger Typ".

Selective Advantages of Intensive Contact

Because of the greater ability of moose to defend their young, there would have been less selective pressure on them than on most cervids to develop means of infant concealment. Just how effective defense has been historically and currently, and thus how little pressure there has been towards minimizing infant exposure, we do not know. Nevertheless, one might wonder why moose infants are not better concealed when separations do occur. Furthermore, one might wonder whether predation losses -- however extensive they may be -- might not be further reduced by augmenting defense with some form of lying-apart. Presumably, a cow could remain close enough to rescue her calf if it was endangered by predators, yet far enough away -- perhaps 30 to 50 m or so -- to avoid revealing its location, thereby reducing the likelihood that she would have to defend it. This would seemingly minimize the danger to both mother and infant. That such a pattern is lacking suggests that the advantages of closer mother-infant association outweigh whatever predation losses occur. Perhaps the mother is more intensely motivated to protect her infant when she is with it. Perhaps the first week or so of life constitute a sensitive period for types of learning that are promoted by maternal contact and guidance (see Cow-Yearling Relationships). This is a problem that should be explored further.

ACTIVITY PATTERNS

Numerous studies have been conducted on the activity patterns of ungulates, especially with regard to relationships between activity and rest versus time of day. This same emphasis characterizes the literature on moose (e.g., McMillan 1954, LeResche 1966). Almost nothing has been published on related topics.

Kenai moose were considered to be resting when they were lying down and as active when on their feet, whether traveling or standing still. Although cows usually rested steadily for long periods, their calves occasionally interrupted rest for a few minutes. This distinction between interruptions and activity periods is illustrated in Fig. 3. On August 6, 1970, Amazon and Arnold rested together nearly 4.5 hrs from 07:23 to 11:58. During this span of time, Amazon arose twice to nurse her calf, dividing the 265-min rest period* into three fragments (rest bouts). The two interruptions averaged 7.5 min. During that same time span, Arnold arose six times, dividing his 258-min rest period into seven fragments (rest bouts). The interruptions averaged 3 min.

In general, as in this example, interruptions were

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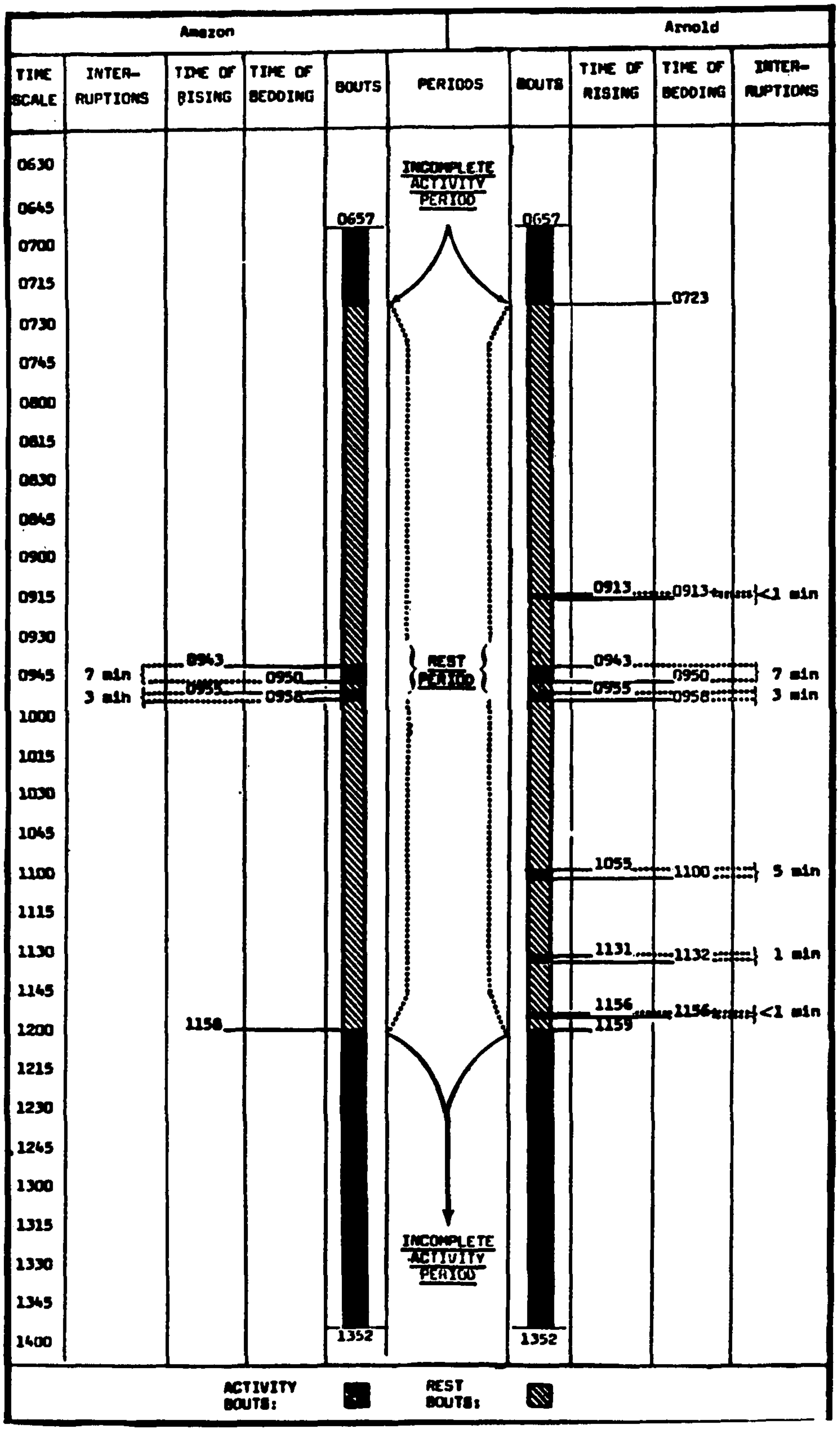
*Interruptions were excluded in calculations of rest period duration.

Fig. 3. Typical joint rest and activity periods for a cow and calf. Amazon and Arnold, 1971. Note the differences between interruptions of the rest period and activity periods, and between periods and bouts.


Amazon
Arnold
TIME SCALE
INTER-RUPTIONS
TIME OF RISING
TIME OF BEDDING
BOUTS
PERIODS
BOUTS
TIME OF RISING
TIME OF BEDDING
INTER-RUPTIONS
0630
0645
0700
0715
0730
0745
0800
0815
0830
0845
0900
0915
0930
0945
1000
1015
1030
1045
1100
1115
1130
1145
1200
1215
1230
1245
1300
1315
1330
1345
1400
INCOMPLETE ACTIVITY PERIOD
0657
0657
0723
0913
0913
<1 min
0943
0943
7 min
7 min
0950
0950
0955
0955
3 min
3 min
0958
0958
REST PERIOD
1055
1100
5 min
1131
1132
1 min
1156
1156
<1 min
1158
1159
INCOMPLETE ACTIVITY PERIOD
1352
1352
ACTIVITY BOUTS:
REST BOUTS:

distinguished from activity periods by their brevity and by the behavioral contexts in which they occurred. From the majority of instances, where identification of an interruption as such was intuitively obvious, several rules were formulated for dealing with cases where judgment was more difficult. They are presented in the Appendix.

In lieu of a biological criterion for determining when an interruption had "seriously" increased or decreased the length of the rest period in which it occurred, any period interrupted by <u>disturbance</u> for more than 10 min <u>and</u> for more than 10% of its total length was omitted from calculations of mean rest period duration. Rest periods truncated by disturbance and the activity periods thereby initiated were also omitted. They were classed as "seriously disturbed". Fifteen rest periods and 5 activity periods by Mary Ann and Amazon were thus discarded as were 8 rest periods and 2 activity periods by their calves. So too, all periods seen only in part were omitted from calculations of mean duration. (On those occasions when a restless cow got up leisurely within a minute or two after mild disturbance, the rest period was <u>not</u> considered to have been truncated; see later.)

Results

Proportion of Time Spent Active

As the Kenai calves matured and increased their consumption of vegetation, they spent an increasing proportion of their time active. During the first few days portpartum, both calves and their mothers were bedded almost constantly, but by the end of the first week, the cows spent over half of their time active; by the fifth week, Rolly and Alfe did so too (Fig. 4). Considering all data on Mary Ann, Amazon, and their calves, the young were active only about three-fourths as much of the time as their mothers were. During nearly 16,000 min of observation, the cows were active 59% of the time; during approximately 14,500 min of observation, their calves were active 43% of the time.

Synchronous Initiation of Rest and Activity Periods

Although Kenai calves frequently began rest and activity periods at the same time their mothers did, they often bedded down much sooner or got up later. The reverse, however, was not true (Table 5). In only three instances did a calf get up more than 1 min before its dam; and in only three instances did one bed down more than 3 min after. One exception involved three-day old Roxy, when she got up 5 min before Mary Ann did. The cow apparently allowed her to suckle, then began foraging. Roxy remained active for 25 min. The other exceptions involved calves at least six weeks old. Fifteen weeks after the above incident, Mary Ann bedded down in dense cover

Fig. 4. Proportion of time spent active as a function of calf age: Mary Ann and Amazon vs. Rolly and Alfe, 1971.

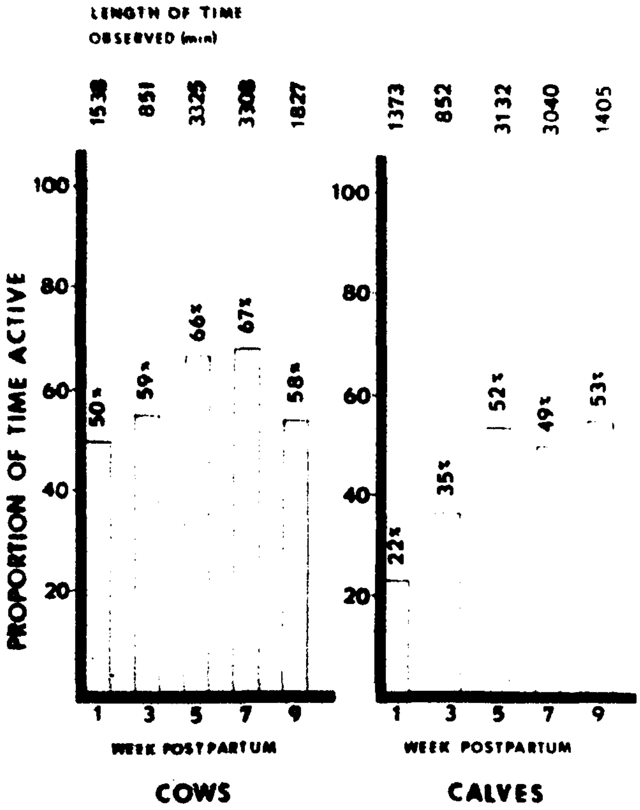

LENGTH OF TIME OBSERVED (min)
1538
851
3325
3308
1827
1373
852
3132
3040
1405
PROPORTION OF TIME ACTIVE
100
80
60
40
20
50%
59%
66%
67%
58%
22%
35%
52%
49%
53%
1
3
5
7
9
WEEK POSTPARTUM
COWS
WEEK POSTPARTUM
CALVES

Table 4. Cow-Calf Synchrony in the Initiation of Rest and Activity Periods (for Mary Ann, Amazon, and their calves)

4a. Initiation lag relative to whether cow or calf bedded down or arose first

	Rest Periods				Activity Periods			
Initiation Lag (cow vs. calf)	Mean (min)	(SD) (min)	No. of Obs.	%	Mean (min)	(SD) (min)	No. of Obs.	%
Simultaneous Initiation								
(x ≤ 1 min)	<1	(--)	20	38	< 1	(--)	29	64
Calf after Cow	5	(5)	8	15	29	(37)	13	29
Calf before Cow	31	(31)	24	46	23	(19)	3	7
Total Joint Periods			52				45	

4b. Absolute value of initiation lag

Initiation Lag (min)	Rest Periods No. of Obs.	Rest Periods %	Activity Periods No. of Obs.	Activity Periods %
$x \leq 1$	20	38	29	64
$1 < x \leq 10$	15	29	9	20
$10 < x \leq 100$	15	29	6	13
$100 < x$	2	4	1	2
Total Joint Periods	52		45	

about 25 m from Roxy. The calf did not reach a spot where her dam was visible to her until 9 min later, whereupon she bedded down too. In July of the following year, her six-week old brother Rolly got up when a yearling approached to within 5 m of him. Although Mary Ann seemed to ignor the yearling for over 20 min, she finally arose and chased it away. Then both cow and calf fed for over 40 min before lying down. The other incidents involved Amazon and her calves. On July 14, 1970, Arnold bedded down six min after his mother. One year later, his nine-week old sister Alfe once arose 42 min before Amazon; two days later, she remained up 16 min after her mother bedded down in plain sight, about 25 m away.

