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    SOME PRELIMINARY OBSERVATIONS ON THE ACOUSTIC
    BEHAVIOR OF SEMI-DOMESTIC REINDEER
    (RANGIFER TARANDUS TARANDUS) WITH EMPHASIS ON
    INTRASPECIFIC COMMUNICATION AND THE MOTHER-
    CALF RELATIONSHIP.

    University of Alaska, M.S., 1972
    Zoology

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SOME PRELIMINARY OBSERVATIONS ON

THE ACOUSTIC BEHAVIOR OF SEMI-DOMESTIC REINDEER

(Rangifer tarandus tarandus)

WITH EMPHASIS ON INTRASPECIFIC COMMUNICATION

AND THE MOTHER-CALF RELATIONSHIP

A

THESIS

Presented to the Faculty of the

University of Alaska in Partial Fulfillment

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for the Degree of

MASTER OF SCIENCE

By

Carol A. Ericson, B.A.

College, Alaska

May, 1972

SOME PRELIMINARY OBSERVATIONS ON

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ABSTRACT

This study provides a general description of the overt acoustically related behavior of reindeer during the calving season by means of a series of observations under naturalistic conditions. Grunts by adults and bleats by calves are the loudest vocal sounds emitted by reindeer. Grunts range from 15 to 1900 Hertz; bleats range from 240 to 4400 Hertz, but the pitch drops with age. Under stress conditions, calves utter longer, louder, more highly-pitched bleats.

While during the calving season all mothers and all calves tend to vocalize in connection with characteristic kinds of situations, particularly mother-infant interactions. Individual differences are evident in propensity to vocalize, but later-born calves tend to vocalize more. It is hypothesized that grunts and bleats serve as alerting signals but play no role in actual individual recognition.

Snorts are frequently used in connection with agonistic behavior and during alarm situations. A wide variety of non-vocal sounds, such as belches, coughs and sneezes, are emitted, particularly by adults, during relaxed rumination. These sounds provide a means of herd cohesion and reassurance of the individual's "in-group" feeling. Bleats are infrequently emitted by calves during apparent paradoxical sleep.

Reindeer show varying degrees of response to environmental acoustic stimuli. Mothers with calves are always more alarmed by any unusual sounds, particularly when accompanied by visual stimuli.

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iv

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INTRODUCTION

Acoustic signals have been frequently mentioned in naturalistic studies of the social species _Rangifer tarandus_[1] with the implication that they form a system of communication. Since any social organization implies that some kind of communication is occurring among its members (Etkin, 1963), the frequent linking of acoustic signals with social behavior in ungulates follows logically if these signals are important components of intraspecific communication. Indeed, intraspecific acoustic communication has been documented for a wide variety of other ungulates, most commonly in connection with the rutting season, alarm situations and the mother-infant relationship. It is upon the last two categories that the emphasis of this study was placed, in an attempt to thoroughly and systematically examine acoustic communication in _Rangifer_ during the calving season.

Sounds emitted by mothers and infants are among the most common acoustic signals of ungulates (see Appendix). These sounds are an integral part of care-soliciting and care-giving behavior, which is a powerful force of attraction

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[1] This includes reindeer and caribou. See Banfield, 1962 for a discussion of the taxonomy within this genus.

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promoting not only the primary socialization of the infant
(Scott, 1960; Etkin, 1963) but also drawing animals together
into a herd (Scott, 1958; Scott, 1969).

References to maternal-infant acoustic communication
in reindeer or caribou are numerous, but the subject has
not been systematically investigated. The sounds produced
by mothers have been described variously as "a racous
mooing or grunting, usually intermittent and coarse ...
[and, to call the calf,] a reedier voice, somewhat like
intermittent combinations of 'KGRAU' and 'KHKHRRAU' "
(Flerov, 1952:217), "gurgling grunts" (Pruitt, 1960:28),
"loud, hoarse grunts" or "soft, intermittent grunts"
(Lent, 1966:735), "low, short, belching grunts" (Banfield,
1954:15), "short grunts resembling swine" (Kelsall, 1968:42),
"a low, coughlike grunt" (Murie, 1935:32), "a low, grumbling
call"(Evans, undated:68), and "a short, exhaled grunt,
similar to swine but not so nasal, it sounds somewhat like
coughing" (Jacobi, 1931:217).

Sounds produced by the calf are described as being
similar to those of the mother (Jacobi, 1931:217; Murie,
1935:32, and 1944:155; Kelsall, 1968:42), or as a "blat"
(Pruitt, 1960:31, 32), a "bleating" (Lent, 1966:735), a
"bawl" (Banfield, 1954:15; De Vos, 1960:255) that De Vos
claims was audible one half mile away, as the sound "avk"

Preobrazhenskii, 1961) or as "a sound intermittent between crying and piping" (Flerov, 1952:217).

Mother-infant acoustic signals have been found to be most frequent during herd movements or disturbances or when, for other reasons, one member of the pair becomes alarmed and cannot locate the other member (Seton, 1929; Murie, 1935: 32 and 1944:155; Lent, 1966:726 et seq.; Baskin, 1969:75; Kelsall, 1968:42). Even when no general distress situation is apparent, the cow grunts while she is searching for her calf or while it is searching for her (Jacobi, 1931:217; Pruitt, 1960:31; Preobrazhenskii, 1961:124; Lent, 1966:738). Grunting is also noted when the cow wishes to elicit approach or following by an infant; most frequently this is done in conjunction with other approach-eliciting behavior (Evans, undated: 68-69, 102, 106; Jacobi, 1931:217; Murie 1944:156; Pruitt, 1960:32; Lent, 1966:734, 735, 750, 752; Kelsall, 1968:42; Baskin, 1969:75).

Aside from vocalizations uttered in the context of the mother-infant bond there are, obviously, many other acoustic stimuli in the environment of the species. All these possible sounds are categorized in Table 1. Stefansson (1921), Murie (1935), De Vos (1960), Lent (1964 and 1966) and Kelsall (1968) have described a range of alarm reactions to gunshots and other noises. The differing responses observed were attributed to differences in weather, size

TABLE 1

THE ACOUSTIC STIMULI IMPINGING UPON REINDEER

	Source of Phenomenon	Type of Acoustic Stimulus
I.	Environment, other species	All environmental sounds excluding those caused or emitted by reindeer
II.	Reindeer - caused	Various sounds incidental to life activities
III.	Reindeer - emitted A. Non-oronasal	Clicking sounds produced by sesmoid bones

	B. Oronasal
	  1. Vocalizations
	  2. Respiratory/ digestive sounds
		
		Grunts, bleats
		Various non-vocal or partially vocal sounds

of the group of animals, or season of the year. Cows with young calves were found to be the most easily alarmed.

The sounds emitted by reindeer, either through the oronasal tract or by some other part of the body, have been mentioned in nearly every behavioral study of the species. Most frequently described are the vocalizations of the rutting male (Caton, 1877; Seton, 1929; Jacobi, 1931; Espmark, 1964a). The clicking noise produced by the sesmoid bones that is incidental to locomotion is described by Seton (1929), Jacobi (1931), Murie (1935), Flerov (1952), Semenov-Tyan-Shansky (1960), Lent (1964) and Kelsall (1968). (Prior [1968] describes a similar sound for roe deer, Capreolus capreolus.) Grunts or snorts emitted by excited animals are mentioned by Murie (1935), De Vos (1960) and Kelsall (1968). Coughing, sneezing and loud, labored breathing accompany infestations of the nasal parasites (Grudin, 1953; Espmark, 1968).

MATERIALS AND METHODS

The Study Herd

The study was conducted from 29 April to 13 June, 1970 by the author and an assistant. The small herd of semi-domestic reindeer observed were confined in a 1.5 hectare (3.6 acre) rectangular paddock 0.5 km south of the town of Cantwell, Alaska. The topography is that of a hilly river valley surrounded on three sides by mountains; the paddock itself was located on top of a small hill. Wire fencing bounded the paddock area, containing over-grazed tundra vegetation (lichen, moss, stunted birch, alder and willow) on an uneven substrate.

At the beginning of the study, the average snow depth in the paddock was 0,5 m, though in the feeding area snow was trampled and hard-packed, while in the drifted areas, which the animals avoided, the snow depth went to 1 m. By 11 May a third of the pasture area was clear of snow and in a wet, muddy condition. Melting continued rapidly and by 21 May no snow remained in the paddock, though the ground stayed sodden until the end of May.

Weather conditions during the study tended to be uniform. Most days were cool (-2 to + 10°C), though in the last three weeks of the study mean daily temperatures generally rose because the number of daylight hours increased.

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Cloud cover and moderate winds were usual, but measurable precipitation was rare.

The herd observed in this study consists of 18 individuals: six calves born immediately before or during the study, the six cows who were their mothers, three cows without current calves, two bulls and one steer. These animals belong to the Reindeer Research Section of the University of Alaska's Institute of Arctic Biology. A brief life history of each animal is given in Table 2. Two of the current calves had been born a few days before the study commenced and the remaining four were born during the study period. The oldest calf was eight weeks of age and the youngest five weeks when the study terminated.

As is evident from Table 2, nine of the adults had been continuously confined for at least 18 months prior to the study. Three had been continuously confined for at least two and a half years. Three animals had been resident at the Cantwell site for 18 months prior to the study, while the remaining nine had been there for nine months. Of the six cows who had calves during this study, four had been mothers at least once before.

During the winter immediately preceding the study, the herd had endured severe snow conditions and food

TABLE 2

LIFE HISTORIES OF INDIVIDUAL HERD MEMBERS

Id. No.	Sex	Age (Years)	Date Obtained	Obtained From	Resident At Cantwell Since	Previous Calves			Current Calves	
						Sex	Date Born	Date Died	Sex	Date Born
2	F	4	May,1968	B.I.A.,Nome*	Aug.,1969	M	1-VI-69	1-VI-69	F	29-IV-70
5	F	3	Nov.,1967	" "	Sept.,1968	-	--	--	M	13- V-70
10	F	4	Nov.,1967	" "	Sept.,1968	-	--	--	F	25-IV-70
12	F	4	Nov.,1968	" "	Aug.,1969	M	23-IV-69	16-IV-70	F	16- V-70
17	F	4	Nov.,1968	" "	Aug.,1969	M	30-IV-69	1-IV-70	F	3- V-70
20	F	8	Fall,1968	Nunivak Is.	Aug.,1969	?	9- V-65	10- V-65		
						?	1- V-66	12-II-68		
						?	29-IV-68	30-IV-68	F	22-IV-70
9	F	4	Nov.,1967	B.I.A.,Nome	Sept.,1968	-	--	--	-	--
14	F	3	Nov.,1968	" "	Aug.,1969	F	27-IV-69	III-70	-	--
						F	27-IV-70	27-IV-70	-	--
21	F	8	Fall,1968	Nunivak Is.	Aug.,1969	?	V-65	65 or 66	-	--
						?	Spring,'66	Spring or Fall,'66		
B5	M	?(Adult)	Nov.,1968	B.I.A.,Nome	Aug.,1969					
B8	steer	?(Adult)	Nov.,1968	" "	Aug.,1969					
S	M	2	May, 1968	" "	Aug.,1969					

* Obtained from Bureau of Indian Affairs, Nome.

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shortage. In early spring a commercial pelleted cattle ration ("Purina Cattle Starter No. 1") was provided every several days to supplement their natural forage diet. Three yearling calves had died during March and April of 1970, and the generally low plane of nutrition was presumably a major factor in these deaths and in the death at parturition of number 14 cow's 1970 calf.

Research personnel of the Institute of Arctic Biology continued their own physiological experiments during the course of the study (for details, see Luick, 1970). In connection with these tests, the animals were handled as follows:

(a) Herding. The herd was lured or driven into a small (approximately 40 m^2) "catching corral" in one corner of the main paddock and retained there in close proximity to each other and to the two to five workers on the other side of the fence.

(b) Sampling. Individual calves were chased and separated from the herd, and carried to just outside the catching corral fence. There, while physically restrained by one or two workers, they were sampled and weighed. Sampling involved the withdrawal of blood from the jugular vein and an intravenous injection of

a small amount of H^3-water solution.

(c) <u>Release</u>. After sampling, the calves were replaced in the catching corral with the rest of the herd. When all the calves had been sampled, a gate was opened and the entire herd was released again into the main paddock.

The duration of the 16 sampling sessions which occurred during the course of this study ranged from 30 to 210 minutes. The average duration was 90 minutes.

The herd was fed a supplementary diet of the commercial food every other day during this study. Until 12 May, the man who had fed them since early spring continued to do so, but after that date the author and her assistant assumed the feeding duties. The feed was hauled into the paddock on a sled and dumped into two wooden feeding troughs. The animals usually became excited as the feed was brought toward the paddock, and crowded around the sled and the troughs as the feed was transferred. Aside from this supplemental feeding the herd browsed and grazed at will throughout the paddock.

Water was available in the form of snow until the melt. Afterwards, the herd drank from the small pools of ground water scattered throughout the paddock.

From the foregoing description of the conditions under which the study herd is maintained, it is apparent that man-made disturbances of the animals are common. Disturbances consist of a spectrum of visual, acoustic, olfactory and tactile stimuli associated with the feeding and physiological sampling sessions, as well as a variety of visual and acoustic disturbances due to the proximity of human habitation: talking and shouting, barking of dogs, vehicular noises, train whistles and occasional low-altitude air traffic.

The Longitudinal Method

This study provides a general description of the overt acoustically related behavior of reindeer by means of a series of observations under non-experimental conditions. It is a survey and tabulation study rather than a hypothesis-testing experiment.

While the goal was the observation of natural behavior, the previously described disturbances associated with the study site, as well as the confinement of the herd, precluded totally naturalistic conditions. Nevertheless, certain spontaneous antecedent behavioral contexts can be related to certain consequences. This is the vital condition for the study of communication, since the key to the meaning of a sound pattern is the context in which it occurs

(Strevens, 1962). The context of what appears to be a communication event must be assessed "... in the hope of dissecting that which is relevant to the selection process from the rest of the background" (Sebeok, 1965:1013). By systematic observations of context, then, important features can be isolated and predictions can be made regarding the behavioral events associated with true acoustic communication. Thus this study provides a framework for future work involving experimental manipulation of the pertinent variables.

Because the ontogeny of acoustically related behavior is an important factor in this study, the data were collected on what is termed "the longitudinal basis": the same group of subjects are observed at different times. As Denenberg and Banks (1969:204) write,

> This procedure of repeated measurement is of considerable importance because it is often possible to relate unique behavioural patterns at one age to known events which occurred earlier in time.

This is the method commonly used in the study of individual developmental changes (Goldfarb, 1960). It has the advantage of dealing with variability, and allows the observer to identify and become familiar with individual subjects.

The use of the longitudinal method in this study had

the disadvantage of precluding the analysis of the effect of long-term environmental changes. While these changes (snow melting, daylight increasing, leafing out of vegetation, etc.) are accurately known, there is effectively no way to isolate their effects from those of age changes, so that it is not possible to determine beyond any doubt that particular behavioral shifts are maturational in origin (Denenberg and Banks, 1969). Major environmental and seasonal changes are considered to exert negligible effects for the purpose of this study.

Data Collection

During the 45-day span of the study, observations were recorded for 38 days. A total of nearly 171 hours (10259 minutes) were spent in observing the herd. Because observations were made under two distinct and very different conditions, the character of the observation period will be distinguished, as described below, for the remainder of the discussion.

First, "general observation" periods occurred on 32 days for a total of 8804 minutes (nearly 147 hours, or 86% of the total observation time). These periods were characterized by little disturbance, so that the animals were engaged in what is considered naturalistic activities and the presence of the observer was generally ignored.

A few disturbances did occur during general observation periods, such as feeding or the distant acoustic/visual stimuli resulting from the proximity of human habitation. Rarely, one individual animal was handled for special purposes, usually to drive it away from the recording equipment. The occurrence of any such disturbances were always carefully noted.

Second, "confined" periods occupied the remainder of the observation time. They occurred on 16 days for a total of 1455 minutes (24 hours or 14% of the total observation time), and were comprised of observations made during the physiological sampling sessions. Conditions were characterized by confinement and crowding in the catching corral, excitement, and reindeer, human and mechanical noise.

