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Pregnancy birth behavioral development of the fawn and territoriality in the pronghorn (Antilocapra americana Ord) on the National Bison Range Moiese Montana

Peter T. Bromley

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PREGNANCY, BIRTH, BEHAVIORAL DEVELOPMENT OF THE FAWN, AND TERRITORIALITY IN THE PRONGHORN (ANTELOCAPRA AMERICANA) ON THE NATIONAL BISON RANGE, MOIESE, MONTANA

by

Peter T. Bromley

B. S. Cornell University, 1964

Presented in partial fulfillment of the requirements of the degree of Master of Arts UNIVERSITY OF MONTANA 1967

Approved by:

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Chairman, Board of Examiners

Dean, Graduate School

[Date] Jul 70 1967

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ACKNOWLEDGEMENTS

I am particularly thankful to Dr. Robert S. Hoffman, Department of Zoology, University of Montana, for suggesting this study, for his continuing support and encouragement, and for his helpful criticism of the manuscript. Data analysis was greatly speeded through methods suggested by Dr. Donald A. Jenni, Department of Zoology, University of Montana. Dr. Ludwig G. Browman and Dr. Philip L. Wright, Department of Zoology, University of Montana freely donated their time and thoughts. Dr. John Craighead, Montana Wildlife Co-operative Research Unit, University of Montana, helped clarify my objectives, and suggested the fawn marking technique and data collection method used. Movie film and encouragement were donated by Dr. Dale Lott, Department of Psychology, University of California, Davis. Mr. Frank Mangels, Mr. Peter Mikelson, Mr. John Mugaas, Mr. Bartholomew W. O'Gara, Mr. Dennis Parker, and Mr. John O. Sullivan aided in capture of fawns. Members of the behavior discussion group contributed their ideas, as well as stimulating my thinking on animal behavior.

I wish to thank the manager of the National Bison Range, Mr. Joseph Mazzoni, and the directors of Region 1 refuges, Bureau of Sport Fisheries and Wildlife of the U.S.
Fish and Wildlife Service for permission to work on the National Bison Range, and for providing quarters during the field study. My appreciation goes to all the National Bison Range personnel and their families for being always friendly and helpful.

I am particularly indebted to my wife, Carol, who supported with encouragement, thought, and a great deal of work throughout the study.
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PREGNANCY, BIRTH, BEHAVIORAL DEVELOPMENT
OF THE FAWN, AND TERRITORIALITY IN THE PRONGHORN
(ANTILOCAPRA AMERICANA ORD) ON THE
NATIONAL BISON RANGE, MOIESE, MONTANA

INTRODUCTION

The science of ethology or the "biological study of behavior" depends in part upon behavioral description of species in their natural environment (Tinbergen, 1963). Such studies on wild ungulates commenced with Darling's (1937) work on Scotland's red deer (Cervus elaphus). Work on North American species began when Altmann (1952, 1958, 1963) described social behavior in elk (C. canadensis) and in moose (Alces alces).

Altmann's findings have been added to, particularly in the area of display postures, by Geist, who has published on moose (1963), mountain goat (Oreamnos americanus) (1964), comparative ethology of the cervids (1966), and bighorn sheep (Ovis canadensis) (1967). Barren-ground caribou (Rangifer tarandus) has been described by Pruitt (1960) and deVos (1960). Social behavior of bison (Bison bison) has been described by McHugh (1958) and Fuller (1960).

Reproductive behavior in African ungulates has been...
more extensively studied than similar behavior in North American forms. The sexual and territorial behavior of Uganda kob (Adenota kob thomasi) has been intensively described by Buechner and his co-workers (Buechner, 1961, 1963; Buechner and Schloeth, 1965; Buechner et al., 1966; Leuchold, 1966). Territorial behavior has also been described in puku (Kobus vardoni), deVos, 1965; deVos and Dowsett, 1966), two species of waterbuck (K. ellipsipimurus and K. defassa, deVos and Dowsett, op. cit.; Kiley-Worthington, 1965), and the lechwe (K. leche) (deVos and Dowsett, op. cit.). Recently, Estes (1967) compared the behavior of Grant's gazelle (Gazella granti) to Thomson's gazelle (G. thomsonii). He also discussed territoriality and taxonomic implications.