Rest and Activity Period Durations

The tendency of Kenai calves to bed down sooner and get up after their dams is reflected in the rest and activity period duration figures given in Table 6. Mary Ann and Amazon averaged over 1.5 hrs for both rest and activity periods. Their calves averaged nearly 2 hrs per rest period and 1 hr per activity period.

Interruptions

On many occasions when I disturbed a cow resting with her neonate, she became motionless (i.e., "froze") except for movements of her ears and eyes. She arose only if

Table 5a. Rest Period Durations (for Mary Ann, Amazon, and their Calves)

	Cows			Calves		
Rest Periods	Mean (min)	(SD) (min)	No. of Obs.	Mean (min)	(SD) (min)	No. of Obs.
Periods Disturbed Mildly or Not at All	103	(58)	40	113	(65)	40
"Seriously Disturbed" Periods	47	(39)	15	48	(53)	8
Total Complete Rest Periods			55			48
Total Incomplete Rest Periods			34			41
Total Rest Periods			89			89

Table 5b. Activity Period Durations (for Mary Ann, Amazon, and their Calves)

	Cows			Calves		
Activity Periods	Mean (min)	(SD) (min)	No. of Obs.	Mean (min)	(SD) (min)	No. of Obs.
Periods Initiated Spontaneously	99	(54)	30	67	(40)	35
Periods Initiated by Disturbance	66	(64)	5	20	(0)	2
Total Complete Activity Periods			35			37
Total Incomplete Activity Periods			87			56
Total Activity Periods			122			93

approached closely. Then the cow would stand, oriented in my direction for as much as half an hour or longer, even if I sneaked away through the brush shortly after she got up. A few days before Mary Ann bore Rolly, she also remained standing like this after spotting me from about 100 m away. She had been acting strangely, and I suspect that she was in labor. When calves were at least a week or two old, they and their mothers usually arose immediately if disturbed. After calming down, which normally took no more than 10 min, they frequently bedded down again, at the same time. But the dams were somewhat more likely than their calves to begin activity periods rather than to resume resting.

Undisturbed cows usually remained recumbent throughout rest periods, but their calves occasionally arose spontaneously for a few minutes, during which they stretched, wandered around, or fed. (By "spontaneously", I mean that the interruption was not elicited by an environmental event obvious to me, such as a passing plane or a branch breaking in the wind -- i.e., by a "disturbance".) Mary Ann and Amazon interrupted rest on only 23 occasions during 89 rest periods (Table 6). Eighteen of these interruptions were elicited by disturbance: 2 by aircraft, 12 by the observer, and 4 by natural events. Three of the spontaneous interruptions occurred when a cow arose to nurse her calf. The two instances by Amazon (Fig. 3) occurred in August and are unusual for that time of the year. The only stage of calf development during which spontaneous interruptions by cows were typical was during the first several days postpartum. A cow may invite nursing by getting up and standing in place with her head elevated. Suzanna and Carie, the only two cows that I could watch regularly at this stage, did this frequently.

In the nine other instances that a calf interrupted rest to suckle, then bedded down again, the dam was already active before nursing and/or remained active afterwards. In two cases, the calf arose again in a few minutes and joined its mother. The longest nursing interruption was 13 min, by a three-day old calf.

The calves also interrupted rest periods on 50 other occasions. Thirty of these interruptions were elicited by disturbance: 2 by aircraft, 18 by the observer, and 10 by natural events. The other 20 were spontaneous. Eighty per cent of the spontaneous interruptions occurred while the dams were resting. Only six were more than 1 min long, and only one was over 5 min in duration, lasting 15 min. That it was so much longer than any of the others is probably attributable to the unusual circumstances under which it occurred. Moose cows usually bedded down within several meters of their young and vice versa. On this occasion, however, Mary Ann bedded down about 50 m from Rolly. Nearly 1 hr later, he got up and walked to her, then lay down. If she had been closer, he would presumably have bedded down sooner, or he might not have gotten up at all. Three of the shorter interruptions were also instances when a calf just arose, moved closer to its dam, then bedded. On another occasion, a cow bedded while her calf was in a playful mood. It joined her, but arose shortly thereafter and romped again for a few minutes. During three other interruptions, the calf fed briefly. In the remaining instances, the calf did nothing but wander around briefly, and perhaps perform a few comfort activities.

Discussion

Influence of Resting Cows on the Activeness of their Young

It was uncommon for a calf to be active for more than a few minutes while its dam was resting. One exception was by a calf only a few days old. The others were by calves more than six weeks old. This suggests that the frequency of exceptions is age-dependent. Perhaps calves are inhibited from activity when aware that their mothers are resting. Exceptions may occur when other factors temporarily outweigh the inhibition.

Spontaneous Interruptions

The one spontaneous interruption more than 5 min long, was described earlier. It was probably motivated by eight-week old Rolly's desire to be closer to his dam. This may have also been true in the other three cases that a calf just moved closer to its mother during an interruption. But, in most of the cases, I suspect that interruptions were "comfort activities". Calves were much more restless than their mothers (yearlings were intermediate). They shifted position (fidgeted), stretched, scratched, shook or yawned far more often. During seven seemingly typical minutes, calves performed 42 comfort activities (not including any interruptions; ear twitches were not counted).

Initiation of Rest and Activity Periods

The instance when 15-week old Roxy did not bed down until 9 min after her mother did, is probably attributable to the fact that the cow could not have been visible to her until just before she did lay down. The fact that six-week old Rolly once got up 20 min before his mother may have been due to the close approach by the yearling. McMillan (1954) and Van Wormer (1972) have both remarked on the tendency moose to act synchronously. When one beds down or arises, others near it tend to do so too. In this instance, the activity of the yearling may have counteracted the hypothesized inhibiting effects of the dam's recumbency. The fact that this sort of thing did not happen more often is undoubtably related to the intolerance of cows with calves towards other moose. That Mary Ann waited so long before chasing this yearling away is unusual.

In the other four instances, intervening factors were not obvious. During their first week or two postpartum, Lightning, Darkness, and other calves I watched closely at this stage, frequently arose spontaneously and wandered around for a few minutes while their dams rested. The fact that on one instance Mary Ann got up while Roxy was still active may merely have been coincidental. Furthermore, during the first few days of life, calves frequently seemed relatively unattentive to what their mothers were doing and to other environmental events. For instance, whereas older calves usually watched me or their mothers intently when I disturbed them, neonates seemed unaware of me and usually paid only intermittent attention to their dams, or they just tried to suckle (see earlier) or bedded down. On one occasion when Mary Ann "froze" after I disturbed her while she was resting, infant Roxy got up and wandered around for a few minutes (which might have been fatal, had I been a predator). If neonates are even intermittently less aware of their mothers than older calves, they may be less subject to activity-inhibition.

As calves matured past age six weeks or so, they became noticably more independent in a variety of ways including a tendency to initiate or continue some behavior even when the dam was trying to initiate or continue some other joint activity. On at least four occasions I saw a calf walk in one direction, bleating for its mother, as she walked in another direction, grunting for it. Growing independence may have also been manifested by an increased tendency for activity while the mothers were resting. Certainly, the few times that I saw this are not obviously indicative of a general tendency; but had I continued regular observations past mid-August, I think that one would have been found.

Cow-Calf Synchrony

According to LeResche (1966:64), when cows in the Matanuska Valley utilized lakes or open meadows in the summertime, their infants:

> most often left hiding after their dams had fed for 3-4 minutes, and bedded down while the females remained feeding. In about half the cases observed, the calf reappeared momentarily one or more times to approach the cow or feed while the cow continued feeding and then returned to hiding on its own. In other cases, the calf re-emerged only to greet the cow as she entered the brush, or was not seen again after bedding down.

In contrast, Geist (1959) reported that during the winter calves usually fed and rested with their dams and implied that they frequently got up and bedded down at the same time the cows did.

Since Geist did not present further details or quantitative data on synchrony, comparison of our findings is not possible. LeResche's statements, quoted above, suggest that Matanuska cow-calf pairs showed considerably less synchrony than Kenai pairs. This may have been due to the fact that, while Kenai calves usually fed with their mothers, Matanuska calves usually remained in cover at a distance from their dams while the cows fed in water or open meadows.

Durations of Rest and Activity Periods

There is no information in the literature on this topic for cows-calf pairs. LeResche's (1966) findings on cows and calves in the Matanuska Valley of Alaska are presented in the form of feeding bouts rather than activity periods. A feeding bout apparently ended whenever the moose stopped eating, even momentarily; when feeding resumed, another bout began (see LeResche 1966:64). These averaged 1 hr for the cows and 0.5 hr for their calves. LeResche did not indicate what proportion of time during activity periods was spent feeding, and I do not have data on this for Kenai moose. Geist (1963) gave a figure of 90% for summer, presumably with reference to adults.

Other investigators have not presented separate data on cow-calf pairs. McMillan (1954) observed Shiras moose during summers. These averaged 3 hrs per rest period during the daylight hours (Table 6). British Columbian

Table 6. Summertime Rest and Activity Period Durations: Cumulative Data for All Classes of Moose.

	Rest Periods		Activity Periods	
Observers	Mean (min)	Range (min)	Mean (min)	Range (min)
McMillan (1954)	180	25 - 390	--	--
Geist (1959, 1963)	150	20 - 280	33	10 - 100
Phillips and Berg (1972)	126	--	102	--

moose watched by Geist (1963) during May and June averaged about 2.5 hrs per rest period and 0.5 hr per activity period. Summer observations by Phillips and Berg (1972) in Minnesota revealed rest periods averaging 2 hrs in length and activity periods 1.5 hrs long.

Rest periods vary widely in duration. McMillan reported a range of 25 min to about 6.5 hrs; Geist reported one of 20 min to about 4.5 hrs, which is equivalent to what I found for Kenai cows and calves. However, we have no further basis for comparison between our findings since, without additional information, we cannot test whether the differences in mean values are statistically significant; nor can we assess their biological implications. Furthermore, our methods of measuring period durations may not be quite the same.

None of these authors explicitly indicated how he determined when rest periods ended and activity periods begun, or vice versa. Did a rest period end whenever a moose arose, however briefly? Or were brief bouts of activity during long rest periods considered interruptions? How was interruption of a rest period distinguished from termination of the period? (My methods are presented in the Appendix.)

It will be noted that the shortest activity period observed by Geist (1963) was 10 min long. Thus, either that was the shortest unit of activity he saw, or else all shorter ones were considered as interruptions. Judging from the ranges and mean values for durations given by McMillan and Geist, they probably measured the total time bedded between successive activity periods, excluding interruptions, as I did; or they measured the total time bedded, plus interruptions. The results of either method should be nearly identical, even if interruptions were as common as for Kenai calves.

Interruption and Truncation of Rest Periods by Disturbance

Whether bedded moose arose upon being disturbed, the abruptness with which they got up, and the length of time they remained active afterwards, all seemed to be associated with the duration and severity of the disturbance. Severity, in turn, was a function of both the disturbing event and the prior psycho-physiological condition of the moose.

Once cow-calf pairs had become accustomed to me, they often bedded down even when I was within 15 m of them. I could usually speak into my tape recorder or rustle leaves as I shifted position during the beginning of a rest period without alarming them. If I kept making small noises now and then, these did not alarm the moose. However, if I had been still for a while, then made noise or moved, they usually got up.