When the day is divided into quarters of six hours each, 3.5% of the general observation time was between 2400 and 0600, 22% between 0600 and 1200, 60% between 1200 and 1800, and 14.5% between 1800 and 2400. No confined periods occurred between 2400 and 0600, but 26% of total confined time was between 0600 and 1200, 64% between 1200 and 1800, and 10% between 1800 and 2400. The distribution of observation time in these quadrants by experimental week, with the first seven days of the study comprising experimental week 1, is shown in Figure 1.

minutes of observation time

quadrant #
experimental
week number
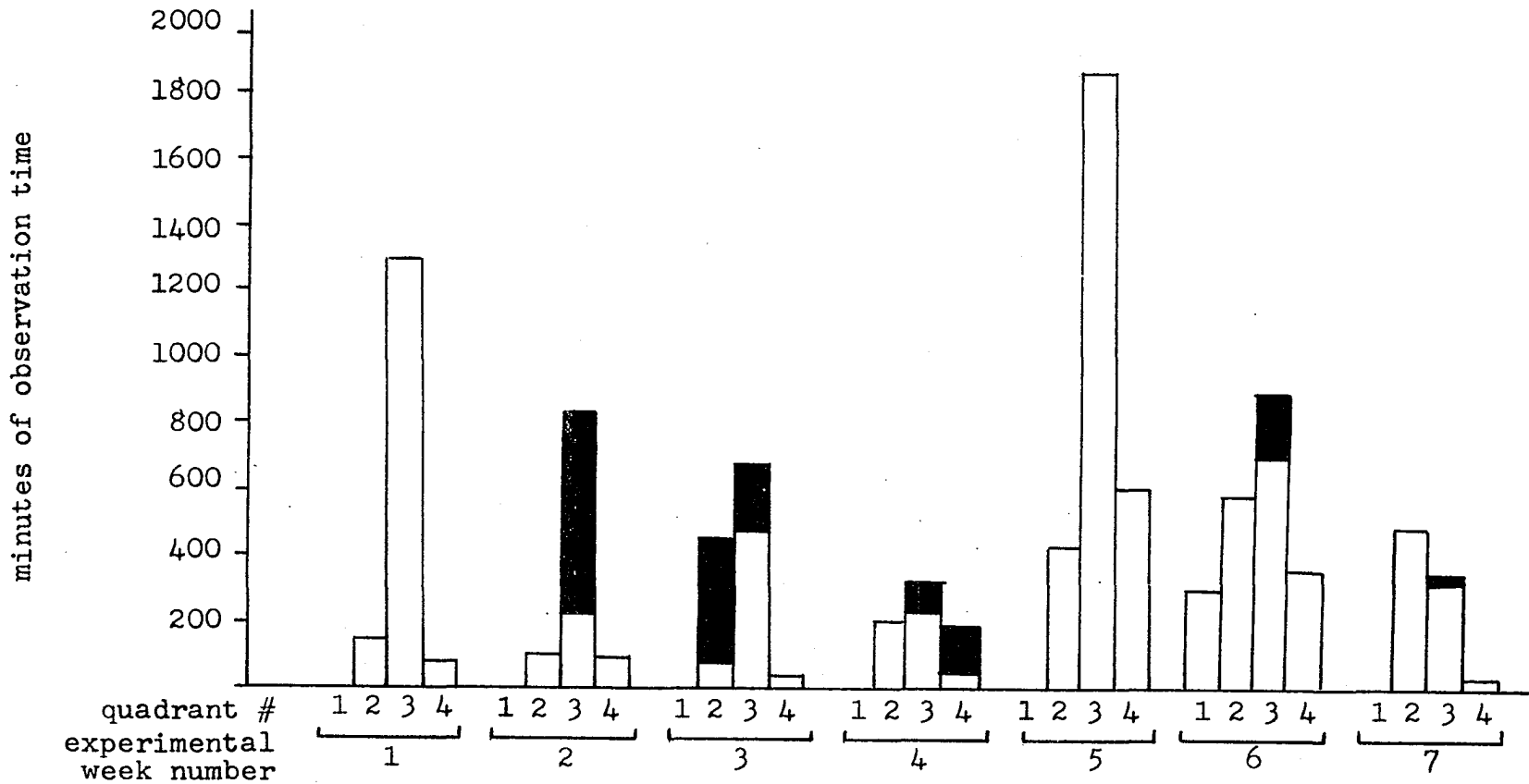
Figure 1.   Distribution of total minutes of observation, within quadrants of the
24-hour period (quadrant #1:   2400-600, #2:   600-1200, #3:   1200-1800,
#4:   1800-2400) for the seven weeks of the study.   Clear areas are
general observation periods, shaded areas are confined periods.   Total
number of minutes of observation = 10259.

In attempting to systematically observe animal communication, the human worker is invariably hampered to an unknown extent by signal detection problems. While these problems are recognized and have been intensively investigated (see Swets, 1964), the signal detection process varies widely between species because of both physiological and morphological differences and species-specific learning processes.

The acoustic events discussed in this study are necessarily only those perceived by a human observer. In the case of reindeer-emitted sounds, they are those sounds heard from observation distances varying from 1 to 65 m, though averaging 8 m. Similarly, associated behavioral or contextual changes are those which could be seen or heard at the same distances.

Observation and accurate recording of as much acoustically related behavior as was apparent were the main goals of data collection. The observer, equipped with 7 X 35 binoculars, a watch, a stopwatch, and paper and pencil stood or sat in an advantageous position within the paddock to view the entire herd. Visual and acoustic observations were written down immediately upon what seemed to be the conclusion of a discrete event or series of events. However, for long and complex events, writing would begin during the event, so

that for a brief time the observer was attempting to both watch and write. While this introduced obvious possibilities for error, such complex events were relatively few. Errors of omission are more serious when there was the possibility that (1) two or more events were occurring simultaneously in different parts of the herd, (2) the observer missed an event in the process of recording a previous one, or (3) occasionally events were missed completely because the observer was too far away to accurately see or hear them.

In addition to written observations, a total of 18 hours (15,400 meters) of magnetic tape was recorded simultaneously with written observations during both general observation and confined periods. Of the 38 days on which observations were made, for 23 of the days there are tape recordings of at least some of the acoustic events. An Uher 4000 Report-L magnetic tape recorder at a recording speed of 7.5 inches per second was used in connection with an AKG model D-900E parabolic range microphone (frequency response range 40-13000 Hertz). The recording equipment was sheltered in a canvas tent in the paddock, though the microphone protruded from the tent and was aimed at sound-emitting individuals. Infrequently, sounds were heard and described in writing which were not distinguishable on playback because of wind or aircraft background noise.

A second major data collection goal was for the observers to remain as inconspicuous to the herd as possible. There were two reasons for this: (1) to observe under circumstances as undisturbed and naturalistic as the study location conditions would allow, particularly during general observation periods, and (2) to minimize an important disadvantage of the longitudinal data collection method whereby the process of obtaining data changes the subject (e.g. some kind of learning occurs) so that future observations on that subject are affected (Denenberg and Banks, 1969). The observers were generally successful in that, after a short habituation period prior to the beginning of the study, they were generally ignored by the herd.

RESULTS AND ASSOCIATED DISCUSSION

The Qualitative Properties of Vocalizations:
Grunts and Bleats

The loudest reindeer-emitted sounds are the vocalizations
which will herein be referred to as "grunts" and "bleats".
These are the most widely described and obvious acoustic
signals emitted by reindeer and seem the most amenable to
investigation as distinct communication signals. This
section will discuss the qualitative properties of grunts
and bleats, while the following two sections will analyze
the number and contexts of these sounds.

Grunts

In this paper, "grunt" refers to the adult vocalization.
It is an explosively harsh and grating sound, rather like
someone attempting very loudly to clear their throat.
Its frequency ranges from about 15 to 1900 Hertz, with
base frequencies very low (15-150 Hz) and from one to
three overtones centered at approximately 500 - Hz
intervals (see Figure 2). Undoubtedly the activity and
posture of the vocalizer as well as the position of the
tongue and lips have great influence on the number and
frequency of overtones. Most often the mouth is open
during the entire vocalization, but in some cases it was

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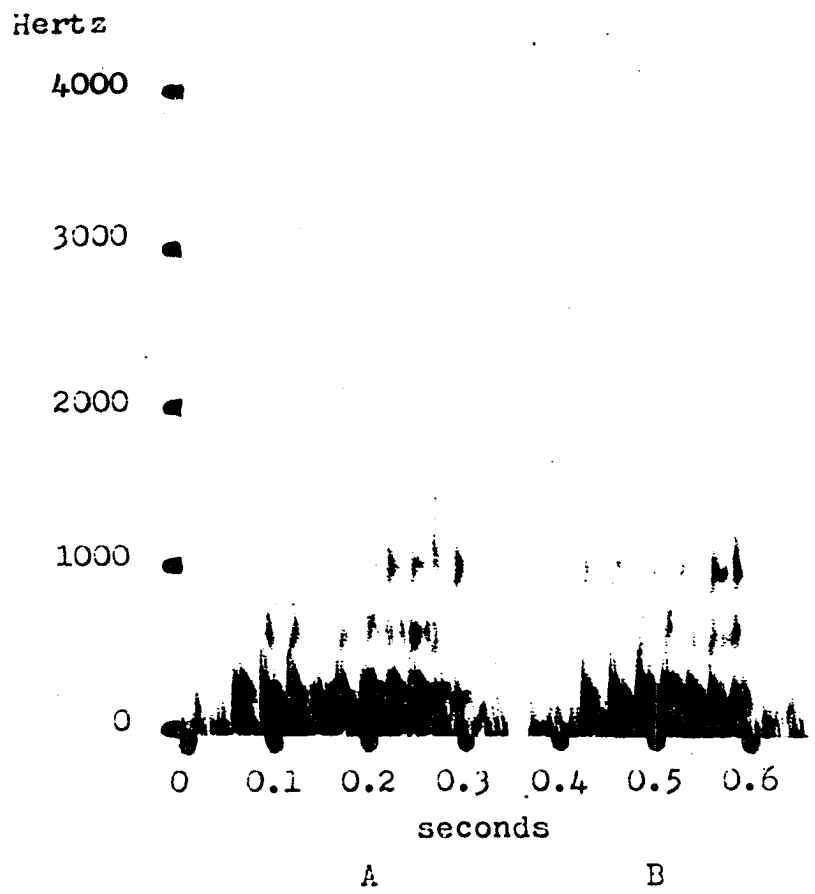
Figure 2. Grunts, number 2 cow. Grunt A and grunt B were emitted in sequence; the original time interval between the start of A and of B was 1.0 seconds.

open for only part(s) of the emission or remained closed entirely.

The grunt vocalization begins in one of two ways: A sudden, cough-like explosion of sound was most common, but, occasionally, the sound commenced slowly and built, within 0.10 second, into a grunt. The average duration of adult vocal emissions was 0.30 seconds (n = 9).

Though there were variations in the intensity of grunts, this was not nearly as marked as the variations of bleats. Maternal grunts were found subjectively to be louder with increased stress and excitement, as during confined periods. Espmark (in press) has also observed this in reindeer, and De Nahlik (1959:28) and Gilbert (1968:870) describe similar findings for fallow deer mothers (Dama dama). The postures of vocalizing adult or infant reindeer are fairly stereotyped. Animals which are walking or trotting during the vocalization assume one of two postures: (1) head extended with dorsal surface of the neck slightly concave, so that the head is level with or slightly lower than the spine -- a posture very similar to the "threat pose" illustrated and described by Pruitt (1960:5-7) or the "attraction pose" illustrated and described by Lent (1966:730, 734-735); (2) head raised high and held horizontally, with an alert expression. Animals which remain standing while they vocalized also assumed an

alert, head-high posture and, occasionally, exhibited the full alarm posture (Pruitt 1960:14). Both Pruitt (1960) and Lent (1966) mention that grunts sometimes accompany these postures. Lent (1966) found that grunts in conjunction with the "attraction pose" were always associated with cow-calf behavior, but the head-bobbing which he described as being frequently associated with this vocal behavior in caribou cows was never observed in this study.

Bleats

A "bleat" is herein defined as the vocalization of infant reindeer (in this study, from birth to the age of eight weeks). It sounds like a short, piercing cry. Spectrographic analysis of 274 separate bleats (153 temporally related sets of bleats) revealed wide variations in intensity, duration, base frequencies and number and frequencies of overtones (see Figures 3, 4 and 5). In many cases the differences for one individual on one day were as great as those between individuals.