Although observations have appeared occasionally in life history works, to date there have been few publications on pronghorn behavior. Buechner (1950) described some aspects of birth, fawn behavior, and reproductive behavior. Hoover et al. (1959) and McClean (1944) also made some behavioral observations. Prenzlow (1964) described some aspects of pregnancy, birth, and social behavior. His review (1965b) of pronghorn behavior was a valuable addition to the literature because many of his sources were unpublished and relatively unavailable. Recently, Howard (1966) described parturition in a pronghorn doe.

Among unpublished theses, Prenzlow (1965a) and Gregg
(1955) described some aspects of doe-fawn and reproductive behavior. Autenrieth (1966) described birth and development of social behavior in two pairs of twins.

The limited knowledge of pronghorn behavior indicated the need for descriptive studies on this species. Originally I planned to describe the social development of the pronghorn fawn, but the objectives of this study were later broadened to include behavior of pregnancy, birth, herd structure, distribution of mature bucks during the rut, and reproductive behavior. These subjects, with the exception of reproductive behavior, are described in this thesis.
Figure 1. Map of the study area.
Legend:

- National Bison Range Boundary.
- Study Area Boundary
- Stream
- Intermittent Streams
- Tour Road
- Jeep Road
- Slaughter House

[1 mile]
METHODS AND MATERIALS

The study was conducted at the National Bison Range, Moiese, Montana during the summer and early fall of 1965 and 1966. Between 30 May and 16 October 1965, 51 days were spent in the field and observations were recorded for 225 hours. In 1965 the general habits of the pronghorns were learned, although little quantitative data were obtained. More detailed observations were recorded for 246 hours from 13 May to 21 October 1966. Pronghorns were less intensively observed for many additional hours during both years. Most of the observations were made during and shortly after fawning and during the rut in both years. The data in this paper, unless otherwise specified, were gathered in 1966.

Study Area

The National Bison Range is a 18,541 acre National Wildlife Refuge located in Lake and Sanders Counties of western Montana. The study area (Figure 1) was roughly 3.5 square miles of range. The several hills and ridges of the area allowed undetected observation of pronghorns from high points. Vegetation of the study area consisted largely of grassland with some brushy drainages. "...The grassland consists largely of Palouse Prairie vegetation, with blue-
bunch wheatgrass (*Agropyron spicatum*) as the principle species." The drainages in the study area commonly contained snowberry (*Symphoricarpos occidentalis*) (Morris and Schwartz, 1957).

Animals

The pronghorn is not endemic to the National Bison Range. From 1910 to 1916, a total of 16 pronghorns were introduced to the Range. The herd dwindled and finally disappeared in 1926. In conjunction with a University of Montana research project, pronghorns were reintroduced in 1951. In the next seven years, the herd increased to 38 pronghorns. Due to reproduction on the Range and to subsequent planting. The pronghorn has survived well on the Range to date (National Bison Range records, unpublished).

During the study, the pronghorn population of the Range was altered by trapping and shooting. From the summer to mid-October in 1965, about 160 pronghorns (36 bucks, 68 does, and 56 fawns) were on the Range. Trapping and shooting reduced the population to about 17 adult bucks, 23 adult does, and 46 yearlings (or a total of 86 pronghorn) by April of 1966. In August and during the rut of 1966, the Range population consisted of 64 bucks, 28 does, and 20 fawns, totaling 112 pronghorns. Thus, the sex ratio changed from 0.5 bucks to 1.0 does in 1965 to 2.3 bucks to 1.0 does in 1966.
Although most of the pronghorns on the Range occupy a native grassland habitat, a few animals are usually kept in exhibition pastures for tourist enjoyment. The behavior of one of these animals, the "tame doe," and her offspring was intensively studied when she gave birth to her first two fawns on 10 June 1966. The tame doe was adopted by Range personnel when she was less than two days old in 1964. According to Range personnel, the fawn was abandoned by her mother; the fawn had been photographed shortly after her birth and was found in a weakened condition when the area was searched the following day.