Sensitivity to mild disturbance seemed to increase as a rest bout progressed. During the beginning of a given period, rustling of leaves and other sounds usually evoked little or no response. But an hour or two later, these same sorts of noises were often enough to stimulate the moose to get up. On those occasions that a moose arose as it was being disturbed or immediately thereafter, association between the two events was obvious, especially so if the moose seemed frightened. However, when the moose did not get up for a minute or two, it was impossible to be completely sure that arising was in response to disturbance. Delayed responses were particularly common if the cows had been bedded long enough to become restless. (I have specified cows since calves were almost always restless while bedded down.)

McMillan (1954) noted that, when a bedded Shiras moose began stretching, this was an indication that it would soon get up. During the beginning and middle of a rest period, Kenai cows typically stretched, scratched themselves, shifted position slightly, yawned, or performed other "comfort activities" only a few times per hour. However, during the last 10 to 15 min before they arose, several comfort movements were frequently made. If a cow began feeding while bedded, this was a reliable sign that she would arise within no more than 10 min, and probably much sooner. Geist (1963) found that moose performed most comfort movements near the beginnings and ends of activity periods, but he did not indicate how comfort movements were distributed through rest periods.

NURSING

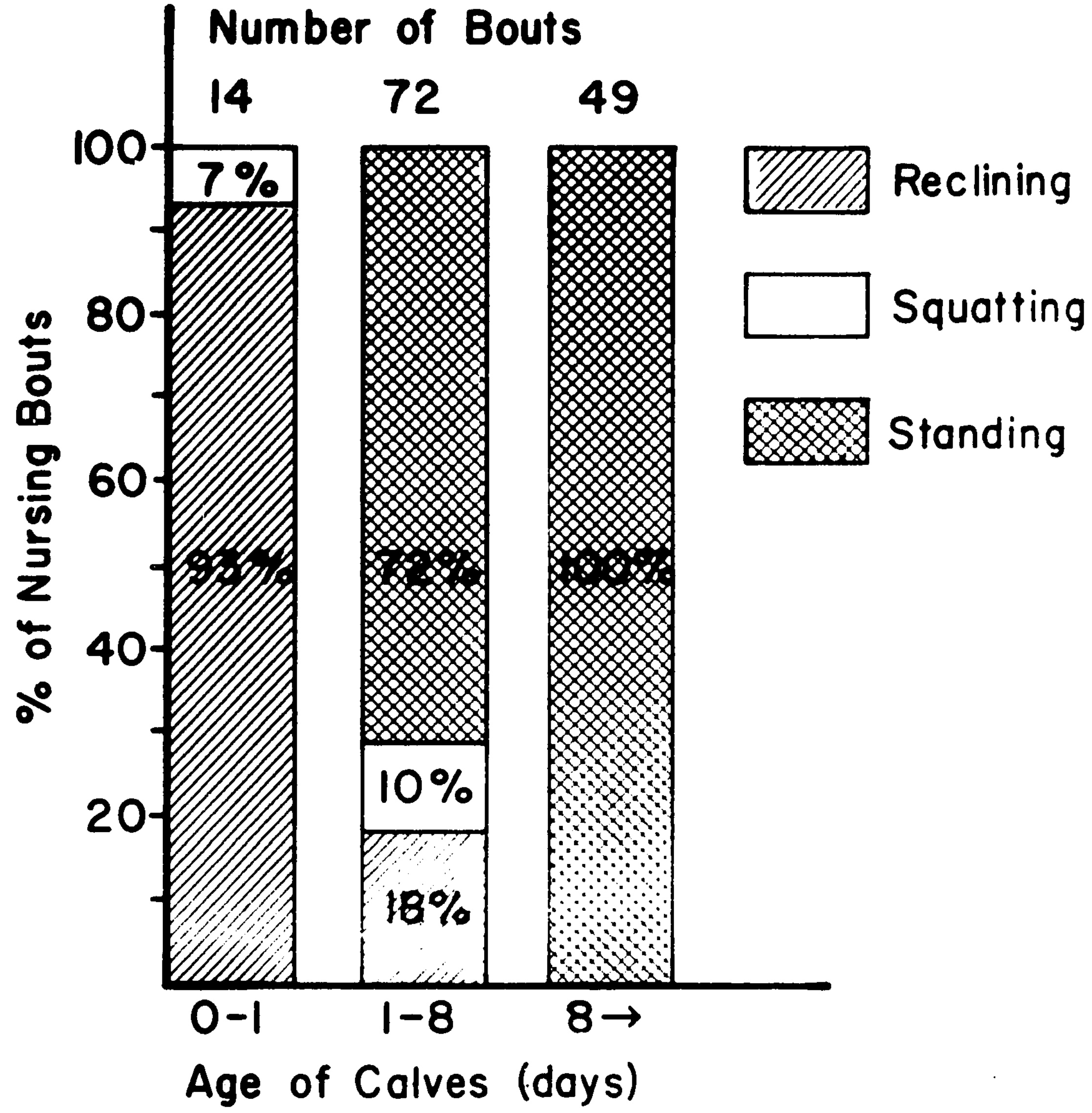
By "nursing" I refer to the transfer of milk from mother to infant, or to the mother's role in this transfer. The calf's activity is called "suckling". In the following discussion I provide various quantitative data on nursing postures, duration of nursing bouts, and other events for Kenai moose. It should be kept in mind that figures for the first two weeks postpartum are based on sporadic observations; except where specified otherwise, they represent data for all calves (Table 2). All quantative data beyond that age are solely for Rolly and Alfe, based on systematic biweekly observations. Other descriptive material for calves more than two weeks old are primarily for Roxy, Rolly, Arnold, and Alfe -- the offspring of Mary Ann and Amazon.

Results

Recumbent Nursing

The manner of nursing changes as calves mature. They first suckle before they are 1.5 hours old, while they and their mothers are bedded (Skuncke 1949; Speidel, In Peterson 1955; Knorre 1959: Fig. 7; 1961). Hediger (1955), Altmann (1963), and Lent (1973) have also reported recumbent nursing. On the Kenai Peninsula, most nursing during the first day was in this position (Fig. 5). In

Fig. 5. Posture of the cow while nursing her calf as a function of the age of the calf.


Number of Bouts
14
72
49
100
80
60
40
20
% of Nursing Bouts
7%
93%
72%
10%
18%
100%
0-1
1-8
8→
Age of Calves (days)
Reclining
Squatting
Standing

all cases, the calf rested with its head by the udder and its rump near its mother's shoulder. This orientation was also used when they were standing. Lent calls it the "reverse parallel" position. A calf initiated recumbent suckling by kneeling on its carpal joints, bunting the udder solidly a few times, and lying down to suckle. Contact with the udder while kneeling seemed to position the calf so that it could reach the udder while bedded. Bunting may have also been easier while kneeling. When the calf was already bedded by the udder, it arose to a kneeling position and bunted the udder before lying down again and sucking. While recumbent, the calf did not bunt the udder but intermittently massaged it with its muzzle at a rate of up to once per second.

During the first few days of life, Kenai calves seemed to suckle at will. Their mothers were available almost continuously. If a cow was feeding nearby, she usually returned when her calf bleated. She assumed the nursing stance, legs fully extended and head typically elevated so that her eyes were higher than her rump. When her infant tried to suckle, she bedded down, usually with her udder exposed towards it. Cows also initiated bouts. When resting by her calf, a cow simply arose and assumed the nursing stance. Typically, her calf arose too, even if it had been resting by her udder before she got up.

If the calf remained bedded, the cow aroused it by nudging. When it tried to suckle, she lay down, enabling it to reach the udder.

Standing Nursing

Kenai calves only a few hours old attempted to suckle while their dams were standing; but they were not tall enough because their hind legs were extended so far out behind them that the tibiae were nearly parallel with the ground, and their fetlocks almost touched the ground (see Fig. 2), instead of being nearly vertical as they are for older calves. As they grew stronger and could stand more normally (Fig. 6), they could sometimes reach the udder if the dam squatted. In one instance, Carie lowered her udder an estimated 10 to 20 cm in this manner. The nursing squat is identical to that used for urination (see Geist 1963).

Calves suckled from between their dam's hind legs in 17% of the bouts (n = 60) seen during their first eight days. After that, they always suckled in the reverse-parallel position. Calves older than eight days also tried to suckle from the rear, but none was successful. They rubbed their muzzles against the udder, perhaps bunted it a few times, then gave up and moved around to a flank to suckle. Altmann (1963) stated that Wyoming calves never suckle from the rear and suggested that the

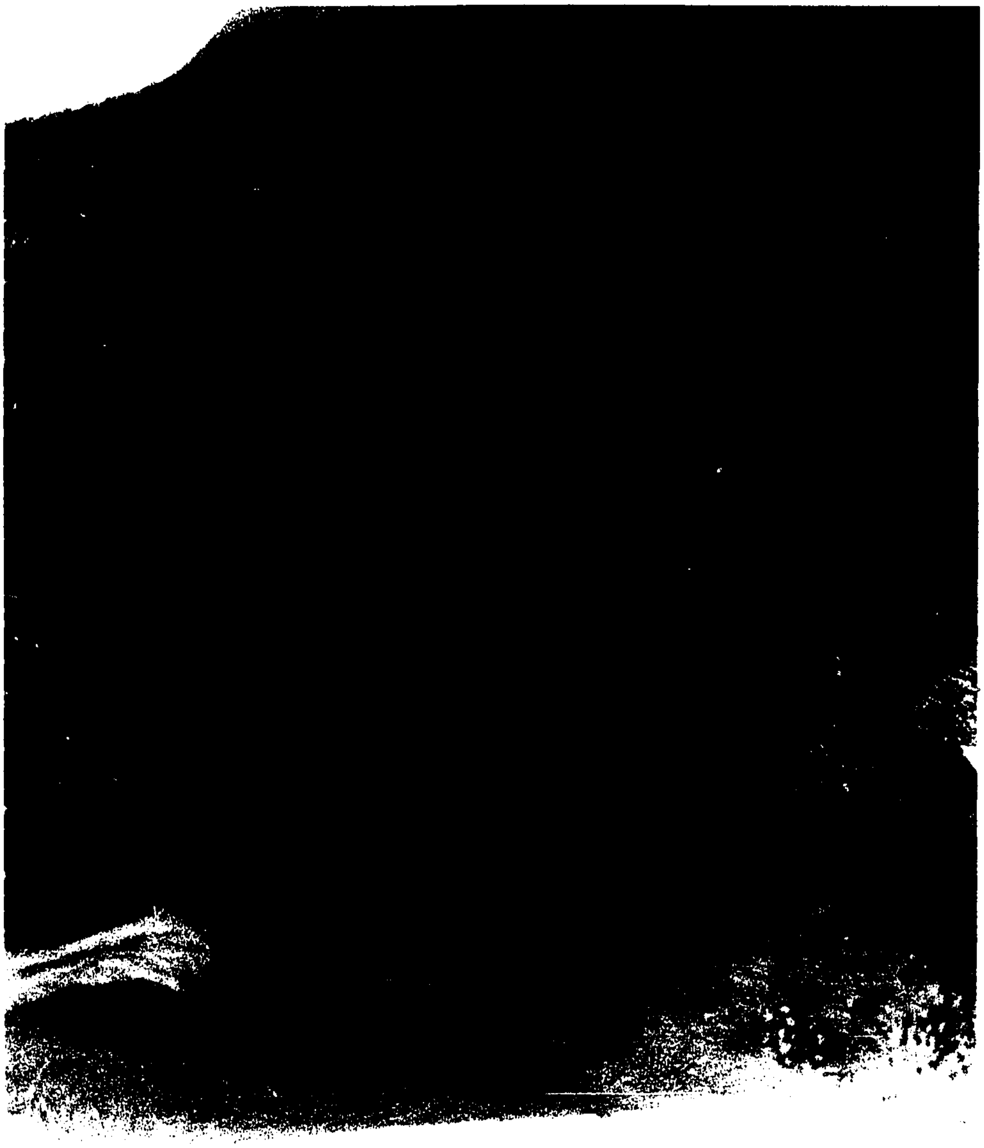
Fig. 6. Boltar, a few days old.

teats might not be accessible from that position. Figure 7 shows the udder and a posteriorly accessible teat of one of the Kenai cows.