Spectrographic variations between vocalizations may be functions of the distance from the recording source (Penney, 1968), the anatomy of the individual's resonating chambers, the open or closed position of the mouth, muscular contractions during the emission which change the shape of
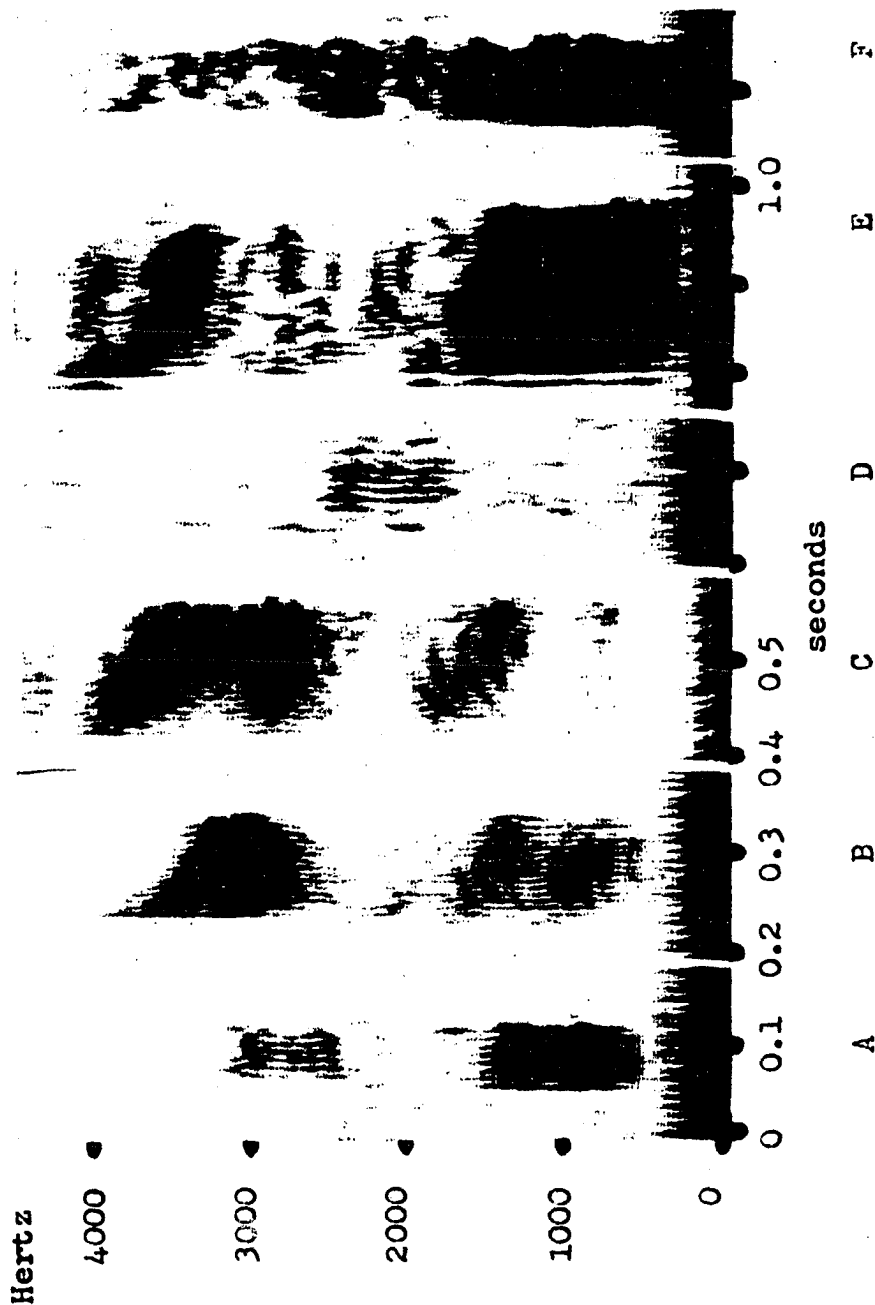
Figure 3. Bleats of different individuals at 1 week of age. A - 20c, B - 10c, C - 2c, D - 17c, E - 5c, F - 12c (i.e. in order of birth, with the first-born calf to the left).
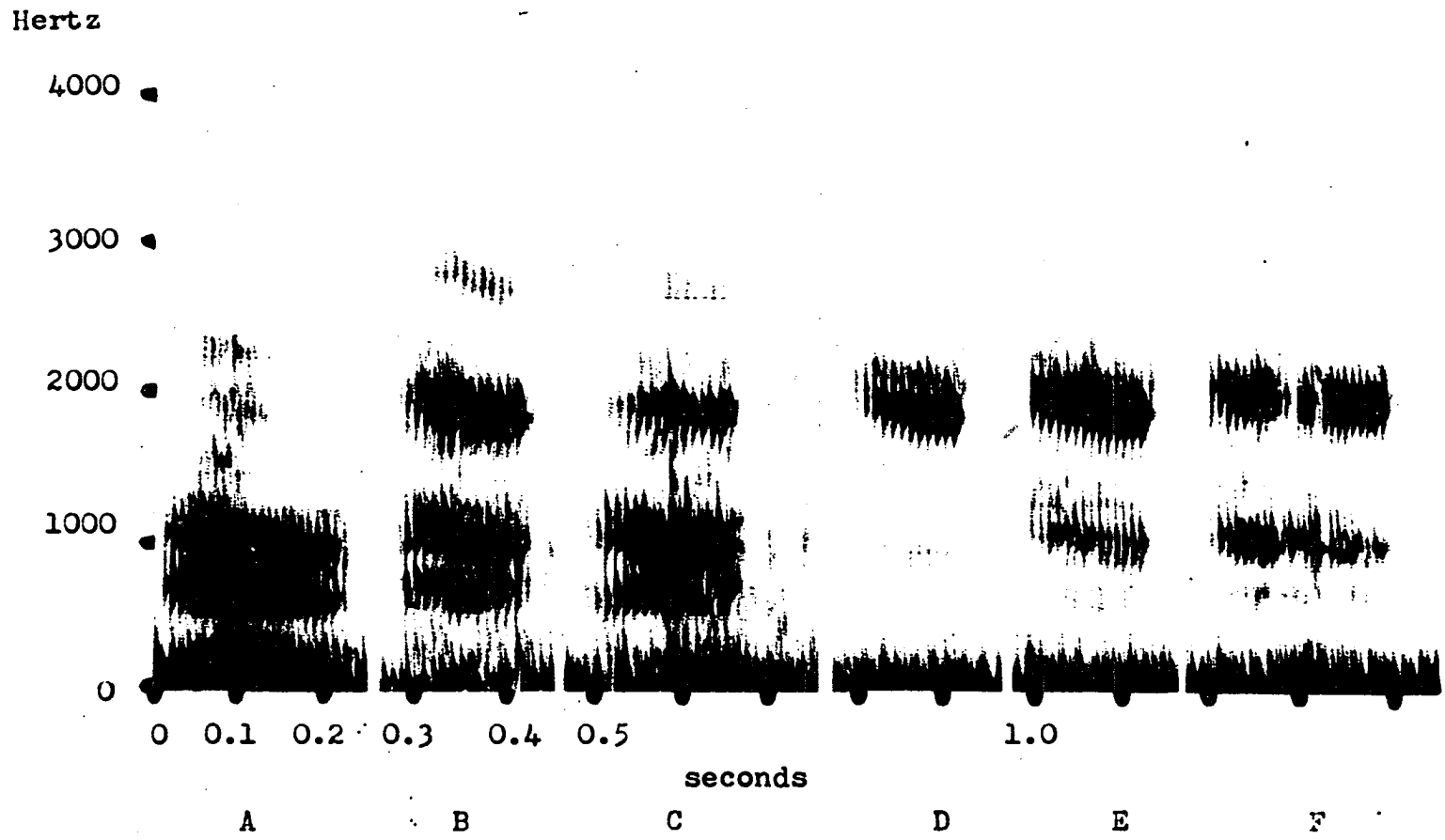
Figure 4. Examples of variations in frequencies of greatest intensity. These are the bleats of number 2 calf, all recorded in its fifth week of life. Bleats B and C were recorded at one time and there were originally 1.6 seconds between the start of B and of C. Bleats D, E and F were also recorded at one time, and originally there were 1.6 seconds between the start of D and of E, and 2.0 seconds between the start of E and of F.
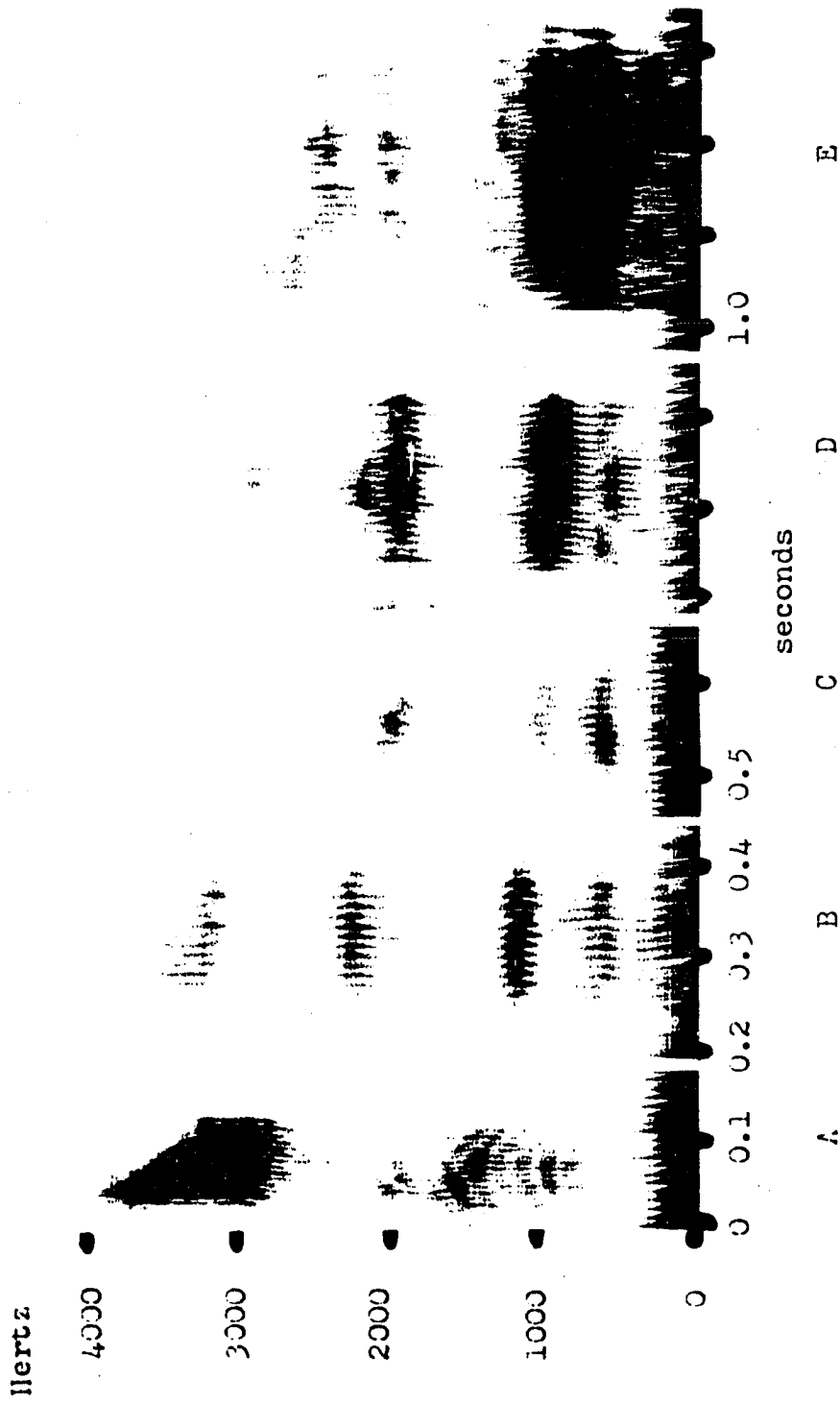
Figure 5. Bleats of one individual (number 2 calf) at different ages. A - 1 week, B - 2 weeks, C - 4 weeks, D - 5 weeks, E - 6 weeks.

the resonating organs and chambers, and the posture and activity of the vocalizer for calves as well as for adults. For calves, qualitative differences may in addition be a function of age-related changes. The data collection method proved inadequate for a complete analysis of qualitative differences in bleats with reference to all of these variables, so that analysis for the possible distinctive characteristics of individual calves (as indicated in Figure 3) could not be done.

However, when the spectrographs were grouped without regard to individual or age, but with respect to stress conditions, some interesting features were noted. One hundred and sixty-eight of the analyzed bleats were recorded while the individual vocalizer was being physically restrained by personnel during physiological sampling or weighing. These bleats are referred to as "physical stress" bleats. The remaining 106 bleats were recorded at other times, when the vocalizer was not physically restrained.

Physical stress bleats were subjectively judged to be louder than other bleats, though both kinds of bleats averaged 130 sound pulses per second. This is statistically different (Student t-distribution, $t = 6.35$, $P < .001$) from the corresponding value for grunts: 60 sound pulses per second.

The mean duration of physical stress bleats, 0.21

seconds (range: 0.05 to 0.47 seconds) is significantly

longer (t = 6.08, P <.0005) than that for other bleats,

0.15 second (range: 0.05 to 0.26 second). Other studies

also have mentioned how the vocal signals of infant reindeer

(Espmark, in press) and of other ungulates increase in

intensity and duration, as well as in frequency of

occurrence, with stress (Gilbert, 1968; Van Wormer, 1969a).

Emotional tension is known to increase vocalization rate

and frequency, and to cause a blurring of the sound quality

(Hoops, 1969). For primates, Andrew (1963) has found

vocalization intensity to be a direct function of the

strength of the arousing stimuli, and, in general for all

vocal mammals "The loudness of the call is always a clue

to the amount of distress involved." (Scott, 1969:9; see

also Gilbert, 1968 and Hoops, 1969)

The analyzed bleats contained frequencies ranging

from 240 to 4400 Hz, which spans nearly the entire range

of human (and possibly reindeer) audition. Commonly, a

bleat is composed of two lower "base" frequencies varying

between 500 and 1500 Hz., with two or three overtones that

were in most cases less clearly separated than those of

grunts. The cumulative effect is a sound much higher in

pitch and more continuous in time (i.e. less raucous)

than a grunt.

The base frequencies are not invariably the most

intense ones: often, an overtone is dominant. Not uncommonly in a series of bleats and, occasionally, within a single bleat, there are changes in intensity among stable frequency positions, so that an exchange of dominant and subordinate frequencies occurs (as an example, compare spectrographs Figure 4, b and c). As a further complication, the frequency bands themselves are not always stable within a series of bleats and sometimes within even a single bleat (note the brief appearance of an overtone in Figure 4a). The sliding of frequencies in a bleat results in a glissando effect which imparts, to human observers at least, a very obvious panic note to the vocalization. The imparting of emotional meaning to a sound through the use of inflectional frequency change is well known for humans (see Pronost and Fairbanks, 1939; Davitz, 1964; Trager, 1965; Vetter, 1969) and occurs in connection with distress and pleasure notes of chicks (Collias and Joos, 1953).

It is not known to what extent such variations in frequency and in pitch dominance are influenced by postural changes, by the open or closed aspect of the mouth, or by the position of the lips, and which are a result of changes in the laryngeal musculature.

Newborn calves, though they are unable to vocalize as loudly as adults, still produce an effective acoustic

signal because higher frequencies are utilized, together with more than twice the number of sound pulses per second. Among vocal mammals, there is an almost universal tendency for the pitch to drop markedly from a high infant level to a lower adult level (Hoops, 1969). Prior (1968) discusses this phenomenon in roe deer. Similarly, for the reindeer calves in this study there was a tendency for the base frequency to drop and for overtones to be lost. This was accompanied by a concurrent increase in intensity, probably due to physical maturation of the vocal tract and musculature as well as to the general increase in body size (Tembrock, 1963) so that the "bleat" vocalization of infants becomes the loud, low-pitched "grunt" of adults (see Figure 5 and cf. Figure 2).

But the wide variations of frequency in the same calf on occasions separated only by hours or even minutes seems to indicate that, if agitated enough, calves retain for a time the capability of producing higher-pitched sounds. High-pitched sounds have a more piercing and more alarming effect on listeners. Ostwald (1963:39, 46) and Gewirtz (1961:233) ascribe the effectiveness of human infant cries as care-soliciting signals to their loud and annoying high-energy components, so that the sound produced is so alarming and unpleasant a stimulus that listeners are unable to ignore or overlook it.

The Quantitative Aspects of Vocalizations:
Grunts and Bleats

Vocal events

Bleats and grunts may occur singly, in pairs or in series in time. These series may be appropriately designated by what Tembrock (1963:764) terms "homotypical sound sequences" in that single vocalizations are produced one after the other with random time intervals between them. The sounds repeat in series of varying lengths, but there are no special sequences characterized by repeated patterns or rhythmic motifs.

Within a series of grunts or bleats, however, sound emissions tend to occur regularly with each expiration of breath. This is particularly true of the vocalization series uttered under alarm conditions. The fastest series rate for adults and calves is approximately 100 bleats per minute. This rate is maintained constant for only up to eight seconds when a breathing pause of one to three seconds duration is taken; every 20 to 30 seconds a somewhat longer pause is taken to breathe several more times.

Because grunts and bleats most frequently occurred in pairs or series such collections of vocalizations, rather than single vocalizations, were taken as the units of analysis. These units were termed "vocal events". A

"vocal event" is herein defined as a grunt or series of grunts (a "grunt event") or a bleat or series of bleats (a "bleat event") emitted by one vocalizer on one occasion which is characterized by a particular behavioral context. The duration of a vocal event includes the time spent in other activities concurrent with the emission period of a vocalization series, but does not include activities prior to or following the single vocalization or the initial or terminal vocalization of a series. (These activities, discussed in the following section, are referred to as pre-vocal event and post-vocal event behavior.) Thus the duration of vocal events varied from the time occupied by the briefest bleat, 0.05 second, to five minutes or more, which was the total time an individual was vocalizing while continually behaving in some consistent manner in an unchanging context. Most vocal events were less than 30 seconds in length. Vocal events of longer than one minute occurred most commonly during sampling periods. During these times a restrained calf would often bleat and its mother grunt continuously and antiphonally. The event ended when workers allowed the calf to rejoin its mother.

Because the length of observation periods varied from day to day, for analytic purposes it was necessary

to divide the actual number of vocal events observed on a given day by the total number of minutes that had been spent in observation on that day. (As indicated previously, general observation and confined period data are treated strictly separately.) The resultant quantity was multiplied for convenience by a constant factor of 10^3, giving a value which is herein referred to, for simplicity, as the "number of vocal events" (i.e. "per unit observation time" is omitted).

Figure 6 clearly indicates that the number of vocal events in the herd per individual[2] was not constant, but varied from day to day, particularly markedly during the first third of the study period. It is logical to ascribe the observed variations in occurrence of vocal events to variations in those factors which account for any adaptive significance vocalization may have.

To examine the observed variations, 5, 17, 25 and 26 May were taken as "high-incidence days", or days on which there was a particularly high occurrence of vocal events. Similarly, 15, 20 and 29 May and 9 June were taken as "low-incidence days". The variables which were

[2]"Per individual present" represents a necessary correction for the increase in the number of possible vocalizers as calves were born during the study period.
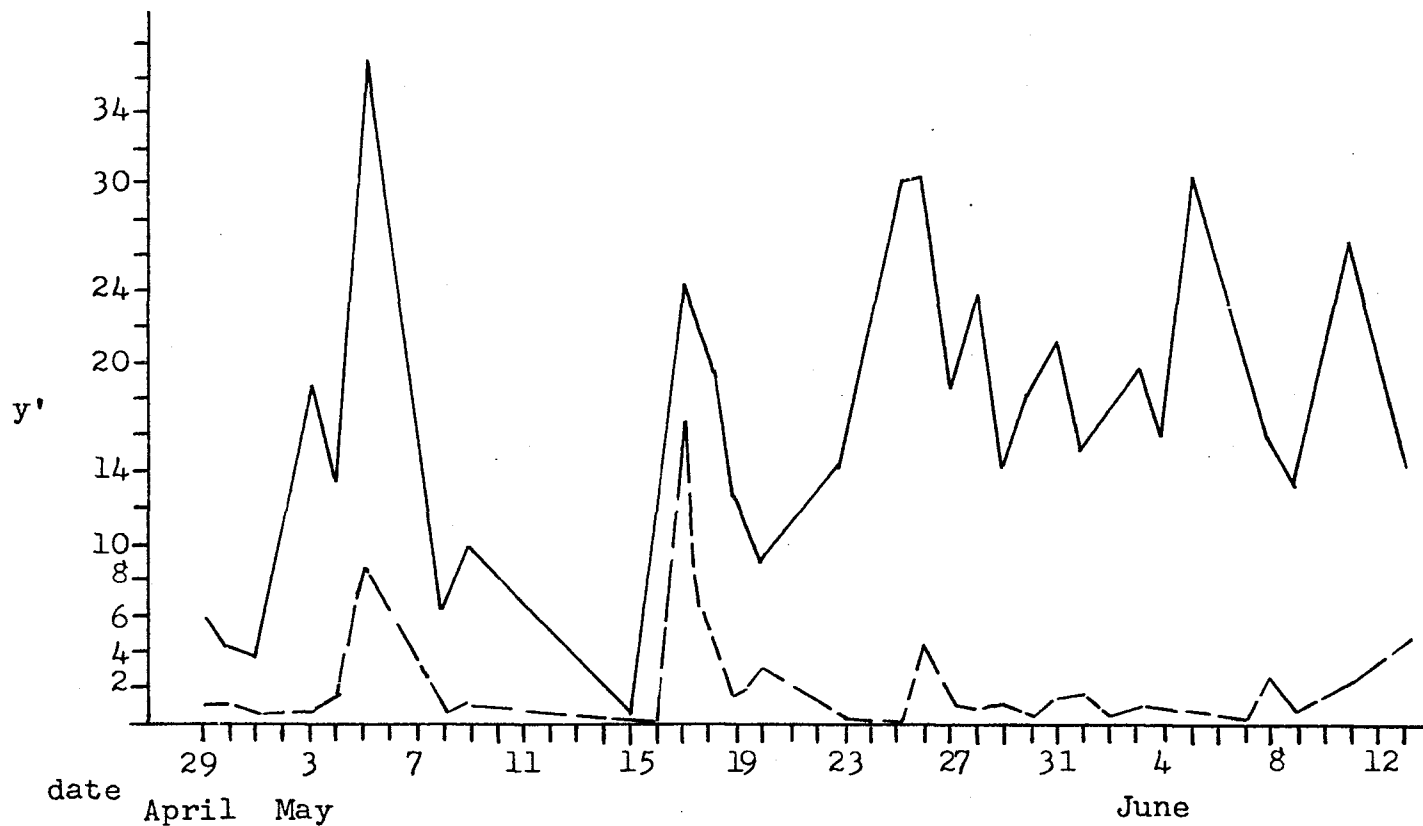
Figure 6. Number of general observation vocal events per individual observed through
the study period (April 29 to June 13). Solid line indicates calf bleat
events, dotted line indicates adult grunt events.

$$y' = \frac{\text{vocal events} \times 10^3 \ / \ \text{general obs. minutes on date}}{\text{no. of potential vocalizers}}$$

examined in this study as being possibly significant in
influencing the incidence of vocal events are (1) daily
meteorological conditions, (2) time of day of observation,
(3) calf age (for calves and mothers) and (4) behavior
of the vocalizer and context of the vocal event. Obviously,
there are many other factors, as mentioned in the second
section of the Materials and Methods, that should be
considered for the sake of completeness, but it was felt
that all possible factors could not be adequately discussed.
One interesting possibility, though, is that motivation
to vocalize may vary from day to day depending on previous
vocal activity. Such a situation might obscure the
effects of any of the four variables to be considered.
However, low-incidence days did not invariably follow
high-incidence days in Figure 6, and, in general, vocal
activity was not consistently low on each day following
a day of human-caused stress in which animals vocalized
frequently.