In 1966, 12 fawns were captured and ear-tagged with colored plastic streamers when they were seven days or less old. Each fawn was tagged in either the left or right ear, and no two fawns were marked with the same color in the same ear (Table 1). Of the 12, eight were frequently observed, although five fawns, similarly marked in 1965, were observed infrequently. In 1966 additional 10 buck and three doe pronghorns could be individually identified by their molt pattern and color in both sexes, and, in the bucks, by the shape, size, and symmetry of their horns. In 1965, one male could be recognized as an individual.

Other ungulates frequently seen on the study area were bison, white-tailed deer (Odocoileus virginianus), and mule deer (O. hemionus). Elk were occasionally seen. Potential pronghorns predators on the Range included coyotes.
Table 1.--Fawns captured and tagged in 1966

<table>
<thead>
<tr>
<th>Number</th>
<th>Date Captured</th>
<th>Capture Age</th>
<th>Sex</th>
<th>Tag Color(s)</th>
<th>Ear Tagged</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>22 May</td>
<td>1 hour</td>
<td>F.</td>
<td>white</td>
<td>right</td>
</tr>
<tr>
<td>7</td>
<td>22 May</td>
<td>1 hour</td>
<td>M.</td>
<td>white</td>
<td>left</td>
</tr>
<tr>
<td>8*</td>
<td>23 May</td>
<td>1 day</td>
<td>M.</td>
<td>orange</td>
<td>right</td>
</tr>
<tr>
<td>9*</td>
<td>23 May</td>
<td>1 day</td>
<td>F.</td>
<td>green</td>
<td>right</td>
</tr>
<tr>
<td>10*</td>
<td>23 May</td>
<td>1 day</td>
<td>F.</td>
<td>green</td>
<td>left</td>
</tr>
<tr>
<td>11*</td>
<td>23 May</td>
<td>1 day</td>
<td>F.</td>
<td>yellow</td>
<td>right</td>
</tr>
<tr>
<td>12*</td>
<td>25 May</td>
<td>1 hour</td>
<td>M.</td>
<td>yellow</td>
<td>left</td>
</tr>
<tr>
<td>13*</td>
<td>25 May</td>
<td>1 hour</td>
<td>M.</td>
<td>white/orange tip</td>
<td>right</td>
</tr>
<tr>
<td>14</td>
<td>29 May</td>
<td>7 days</td>
<td>F.</td>
<td>white/orange tip</td>
<td>left</td>
</tr>
<tr>
<td>15</td>
<td>29 May</td>
<td>7 days</td>
<td>M.</td>
<td>white/green tip</td>
<td>right</td>
</tr>
<tr>
<td>16*</td>
<td>1 June</td>
<td>2 days</td>
<td>M.</td>
<td>white/green tip</td>
<td>left</td>
</tr>
<tr>
<td>17*</td>
<td>1 June</td>
<td>2 days</td>
<td>M.</td>
<td>white/yellow tip</td>
<td>right</td>
</tr>
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Legend:
*Fawns most often observed.
F. -- female
M. -- male
(Canis lantrans), dogs (Canis familiaris), bobcats (Lynx rufus), and golden eagles (Aquila chrysaetos).

Methods

Capture and Marking: Fawns less than one week old are captured and tagged. When a newborn fawn was observed, its location was memorized. I then walked to the spot (the distance varied from a few hundred yards to nearly 1/2 mile), found the lying fawn, and captured it by hand, or, less frequently, with a large net. Fawns were marked with colored, half-inch wide plastic tapes which hung down 10-12 inches below their ears. A 3/4 inch cut was made near the ear's base in the thick, median cartilage ray: one end of the tag was slipped through the slot; four holes were punched in the tag; and two pinch-tight rivets secured the tag to itself when pinched with pliers (Craighead et al., 1960). None of the five animals tagged in 1965 was seen with tags in 1966. However, 11 of 12 tagged in May, 1966 retained their tags until at least October, 1966.