During the first week or so, bunting was relatively gentle. It involved mainly head and neck movements. However, by age two and a half to three weeks, bunting was so vigorous that the calves' ears flopped wildly. Thrusting was performed using the whole body, especially the head, neck, and forequarters, at a continuous rhythm of about twice per second throughout each bout. The two calves reared by Markgren (1966) bunted mildly when only a few days old but very vigorously by the second month.

Stimuli Which Elicit Suckling Behavior

I have already described how a calf will usually attempt to suckle when its dam assumes the nursing stance. Prior to sucking, it will typically nuzzle her, especially around the udder. Further insight is provided by observations on the objects towards which Boltar, the hand-reared calf, directed suckling attempts. He was abandoned by his mother when no more than six hours old, due to human disturbance. After 17 hours of abandonment, she had not returned and he was taken to camp. Boltar anxiously explored my clothing with his lips, especially around my groin, bunting weakly. When I knelt down, he knelt too, shoved his nose into my groin and bunted



upwards with considerable force. He made similar thrusts into my armpits when I held my arms a few inches from my sides. He seemed to search for a semi-enclosed area and, finding one, would begin bunting. He also directed suckling attempts against the undersides of moderately large objects with space beneath them, including a table, a bench and a bed, each of which was set against the wall of a building. He approached our truck, explored its surfaces with his lips ("lip-exploration") and bunted upwards under the runningboard, fenders and the open door, inspite of the fact that this was apparently painful for him to do so, judging both from his vocalizations and the sounds of his muzzle hitting the truck. When I prepared his bottle, Boltar became very excited; he bunted against me and explored the furniture with his lips. He seemed to bunt most forcibly against me and possibly against the underside of my table. Markgren (1966) stated that when he approached his two moose calves with their milk bottles, they bunted into the air and against the fence separating him from them.

A dam's vocalizations also seemed to elicit suckling attempts. In cases where a Kenai cow assumed the nursing stance, but her calf did not look up, grunting attracted its attention. Furthermore, grunting apparently released approach in conflict situations. Calves were sometimes rebuffed when they tried to suckle (see below). Consequently, they often approached hesitantly, or did not approach at all. But upon hearing its mother's grunting, a calf would run to her and begin suckling immediately. In no case was a calf rebuffed or avoided after this combination of signals.

Pre-Suckling Behavior

When Kenai neonates approached their mothers to suckle, whether after being invited or on their own initiative, they commonly bleated, phantom-sucked and flicked their tongues. Markgren (1966) also reported tongue-flicking when his calves approached him to suckle. In Pens 2 and 4, Kenai calves more than about one week old did not phantom-suck and when more than two weeks old seldom nuzzled their dams prior to nursing.

"Phantom-sucking" is an exaggeration of the mouth and tongue actions used in actual sucking. The designation "phantom" refers to the fact that actual sucking does not occur, and the mouth actions are usually performed without contact with any object. It may be directed towards the dam or caretaker from at least 30 m away as the calf approaches to suckle. However, a calf may phantom-suck while its lips explore surfaces such as the dam's flank. These characteristics were determined primarily by watching Boltar. I could hear his phantom-sucking over 5 m away.

During phantom-sucking, the gums were sometimes exposed, producing highly visible flashes of color. Tongue-flicking (alternate extension and retraction of the tongue during which the muzzle sometimes appears to be licked) also produced flashes (Fig. 8). Both gums and tongue are bright pink.

Sucking sounds and flashing of gums were rhythmical and were performed about once to twice a second, roughly the same rate at which calves uttered bleats. Phantom-sucking and bleating sometimes occurred simultaneously and might be interspersed with tongue-flicking. These activities may be displays which help induce the mothers to permit suckling.

Nuzzling, lip-exploration, tongue-flicking, and bunting all virtually ceased after Boltar was fed, then reappeared a few hours later, becoming progressively more frequent and, in the case of bunting, more intense. They might be interpreted as manifestations of hunger Bleating also became more frequent and intense on these occasions. Likewise, Boltar's phantom-sucking increased until he was fed, then virtually ceased afterwards.

Phantom-sucking also appeared when Boltar was bedded, whether alert, drowsy, or apparently sleeping. Under these conditions, phantom sucking did not indicate hunger. He did not attempt to suckle when I held the bottle near

Fig. 8. Boltar flicking his tongue as he approached me to suckle; one day old.

his muzzle; nor did he bunt, explore the bottle or me with his lips, or tongue-flick.

By the time Boltar was three weeks old, recumbent phantom-sucking had gradually been transformed into "phantom chewing". His jaw movements had become progressively more lateral. Grinding of the molars was audible, in addition to sucking sounds, but he had not yet begun to ruminate. When he died one week later, autopsy revealed no more than a few millimeters of chewed vegetation in his digestive tract. Markgren (1966) likewise saw phantom-chewing in calves he reared. He interpreted this as incipient cud-chewing. That interpretation might also be applied to Boltar. However, Dieterich (viva voca) has reported that domestic cattle calves that were scouring badly, sometimes make grinding sounds with their teeth; most of them died. Since Boltar had been scouring badly for over two weeks, and died shortly after phantom-chewing appeared, the trait may have been a symptom of his poor condition.

Interruption and Termination of Nursing

During their first eight days of life, Kenai calves frequently interrupted nursing bouts temporarily; their mothers occasionally did so too, as they stepped forward to feed. Interruptions rarely (5%; n = 66) lasted over 30 sec. After two weeks of age, interruptions were almost never more than 1 sec long, occurring mainly when calves switched teats. Interruptions were longest in cases where calves bunted the udder a few times before regrasping a teat. On the few occasions that I was close enough to see, it was noticed that cows began terminating after the fourth switch, presumably when a calf began suckling from one of the teats a second time. In contrast, beef calves may change teats many times during nursing bouts, leaving each quarter of the udder even before it is emptied and returning again later; switches and bunting become more frequent as the nursing bout nears its end (Hafez et al. 1968). Bunting by moose calves also seemed to become more vigorous towards the end of a bout, perhaps due to the dwindling flow of milk.

During the first day, while cows and calves were recumbent for nursing, calves apparently terminated all bouts. They suckled at will and quit on their own initiative. Once they began to suckle standing, sometime on the first or second day, their mothers also ended many bouts: 51% during the first eight days (n = 86) and 100% thereafter. Espmark (1969) reported that in a small group of roe deer the fawns terminated all bouts on the first day, and the does terminated all bouts after the seventeenth day.

A calf terminated nursing simply by releasing the teat; it usually remained with the mother for a short while, nuzzling or licking her and being licked by her, before it moved away. A cow terminated nursing by stepping forward, usually lifting her adjacent hind leg over the calf (if it was nursing from her flank). Frequently the leg bumped the calf, sometimes making it stumble or fall. Since calves usually held on to the teat and were often dragged momentarily, this may have helped to detach them. As early as the seventeenth day, stepping forward was accompanied by a moan-like vocalization from the cow. Although moaning soon became typical, it did not occur in all instances even as late as the ninth week postpartum. Moaning often began before a cow stepped forward and sometimes continued several seconds after the calf was loose. Cows also moaned when discouraging attempts by their calves to suckle or play-fight. Calves responded by withdrawing.

Milk Consumption

The duration and frequency of nursing bouts decreased rapidly with age. Bout duration indicates the amount of time that a calf appeared to have its mouth on a teat. Detectable interruptions are not included. Data for the calves Rolly and Alfe are shown in Figs. 9 and 10. They could not be observed at night, nor could they be followed continuously throughout the day. Data are most complete

Fig. 9. Mean durations of nursing bouts between 10:00 and 22:00 hr (Alaska Standard Time) as a function of calf age (Rolly and Alfe, 1971). (<u>Note</u>: some of the bouts shown in Fig. 9 could not be timed.)

Number of Bouts								
15		4		8		5		2
Standard Deviation (sec)								
282		27.5		2.5		1.5		1.4

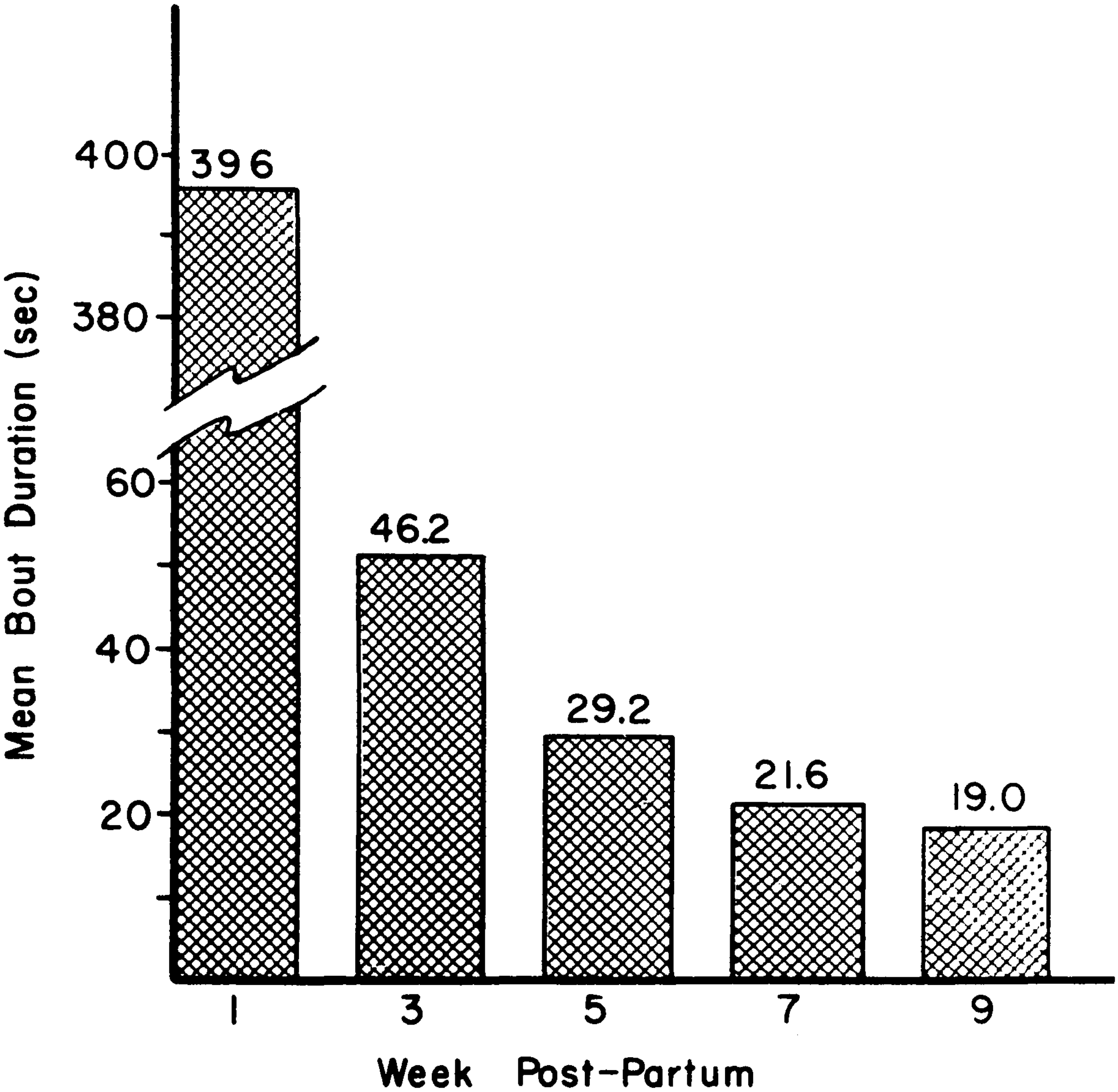
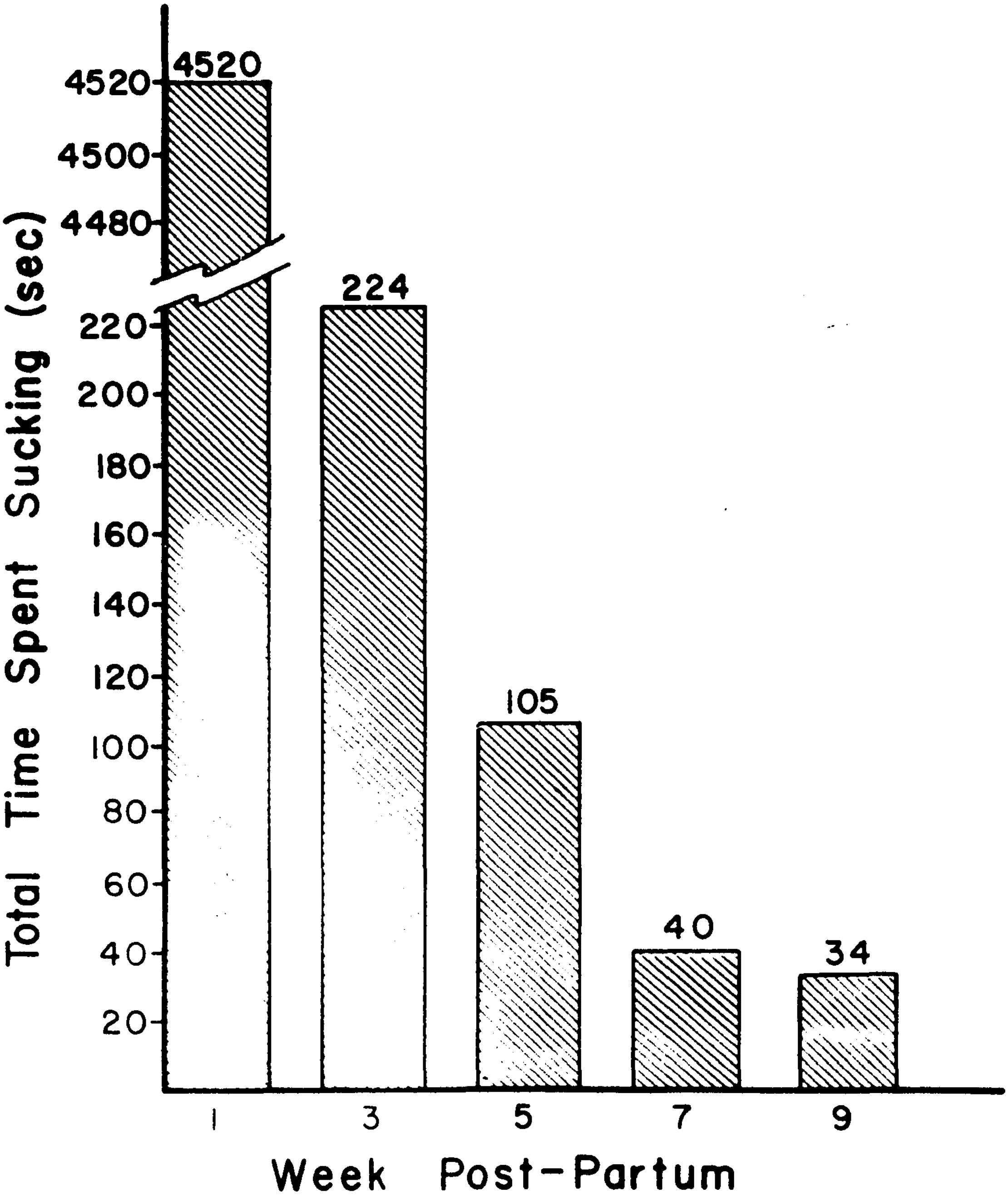