Effect of changing meteorological conditions

No particular characteristic conditions of temperature,
cloud cover, precipitation or wind, or combinations of
these, were found to be consistently associated with
high- or low-incidence days. However, the study site

failed to provide a range of meteorological conditions wide enough so that the effect of such variations on the occurrence of vocal events could be conclusively determined. Because conditions were so consistent, weather can effectively be dismissed as an important factor influencing the variations in occurrence of vocal events seen in this study.

On most days the temperature was between -2 and +10°C, with some cloud cover but no precipitation, and moderate wind. The one day, 11 June, when precipitation was constant for the nearly eight hours of observation time was a day in which there was a high incidence of vocal events. This is in agreement with Lent (1966:735), who found an increase in calf vocalizations "presumably as a result of discomfort" during rain storms. But the six other days of the present study which were characterized by intermittent precipitation were neither high- nor low-incidence days.

Effect of different time quadrants of observation

The quadrants of the day during which observations were made have been described previously (page 14) and illustrated in Figure 1. Quadrants during which observations were made on days of high vocal activity were not consistently

different from those of low-incidence days. However, since
all quadrants were not sampled with equal intensity, the
effect of time of day on the occurrence of vocal events re-
mains open to question. For the purposes of this study
any possible effect is minimized because of the relative
uniformity of observational quadrants (i.e. 88% of general
observations were made between 0600 and 1800).

The major factor in determining the influence of
observational quadrant on the occurrence of vocal events
is not really the time of day per se, but rather the
herd's diurnal cycle of activity and resting. Banfield
(1954) found that the peak occurrence of vocalization
was reached during feeding periods, and that resting
periods were characterized by few vocalizations. Similar
correlations between activity and vocalization level
have been made for domestic lambs, Ovis aries (Cairns, 1966)
and young cattle, Bos taurus (Hafez, Schein et al, 1969).

Compton and Brundage (1971) and Hafez, Cairns et al
(1969) found that free-ranging cattle and domestic sheep
are active during daytime and rest at night, but Tribe (1950,
cited by Hafez, Schein et al, 1969) feels that often these
animals graze and walk around considerably during the
nocturnal hours. Banfield (1954) observed reindeer
and caribou in the arctic to feed casually during nearly

the entire 24-hour daylight period. Jones (1966) found
that the activity of caribou calves on Adak Island, Alaska
was influenced by weather. Despite daylight and weather
effects, however, there are still pronounced peaks of
caribou herd activity during *midmorning*, afternoon
and evening (Banfield, 1954; Harper, 1955; De Vos, 1960;
Kelsall, 1968).

In this study herd, each observational quadrant
seemed to span at least one hour-long resting period,
so that approximately four resting periods were distributed
through 24 hours. In agreement with the authors cited
above, vocal activity during these periods was invariably
infrequent or absent. (Vocal sounds produced by sleeping
calves were ocassionally heard, however, and are discussed
separately in a later section.) The occurrence of vocal
events in the context of specific activities is examined
in detail in the following section.

Thus the fluctuations in occurrence of vocal events
observed during this study are not primarily functions
of meteorological conditions or time of the observation.
There remains the analysis of these fluctuations with
respect to individual differences, time since parturition,
and behavioral context.

Individual differences and the effect of calf age

Marked differences in the total number of vocal events per individual were observed (Table 3).[3] But there were consistencies such that three distinct groupings of individuals may be differentiated, without overlapping, on this basis alone. These groupings coincide exactly with the social divisions "calves", "mothers" and "calfless adults".

Of the 202 total observed grunt events, 188 (or 93%) were emitted by the six cows which were mothers of calves, and 14 were emitted by the six other adults. Because motherhood is apparently such an important factor influencing the occurrence of vocalization, grunt events by mothers were analyzed with respect to time since parturition (i.e. calf age).

There were sharp variations among total vocal events uttered per individual within the calf group and within the mother group. Certain individuals were far more vocal than others. No clear or inverse relationship was noted for the vocal propensities of calves compared to those of their mothers. No correlations were found

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[3]In Table 3 and in following tables dealing with individuals, both calves and mothers are listed in order of parturition date (earliest first). The identification number of each calf is its mother's number followed by a lower-case "c".

TABLE 3

TOTAL NUMBER OF VOCAL EVENTS FOR INDIVIDUALS

Individual	General Observation Periods: No. Vocal Events x 1000 / Total Gen. Obs. Time	Confined Periods No. Vocal Events x 1000 / Total Confined Time
Calves	(n - 815 Bleat Events)	(n = 75 Bleat Events)
20c	4.8	6.9
10c	11.5	8.9
2c	10.5	11.7
17c	13.2	6.2
5c	45.7	21.1
12c	22.5	34.4
Mothers	(n = 145 Grunt Events)	(n = 42 Grunt Events)
20	1.5	8.9
10	1.0	2.1
2	3.9	6.9
17	2.3	4.8
5	2.3	2.8
12	7.9	21.9
Other Adults	(n = 14 Grunt Events)	(n = 0 Grunt Events)
21	0.1	0
9	0.5	0
14	0.1	0
B5	0.2	0
B8	0.2	0
S	0.5	0

between parturition date sequence and amount of grunt

events for individual cows. However, there appears to

be a tendency for calves born later to vocalize more,

as is evident from Table 3.

Calf age was examined as a factor influencing the

occurrence of bleat events and of grunt events by mothers.

Table 4 shows the occurrence of general observation

vocal events with respect to the number of weeks post-

partum[4] for the vocalizer. (For comparison, the occurrence

of grunt events by the six calfless adults is given with

reference to weeks since the beginning of the study.)

This information is presented graphically in Figure 7.

The grouped data indicate a decrease in the occurrence

of maternal grunt events over the three-week period

following parturition. Also indicated is a distinct

peak in bleat events by calves during their third week

of life, but information discussed below shows that this

is erroneous. The error is due to an amplification of

individual calf differences as a result of more observation

periods in the later weeks of the study, just at the

time when the more vocal later-born calves were in their

third week of age. The three less-vocal earlier-born

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[4]Week 1 was comprised of the time from parturition
to 7 days thereafter, week 2: days 8 to 14, etc.

TABLE 4

TOTAL NUMBER OF VOCAL EVENTS VS. CALF AGE

	Time (Weeks)	No. Vocalizers Observed	General Observation Periods: Total Vocal Events x 1000 / Total Gen. Obs. Time	Confined Periods: Total Vocal Events x 1000 / Total Confined Time
Calves				
	1 Week Age	5	21.5	10.9
	2 Weeks Age	5	16.9	10.5
	3 " "	6	30.1	7.1
	4 " "	6	22.1	8.0
	5 " "	6	16.8	7.4
	6 " "	4	8.9	4.8
	7 " "	3	11.3	11.1
Mothers				
	1 Week Postpartum	5	10.1	7.6
	2 Weeks Postpartum	5	6.0	6.9
	3 " "	6	2.4	2.0
	4 " "	6	1.9	1.8
	5 " "	6	2.5	1.8
	6 " "	4	1.5	0
	7 " "	3	2.5	8.3
Other Adults				
Study Week	I	7	1.4	0
" "	II	7	0	0
" "	III	6	1.7	0
" "	IV	6	4.1	0
" "	V	6	1.0	0
" "	VI	6	1.6	0
" "	VII	6	3.6	0

Figure 7. Total number of general observation vocal events (bleat events for calves: solid line, grunt events for mothers: dashed line) associated with calf age. For comparison, the number of grunt events by calfless adults (dotted line) is given with reference to weeks since the beginning of the study.

$$y = \frac{\text{vocal events in week} \times 10^3}{\text{general obs. minutes in week}}$$

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calves were the only ones observed at ages seven and
eight weeks.

The occurrence of general observation vocal events
for each individual calf and mother for each week post-
partum is shown in Table 5 and Figure 8. Clearly, Table 4
and Figure 7, which ignore individual differences, are
biased in the case of calves as explained in the previous
section: none of the individual calves show a clear
peak in vocal activity during the third week of age as
indicated by the grouped data. For calves, enormous
individual differences are evident in both the amounts
of bleat events and changes in their occurrence over time.
It is impossible to distinguish any generalized way
in which the frequency of bleat events is influenced
solely by increasing calf age from parturition to seven
weeks.

For five of the six mothers, Table 5 and Figure 8
confirm a decrease in occurrence of grunt events in
the first three weeks following parturition. After that
time, great individual differences are evident: in four
cases occurrence of grunt events generally drops during
the entire study period, but for the two most vocal
cows (numbers 12 and 2) there is a sharp increase in
vocal output.

TABLE 5

NUMBER OF GENERAL OBSERVATION VOCALIZATIONS ASSOCIATED WITH INDIVIDUALS AND WITH CALF AGE

I   Bleats

$$\frac{\text{No. of Gen. Obs. Bleats (Wk)}}{\text{Gen. Obs. Time (Wk)}}$$

Individual	20c	2c	5c	10c	12c	17c
Age (Wk) 1	x	8.25	53.73	8.28	20.98	34.97
" " 2	4.81	3.28	54.66	15.7	22.75	Ø
" " 3	13.12	8.67	46.63	13.33	24.75	7.96
" " 4	3.47	18.22	38.97	7.72	25.40	13.92
" " 5	10.12	12.09	62.80	6.28	25.00	12.09
" " 6	5.18	10.01	x	12.37	x	8.61
" " 7	3.69	13.29	x	19.21	x	x

II. Grunts
(a) By Cows with Calves

$$\frac{\text{No. of Gen. Obs. Grunts (Wk)}}{\text{Gen Obs. Time (Wk)}}$$

Individual	20	2	5	10	12	17
Age of Calf (Wk) 1	x	1.38	10.40	3.55	40.21	10.93
" " 2	5.50	6.56	4.05	6.54	7.84	Ø
" " 3	3.28	5.20	1.04	Ø	3.38	1.59
" " 4	1.73	6.07	1.58	Ø	3.10	0.61
" " 5	2.02	2.07	2.42	Ø	14.00	0.90
" " 6	0.69	4.21	x	Ø	x	2.03
" " 7	Ø	12.08	x	0.62	x	x

Figure 8. Number of general observation vocal events (bleat events for calves: solid lines, grunt events for mothers: dashed lines) for each individual mother and calf, associated with each week post-partum.

$$y = \frac{\text{number of vocal events} \times 10^3}{\text{general obs. minutes in week}}$$

The Behavioral Context of Grunts
and Bleats

Kinds of behaviors associated with vocal events

Each observed vocal event was associated with some pre-event and post-event behavior(s) by the vocalizer. The following categories were used to describe these behaviors:

I. Cow-calf interactions

Ia. vocal interactions

Ib. other (non-vocal) interactions (i.e. nursing, licking, sniffing, etc.)

II. Overt interactions with other reindeer (other than between mothers and offspring)

IIa. vocal interactions

IIb. other (non-vocal) interactions (i.e. agonistic encounters, sniffing, etc.)

III. No overt interactions seen, but vocalizer is proximate (within 8 m) to other reindeer

IV. Vocalizer is grazing or browsing, and is not proximate to other reindeer

V. Vocalizer is engaged in other behavior independent of and not in proximity to other reindeer

VI. Vocalizer is apparently reacting to non-reindeer or human disturbances

VIa. Stimulus is an acoustic disturbance (talking, mechanical noise, etc.)

VIb. Stimulus is a visual/olfactory disturbance

(Obviously, categories Ia, IIa and VIa and b are not appropriate designations of post-vocal event situations, hence they are not used in that sense). These categories were compared to determine which kinds of behavior most frequently accompanied a vocal event. The actual value used in this comparison was the percentage of the total number of vocal events which was associated with a particular category. This percentage was computed separately for categories dealing with pre-event and with post-event behavior. Further, distinction was made between general observation and confined period vocal events. Calves, mothers and other adults are examined as three distinct groups. Table 6 compares the different categories, which are ordered according to decreasing percentages of the vocal event groups involved.

There is a clear increase in cow-calf interactive behavior following vocal events, and is particularly large following bleat events. For calfless adults, where the mother-infant relationship cannot be a factor, the few vocal events which did occur were associated with proximity to and interactions with other individuals, and with disturbances.

TABLE 6

CONTEXTS ASSOCIATED WITH ALL VOCAL EVENTS

(A) General Observation Periods

| | Calves | | | | Mothers | | | | Other Adults | | | |
| | Pre | | Post | | Pre | | Post | | Pre | | Post | |
Rank	Category*	%Value**	Category	%Value	Category	%Value	Category	%Value	Category	%Value	Category	%Value
1	IIa	19.9	Ib	43.1	Ib	32.4	I	55.2	III	42.8	III	35.8
2	Ib	19.0	V	18.2	IIa	22.8	III	11.0	VIb	35.8	IIb	7.1
3	IIb	19.0	III	15.2	Ia	21.4	II	4.8	IIa	28.6	IV	7.1
4	V	15.7	IIb	13.3	VIa	9.7	IV	2.1	IIb	7.1	Ib	0
5	III	14.0	IV	12.6	III	9.0	V	0	IV	7.1	V	0
6	VIb	12.4			IIb	6.2			VIa	7.1		
7	IV	6.8			VIb	6.2			Ia	0		
8	Ia	4.3			IV	2.8			Ib	0		
9	VIa	1.0			V	0			V	0		

(B) Confined Periods

| | Calves | | | | Mothers | | | |
| | Pre | | Post | | Pre | | Post | |
Rank	Category	%Value	Category	%Value	Category	%Value	Category	%Value
1	VIb	61.3	I	30.7	Ia	71.4	I	76.2
2	Ia	42.7	II	6.7	Ib	50.0	II	4.8
3	IIa	20.0	V	6.7	IIa	9.5	III	0
4	Ib	9.3	III	2.7	VIb	9.5	IV	0
5	V	8.0	IV	0	VIa	7.1	V	0
6	IIb	2.7			IIb	2.4		
7	III	1.3			III	0		
8	VIb	1.3			IV	0		
9	IV	0			V	0		

Total Vocal Events By Other Adults During Confined Periods = 0

* (For a fuller explanation of these categories, see text, p. 46)

I Cow-calf Interactions
  (a) vocal
  (b) other
II Overt Social Interactions
  (a) vocal
  (b) other
III Non-overt, Proximate
IV Grazing or Browsing
V Other Independent Behavior
VI Non-reindeer Stimuli
  (a) acoustic
  (b) other

** Percent of total vocal events in group

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Vocal events and the mother-calf relationship

Table 7 shows the behavioral categories with which the vocal events of individual mothers and calves were associated. Particularly obvious is the high occurrence of mother-infant interactive behavior for all individuals following vocal events. Individual differences among mothers and calves, then, are manifested as differences in the quantity of vocal events produced, as discussed previously, rather than in the kinds of behavioral contexts within which these events occur.

The different behavioral categories in which vocal events occurred at specific calf ages is examined for calves and mothers, as two groups, in Table 8. The high occurrence of mother-infant interactive behavior is again noticeably associated with grunt and bleat events, particularly during the first two weeks post-partum.