Observation: Pronghorns were observed with the unaided eye, 8X32 binoculars, and a variable, 15-60 power Bausch and Lomb spotting scope. After the pronghorns' habits were learned, observations from hill and ridge tops replaced the random observation points employed at the start of the study. Presentation of the observer's silhouette to the pronghorns' view was avoided. Observation from high
points was used through the summers of 1965 and 1966. When the rut commenced, observations from a car or pick-up truck were made during morning and late afternoon trips on the Range tour road in both 1965 and 1966. Due apparently to summer tourist and Range personnel traffic, the pronghorns were somewhat habituated to cars. Pronghorns 300 yards away and occasionally less appeared unaffected by cars, but took flight if humans on foot were within 500 yards.

Data recording: During 1965 several inexpensive but reliable tape recorders were used to record field observations. Most of the first year's observations were recorded in a field notebook. In 1966 a Channel Master portable tape recorder (model 6549) was used almost exclusively. Taped observations were usually transcribed from the tape to form sheets (described below) within a week. During the rut of 1966, the approximate positions and movements of seven naturally marked adult bucks were plotted on acetate overlays of a study area contour map, mounted on a clipboard. Between 1 September and 21 October, 31 overlays were prepared, one per day in the field. In addition to notes, 35mm slides and super 8mm movies were taken.

Data treatment: The tape recorded observations of 1966 were transcribed from tapes to form sheets. The forms had spaces for the date; the fawn's number or naturally marked animal's identity; the animal's sex; the location; description of behavior; and a code number for each ob-
observation. Chronological accounts of individual fawn behavior; fawn-mother behavior; fawn-unfamiliar doe behavior; fawn-herd behavior; and fawn-fawn behavior were kept for each marked fawn. The records of breeding behavior were filed as male-female and male-male observations.

Quantification of observations was attempted when the observations were made and when the data were compiled. Events were timed with the aid of a wrist watch. Records of seconds were probably accurate to within two seconds. Occasionally times were estimated without the use of a watch. Distances were estimated by eye. Up to 20% error might have occurred in such estimates.

Due to the variability of the measurements, elaborate statistical treatment of the data would be unrealistic. Averages and percentages of variable levels were frequently used. Because the number of events observed during an observation period is, in part, a function of the observation period's length, daily records or sums of observations must be adjusted before they are compared. Data were converted into comparable, "relative frequencies" by dividing the number of events recorded during a time interval by its length. The most commonly used unit of time, the hour, was not always equal to the actual time spent observing. A fawn-mother hour was equal to one hour spent observing a fawn with its mother, but if two siblings were observed with their mother for one hour, two fawn-mother hours were
counted. The assumption was made that a constant percentage of the significant events per observation hour was recorded, regardless of the number of individuals under observation. In the same way, if a group of five fawns was observed for one hour, five fawn-fawn hours were counted.

To emphasize peak variable values and to illustrate more than one variable simultaneously, the percentages of maximum variable values for specified time lengths were graphed against a single time scale. In this way, frequencies of three different behaviors were illustrated in Figure 13. The five-day interval during which a variable's greatest magnitude occurred was designated as 100%, and this variable's level for the remaining intervals was a percentage of its minimum level. This method was suggested by Dr. D. A. Jenni (pers. comm.).

The $X^2$-test was used occasionally, and the statistical basis for its use is explained where used.

The daily position records of the naturally marked bucks were transferred from the acetate overlays to seven sheets of tissue paper, one per buck. A location record was transferred in the following way: (1) the section corner marks on an acetate overlay were matched to similar marks on the overlying tissue paper; and (2) the original record was subsequently plotted on the tissue paper. By contrasting concentric circles from an apparent chosen distribution center, the smallest possible circle which en-
closed two-thirds of the points was determined for each buck's record. The outlying points encompassed by the circle were joined by straight lines. The most distant points recorded for each buck were joined by dashed lines (Figures 20-26).