Fig. 10. Total time nursing between 10:00 and 22:00 hr (A.S.T.) as a function of calf age (Rolly and Alfe, 1971).

Total Seconds of Nursing								
6630		211		282		107		55
Total Hours of Observation								
17.6		11.3		32.3		31.7		19.2



for the 12-hr interval from 10:00 to 22:00 (Alaska Standard Time) (Fig. 11); the values given are for that time span only. Total sucking was estimated using the cumulative data for the given period by the following formula:

$$\frac{\text{(total seconds of nursing observed)}}{\text{(total hours of observation)}}\ (12\text{ hrs}) = \text{(estimated seconds of nursing 10:00-22:00)}$$

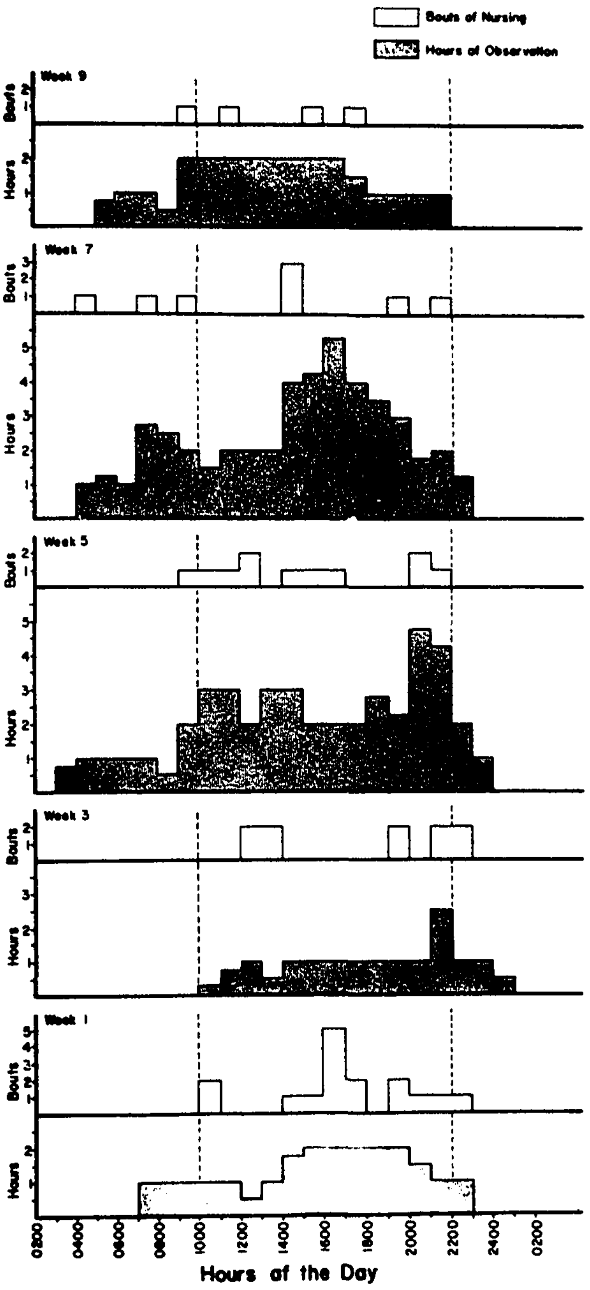
For instance, during the first week postpartum, 6630 sec of nursing were seen during 17.6 hrs of observation on Rolly and Alfe between the hours of 10:00 and 22:00. If one assumes that nursing bouts during the rest of the day and night were equivalent in frequency and duration, 24-hr estimates are obtained by doubling the 12-hr values.

Mean duration of nursing bouts for Rolly and Alfe decreased more than 20-fold from about 400 sec each during the first week postpartum to about 20 sec each by the ninth week (Fig. 9). This was accompanied by nearly a 5-fold decrease in frequency from about 10x/12 hr, and more than a 100-fold decrease in total time nursing (Fig. 10).

Foraging

Kenai calves began mouthing and, later chewing on leaves before they were one week old; but most did not start foraging regularly until at least two or three weeks postpartum. The one exception to the norm was

Fig. 11. Number of nursing bouts and number of hours of observation of Rolly and Alfe for each 1-hour interval of the 24-hour day (A.S.T.), for each semi-weekly observation period in 1971.


Bouts of Nursing
Hours of Observation
Week 9
Week 7
Week 5
Week 3
Week 1
Bouts
Hours
1
2
3
4
5
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
2400
0200
Hours of the Day

Twister; he was browsing regularly when only five days old, probably because he was not obtaining enough milk to satisfy his hunger. His head and neck were twisted to one side, presumably due to an injury. I saw no evidence of this problem on his first day of life. The handicap prevented him from suckling while his dam was standing. Whenever he stretched towards the udder, he fell down. Although his mother may have continued to bed down to let him nurse, as she had done on his first day, I never saw her do so. In fact, she seemed to ignore his almost constant bleating when he tried to follow her through dense brush and windfall. He may have begun subsisting on foliage when just a few days old. When Twister was again seen in late July, only a vestige of the twist remained. He appeared to be as large and vigorous as other calves in the enclosures.

Discussion

Stimuli Which Release and Orient Suckling

Kenai calves usually tried to suckle when their mothers assumed the nursing-stance or, frequently, the alert-stance. This suggests that common visible aspects of the stances were releasors.

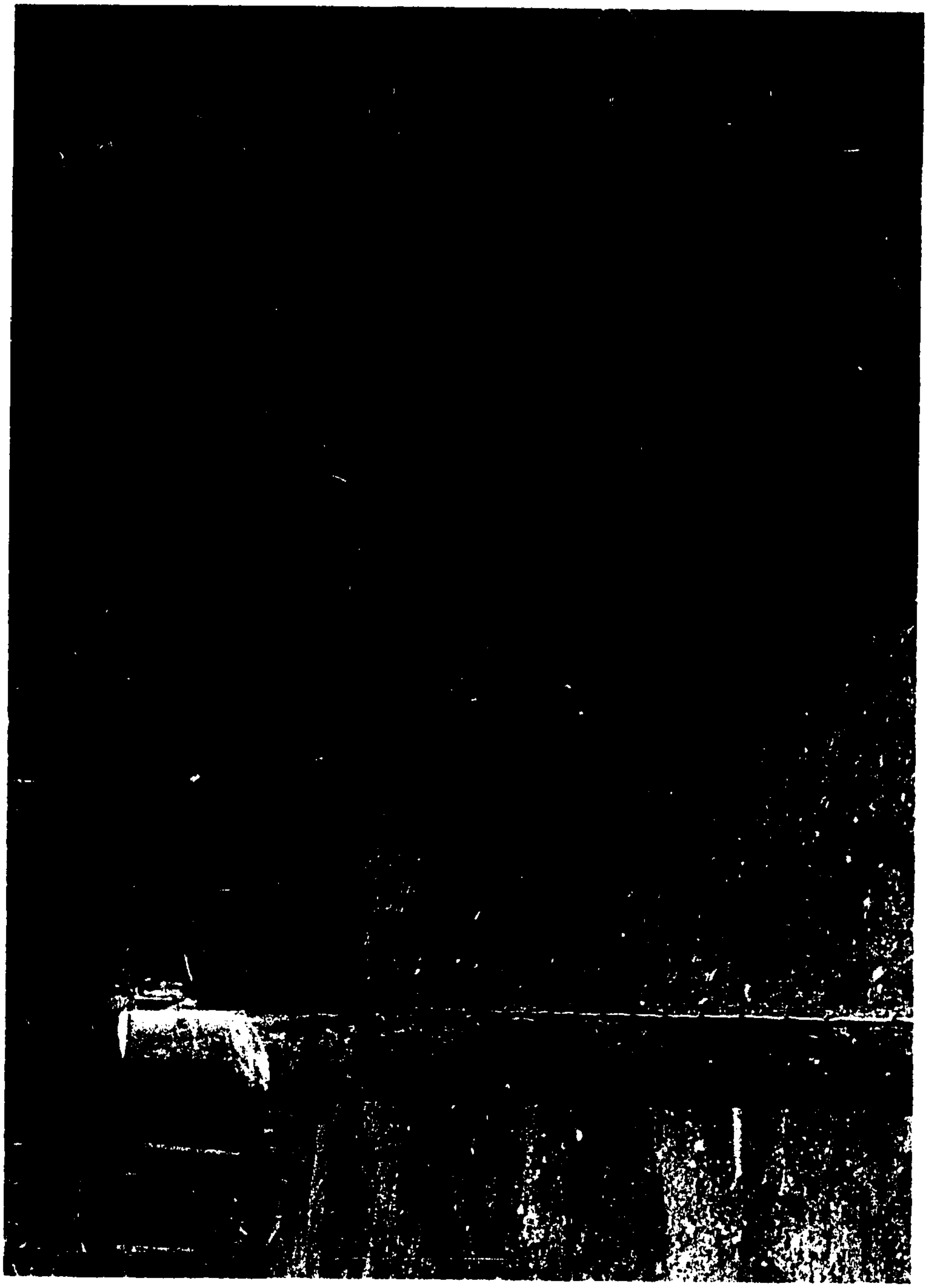
Although position of the dam's head seemed to be crucial once calves were a few weeks old, this was not apparent during the first week or so. Neonates frequently tried to suckle when their mother's heads were lowered below rump level. But I never saw an older calf attempt suckling except when the dam's eyes were more than rump high -- i.e., when her neck was above horizontal. Thus, other aspects of the nursing stance must have been more important initially postpartum.