When mother-infant interactive behavior is examined separately (Figure 9), it is seen to decline sharply with calf age (1) as a pre-bleat event behavior and (2) as a post-grunt event behavior. In connection with the acoustic aspect of interactive behavior specifically, for all cow and calf pairs, 34% of grunt events by mothers were preceded by the bleating of their own calf, while only 4% of calf bleat events were preceded by

TABLE 7

BEHAVIORAL CATEGORIES ASSOCIATED WITH INDIVIDUALS:
PERCENTAGE OF TOTAL VOCAL EVENTS
FOR INDIVIDUAL

I.   Calves
     (A) General Observation

Prevocal Category — Individual

Prevocal Category	20c	10c	2c	17c	5c	12c
I	23.8	19.8	20.7	25.0	22.3	20.4
II	40.5	39.6	35.9	29.8	35.7	45.9
III	9.5	11.9	12.0	19.2	16.3	9.6
IV	2.4	9.9	4.4	2.9	7.8	7.6
V	16.7	17.8	12.0	13.5	16.9	15.3
VI	11.9	13.9	12.0	15.4	12.5	12.7

Postvocal Category — Individual

Postvocal Category	20c	10c	2c	17c	5c	12c
I	52.4	41.6	44.6	42.3	44.2	38.9
II	11.9	13.9	16.3	15.4	12.5	11.5
III	7.1	11.9	16.3	18.3	16.9	13.4
IV	2.4	18.8	9.8	6.7	14.7	12.7
V	14.3	14.9	20.7	18.3	19.4	17.2

     (B) Confined

Prevocal Category — Individual

Prevocal Category	20c	10c	2c	17c	5c	12c
I	90.0	15.4	52.9	33.3	33.3	72.7
II	0	23.1	41.2	33.3	20.0	9.1
III	10.0	0	0	0	0	0
IV	0	0	0	0	0	0
V	0	7.7	5.9	11.1	13.3	9.1
VI	70.0	76.9	70.6	33.3	46.7	72.7

Postvocal Category — Individual

Postvocal Category	20c	10c	2c	17c	5c	12c
I	40.0	23.1	11.8	33.3	40.0	45.5
II	0	7.7	17.7	11.1	0	0
III	10.0	7.7	0	0	0	0
IV	0	0	0	0	0	0
V	0	7.7	5.9	11.1	13.3	0

Table 7 continued

TABLE 7 continued

II. Cows
   (A) General Observation

Prevocal Category	Individual					
	20	10	2	17	5	12
I	76.9	22.2	47.1	50.0	56.3	34.6
II	38.5	55.6	32.4	5.6	31.3	27.3
III	7.7	33.3	11.8	11.1	0	5.5
IV	0	0	2.9	5.6	0	3.6
V	0	0	0	0	0	0
VI	7.7	0	55.9	44.4	37.5	34.6

Postvocal Category	Individual					
	20	10	2	17	5	12
I	69.2	33.3	50.0	66.7	56.3	54.6
II	7.7	44.4	0	0	0	3.6
III	7.7	11.1	11.8	11.1	6.3	12.7
IV	0	11.1	2.9	0	0	1.8
V	0	0	0	0	0	0

   (B) Confined

Prevocal Category	Individual					
	20	10	2	17	5	12
I	76.9	100.0	90.0	71.4	100.0	71.4
II	0	0	10.0	28.6	0	28.6
III	0	0	0	0	0	0
IV	0	0	0	0	0	0
V	0	0	0	0	0	0
VI	7.7	0	10.0	0	0	42.9

Postvocal Category	Individual					
	20	10	2	17	5	12
I	84.6	100.0	70.0	57.1	100.0	71.4
II	0	0	20.0	0	0	0
III	0	0	0	0	0	0
IV	0	0	0	0	0	0
V	0	0	0	0	0	0

TABLE 8

BEHAVIORAL CATEGORIES ASSOCIATED WITH CALF AGE:
PERCENTAGE OF TOTAL VOCAL EVENTS
FOR EACH WEEK POSTPARTUM

I. Calves
(A) General Observation

Prevocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
I	48.9	22.4	14.3	18.7	22.8	16.7	18.4
II	19.2	42.1	40.6	41.3	37.5	42.9	36.7
III	12.8	9.2	14.8	14.2	16.9	11.9	16.3
IV	3.2	6.6	4.2	11.6	7.4	4.8	12.3
V	12.8	29.0	15.2	11.6	14.0	19.1	16.3
VI	16.0	18.4	13.8	9.7	10.3	14.3	10.2

Postvocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
I	67.0	50.0	33.6	42.6	46.3	31.0	42.9
II	5.3	15.8	15.2	11.6	16.2	15.5	8.2
III	5.3	10.5	17.1	14.8	19.1	22.6	12.3
IV	2.1	7.9	10.1	16.8	16.2	16.7	20.4
V	11.7	18.4	28.1	11.0	15.4	22.6	10.2

(B) Confined

Prevocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
I	76.9	39.1	47.1	41.7	25.0	0	75.0
II	7.7	30.4	23.5	8.3	50.0	0	50.0
III	0	0	0	8.3	0	0	0
IV	0	4.4	11.8	16.7	25.0	0	0
VI	.61.5	60.9	64.7	58.3	50.0	100	75.0

Postvocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
I	69.2	21.7	17.7	33.3	25.0	0	25.0
II	0	13.0	11.8	0	0	0	0
III	0	0	5.9	8.3	0	0	0
IV	0	0	0	0	0	0	0
V	0	4.4	11.8	8.3	25.0	0	0

Table 8 continued.

TABLE 8 continued

II. Cows
   (A) General Observation

Prevocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
I	51.2	48.2	41.2	38.5	45.0	42.9	27.3
II	14.0	37.0	41.2	38.5	20.0	35.7	45.5
III	2.3	11.1	5.9	7.7	5.0	28.6	18.2
IV	2.3	3.7	0	0	5.0	7.1	0
V	0	0	0	0	0	0	0
VI	23.3	14.8	35.3	46.2	55.0	64.3	63.6

Postvocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
1	79.1	48.2	64.7	46.2	35.0	50.0	18.2
II	2.3	22.2	0	0	0	0	0
III	2.3	7.4	17.7	15.4	10.0	28.6	18.2
IV	0	3.7	0	0	10.0	0	0
V	0	0	0	0	0	0	0

(B) Confined

Prevocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
I	100	86.7	72.7	33.3	100		66.7
II	11.1	20.0	9.1	0	0		0
III	0	0	0	0	0		0
IV	0	0	0	0	0		0
V	0	0	0	0	0		0
VI	22.2	0	9.1	33.3	0		33.3

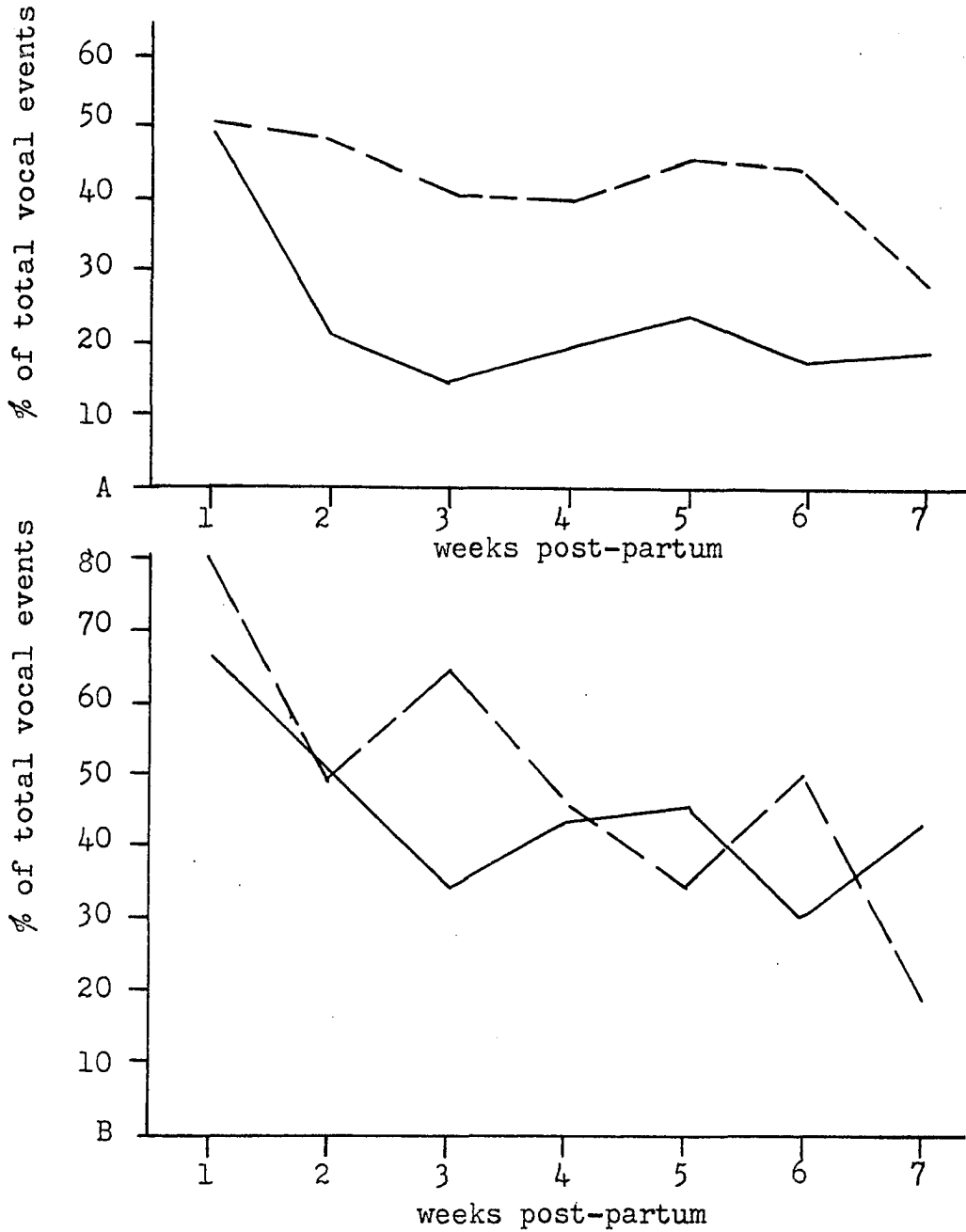| Postvocal Category	Weeks Postpartum						
	1	2	3	4	5	6	7
1	77.8	73.3	72.7	100	100		66.7
II	0	13.3	0	0	0		0
III	0	0	0	0	0		0
IV	0	0	0	0	0		0
V	0	0	0	0	0		0

Figure 9. Percentage of total general observation vocal events (bleat events: solid line, grunt events: dashed line) in each week post-partum emitted (A) prior to and (B) following mother-calf interactive behavior (i.e. behavior class I, explanation in text).

maternal grunts. There was a tendency for calves which frequently "replied" to maternal grunts to have mothers which usually did not "reply" to their bleats, and vice versa. Figure 10a indicates how such "replying" behavior varied with calf age. While a consistently low percentage of calf bleats follow maternal grunt events, a sharp drop in the vocal response of mothers to their calves' bleats as the calves grew older.

One of the most important interactions between mother and infant mammals is nursing. In this study 25% of all nursing events observed (n = 368) were preceded by the bleating of the calf, while only 4% were preceded by maternal grunts. Figure 11a indicates that the percentage of bleat-preceded nursing declines sharply after the age of five weeks (only a small number of nursings were observed for ages seven and eight weeks). For all six cow-calf pairs, 9% of all bleat events and 6% of all grunt events were followed by nursing. These data imply that, while vocalization is used in connection with nursing, neither cows nor calves vocalize primarily to effect that behavior alone. Rather, as seen above, the use of the voice is followed most frequently by many other kinds of mother-infant interactions. That so many more nursing events followed bleats than followed grunts may simply
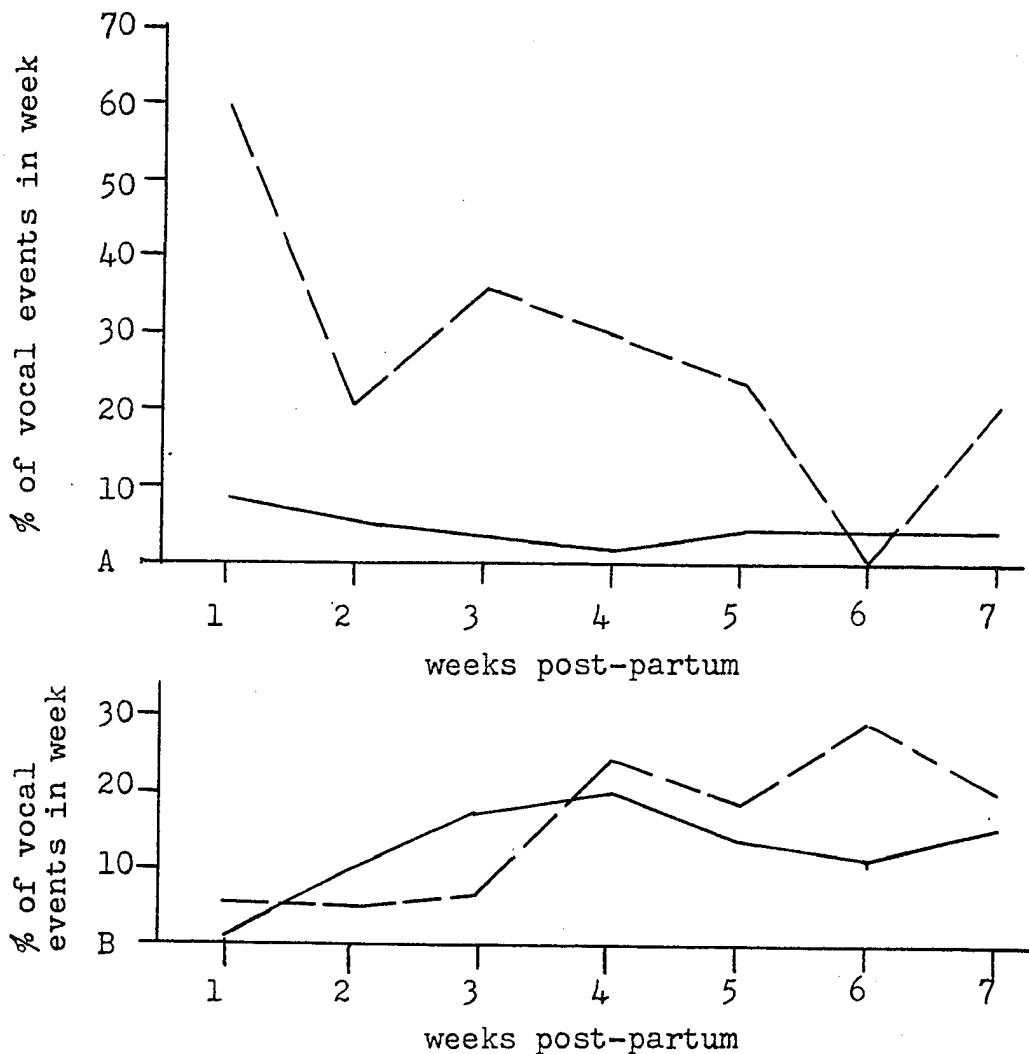
Figure 10 (A). "Replying behavior": percentage of all
bleat events by calves (solid line) at
each week post-partum which were preceded
by their mothers' grunting; percentage of
all grunt events by cows (dashed line) at
each week post-partum which were preceded
by their own calves' bleating.

(B). Percentage of all bleat events by calves
(solid line) which followed within 1
minute of grunts by cows other than their
mothers, and of all grunt events (dashed
line) similarly following the bleats of
strange calves, at each week post-partum.