The accuracy of the distribution center was checked by: (1) measuring the distance between the two most distant points in the two-thirds distribution area; (2) drawing a circle with a radius equal to one-half of the measured distance on an acetate sheet; (3) moving the circle over the point distribution; (4) counting the number of points encompassed by the circle; and (5) accepting the chosen center if the greatest number of points was counted when the circle encompassed the already determined two-thirds distribution.

A 1/2 inch grid was used to approximate the 2/3 and total distribution areas for the seven, mature bucks. Because the original data were keyed to a map scale of two inches per mile, each grid square was equal to 1/16 square miles. The estimated number of grid squares enclosed by the distribution polygons was multiplied by 1.16 to yield the approximate size in square miles of each distribution area.
RESULTS

Behavior Involved with Parturition

Tame Doe

During the spring of 1966, parturition was observed twice in wild does and once in a two-year-old tame doe. Two fawns were born to the tame doe at 1606 and 1637 on 10 June. Detailed observations at short distances were made from 0610 to 1244, from 1330 to 1827, and from 2008 to 2045.

Pregnancy: The tame doe had a noticeably distended abdomen about one month prior to parturition. Five days prior to giving birth, her udder was noticeably swollen, but fully covered with hair. On 9 June bare skin was visible between the hairs of the lower two-thirds of the distended udder. The udder appeared dark to the naked eye at 30 yards. The doe appeared to have difficulty walking on 9 June.

Labor Postures: Observations on the birth day began at 0610, but there was no sign of labor until 0644, when the doe vertically elevated her tail. The tail is always erected during elimination (defecation and urination) in the pronghorn (Gregg, 1955), but elimination did not occur this time. The "tail-up" was often observed simultaneously with
abdominal stretching when the doe stood with hind legs parallel and well posterior to their normal position (Figure 3). The doe was observed to tail-up 161 times during the 596 minutes prior to her fawn's birth (total observation time equalled 550 minutes during this period). The tail-up was assumed constantly during intense periods of labor and while the young remained partly in the birth canal. There was no apparent pattern to the length of tail-ups. The frequency of tail-ups increased up to birth time (Figure 7).

The first sign of strong labor contractions came at 0947, when she arched her back three times while lying down. This was noted again at 1027 and at 1100, when the doe appeared to try to rise from a lying position, but failed.

At 1108 she assumed a posture seen during the most intense periods of labor. While lying down, she fully extended her neck in an antero-dorsad direction and placed her head on the ground. She twisted her neck so that her head was upside down several times. This posture with and without the head-upside-down addition was observed 10 times during parturition and varied from 1 to 10 minutes in duration. A curled posture of the lying parturient doe, similar to a sleeping dog's posture, was observed several times. At 1339 the doe lay down. After lying in the normal position for 3 minutes, she rolled over on her side. At 1345 she arched her back. She lay curled with eyes
nearly shut and tail erected until 1348 when she again rolled over on her side with her eyes closed. Labor postures were frequently accompanied by tail-ups and kicking of the hind legs. A labor period constituted sequential manifestation of one or more of the above postures by the parturient doe.

**Parturition:** At 1544, 18 minutes before its birth, a front hoof of the first fawn (#1) appeared within the fetal sac at the tame doe's vulva. The above labor period was 8 minutes long. Separated by standing periods of less than 1 minute, the remaining labor periods lasted 7, 3, 1, 2, and less than 1 minute. Four series of abdominal contractions passed within 15 seconds, 22 minutes before birth. Six series of contractions occurred during a one-minute period, 12 minutes before birth. Four minutes before her fawn's birth, the doe stood, inspected the ground where her rump had been, and then lay down with her head near that area. One minute later she grunted during a labor period. The first fawn's birth resulted in no visible loss of maternal blood. The male fawn was born head first, eyes open, tongue approximately 1/4 inch out of its mouth, and breathing.