Fraser (1968) stated that a neonatal foal quickly focuses teat-seeking in the angles between his mother's limbs and body. This has also been reported for goats Capra hircus (Blauvet 1956), llamas Lama glama (Kraft 1957), giraffes Giraffe camelopardalis (Lang 1955; cited by Thomas 1956) and domestic cattle (Adler, Linn and Moore 1958), according to Majoribanks-Egerton (1962).

Fraser (1968) also proposed that among some equidae, the dam's lower outline with shaded area beneath may release and orient suckling. Boltar's choice of objects towards which he directed suckling behavior (especially bunting) suggest that this is also true for moose. These objects included the observer, a bench, a bed, a table, and the running board, fenders, and open door of a truck. All were large or moderately large, and had open space beneath them.

Precisely what aspects of the dam's lower outline might release suckling are unknown. But it may be the dark/light interface. If so, this might explain the ventral-lateral color-shading pattern of cows (Fig. 12).

Fig. 12. Mary Ann: note the color-shading pattern of her pelage, particularly the dark chest and ventral flanks. (This photograph was taken *after* her winter coat was shed, the stage when the pattern is *least* accentuated.)



Essentially all cows that I have seen, live or in photographs, have been blond on ther backs and upper flanks, rump and shoulders; their chests, lower flanks and lower rump were darker and often black; the legs are typically much lighter in color, being whitish or blondish. (However, they may be almost uniformly dark just after shedding in early or mid summer; their backs turn blond as the season advances, perhaps through sun-bleaching.) This pattern of color-shades would accentuate the lower outline, especially its shaded aspect. Young bulls are also color-shaded in this way, but it is my impression that mature bulls tend to be much darker. All of the moose that I have seen that were almost completely black (except for their legs) were mature bulls. The similarity in color-shading between females and young-males is not surprising considering the widespread sexual automimicry of this type, morphological and behavioral, among mammals (e.g., Geist 1966, 1971). Fraser (1968) further noted that the lower outline of a mare closely resembles the equid mounting releasor ("Torbogen"). He states (p. 147) that: "It is an interesting speculation that the basic releasors for the two most fundamental activities of mounting and nursing should be nearly identical". Geist (1963:197) illustrates the posture of a cow moose while being naso-genitally "tested" by a rutting bull. Whether this pose is also assumed when inviting copulation, I do not know; but it is intriguing to consider its similarity to the nursing stance, in view of Fraser's remarks. It differs from the nursing stance only in the position of the ears.

While the hypothesis that the dam's lower outline releases suckling is consistent with Boltar's response to the truck and to other large objects with space beneath them, it does not explain why he bunted my groin much more forcefully while I was kneeling than while I was standing, or how a neonate finds the udder when its dam is bedded. Search for a semi-enclosed space may facilitate teat location while the mother is recumbent. In that posture, the cow's blond udder and adjacent underbelly are exposed in a rough semi-circle surrounded by the dark pelage of her chest, flank, and hindleg. The teats are grey or pink (Fig. 13). This pattern of contrasting shading may also help neonates to find the udder.

LeResche (1966) reported that Matanuska cows initiated reunions by grunting; their calves responded by bleating and approaching them; the calves stopped vocalizing only when they began to suckle. Knorre (1961) and Lent (1973) have also reported vocal nursing solicitation among moose. Lent noted that it is common in ungulates. Markgren (1966) reported that the calves he reared responded to his "food whistle" by running to him, licking their

Fig. 13. Ventral view of an udder and surrounding areas.

muzzles. There was no indication that vocalizations, per ce, elicited suckling attempts by Kenai calves. But, as noted earlier, grunting often complemented a cow's visible invitations.

The especially hard bunting by a calf at the onset of a nursing bout and when switching teats, probably served to stimulate milk letdown (see review by Fraser 1968). Ejection depends upon muscle contractions which are controlled by oxytocin released from the posterior pituitary upon stimulation of the udder. Letdown may also be stimulated by "visual factors" (Fraser, p. 146) including, presumably, sight of the young.

Milk Consumption

During their first week of life, Rolly and Alfe suckled for an average of about 4500 sec per day during the 12-hr interval between 10:00 and 22:00 hr, which suggests a value of 9000 sec per day. This is about twice as high as the values for roe deer *Capreolus capreolus* (4100 sec) and reindeer *Rangifer tarandus* (4500 sec) which may be calculated from the data on duration and frequency of suckling in Espmark (1969: Figs. 5,6; and 1971: Figs. 12, 13). Munro (1956; cited by Hafez et al. 1969: Fig. 45) observed approximately 1900 sec of suckling by a three-day old domestic lamb *Ovis aries* during the 10-hr interval between 09:00 and 19:00 hr. Extrapolation suggests a value of 4560 sec per 24-hr. New Forest ponies observed by Tyler (1972: Fig. 21) suckled for an average of 300 sec per hour during their first week of life. If one assumes that this average is based on data for all hours of the day and night, a 24-hr value of 7200 sec is obtained. Although it is possible that suckling by Rolly and Alfe was concentrated during hours between 10:00 and 22:00, it is more likely that they suckled equally long during the rest of the day.

Under the conditions of observation, there was no way to determine how much of the time during a suckling period that Rolly or Alfe was obtaining milk. One must expect a lag to have occurred between initial stimulation of the udder and letdown, at least during the early part of the lactation period. In some cases, it can be from 45 to 90 seconds long for cattle calves. However, letdown can also be stimulated by sights and sounds that a cattle cow has learned to associate with being milked (Davis 1962). One would expect a cow to respond similarly to the sights and sounds of her calf, and for the lag to decrease as she gains experience during the lactation period as well as with each calf born to her. Furthermore, infants may retain teat contact even after letdown has ceased. Prolonged teat contact after milk flow stopped might have occurred when both cow and infant were recumbent but would seem unlikely when the cow was standing or squatting. That would demand considerable effort by the infant to stretch so high for an extended period. If prolonged contact did occur only while both cow and infant were lying down, one would expect recumbent bouts to have been significantly longer than bouts when cow and infant were on their feet. That was not the case. Considering all calves observed during the first two weeks recumbent bouts averaged 342 seconds (n = 21, SD = 364); standing and squatting bouts together averaged 318 seconds (n = 50, SD = 324). However, calves did sometimes hold onto a teat for a second or two as the mother was terminating the bout (see above).

As the calves matured, their rate of suckling probably increased. The only figures available are for Boltar; they can serve only as a rough estimate, since the hydrodynamics of teat sucking are undoubtedly different from those of bottle sucking. His rate increased nearly 12-fold between his third day and his eighteenth. Initially, he sucked on a bottle for 20 min without consuming more than 1 pint ($\frac{1}{2}$ liter). Changes in letdown may have also increased the rate of milk flow, but we have no figures.

On the otherhand, the enormous amount of time that Rolly and Alfe apparently spent suckling during their first week of life, relative to later weeks, and relative to what has been reported for roe deer, reindeer, sheep and ponies, may in part be an artifact. If a neonate rested its muzzle on or near the udder or nuzzled it part of the time, that could not always be distinguished from suckling. Bunting was very mild and sporadic at that stage, and the moose were usually screened from view by vegetation. By the third week, however, there was little likelihood of such error. Bunting was vigorous enough and the cow-calf pairs visible enough that teat contact was readily distinguishable. At this age, these two calves suckled for an average of about 500 sec per day. Roe fawns and reindeer fawns both suckled over 1000 sec per day. This might suggest that moose calves actually suckled less than roe and reindeer fawns during their first week. But, it may merely indicate that the moose calves were being weaned more rapidly. By the ninth week these calves suckled an estimated 70 sec per day; roe fawns 40 to 59 days old averaged about 120 sec per day, and reindeer fawns averaged roughly 250 sec per day during their eighth week, and 184 sec per day during their eleventh (Espmark 1969, 1971). (Weaning is discussed below.)

Considering the probable decreases in non-sucking teat contact, increases in milk flow, and the possibility of systematic error during the first week, there is no reason to think that the observed 100-fold decrease in total time "nursing" was accompanied by a proportional decrease in total milk consumption during the first nine weeks of life.

Knorre (1961) indicated that the stomach (abomasum?) capacity of newborn moose calves was only about 1.5 liters. By weighing tame calves before and after suckling from their mothers, he determined that consumption varied from 0.1 to 0.5 liters of milk per nursing, according to the age of the calf. He claimed that on each of their first days of life calves ingested 0.5 to 1.0 liters/24 hr and that when consumption was greatest (about age 5 to 6 weeks), they sucked 1.5 to 2.0 liters/24 hr. Bubenik (*viva voce*) has pointed out that 0.5 to 1.0 liters/24 hr is much lower that one would expect for an infant the size of a moose calf. Calculations by Gasaway and Coady (in press) based on reindeer data support Bubenik's criticism. They estimated that a moose calf would need 3 to 4 liters/24 hr. during the first week of life. Yazan and Knorre (1964) have stated that by improving milking techniques, the daily yield of domesticated moose was increased from 2 to 6 liters, over a period of years. Thus, one must wonder whether cows gave full yield to their infants under the test conditions that Knorre used to arrive at the figure of a maximum of 2 liters per day, and whether it was possible to weigh calves accurately before and after they had suckled.

According to Knorre, during the entire suckling period pluriparous cows produced a total of 100 to 200 liters of milk, depending upon inherant capability, nutritional state, and age. Primiparous cows produced only 50 to 75 liters per season. Knorre concluded that, on the average, wild cows in the Pechora region of Russia produce about 150 liters. He states that domesticated calves achieved optimum nourishment when given milk five times per day. Furthermore, milk production by cows was also greatest when they were milked five times per day. Three cows cumulatively produced at least one-third again as much at that frequency as when milked only two to three times per 24 hr. Furthermore, Yazan and Knorre (1964) indicated that by improving milking techniques, the average yield of cows was increased from a maximum of 150 liters per season to 430 liters. Knorre's domesticated calves suckled eight to ten times per 24 hr when a few days old; my data suggest frequencies about twice that for Rolly and Alfe (see Figs. 8 and 9).

Foraging

Bierwirth (1949; cited by Markgren 1966) told of one calf that began chewing on foliage when it was only three days old. But most calves in Scandinavia and Wyoming do not start foraging regularly until at least two or three weeks old (Markgren 1966, Altmann 1963, respectively). This is equivalent to what I saw. A calf reared by Dodds (1959) did not begin until one month of age.

The fact that Carie apparently did not modify her behavior so as to regularly permit Twister to suckle, inspite of his handicap, cannot be explained by lack of maternal experience or by immaturity. She raised at least one calf successfully, in 1969.

Selective Advantages of Delayed Weaning

Suckling phases several months long are typical for ungulates; in some cases the young are not weaned until the following spring when they are a year old (Lent 1973).

Ewer (1968) has expressed doubt that it takes so long for rumen digestion to become fully established and has suggested that the function of prolonged lactation is to keep the infant under its mother's vigilant care. The extended nursing phase does appear to play an important role in the protection of moose calves.

I have already described the cow's nursing stance: legs fully extended and head elevated. The alert stance is essentially the same, but the head is usually held higher and the ears cocked forward in the direction the animal is facing (see Geist 1963: Fig. 53); in nursing, the ears are usually directed sideways. The similarity between the nursing and alert stances frequently led to mistakes by calves. When a cow lifted her head in alarm, her calf was likely to attempt to suckle. Cows normally avoided such attempts by stepping forward or discouraged them with a moan. Nevertheless, even calves three months old still reacted to alert stances by trying to suckle in cases where their mothers were disturbed. (In no case did a calf attempt to suckle when it was obviously disturbed.) A cow could seldom lift her head to look at something or stand in place with her head elevated without her calf watching her intently and perhaps even approaching. It is presumably the desire to suckle that keeps the moose calf so keenly attentive of its mother. Lent (1973) stated that "Such use of generalized attention-getting cues is of obvious value, particularly when the mother can more easily communicate further information after close contact is established with her offspring". Infant moose usually watch their mothers during disturbance, occasionally glancing towards the source of disturbance, but seldom staring at it. As they mature, however, they orient more towards the source of disturbance but are obviously still highly aware of what their mothers do and are quick to follow in case of flight or charging. The similarity between the nursing stance and alert stance may be adaptive beyond the simple fact that desire to suckle motivates attention to the cow. It maintains this attentiveness and alerts the calf in case of disturbance without frightening it unnecessarily and, thus, without producing undue emotional stress.