(Both 10A and 10B are from general
observation data only.)
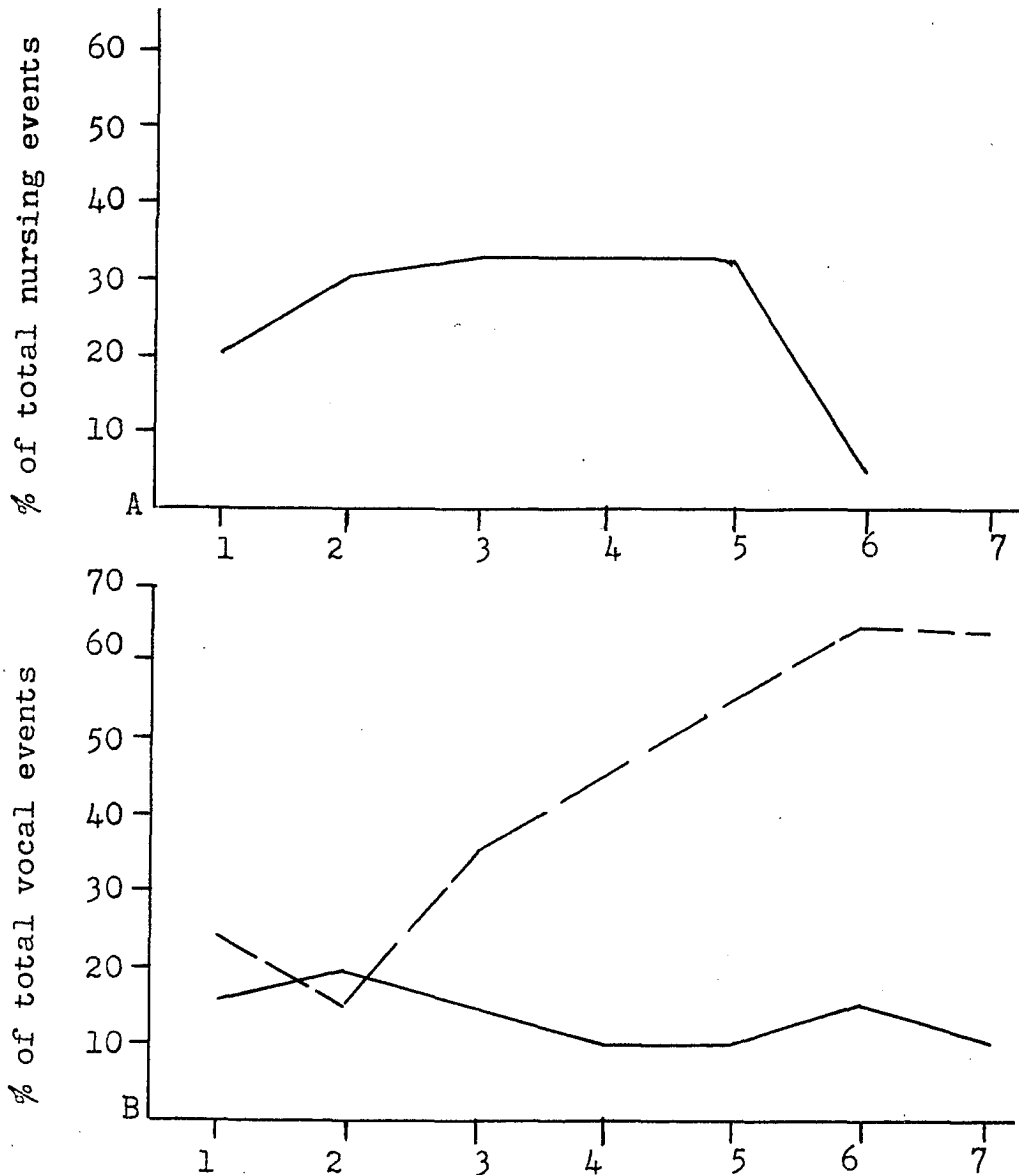
Figure 11 (A). Percentage of total nursing events observed
(n = 326) in each week post-partum which
were preceded by bleating of the calf.
(The percentage preceded by grunt events was
too small for analysis in this manner.)

(B). Percentage of total general observation
vocal events (bleat events: solid line,
grunt events: dashed line) in each week
post-partum which were preceded by an acoustic
and/or visual/olfactory non-reindeer disturbance
(i.e. behavior class VI, see text for
explanation).

be because bleats were more numerous than grunts. Reasons for this numerical disparity are discussed below. Even so, it is also understandable that a vocalizing calf attempting to reunite with its mother may be more interested specifically in the nursing aspect of the interaction than is the cow.

Because vocal events were so often followed by mother-infant interactions during the first weeks post-partum, particularly during disturbances (Table 8, Ib, IIb), the value of voice in reuniting cows and calves cannot be denied. The calf vocalizes much more frequently because it must solicit care, and the maternal instinct is sufficiently strong to cause the cow to search out and approach her calf in response to its bleats. Grunts are necessary only when the calf cannot be located, or when the mother is agitated or suspicious and wishes to orient the calf toward herself and encourage it to remain close to her. This author's findings confirm those of Baskin (1969) that a cow which is sufficiently motivated to vocalize will continue to search and call until her maternal instinct is satisfied. In agreement with Lent's (1966) observations, it is only by the persistent efforts of the cow that the cow-calf bond is formed and maintained in the first days of life.

The very first stage in the ontogeny of the calf's vocal communication was over when its mother ceased to respond to its bleats as if they were all solicitations of care. Instead, beyond three weeks post-partum, the frequency of actual cow-calf reunifications following bleat events dropped; apparently the cow, if anything, received the bleats as merely reassuring signals that the calf was somewhere in the herd. Gradually, it became the infant who had to initiate the bond-maintaining interactions. Schneirla (1959) discusses in detail a similar change in roles he observed with kittens.

But for a time, disturbed situations remained an exception to this role change. While the change in percentages of vocal events which were associated with disturbances at different calf ages (Figure 11b) is only slight for calves, there is a large apparent increase for mothers. This is a reflection of the fact that, while grunt events in general became increasingly rare, an agitated mother grunted and responded to the high-pitched bleat of her alarmed calf just as she had earlier in its infancy. Antiphonal vocal exchange during times of stress continued to be important.

Despite the fact that their vocal emissions began to lose value as care-soliciting signals, most growing

calves remained very vocal. The calf behaved in the same way both before and after vocalizing for approximately 57% of the bleat events observed in this study. There was some tendency for calves to vocalize while interacting socially with other individuals (aside from the mother) and to afterwards retire to browse or wander alone. Many of the changes in bleat-associated contexts noted with increasing calf age are due simply to the calf's widening range of activities, particularly herd social interactions and independent explorations.

Vocal interactions other than between mothers and infants

Vocalizations were considered to be "vocal interactions" if they were emitted within one minute of a vocal event by another individual (other than the mother or offspring of the vocalizer). A total of 14% of all grunt events by mothers followed bleats of calves other than their own, as compared to 34% after bleats of their own offspring. Maternal grunt events following grunts by other adults formed 12% of the total. At first a measure of voice discrimination and recognition seems likely because of the much greater vocal response of mothers to their offsprings' vocalizations than to those emitted by other individuals. But while vocal response by mothers to grunts

by other adults increased sharply in the weeks following
parturition (Figure 10b), there was a decrease in the
proportion of grunts that followed the bleats of their
own calf (cf. Figure 10a). These findings are compatible
with the increased proportion of grunt events by mothers
during disturbances (Figure 11b) but general decrease in
frequency of cow-calf interactions (Figure 9) as the calf
grows.

For calves, 4% of all bleat events occurred after
maternal grunts and 2% followed the grunts of other adults.
In contrast, 14% of calf bleat events followed bleats
by other calves. This vocal response to peer-group
vocalizations increased with calf age.

It is not known to what extent visual and olfactory
stimuli were important in the apparent social facilitation
of vocalization.

Vocal events associated with postural changes

While only 2% of grunt events were emitted by adults
as they assumed or arouse from a lying position, fully
38% of all bleat events were so emitted. Most commonly
the calf vocalized as it stood up or immediately after
arising. A particularly high incidence of this behavior
was seen for calves from three to five weeks of age
(Figure 12). This period coincides precisely with the
maximum rate of rumen development (Krebs and Cowan, 1962;
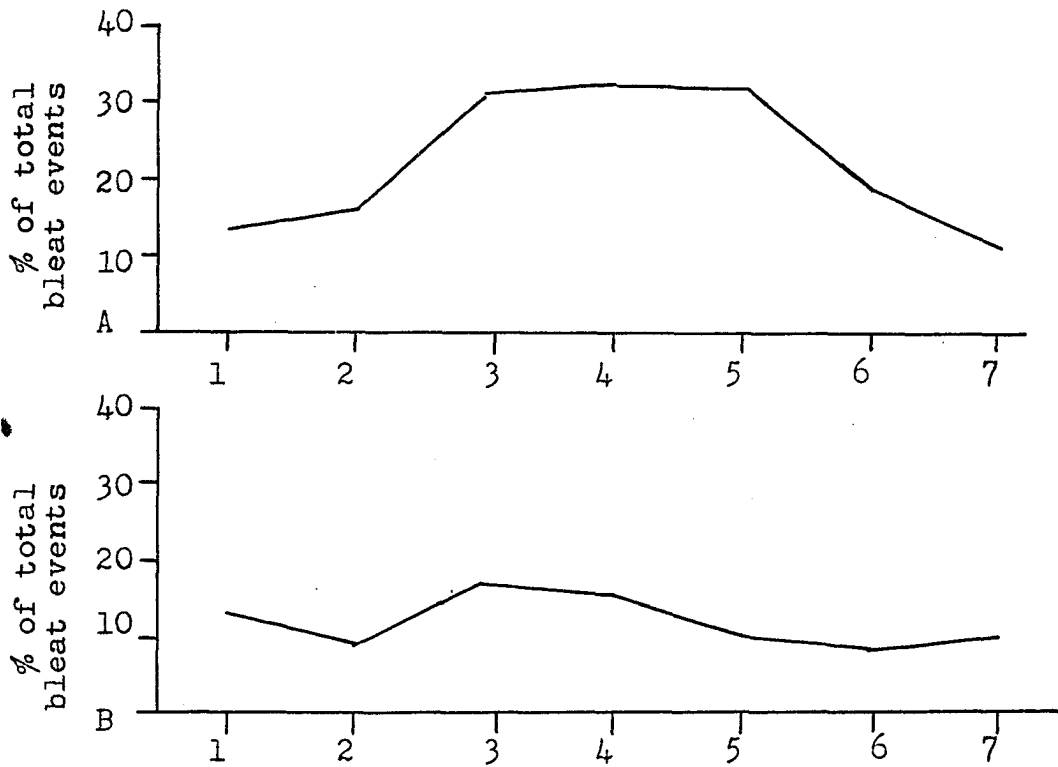
Figure 12. Percentage of total general observation bleat events in each week post-partum which occurred (A) prior to and (B) following a change of posture (i.e. assuming or arising from a lying position).

Warner and Flat, 1965), and it is possible that such behavior is in part due to the discomfort of gas in the digestive tract.

Other Reindeer-emitted Sounds

Non-vocal sounds

While the emphasis of this study was upon the loudest, most widely described vocal communication signals of reindeer, grunts and bleats, a wide variety of other sounds were also emitted by the animals observed. Grunts (and bleats, for infants) are primarily sounds produced by the action of the vocal cords and associated laryngeal musculature. But there are numerous other sounds produced by a variety of other patterns of motion in the upper respiratory and alimentary tracts which are enhanced and made more audible, just as are grunts or bleats, through resonance in the nasopharyngeal cavities. These include sounds associated with the respiratory and digestive processes, and include coughs, sneezes, wheezes, snores, belches and sounds associated with yawning, swallowing and regurgitation. Such sounds will herein be referred to as "non-vocal sounds". A total of 394 non-vocal sounds were emitted by adult reindeer during the study, compared to 202 total grunt events. In contrast, calves emitted only 25 non-vocal sounds but 890 bleat events.

Listed and described below are the kinds of non-vocal sounds emitted by the adult reindeer. The percentage of the total 394 comprised by each kind of sound is given in parentheses.

(1) The <u>snort</u> (30%) is produced by the quick expulsion of air through the nose, with the mouth closed. This is described for caribou by Kelsall (1968).

(2) The <u>cough</u> (19%) is a sudden and noisy expulsion of air from the lungs through the glottis as a result of a muscular spasm in the throat in an effort to clear the air passages.

(3) The <u>wheeze</u> (12%) is a repeated whistling, breathy sound produced by the prolonged and labored expulsion of air through the nose or mouth.

(4) <u>Grunt-compound sounds</u> (12%) are those which are not entirely non-vocal, but rather sounded as if a typical non-vocal sound was emitted simultaneously with a quiet grunt vocalization. They are best described by hyphenating the word "grunt" (to denote the vocal aspect) with the following kinds of sounds: belch, cough, moo, rumble, sigh, snort, wheeze, whine and yawn. These sounds were always uttered in the same relaxed manner as their non-vocal

components rather than in the usual behavioral
contexts of grunt events.

(5) The <u>sneeze</u> (8%) is a sound resulting from
the sudden, involuntary, explosive exhalation of
air through the nose and mouth as a result of
irritation of the nasal mucous membranes.

(6) <u>Groans</u>, <u>whines</u>, <u>moos</u> and <u>rumbles</u> (5%) are
sounds with incidental vocal components, yet do
not sound at all like grunts. The groan is a low,
deep, muffled, harsh sound. The whine is a high-
pitched, protracted, quiet, nasal humming. The moo
is similar to that of a domestic cow, although it
is quieter and briefer. The rumble is a low,
harsh, grating sound originating in the back of
the throat, similar to gargling noises. In
addition, one of these sounds often would accompany
the expulsion of air at the conclusion of a yawn.

(7) <u>Sighs</u>, <u>snores</u> and <u>gulps</u> (5%) are very quiet sounds.
The first two are protracted and breathy: the
sigh is merely a quiet, prolonged expiration of
air through the nose, while the snore is a louder
expiration accompanied by a hoarse vibrating of
the relaxed mucous membranes of the pharynx and
throat. The gulp is a brief sound produced

occasionally during the act of swallowing.

(8) Belches and regurgitations (4%) are sounds associated with the expulsion of gas from the upper alimentary tract (primarily the rumen and reticulum) and the voluntary bringing up of a bolus of food from the rumen into the mouth for leisurely chewing.

(9) The yawn (3%) is a breathy sound accompanying the quick inspiration of air (and imparted with a hollow tone due to the rounded configuration of the mouth and lips), followed by a quiet sigh or soft humming sound during exhalation.

(10) Other compound sounds (3%) are those best described by hyphenating two of the previous categories: cough-belch, cough-sneeze, cough-wheeze, cough-whine, snort-sneeze and snort-yawn.

The kinds of non-vocal sounds emitted by calves are listed and described below. The percentage of the very small total of 25 comprised by each kind of sound is given in parentheses, as are the actual number observed.

(1) Bleat-compound sounds (24%, n = 6) are those similar to the grunt-compound emissions of adults, except that the vocal component of the sound is

the higher-pitched bleat. They sound like the spontaneous emission of a bleat with the non-vocal cough, moo or sigh sounds.

(2) The cough (24%, n = 6) is similar to that described for adults but is generally quieter and more highly pitched.

(3) The yawn (16%, n = 4) is also similar to the adult sound but the occasional terminal hum is higher in pitch.

(4) Sighs and snores (12%, n = 3) are similar to those of adults.

(5) Compound sounds (12%, n = 3) are cough-sigh and sneeze-snort sounds.

(6) A whine and a moo (8%, n = 2) also sounded similar to those of adults, and occured at the terminal stage of yawning. The whine was high-pitched and modulated about a central frequency.

(7) A wheeze and a sneeze (8%, n = 2) were as described for adults.

In addition, panting sounds were commonly made by young calves during resting on warm days, as observed also by Jones (1966).

Even aside from the large disparity between the adult and calf groups, the emission of these sounds even within the two groups was not evenly divided among individuals.

Among the 12 adults, individuals accounted for from 3%
to 18% of the total such sounds, while for calves (with
a much smaller total sample) the range was from 0% to
32%. No correlations were found between the emission
of non-vocal sounds by mothers or calves and calf age.

For adults and calves, approximately 80% of the
total observed non-vocal sounds occurred while the emitter
was lying, standing or, occasionally, leisurely browsing
in a relaxed manner. These emissions were never accompanied
by any overt behavioral change in either the emitter
or other individuals. The remaining 20% of the observed
non-vocal sounds were adult snorts associated with
agonistic interactions.

Snorting was the most common kind of non-vocal
sound. Sixty percent of the snorts were emitted by
individuals which were actively dominating other animals.
The antler threat and similar agonistic displays (described
by Pruitt, 1960 and Lent, 1966) were frequently emphasized
with a loud, sharp snort. Other ungulates are also
known to use the snort or similar sharp respiratory sounds
in conjunction with threat (Fuller, 1960; Cowan and Geist,
1961; Geist, 1966; Hunsaker and Hahn, 1965; Leuthold,
1966; Park, 1969; Van Wormer, 1969b). All snorts
observed were emitted by adults. The absence

of snorting in calves is in part due to simply the lack of opportunity, since young calves, at the bottom of the social hierarchy (Espmark, 1964b; Lent, 1966), never dominate other individuals.

Snorts are also frequently utilized by adults as alarm signals, since they occurred during disturbances and in conjunction the alarm postures and gaits. Snorting is a common alarm signal among ungulates, and both De Vos (1960) and Kelsall (1968) have described its occurrence in this connection for caribou. The latter author (1968:42) believes that the alarm snort is involuntary, "...caused by a quick expulsion of breath as the [alarm] leap is made." This is possible, but alarm snorts were heard in this study even though no alarm leaps (also called "excitation leaps" and described by Murie, 1935; Pruitt, 1960 and Lent, 1966) were observed.

A few snorts were emitted by relaxed, ruminating, resting individuals, as were the other non-vocal sounds. The very small number of such sounds emitted by calves is attributed mainly to the young calves' method of digestion. Most of the adult non-vocal sounds were clearly associated with rumination, and, when not actively browsing, healthy adults ruminated while standing or lying in a relaxed manner. Although calves

begin to develop ruminant digestion in their second week
of life, they do not achieve a full adult-type ruminoreticulum
until the age of four months (Krebs and Cowan, 1962;
Warner and Flat, 1965). Therefore, the young calves
observed in this study still lacked to a large extent
the physiological processes which induce in adults the
apparently involuntary emission of many respiratory and
digestive non-vocal sounds. Several times calves coughed
following rapid suckling, but no overt behavioral responses
by either mothers or calves were noted.