In regard to the similarity between nursing and alert stances, it is interesting to further consider Fraser's (1968) suggestion that suckling by a foal and mounting by a stallion might both be released by the same stimulus -- the lower outline of the mare with shaded area beneath. To carry his speculation one step further, perhaps for moose the posture with legs extended and head elevated releases approach in general, from the side or from behind. (Frontally, it is aggressive for Kenai moose; see Geist 1963, 1966 about the "head-high threat".)

Weaning

When a moose cow moans to her calf, this appears to be a mild threat which is probably reinforced whenever it is bumped by her leg during nursing termination. In no case did a cow visibly threaten her calf. However, that may occur during the final stages of weaning. Lent (1973) noted that vigorous bunting appears to be painful to the mothers in many ungulate species. In some, the mothers terminate nursing or discourage suckling attempts with agonistic behavior including threats, biting, and blows with head or horns. It is probably also painful when a calf holds only its mother's teat with its incisors. This may explain the "agonized" quality, anthropomorphically speaking, which characterizes nursing-termination moans. When cows discouraged suckling or play-fighting, their moans were usually more whiny, shorter, and quieter.

Lent (1973) considers that for ungulates the complex of these events during nursing is associated with weaning. As the infant matures, its suckling efficiency increases, and its mother's milk supply decreases. The infant seeks more milk by bunting harder (or, perhaps, by holding onto the teat after letdown has ceased even when the cow steps forward), which is painful to her. This increases her reluctance to nurse the calf on future occasions and reinforces her tendency to react aggressively when the calf attempts to suckle.

Knorre (1961) stated that in the U.S.S.R. most wild calves are weaned by mid-September, when their dams come into heat. Those cows that he found lactating in January "as a rule" (p. 88 of translation) did not have embryos in their uteri. However, in one case a tame cow weaned her twins when they were two months old. They continued developing normally and reproduced. Denniston (1956) reported that weaning occurred in early September for Wyoming moose, but Altmann (1958) indicated that calves continued suckling through the rutting period and were not weaned until the onset of winter. Dodds (1955) stated that he knew of no confirmed instances of suckling after September 10 in Newfoundland, but that the natives reported seeing instances in late winter. Johnson (viva voce) saw one case of suckling in January (1973) at the Moose Research Center. Cooney (1943) reported that weaning begins in December. Hosley (1949) believed that calves are not weaned until the next infant is born.

Dependence of Calves on Their Mothers After Weaning

Kenai calves became increasingly independent through their first summer. Whether this change continues during the winter is unknown. Johnson (viva voce) has occasionally seen calves widely separated from their mothers for more than a day in Pen 4, during the past two winters (1971/72 and 1972/73).

Numerous observers attest to the fact that the bond between cow and calf continues after weaning and that the calf continues to be dependent upon its mother at least until the following spring (Brown and Simon 1947; Daniels 1953; Denniston 1956; Altmann 1958, 1963). This problem is currently under study by Mr. David Johnson of the Cooperative Wildlife Research Unit, University of Alaska, at the Moose Research Center. Although many orphaned calves survive (LeResche, pers. comm.), some that lose their mothers even as late as November (age seven to eight months) may succumb to exposure and malnutrition. To account for this mortality, Denniston (1956: 112) has proposed two hypotheses:

> 1) . . . the cow initiates movements from one locale to another. In the crucial winter period an inexperienced calf is likely to stay in an area of deep snow and poor browse until too weak to escape it.
>
> 2) A calf shares the social rank of the cow: intraspecifically and interspecifically. A lone calf is on the bottom of the peck order and unable to compete.

Denniston's first hypothesis is supported by Altmann's (1963) observations. She agreed that maternal guidance was essential through the winter. By "guidance" she meant (p. 247): "choice of feeding and shelter places, safety and flight decisions, and later the selection and timing of winter groupings in the river drainages. . . . The winter group in moose does not take care of an orphan". However, calves may follow other adults (Bubenik, viva voca). It is not clearly established that maternal guidance per ce is more advantageous to a calf.

Denniston's second hypothesis is supported by the observations of Houston (1973). He noted that cow-calf pairs rarely associated with other moose during the winter and attributed this largely to the cow's aggressiveness. Since adequate winter range was very limited, "better established and/or more aggressive females might be comparatively more successful than others in bringing calves through the winter" (p. 6). However, on the Kenai Peninsula, cow-calf pairs associate substantially with other moose during winter (LeResche, pers. comm.).

My observations are consistent with the idea that a calf shares the rank of its mother. During 1971, there were five cow-calf pairs in Pen 4. (A sixth cow, probably Prudence, was accompanied by a calf on June 3 but was never seen with it again.) These five cows displayed a linear hierarchy which was stable through the summer of 1971, from the time I first saw interactions in mid-June through early August when my field work ended. Furthermore, cows with calves always displaced those without calves as well as yearlings. They usually, but not always, displaced the two young bulls. I saw no interactions between the one mature bull and any of the cow-calf pairs. However, Geist (1963) indicated that cows with calves may even dominate adult males. In all agonistic encounters between two pairs at the Moose Research Center, the dominant pair was predictable from knowledge of previous encounters. Calves shared the status of their mothers in the sense that, when calves accompanying their mothers interacted, the calf of the dominant cow was usually dominant. That seemed to be associated with the fact that when a subordinate cow retreated, both calves remained near the dominant cow. The calf of the dominant cow thus had its mother for back-up. The dominant cow usually threatened the alien calf, as was typical of all cows with calves when approached by alien calves. If the mother's threat included a short charge, her calf was likely to run with her and continue chasing the alien calf when it ran. As calves matured, they became increasingly more likely to join their mothers in threatening and chasing subordinates. However, when alone, these same calves were themselves subordinate to low-ranking older individuals and to cow-calf pairs. Altmann (1963) and Geist (pers. comm.) have also seen this.

COW-YEARLING RELATIONSHIPS

It appears as though moose calves generally accompany their mothers at least until early spring of their second year. When the dams calve again, the yearlings are driven away (see earlier). This disassociation may be temporary or permanent.

Results

I observed a variety of cow-yearling relationships in Pen 4. There is reason to believe that all cows with calves of the year associated only with their own yearlings. The evidence is circumstantial since individual juveniles could not be positively identified from one semi-weekly observation period to the next. Each of these cows tolerated only one yearling at a time near her; any other that approached was driven away. When an association could be observed over a period of several days, it was always the same yearling with the same cow. In 1971, the yearling with a cow was always the same sex as her calf of the previous year. Furthermore, all cows associated only with their own calves; they threatened and often chased alien calves.

I saw no instance in which a yearling continued to follow its mother, at a distance, after the new calf was born ("life on the margin"; see below). Mary Ann tolerated her yearling Roxy within 10 m of Rolly when he was only two to three days old. Roxy was frequently associated with them for the next few weeks, but progressively less so thereafter. Mary Ann was seldom aggressive towards Roxy even during the first week after Rolly was born. Associations between other cow-infant pairs and yearlings were occasional, especially in the case of the two male yearlings. The cows were not obviously more aggressive towards the males, however.

The closest cow-yearling association was between Olga and Olivia in 1970, a year in which Olga was not seen with an infant. Olivia was especially immature physically and perhaps behaviorally. She followed Olga more consistently and synchronized activities with her more closely than the calf Rolly did with Mary Ann at two and one-half months of age. During summer 1971, Roxy and the two other female yearlings were often associated with one another and sometimes with Prudence (who did not have a calf), singly or as a group, for up to several hours at a time. One of these females may have been Prudence's daughter Prucilla. The two male yearlings were frequently seen together.

A yearling sometimes drifted from association with a cow-infant pair to the company of other yearlings (usually of its own sex) to following a lone adult, all in a single day. Yearlings also spent much of their time alone.

Discussion

According to Denniston (1956), in Wyoming most yearlings were seen in the company of adult cows during their second summer; but, as he pointed out, he had no proof that these yearlings were with their mothers. Altmann (1958, 1959, 1960, 1963) provided a more detailed picture. She claimed (1959) to have relied primarily on natural markings (antlers, bell, and pelage) for recognizing individuals. She stated that most yearlings continued following their mothers closely until chased away prior to the birth of new siblings. Some became fully independent at that time. In most cases, however, a yearling continued to feed and rest in synchrony with its dam, remaining at the margin of her postpartum social distance ("life on the margin"), which was up to 100 yards (90 m) in radius at its peak. As summer advanced, some yearlings were allowed to rejoin their mothers; but, when rut began, all but the most immature and submissive were treated as rivals and driven away by either the cow or her suitor, depending upon the sex of the yearling. Juvenile males frequently tried to court their mothers. Most yearlings became fully independent at this time. Geist (1963) has seen yearling bulls chased by cows.

LeResche (1966) provides quantitative data on cow-yearling disassociation in the Matanuska Valley of Alaska. He first saw new calves in late May. Thereafter, he observed only one instance (on June 1) of a yearling ("loosely") accompanying a cow with a new calf, and only three cases (June 21 to June 23) where the relationship between a yearling and a lone cow was of an "offspring-maternal nature" (p. 53). Of 70 yearlings sighted before June 24, 31% accompanied a cow without a calf; between June 24 and August 21, this was true of only 25% of 73 yearlings seen. Whether these cows were their mothers is unknown. In many cases, there was no discernable interaction between them. (When interpreting this data, it should be kept in mind that some yearlings may have been counted repeatedly; LeResche, *viva voca*.)

Cow-Yearling Association versus Cow-Infant Association

It is interesting to note the parallels between the amount of cow-yearling versus cow-infant association in various parts of North America. In Wyoming, it was rare for a calf to be separated from its mother, and then only when the dam fed in water (Altmann 1958, 1963). Furthermore cows were commonly accompanied by yearlings. In contrast, Matanuska calves were regularly separated from their dams for most of the day, while the cows fed in lakes or large open meadows. These cows were seldom accompanied by yearlings, and then rarely with a calf-like degree of activity/rest synchronization. This parallel also holds for Kenai cow-calf pairs. Cows did leave their infants, now and then, even during the first few days postpartum; cows associated with their own yearlings, at least occasionally, and in two cases, frequently. For Kenai moose, however, yearling-cow association was probably heightened by captivity, which prevented the juveniles from dispersing, had they been so inclined. If such parallels are confirmed by future investigation, it would be worth considering how greater dam-infant contact might influence the duration of their reciprocal bond as the young mature. As was discussed earlier, greater contact during early infancy may promote certain kinds of learning. This may include imprinting.

OVERVIEW

As will have become obvious, the published information on moose is sparse and fragmentary. We do not have thorough behavioral data on even one cow-calf pair, much less on an entire population or representatives from populations of each subspecies. In my own research I tried to learn as much as possible about two cows and their calves and to obtain supplementary information on other families. Yet, I was able to observe them only a fraction of the time during two summers. We know nothing about their behavior during the rest of the year; nor can we yet assess how representative they were of other cow-calf pairs at the Moose Research Center and elsewhere. Furthermore, where differences exist between the findings of various observers, we have few clues as to what genetic, social, habitat, or pathological factors underlie these differences. Such questions can be answered only by following the development of individual moose in many populations over several generations. The generalizations and conclusions presented here are all tentative. They are put forth as hypotheses, for their heuristic value, not as proven facts.

SUMMARY

These observations and tentative generalizations are the products of investigation by a variety of workers.

1. Nearly all cervids, except moose, caribou, and reindeer, exhibit a postpartum "hiding" phase of periodic isolation between mothers and young during which contact periods are infrequent. Thus, they are called "hiders" ("Ablieger Typ"). The primary function of this isolation, called "lying-apart", is to help conceal the fawns from predators. Moose cows, too, may leave their calves in hiding even during the first two weeks postpartum. However, these separations are infrequent, brief, and there is no evidence that they are adaptive for concealment. Rather, they appear to be an incidental consequence of other activities. For instance, although it may normally accompany its mother when she is browsing and grazing, an infant typically remains on shore in cover while she is feeding in a lake. This isolation between mother and young seems to be due to greater preference for cover by calves -- a difference which diminishes as they mature -- and perhaps to an aversion to water as deep as their mothers typically feed in. Although these preferences may help reduce the vulnerability to predators, the resultant isolation probably does not. In this and a variety of other ways, moose

calves are less completely adapted for concealment then are the young of most cervids. In addition, they are not well adapted for flight soon after birth, as are caribou and reindeer young (which are hence called "followers", "Nachfolger Typ"). However, moose cows are especially formidable and can sometimes defend their calves even from wolves and bears by combat and intimidation. It is probably this capability which allows moose infants to avoid predation in sufficient numbers to perpetuate the species in spite of their limitations for concealment and flight. Therefore, they fall into a new class called "defenders" or "Verteidiger Typ".

2. Although calves frequently began rest and activity periods at the same time as their dams did, they often bedded down much sooner or got up later; but they were rarely active for more than a few minutes while the cows were resting. Not only did they not remain up after their mothers bedded down or get up much before their mothers, but, when they arose in the middle of a rest period, it was briefly. Exceptions appear to have been age dependent; nearly all were by calves over six weeks old.

Young moose were far more restless than their mothers. Whereas an undisturbed cow usually remained recumbent throughout a rest period, her calf sometimes arose once or twice to stretch, wander around, or feed. Interruptions may have helped to relieve the monotony of prolonged inactivity.

3. The tendency for Kenai calves to bed down sooner and get up after their dams was reflected in the differences in rest and activity period durations. Mary Ann and Amazon averaged 1.5 hrs for both rest and activity periods. Their calves averaged 2 hrs per rest period and 1 hr per activity period. Overall, Roily and Alfe were active only about three-fourths as much of the time as their mothers.

4. During the first few days postpartum, cows remained bedded most of the time. If disturbed, they usually became motionless except for movements of their ears and eyes; but, if approached closely, they got up and often showed extreme agitation. They sometimes remained up and oriented towards the source of disturbance for over half an hour. Once their calves were a few weeks older, the cows arose immediately if alarmed; but they usually calmed down more quickly and often bedded down again.

5. Moose give birth lying-down and first nurse their calves in that posture. Within one or two days, however, Kenai calves could suckle if their mothers squatted. In a few days, they could suckle even if their dams were standing, Suckling from between the mother's hind legs occurred only during the first week. Thereafter, all suckling was from her flank.

6. Certain visible characteristics of the dam's nursing stance may have released and oriented suckling attempts, including her ventral outline and her color-shading patterns. The blond udder area and pink teats contrast markedly with surrounding areas of the body and legs.

7. Calves apparently solicited nursing by tongue-flicking, vocalizing, making sucking mouth-movements which produced sucking sounds and exposed the bright pink gums and tongue in flashes, and by nuzzling the mother.

8. When cow-calf pairs nursed lying-down, the calves terminated all bouts. When they nursed standing up, the mother did so in all instances after the first week. A cow terminated nursing by stepping forward, pulling her teat from her calf's mouth. Beginning in the third week, this was often accompanied by loud moan-like vocalizations which were mildly threatening to the calf.

9. During their first week of life, Rolly and Alfe were apparently in contact with the udder for at least 4500 sec between the hours of 10:00 and 22:00 each day. By the ninth week, this had dropped to about 34 sec per day during the same 12-hr period. This decrease of more than 100-fold in apparent nursing time does not reflect a proportionate decrease in milk consumption. Increases in flow rate, due to increased efficiency of sucking and letdown, and

decreases in non-sucking teat contact probably account for a significant proportion of the change, especially between the first and third weeks. Furthermore, the figures for the first week may have been exaggerated due to the difficulties of observing nursing while cow and calf were screened by vegetation.

10. A calf's desire to suckle and the similarities between the nursing-stance and alert-stance of its dam seemingly kept it highly attentive to her and prepared to receive appropriate information in case of disturbance.

11. Calves may begin browsing and grazing as early as the first week postpartum but usually not until the second or third. They may be weaned as early as the second month or as late as the twelth, but the fourth or fifth is more common. Some investigators feel that continued association with the mother through the first winter greatly increases the calf's chances of survival. There appears to be considerable local variation in the tendency of calves to associate with their dams during their second summer of life.

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APPENDIX: ACTIVITY PATTERNS

The type of cow-calf synchrony illustrated in Fig. 3 was very common for Kenai moose. Calves were rarely active for more than a few minutes while their mothers were resting. They almost always rested as long or longer than their dams did, although they interrupted rest far more often, as was shown earlier. In most instances, interruptions were readily distinguishable from activity periods by their brevity and by the behavioral contexts in which they occurred. Many were no more than 1 min long, and most were no more than 5 min. However, in some cases, it was not obvious whether a given "bout" of activity was a long interruption or a short activity period. To deal with such problems, criteria were derived from the cases when interpretation was obvious.

In order to discuss criteria for judging whether a given unit of activity or rest is an interruption or a period, it is easiest to use an alternate system of units which I call bouts. Kenai moose were considered to be resting when they were lying down and as active when on their feet, whether they were traveling or standing still. A rest bout began when a moose bedded down, and ended when it got up, however, briefly, thereby beginning an activity bout. As was illustrated in Fig. 3, a rest period is comprised of one rest bout or of a succession of them, separated by interruptions -- which are brief activity bouts. Conversely, each rest bout is either a whole period, a fragment of a rest period or, rarely, an interruption of an activity period. (Only one interruption of an activity period was seen. In that instance, Rolly bedded down after feeding for over 42 min; 10 min later, he arose spontaneously and fed for another 2 hr.) Essentially all activity periods consist of a single activity bout (the instance just mentioned was the only exception observed). Conversely, essentially all activity bouts are either whole activity periods or interruptions of rest periods (Table 7).

Criteria for Distinguishing Activity Periods from Interruptions and Fragments of Rest Periods from Whole Rest Periods

1) Whenever a Kenai cow bedded down, she was either beginning or resuming a rest period.

2) Whenever a calf was resting with its mother, it too was engaged in a rest period.

3) Whenever a calf arose, wandered around or fed for a few minutes, then bedded down again while its mother was resting, this was an interruption.

4) Whenever a cow and calf arose just long enough for

Table 7. Interruptions of Rest Periods

	Cows			Calves		
Interruptions	Mean (min)	(SD) (min)	No. of Obs.	Mean (min)	(SD) (min)	No. of Obs.
Interruptions Initiated by Manmade Disturbances	9	(6)	14	7	(6)	20
Interruptions Initiated by Natural Disturbances	12	(6)	4	9	(8)	10
Spontaneous Interruptions	4	(2)	5	2	(3)	20
Interruptions for Nursing Elicited by the Dams	--	--	--	5	(4)	12
Total Interruptions			23			62

nursing and perhaps for brief feeding, then lay down, that was an interruption for both of them. Furthermore, whenever a calf arose just to suckle and perhaps to forage or wander around for a few minutes, this too was an interruption, whether or not its dam was recumbent when nursing occurred, and whether or not she had been active before nursing or remained active afterwards.

5) If a bedded moose arose upon being disturbed, then lay down again within several minutes after calming, this was considered as an interruption. However, if the moose fed without sign of alarm for more than about 10 min afterwards, this was considered as the beginning of an activity period.

6) All long rest bouts separated from adjacent rest bouts by long activity bouts, were considered as whole rest periods, and the intervening long activity bouts as activity periods. Furthermore, all pairs, triads or larger groups of successive rest bouts separated internally by brief activity bouts (interruptions), and flanked externally by long activity bouts (activity periods), were considered as fragmented rest periods. On this intuitive basis, numerical criteria were devised in accordance with the relative and absolute lengths of known interruptions:

a) Any two undisturbed rest bouts flanking an activity bout no more than 10 min long or 10% of their combined durations, constitute two fragments of a single rest period; the intervening activity bout is an interruption. (Some rest periods were interrupted more than once.)

b) Any two activity bouts flanking a _spontaneously-terminated_ rest bout no more than 10 min long _and_ no more than 10% of their combined durations, constitute two fragments of a single activity period; the intervening rest bout is an interruption. (As noted above, only one of these was seen. However, calves were frequently lost from sight for 10 to 15 min amid the immature birch and spruce, the sort of habitat where they normally bedded. So other interruptions of activity might have gone unnoticed.)

7) The rest bout separating two activity periods is a rest period; and vice versa.

Maternal Activity Periods and Interruptions of Rest Periods

Of the 58 maternal activity bouts seen from beginning to end, 23 were initiated by disturbance; these ranged from 1 min to 180 min. In five of these cases, the cows began feeding steadily after they calmed down, so they were considered as activity periods. In the other 18 cases, the moose bedded down shortly after calming down, so they were considered as interruptions (criterion 5). Only three of these were longer than 7 min; the longest was 22 min. All but five of the others were complete activity periods (ranging from 15 min to 233 min long). These five were considered as spontaneous interruptions of rest periods because of their relative brevity, and because they separated pairs or triads of fairly long rest bouts that were flanked externally by activity periods. One of these triads was shown in Fig. 3 (see Tables 7 and 8).

Maternal Rest Periods

Of the 79 complete rest bouts by Mary Ann and Amazon, 37 were complete periods, none of which was "seriously disturbed". Another 10 were fragments (2 pairs and 2 triads -- see Fig. 3) of 4 complete periods, 1 of which was seriously disturbed (Table 5). The only other 3 fragmented rest periods containing a complete, undisturbed rest bout, also included an incomplete rest bout. The remaining 29 complete rest bouts, all of which had been terminated by disturbance, were fragments of 15 "seriously disturbed" rest periods.

Calf Rest Periods, Activity Periods and Interruptions

All but nine of the calf rest periods were identifiable as such because they coincided with maternal rest periods; these others were identified by the fact that all were longer than 10 min, and most were over 20 min. None could have been interrpreted as an interruption of an activity period. Furthermore, most interruptions were identifiable

Table 8a. Interpretations and Durations of Rest Bouts by Mary Ann, Amazon and their Calves

	Cows			Calves		
Rest Bouts	Mean (min)	(SD) (min)	No. of Obs.	Mean (min)	(SD) (min)	No. of Obs.
Bouts Terminated by Manmade Disturbances	28	(33)	25	20	(25)	20
Bouts Terminated by Natural Disturbances	29	(26)	7	26	(30)	7
Bouts Interpreted as Spontaneous Interruptions of Activity Periods	--	(--)	0	10	(--)	1
Undisturbed Bouts Interpreted as Rest Periods or Fragments of Rest Periods	92	(54)	47	60	(46)	83
Bouts Which Could Not be Interpreted Due to Lack of Data	--	(--)	0	4	(2)	3
Total Complete Rest Bouts	66	(56)	79	50	(44)	114
Total Incomplete Rest Bouts			37			52
Total Rest Bouts			116			166

Table 8b. Interpretations and Durations of Activity Bouts by Mary Ann, Amazon and their Calves

	Cows			Calves		
Activity Bouts	Mean (min)	(SD) (min)	No. of Obs.	Mean (min)	(SD) (min)	No. of Obs.
Bouts Elicited by Manmade Disturbances	22	(43)	17	8	(7)	22
Bouts Elicited by Natural Disturbances	20	(15)	6	7	(6)	22
Bouts Interpreted as Spontaneous Interruptions of Rest Periods	4	(2)	5	2	(3)	20
Spontaneously Initiated Bouts Interpreted as Activity Periods or Fragments of Activity Periods	99	(54)	30	68	(40)	34
Bouts Which Could Not be Interpreted Due to Lack of Data	--	(--)	0	10	(--)	1
Total Complete Activity Bouts	60	(61)	58	27	(38)	99
Total Incomplete Activity Bouts			107			94
Total Activity Bouts			165			193

because they occurred while the dam was resting, for nursing, or were elicited by disturbance, or because they were only a few minutes long. In only a few instances was it necessary to calculate whether the activity bout separating two long rest bouts was less than 10% of their combined lengths. All of the other activity bouts were activity periods.