Non-vocal sounds, with the exception of the snort,
are not used as communication signals in the same sense
that grunts and bleats are used. Sounds such as wheezes,
whines and regurgitation noises are frequently overlooked
by observers because (1) the sounds are quiet, so that
it is necessary to be within 8 m of the animals to hear
them, and (2) the sounds seem "unimportant". But it
cannot be ignored that such sounds, associated with vital
life processes, are virtually continuously evident,
particularly in a large herd. McCullough (1969:71) has
found a similar "continuous array of sounds" in a herd
of Tule elk (Cervus canadensis nannodes). He believes
that such noises constitute continuous integrative
signals for maintaining herd cohesion, and this
author agrees. Etkin (1963:156) describes how the

"in-group feeling", so vital to the psychological well-being of highly social animals, is developed and maintained "...by the interchange of mild stimuli with other members of the group." Clearly, the continuous undercurrent of respiratory and digestive sounds inevitably present in a large herd of reindeer can serve as a source of these stimuli. The reassuring effects of non-vocal sounds discussed in the following section, must contribute to the marked reduction in alertness of individuals in large aggregations that has been described by numerous writers (Murie, 1935; Banfield, 1954; De Vos, 1960; Lent, 1964; Kelsall, 1968).

Reindeer-caused sounds

During the course of their usual activities, reindeer cause a variety of sounds in the process of interacting with the physical environment: hooves strike the substate, branches break, snow is crunched, water is splashed, etc.

A sound incidental to *Rangifer* activity in particular is the clicking noise produced by the sesmoid bones, as described in the Introduction. Lent (1964:173) writes that this sound "...might permit caribou to identify approaching but unseen animals as either 'caribou' or 'non-caribou' ", but he adds "However, I was never able

to hear the clicking noise until the caribou were very close, long after I could hear the noise of their hooves on the snow surface."

The sounds of rapid locomotion, ritualized in some ungulates into in-place drumming with the hooves (see Tembrock, 1963:761), and sudden, loud crashing in the vegetation tend to be effective acoustic alarm signals for all ungulates because they usually accompany a startled flight from danger (see, for example, Geist, 1963:406). On several occasions in this study, the sound of an adult moving rapidly obviously alerted other individuals, although running calves never overtly attracted the attention of adults.

Under particularly cold, clear arctic conditions when sounds propagate extremely well, Lent (1964) feels that caribou bands might actually be frightened by the incidental noises of distant caribou. Probably the alarming effect is a result of acoustic stimuli which seem very close but lack the usual accompanying olfactory or visual stimuli which denote proximate conspecifics. Under normal conditions such close-sounding signals are constantly reinforced by olfactory and visual stimuli, so that "The animals become so accustomed to hearing sounds made by others nearby that as a rule they pay

little attention to the snapping of twigs or to other noises made by a hunter." (Murie, 1935: 28-29) Thus the numerous sounds caused by other reindeer, together with the non-vocal sounds discussed previously, form a continuous flow of quiet signals that is reassuring to the individual herd member.

Sounds vocally emitted by sleeping calves

One type of calf-emitted sound deserves separate attention because of the unusual context in which it occurs. On twenty separate occasions, calves bleated while they slept (i.e. the calves, lying in a relaxed position with their eyes closed and breathing deeply and regularly, gave all appearance of being asleep). Prior to the vocalization there were no unusual stimuli, and following it no overt changes were noted in the behavior of other reindeer. In sixteen cases the vocalizing calf also did not exhibit overt behavioral changes but, rather, continued to sleep. In the remaining four cases the vocalizer moved its limbs slightly and opened its eyes. In only one case did the calf stand up within two minutes of emitting the sound.

The twenty observations were evenly distributed among the different calf age classes. Five of the six calves exhibited this behavior at some time during the study.

However, for one quarter of the observations, the identity
of the vocalizer could not be determined. The single soft
bleat was often difficult to localize because frequently
no overt mouth or other movements were made by the vocalizer.

In considering the significance of these "sleep bleats",
the primary problem lies in determining if the calves
were "conscious" or, as that state is defined by Simon
and Emmons (1956:1066-1067), "aware of external stimuli"
when they bleated. Clearly, if the calves were conscious
when they uttered the sounds, then these bleats should
be considered with all other sounds emitted by reindeer
which appeared to be conscious of their physical location,
social situation and current activity. But if the calves
were not aware of their surroundings while bleating, the
use of these bleats as meaningful communicative signals
can be questioned. Then, the sounds, independent at
the time of emission from external stimuli or context,
must be the result of some kind of central nervous
system activity.

Instances where individuals appeared to be soundly
asleep and oblivious to their surroundings have been
cited for both adult caribou (Murie, 1935:29-31; Pruitt,
1960:35) and caribou calves (Kelsall, 1968:44). While
sleep is rare in adult ruminants (Klemm, 1966), it
is far commoner in the infant and immature stages

of development (Balch, 1955:940; Hafez, Cairns et al 1969:
340-341). "Paradoxical sleep" comprises 30% to 40% of
total sleep time (Loizzo and Longo, 1968). It is the
kind of sleep during which dreams are known to occur in
man, and is characterized by rapid eye movements, phasic
twitching of the limbs and facial muscles, and an arousal-
type electroencephalogram (Best and Taylor, 1950; Oswald,
1962; Klemm, 1966; Johnson et al, 1969). During paradoxical
sleep an animal may exhibit an electroencephalogram
pattern indistinguishable from the waking state, yet by
many other indicators the animal is asleep (Johnson et al,
1969). While dreaming, in humans at least, involves
memory of past experiences and the ability to associate
various sensary impressions (Best and Taylor, 1950:1054),
very young infants are known to dream (Wiggers, 1949:106;
Kleitman, 1963:102).

Observations of apparent sleep in reindeer during
this study and in caribou by other workers, coupled with
(1) the proven incidence of paradoxical sleep in ruminants
(Klemm, 1966), (2) the higher frequency of paradoxical
sleep in younger animals than in adults (Loizzo and
Longo, 1968), and (3) the known occurrence of vocalizations
during paradoxical sleep (Wiggers, 1949), provide bases
for postulating that the reindeer calves in this study

bleated during periods of paradoxical sleep or "dreaming". Since the content of young children's dreams, known to be age-related, first expresses anxiety (Kleitman, 1963), it is possible that the reindeer calves vocalized in response to dreamed anxiety. This speculation is substantiated only by the preponderent occurrence of similar vocalizations by "conscious" ungulates in anxiety and alarm situations as often described in other studies (see Introduction and Appendix) and also indicated in this study.

It is possible that bleating by a sleeping calf is adaptively significant because the mother is in this way informed of her calf's location. There are two reasons, however, that this is not likely: (1) because of the very low intensity of the sound, a sleep bleat is audible only within a distance (approximately 10 m for the human observer) where the calf's location should be visually or olfactorally obvious, and (2) the incidence of sleep bleats is very low compared to the total number of "conscious" bleats observed (i.e. 20 sleep bleats compared to 890 other bleats). It is also possible that the occurrence of vocalization in sleeping calves lacks any real significance and is either a result of indigestion or merely a neurological phenomenon. But the elucidation

of such neurological processes causing vocal emission
during sleep could clarify the causation of vocalization
at any time in the life of the individual.

Response to Environmental and Interspecific Acoustic Stimuli

No effort was made to introduce acoustic stimuli in
a systematic manner in order to observe the herd's response.
However, in connection with the study conditions as
previously described, observations could be made of the
overt behavioral changes which accompanied numerous
incidental acoustic or acoustic-visual disturbances.
(The frequency of actual vocalization following such
stimuli has been discussed previously.)

Many of the disturbances associated with the proximity
of human habitation were acoustic only, since the town,
road and airfield were not visible from the paddock. The
herd appeared to be habituated to commonplace sounds such
as distant shouting, motor noises and train whistles.
Only rarely, when a distant noise was unusually loud,
would several individuals look up from browsing. On
two occasions sneezes and coughs by the observer briefly
attracted the attention of animals 2.5 m away. A pitch
pipe (musical A) was sounded quietly several times
during the first two weeks of the study, with animals

ranging from 2 to 10 m away, but no reaction to the sound was observed.

The herd also appeared to be habituated to air traffic over the paddock at altitudes above 100 m. On a few occasions when small airplanes flew directly over the paddock at a height of 30 m, animals which were lying arose, and the herd members crowded together, snorting and moving nervously. On a single such occasion, the herd trotted rapidly down the paddock, with the cows with calves initiating this movement. Kelsall (1968) also noted that aircraft noise stimulates alarm only at short range. My findings of greater alarm reaction to the louder, modulating noise of helicopters as compared to fixed-wing aircraft agree with those of Espmark (unpublished manuscript). Proximate acoustic stimuli reinforced by unfamiliar visual stimuli produced many more overt alarm reactions than acoustic stimuli alone.

The herd tended to ignore the occasional personnel talking and working near the paddock unless the animals were hungry, at which time the arrival of a person in the paddock area would initiate crowding around the paddock gate and some vocalizations. During the second week of the study when physiological sampling was conducted daily (see Figure 1), the herd exhibited what

appeared to be a learned response to the sound of a
snow machine coming up the hill. After approximately
four snow machine arrivals and departures in conjunction
with the presence of workers who were chasing the herd
and capturing the calves, the animals would assume an
alert posture upon hearing the snow machine and then
would trot quickly to the far corner of the paddock
when the vehicle appeared in the distance. It is
difficult to determine if this was a general herd
reaction or if, as Albright et al (1966) describes for
dairy cattle, only two or three individuals were reacting
in a learned manner to the sound and the rest of the
herd merely followed them. In any case, in this situation
and in all general alarm situations, the cows with
calves were always the first to move away from any
disturbance. They not only moved first, but went the
farthest distance from the source of disturbance and
remained away for the longest time. This is in agreement
with observations by De Vos (1960:258) and with those
of Lent (1966:729), who cites instances in which a

> ... cow and calf in a group with few or
> no other cow-calf pairs... may leave the
> group when disturbed without the others
> being alarmed. Or, if the others are
> acting nervous and alert, the cow may
> lead her calf away without actually
> observing an external source of
> disturbance.

Lent also describes (1964:166 and 1966:729) how this extrasensitive alarm behavior varies directly with the proximity of the disturbance and inversely with the age of the calf. My observations substantiate these variations.

GENERAL DISCUSSION AND CONCLUSIONS

Qualitative Properties of Grunts and Bleats

Grunts by adults and bleats by calves are the loudest vocal sounds emitted by reindeer. They may be uttered singly or in homotypical sound sequences. While analyzed grunts contained frequencies ranging from 15 to 1900 Hz., bleats contained frequencies from 240 to 4400 Hz. Generally the pitch of the calf's bleat drops with age, so that it apparently develops into the adult grunt. These two kinds of vocalizations differ not only in component frequencies, but also bleats have more than twice the number of sound pulses per second as grunts. Bleats vary widely in intensity and duration: bleats emitted during periods of agitation and alarm tend to be louder and of longer duration. Variations of analyzed bleats for each individual calf were often as great as that between individuals, contrary to the preliminary findings of Espmark (in press) who, however, worked with a much smaller sample size of recorded bleats. Because of this variation it was not possible to spectrographically characterize all the bleats of one individual in comparison with the others.

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The Use of Snorts, Grunts and Bleats as Communication Signals

Snorts are frequently used in connection with agonistic behavior, particularly as if to emphasize a visual threat display, and with alarm behavior. In both these kinds of situations, the snort clearly has more of an immediate signal value than it does when occasionally emitted by relaxed, ruminating adults.

Grunts do not occur randomly but, during the calving season, are overwhelmingly associated with mother-infant interactions. Mothers vocalize far more frequently than other adults but, even so, are less vocal than their calves. While the occurrence of calf bleat events is not a clear function of age within the first seven weeks of life, the occurrence of grunt events by mothers decreases sharply after three weeks, consistent with her declining maternal instinct. Calves, in turn, associate increasingly with other individuals, often with other calves. De Vos (1960) makes a similar observation for caribou, and other workers (Collias, 1956; McHugh, 1958; Espmark, 1969) describe both the increasing maternal indifference and the increasing calf independence in other wild and domestic ungulates.

While all mothers and all calves tend to vocalize in connection with characteristic kinds of situations

(mother-infant attractive and bond-strengthening inter-
actions for mothers and young calves, a variety of
exploratory and social interactions for calves older
than three weeks), individual differences are evident
in propensity to vocalize. Certain individuals vocalize
more frequently and for longer periods of time than others.
Previous maternal experience is not a consistent factor
in determining the vocal propensities of either a mother
or her offspring, nor is there a clear direct or
inverse relationship between the vocal propensities of
a cow-calf pair.

Mother-infant Vocal Recognition

Because non-vocal cow-calf interactions were not
systematically quantified, the importance of vocal
events for maintaining the mother-offspring bond is
not precisely clear. The major potential uses of acoustic
signals for bond maintenance are (1) to provide a means
of reassuring stimulus exchange indicating mutual proximity,
particularly during stress situations, and (2) to locate
and recognize the other pair member. The importance
of use (1) is indicated by the frequent occurrence of
grunts and bleats when mothers are together with their
offspring. Use (2) will now be discussed.

Many observers of ungulate behavior have hypothesized that mothers are able to recognize their offspring on the basis of its vocalizations alone, or calves are able to so recognize their mothers, or both. Maternal recognition of the calf's voice is surmised by Smith (1965) and Smith et al (1966) for domestic sheep, and by Gilbert (1968) for fallow deer. Espmark (in press) describes evidence of the ability of both reindeer mothers and calves to identify each other by voice, and McHugh (1958) and Marjoribanks Egerton (1962) also describe supposed mutual recognition by bisons cows and calves, (Bison bison). The most widely held theory, however, is that it is the calf which recognizes its own mother's call. This is noted for reindeer (Baskin, 1969) and caribou (Lent, 1964 and 1966) as well as for dall sheep, Ovis dalli (Murie, 1944), mule deer, Odocoileus hemionus (Einarsen, 1956), the Indian antelope, Antelope cervicapa (Tembrook, 1968) and domestic cattle (Hafez, Schein et al, 1969).

A wide difference was found in this study between the vocal response of mothers to bleats by their own calves (34% of all grunt events) and to the bleats of other calves (14%). There was also a difference for the similar vocal response of calves to their own mothers (4% of all bleat events) as compared to other adults (2%).

It cannot be overlooked, however, that on a long-term basis, the average mother-offspring distance tends to be less than the distance between mothers and strange calves. The observations of this study substantiate those of Lent (1966) that mothers, in fact, frequently threaten away strange calves. It is possible, therefore, that what appears to be a preferential response to a recognized voice actually involves elements of visual and particularly olfactory recognition as well because cow and calf were close enough to utilize these senses effectively.

With the exception of Espmark (in press) and Smith (1965), neither in the studies cited above which discuss supposed vocal recognition nor in other accounts of vocalizing mothers locating vocalizing calves (the red deer, Cervus elaphus: Darling, 1937:139; the saiga, Saiga tatarica: Bannikov, 1961:148) were visual and olfactory clues effectively eliminated. But Espmark (in press) describes his playback experiments with vocal recognition in reindeer in which these clues were absent. He observed that if he removed one calf from a herd of 150 animals (total number of calves = 23?) and then played the previously recorded calls of this calf back to the herd, the mothers responded specifically to the recording of their own calf in seven out of

eight cases. Unfortunately Espmark himself, in the same
study, points out that neither calves nor mothers responded
to each others recorded calls when both were already
together. Smith (1965) also found that domestic sheep
mothers responded to the recorded call of their lambs
only as long as the lambs were not beside them. Therefore,
it is possible to question whether either Espmark's
(in press) or Smith's (1965) studies demonstrate maternal
vocal recognition or merely the alerting effect of any
infant call on the mother when she is not with and
cannot contact her offspring. This argument does not
apply, however, to Espmarks observations in the same
study of apparent calf vocal recognition. Three isolated
calves, aged ten to thirty-two days, showed when tested
greater responses to the recorded grunt of their own
mothers as opposed to the recordings of a strange mother.
It is regrettable that the sample size in this experiment
was so small.

In experiments with sheep in which all stimuli except
acoustic signals have been eliminated, mothers were unable
to identify their own offspring (Collias, 1956; Tschanz,
1962; Lindsay and Fletcher, 1968). Herscher et al
(1963:218) write that

Auditory aids to recognition are probably
not very significant, since it has frequently

> been observed that several mothers will
> respond to the bleat of a young animal
> they cannot see

and even to the young of another species. If the calves

attempt to approach a strange female who answers their

bleating, they are rebuffed (Herscher et al, 1963).

In addition, in Rangifer and in many other genera

of ungulates, both mothers and calves respond to a wide

variety of artificial or crude human imitations of

maternal or infant sounds. Such observations are quite

numerous for reindeer and caribou (Murie, 1944:156; Pruitt,

1960:31; Preobrazhenskii, 1961:114, 124; Lent, 1966:732)

as well as for musk deer, Moschus moschiferus (Egorov,

1965:38), roe deer (Prior, 1968:56, 57) and domestic

cattle (Ewbank, 1968:173).

The physical appearance of the individual mother,

coupled with the attraction posture frequently accompanying

vocal emission (see Results and Associated Discussion,

first part; Lent, 1966) undoubtedly provides important

visual clues in what might otherwise seem to be totally

acoustic recognition of mothers by calves. In support

of this, Herscher et al (1963:218) describe an interesting

situation in domestic sheep:

> By shearing time in May or June, when the
> young lambs are about four or five months
> old, they ... will run to the bleat of
> their newly sheared mother but, failing to

recognize her new shape and color, will
run past her and not be able to find her.

With regard to maternal visual recognition of their
own infant, during the course of this study, the mothers
of the two very dark older calves would frequent reject
each other's calf only after olfactory inspection,
but they both repeatedly rejected the similar-sized
piebald calf from a distance of one to two meters,
without ever sniffing it. Jones (1966) found that even
workers who had become familiar with groups of ten and
thirty-one caribou calves were able to distinguish individuals.

This author agrees with Tschanz (1962), Altmann (1963),
Baskin (1969) and Hafez, Cairns et al (1969) that
individual recognition between mothers and calves is a
complex of visual, olfactory and acoustic clues. It is
probable that olfactory recognition is the first to
develop (Tschanz, 1962; Altmann, 1963) and is most
important (Collias, 1956; Bartholomew, 1959; Smith et al,
1966; Thorpe, 1968; Baskin, 1969). Visual recognition
follows olfactory. In this study visual recognition was
apparent in cows approximately two days post-partum,
but, up to the age of two weeks, calves persisted in
approaching any adult which glanced at them or which did
not threaten or avoid them. Altmann (1963) gives a
similar period for elk calves (Cervus canadensis nelsoni)

and Lent (1966) describes how young caribou calves frequently follow strange cows, even leaving their own mothers to do so.

During the critical first two weeks of the calf's life, the burden of recognition is on the strongest member of the pair -- the mother. It is selectively advantageous that she respond quickly to a wide range of alarm signals. Thus she is not only more easily alarmed by unusual stimuli, but also by any acoustic stimulus resembling the often-varying vocal distress signal of a young calf. The observations of this study lead the author to support Lindsay and Fletcher's (1968:416) hypothesis, which concerns domestic sheep but might well apply to many other ungulates. It maintains that the very young infant's call acts as a non-specific alerting signal which stimulates a mother separated from her offspring to search for it, but the infant call itself "... plays no part in actual recognition." In a like manner calves may be stimulated to seek their mother upon hearing any adult grunt, but Espmark's (in press) preliminary evidence for older calves' recognition of maternal calls indicates that further investigation of this question is necessary.

Some Theoretical Aspects: Individual Differences in
Vocal Behavior, and the Possible Causes of Vocalization

That the occurrence of vocalization in a group of
ungulates is invariably associated with stress activities
and increased movement, ranging from mild hyperactivity
to extreme agitation, has been observed by many workers
for a variety of ungulates (Herscher et al, 1963; Lent,
1966; Hafez, Cairns et al, 1969) and is substantiated
also in this study. Further, Spitz (1963:41) has dis-
cussed how vocal sounds can be considered "discharge
phenomena" in response to unpleasant stimuli or, for
experienced individuals, the anticipation of such
stimuli. Similarly, Murie (1932) postulates that
vocalization is a reflex response to stress, and as
such it is selectively advantageous because the entire
group is immediately alerted to the potentially dangerous
situation perceived by one individual. Other animals
look first toward the vocalizer, then toward the direction
in which he is looking or from which he is moving and,
hence, toward the scene of the disturbance (Struhsaker,
1967). Thus, reindeer vocalizations in general have an
alerting function, just as calf bleats serve as alerting
signals to mothers during calving season. The intensity,
duration and number of calls expresses the urgency of
the situation as the vocalizer perceives it (Gilbert,

1968; Scott, 1969; Van Wormer, 1969a; Espmark, in press).

Individual differences in the propensity to
vocalize may be explained as differences in the individual
thresholds of alarm. Baryshnikov and Kokorina (1964; see
also Hafez, Schein et al, 1969) have classified cattle
into different "personality types" according to their
variations in excitability. Excitable individuals
were found to differ from lethargic ones in many facets
of their responses to disturbing stimuli. These variations
in temperament may explain both the large differences
in the occurrence of maternal grunts seen in this study,
particularly after bleat events, and Herscher, Richmond
and Moore's (1963:218) corresponding observation for
sheep and goats that "Some dams are particularly responsive
to the bleating of the young, answering almost any call of
distress from any young, other dams almost never show vocal
responsiveness."

Lent (personal communication) has found an interesting
counterpart to the widely different vocal propensities of the
reindeer calves discussed in this study. In two muskox
Ovibos moschatus calf births which he observed in 1971, one
calf vocalized 50 times during its first hour of life while
the other did not vocalize once in the same period.
There was a tendency for the reindeer calves in the

present study which were born later in the season to vocalize more in all situations. Since it has been shown that domestic calves or lambs isolated at birth vocalize infrequently or not at all (Collias, 1956; Hafez, Schein et al, 1969), stimulation to vocalize may be socially facilitated by hearing the mother's or other individuals' vocalizations. But the percentage of total bleat events which actually followed maternal grunts or the vocalizations of other calves or adults was small. Lent (personal communication) has observed some newborn muskox calves to vocalize frequently even if they have not yet had the opportunity to hear others including, in one case, the mother. Social facilitation, then, is not the entire explanation for the more frequent vocal behavior of later-born calves.

Later-born calves are born into an acoustic environment already containing the bleats of calves. It is possible that, because of this, later-born calves must vocalize more frequently to attract the same amount of maternal attention, particularly during the critical first several weeks post-partum. Lent (1966) has described how caribou calves born early in the calving season spend their first days in relatively small, slow-moving nursery bands, while calves born later find

themselves part of large and noisy aggregations that are rapidly moving out of the calving areas. Maternal interest declines rapidly during the post-calving period, so that calves which become separated from their mothers during mass herd movements and stress conditions are often abandoned (Lent, 1966). The smaller and weaker younger calves clearly have a greater chance of becoming separated from their mothers in these situations than do older calves. In addition, a cow-calf bond formed late in the calving season is frequently not as strong as a bond formed earlier, so that in other situations (such as at river crossings) later-born calves are more frequently abandoned.

In summary, then, it is advantageous for later-born calves to vocalize more frequently, though the mechanism accomplishing this was not made clear in this study. Besides social facilitation, differences in temperament, excitability and consequent "thresholds of vocal emission" remain potential explanations.

It is possible that the bleating of calf may also be a means of auto-stimulation when the environment fails to provide an optimum stimulus level. Lent (1966) discusses environmental stimulation and caribou calf behavior, and Schneirla (1959) postulates that sudden, proximate stimulus changes cause vocal emission in

very young infants. Andrew (1963) also relates vocalization to stimulus contrast.

An important function of animal communication, in addition to eliciting motor responses, is to provide in listeners an appropriate emotional framework (Eisonson et al, 1963). It is widely accepted that animals tend to emit sounds (excluding those used for navigation) only when emotionally aroused (Murie, 1932 and 1951; Liddell, 1954 and 1956; Scott, 1958 and 1968; De Vos, 1960). This author agrees, concluding from the present study that vocal activity in reindeer in general and within the mother-infant relationship in particular, is a direct result of a state of emotional arousal. The mother-infant bond is clearly an emotional relationship, hence the high level of occurrence of vocalizations by mothers and offspring is explained. But as the calf grows the bond becomes less important, particularly for the cow, and the incidence of bond-related vocal activity drops.

The Use of Non-vocal Sounds as Communication Signals

The numerous sounds caused incidentally by a reindeer herd during feeding, locomotion and other life activities as well as the wide variety of sounds associated with respiration and digestion form a quiet but continuous

background of noises. These sounds provide a means
of herd cohesion and reassure the individual's "in-group"
feeling, hence, according to Etkin (1963) they form a
system of social communication.

Vocal Emissions by Sleeping Calves

Bleats are infrequently emitted by calves during
apparent paradoxical sleep. Since the signal is not in
response to any obvious environmental factor because the
vocalizer is not conscious, sleep bleats instead must
be the result of internal processes, either physiological
discomfort or merely activity in the central nervous
system. It is hypothesized that the emission is a
response to dreamed anxiety.

Response to Environmental Acoustic Stimuli

Reindeer show varying degrees of response to
environmental sounds. The herd showed no apparent
response to repeated acoustic stimuli but, instead,
seemed to be habituated to them. When reinforced by
unfamiliar visual or olfactory stimuli, however, acoustic
stimuli are more alarming. Mothers of young calves are
more easily alarmed than other adults by anything
unfamiliar.

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APPENDIX

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APPENDIX

MOTHER-INFANT ACOUSTIC INTERACTIONS IN
UNGULATES (OMITTING RANGIFER)

(A) Mother-Infant Interaction: Acoustic Signals by Both Mother and Infant

	Animal	Context	Kind of Signal	References
1.	Swine	voice contact	numerous sounds	Gill & Thompson, 1956
2.	Camel	close communication distant communication	growling bleating	Tembrock, 1968
3.	Red Deer	continuous in herd in July	hinds: grunts calves: bleats	Darling, 1937
4.	Wapiti	when cow and calf separated: to effect reunion	cow: high-pitched neigh, deeper and mature squeal calf: squeals	Altmann, 1963 Murie, 1932 and 1951 Struhsaker, 1967 Van Wormer, 1969a
		during calf play	alternate calls	
		during migration	cow: deep squeals calf: squeals	
		when herd fleeing from danger	cow: deep squeals calf: squeals	
5.	Moose	disturbance	cow: grunt calf: whine	DeVos, 1958
		communication (used with gestures and postures)	cow: low, anxious call calf: feeble call	Altmann, 1963 Caton, 1877
6.	Roe Deer	calf, when chased or when left behind: doe, upon approach to calf	doe: low grunts calf: high-pitched squeal with probably ultrasonic components	Prior, 1968

	Animal	Context	Kind of Signal	References
7.	Giraffe	alarm signal by any adult, to which calf responds and flees	snort	Innis, 1958
8	Pronghorn	postpartum to effect reunion	"Mewing" sounds by both cow and calf	Bromley, 1967 Van Wormer, 1969b
9.	Eland	fright	cow: soft bleat calf: bleat like domestic calf	Burton, 1956
10.	Domestic Cattle	approach long-distance communication	call and response cow: moo calf: bleat	Ewbank, 1968 Brownlee, 1950
11.	Camangue Cattle	short-range communication long-range communication voice contact when separated	cow and calf: grunt cow: moo calf: bleat cow: bawl calf: bleat	Schloeth, 1958a and b
12.	Indian Wild Cattle	communication	voice-contact sounds	Tembrock, 1968 Holzapfel, 1939
13.	Wisent (European Bison)	communication	cow and calf: grunts	Jaczewski, 1958

	Animal	Context	Kind of Signal	References
14.	American Bison	when separated prior to or during herd movements calf fails to follow herd	cow: deep, belching grunt more nasal grunt	Marjoribanks-Egerton, 1962 McHugh, 1958 Park, 1969
		during danger prior to nursing by either in answer to the other	cow and calf: grunts	
15.	Hybrid Bison-Domestic Cattle	to maintain contact	prolonged grunts	Deakin et al., 1955
16.	Saiga	mother searching for calf	cow and calf: crying	Bannikov et al., 1961
17.	Chamois	communication	auditory signals	Altmann, 1963
18.	Domestic Goat	postpartum: licking	ewe: low-pitched repetitive, segmented bleats (single or series) Kid: bleats	Collias, 1956 Herscher et al., 1963
		postpartum: brief separation	ewe: grunts kid: loud, long (2 sec.), high screams	
19.	Sheep and Goats	separation	"Baa" or "Bleat"	Hafez, Cairns et al.,1969

Animal	Context	Kind of Signal	References
20. Domestic Sheep	postpartum: licking	ewe: repetitive, low-pitched segmented "Maa" lambs: bleat	Collias, 1956 Herscher et al.,1963 Smith, 1965
	when separated	acoustic signals	Lindsay & Fletcher,1968
21. Mouflon Mt. Sheep	to effect reunion	voice contact	Tschanz,1962
22. Dall Sheep	to effect reunion	cow: "Ba-a-ing" calf: softer answer	Murie,1944

(B) Mother-Infant Interaction: Acoustic Signals By Mother Only

Animal	Context	Kind of Signal	References
1. Domestic Swine	warning, causes piglets to come	grunt	Altmann, 1963b
	during and after parturition		Tembrock, 1968 Hafez and Signore,1969
	maternal behavior in many varied situations	numerous sounds	
2. Wild Boar	warning, to cause piglets to disperse and lie motionless	grunt	Altmann, 1963
3. Fallow Deer	used subtly alert fawn to hide (if young) or to come (if older)	bleat or sound comparable to temporary compressed sigh with mouth closed	DeNahlik,1959 Gilbert,1968
	warning signal	cough	

	Animal	Context	Kind of Signal	References
4.	Genus *Cervus* in general	to induce hiding fawn's approach after danger has passed	call	Flerov, 1952
5.	Red Deer	to induce fawn's approach	short, piping, melodic noises resembling squeaks; sometimes mooing	Flerov, 1952
6.	Wapiti	warning and challange pre-and postpartum	bugling	Altmann, 1958 and 1963
		alarm, alerting calf and causing it to hide (if young) or look for disturbance (if older)	bark	Harper, 1966 Murie, 1932 and 1951 Van Wormer, 1969a
		migration		
		to locate calf in heavy timber, to call it to nurse	high-pitched neigh	
7.	Mule Deer	warning	low, reedy call requiring effort; low bleat (scarcely audible to author at 60 yds.)	Dixon, 1934 Einarsen, 1956
		doe searching for fawn		
		doe inducing fawn's approach		
8.	Moose	to induce calf approach	grunt (similar to alarm call)	DeVos, 1958
9.	Pronghorn	to warn fawn	"Short sound, similar to sneeze or snort but with reed-like vibrations	Van Wormer, 1969b

Animal	Context	Kind of Signal	References
	cow and calf together	lowing sound	Brownlee, 1950
10. Domestic Cattle	cow and calf separated	agitated bellowing and lowing	Hafez, Schein and Ewbank, 1969
11. Wildebeest	communication to calf	special snort	Talbot and Talbot, 1963
12. Domestic Goat	searching for cached kid	bleat	Collias, 1956
13 Bighorn Sheep	communication to lamb	wailing sounds	Egorov, 1955

(C) Mother-Infant Interaction: Acoustic Signals By Infant Only

Animal	Context	Kind of Signal	References
1. Collared Peccary	separated from mother (by even a few yds.)	sharp squeal (audible to author 1/4 mi. away)	Neal, 1959
	when it wishes to nurse		
2. Musk Deer	when in danger, to induce maternal approach	call	Egorov, 1965
3. Fallow Deer	unable to lie down in thick brush	high-pitched mewing or peeping	Gilbert, 1968
	nipped by strange doe		
	arising from hiding and desiring maternal attention		
	intense distress during handling	piercing wail	

Animal	Context	Kind of Signal	References
4. Red Deer	separated from mother	bleat	Darling, 1937
	lone immature male surprised by author	bark	
5. Wapiti	during distress, to induce approach of mother or other adults	high-pitched, loud piercing ("E-e-e-uh!")	Altmann, 1952 and 1963. Murie, 1932 and 1951 Van Wormer, 1969[a]
	calf frightened or captured, to induce maternal approach	long, drawn-out scream; medley of squeals and screams	
	beside mother and undisturbed	low bleat	
6. White-Tailed Deer	wandering alone (a pair of 3-day-olds)	call similar to that of catbird or nuthatch, but louder and with different quality	Hatt, 1937
	alone	blatting call	Rue, 1962
	expressing fear or discontent	a sharp "wah" (same pitch and penetrating quality as a lamb bleat, but lacking tremolo effect)	Severinghaus and Cheatum, 1956
	captured	protesting bleat	Hatt, 1937
7. Mule Deer	captured	plaintive bleat	Einarsen, 1956
8. Roe Deer	?	short, piping, melodic noises resembling squeaks	Flerov, 1952
	when left alone and and hungry	loud, shrill, rhythmic crying interspersed with squeaks	Prior, 1968
	hurt or in terror	long, drawn-out scream	

Animal	Context	Kind of Signal	References
9. Giraffe	captured	bellow	Spinage, 1968
10. Pronghorn	to induce maternal approach	high-pitched, quavering note; loud, high-pitched bleat (audible to author at 500 yds.)	Van Wormer, 1969b
11. Domestic Cattle	distress	bawl	Hafez, 1969
12. Musk Oxen	?	bleat	Pederson, 1966
13. Domestic Goat	stress	lusty bleat	Liddell, 1954
14. Domestic Sheep and Goats	postpartum: lamb sees ewe or hears her	bleat	Herscher et al., 1963
	separated hungry hurt or captured	"baa" of distress	Hafez, Cairns et al., 1969