The amber, fluid-filled fetal sac of the doe's second fawn appeared at 1609. As before, the tail of the doe was elevated from this point on until the birth of her second fawn. One front hoof of the second fawn (#2) appeared
at 1618. At 1622 the second hoof appeared. The mother lay down at 1626 and struggled. The second fawn's nose appeared when it slowly emerged from the vulva at 1626. The mother lay her head back on the ground at 1627 and struggled, and the head and forelegs of the fawn appeared. Toward the end of 1627, she experienced a five-second period of intense abdominal contractions. The mother licked herself, then (#1), then herself again, and then (#1) again prior to a series of vigorous labor periods, evidenced by hindleg struggling, head reversal to the upside-down, on-the-ground position, and grunting at 1628. The second fawn was three-quarters out at 1628. The fawn wheezed when it breathed. Number 2 struggled at 1629. The mother attempted to lie down at 1631, but did not, due apparently to the presence of #2 under her. She licked the ground where fluids from #2 had fallen.

Droplets of blood on the vulva's surface appeared and were the first signs of maternal bleeding. At 1633 the doe attempted to lie down, but did not. The mother licked the ground where fluids from #2 had fallen. Number 2 struggled. The doe attempted to lie down, but did not. The doe lay down at 1634 and during 1635, she experienced three labor periods. Another labor period occurred at 1636. Number 2 struggled at 1637, and was nearly born. Late in 1637, the mother stood with embryonic membranes hanging from her vulva, and #2, a female, lay on the ground fully
free of its mother. Thirty-one minutes passed between the births of the tame doe's twins.

Wild Does

**Pregnancy**: Parturition was observed in two wild does. The observations were made at distances of two to four hundred yards with the aid of a spotting scope. In both cases extensive observations on pregnancy prior to parturition were not made. Labor postures and frequency and length of labor periods were not recorded, as both does lay obscured in depressions during parturition.

**Labor Postures and Parturition**: Tail-ups were seen in the two wild does shortly before birth. In the first doe, a tail-up was recorded 2 hours and 40 minutes before the new-born were seen. In the second doe, the first of 42 recorded tail-ups occurred 3 hours and 20 minutes before parturition. The second doe's tail-ups averaged 21 seconds (range, 3-60 seconds) for 18 observations.

One wild doe preened her rump at least six times during parturition. The first wild doe delivered both fawns while lying. One fawn was born to the other doe while she lay, and the second was born while its mother stood. Approximately 30 minutes passed between the births of the second doe's twins.

**Association with other Pronghorns**: Other pronghorns were present before and during parturition in both wild does.
The first doe was followed closely by three yearling females to the parturition site. One yearling doe investigated the pregnant doe’s rump. The second doe was in a herd of 11 does and one buck. Three hours prior to parturition, the doe was followed by up to six other does and the buck. The buck approached and followed the doe twice, and herded her twice. The buck did not display sexual behavior. The rump of the pregnant doe was investigated 16 times by yearling does, and areas where the pregnant doe had been lying were investigated five times. The yearling does followed the pregnant doe closely 10 times, once at a run. Shortly after birth, a yearling doe approached the mother and young, turned, and walked away with erected rump rosettes.
Figure 2. "Tail-up" in the tame doe. Note the stretched, enlarged abdomen.

Figure 3. "Head-low" posture in a newborn pronghorn.
Figure 4. "Greeting" between the tame doe and her fawn. Note the fawn's flared rosettes.

Figure 5. Nursing in the tame doe and her fawn. Note the tame doe's arched back.

Figure 6. "Rump-licking" in the tame doe and her fawn. Note the erected tail and raised rump of the fawn.
Figure 7. Frequency of "tail-ups" in the tame doe during labor. The dashed line on the absissa indicates that no data was collected during that age interval.

Figure 8. Frequency of vocalization sequences in tame doe and her newborn fawns. Pattern "a" represents the tame doe, pattern "b" represents her second fawn (#2), and pattern "c" represents her first fawn (#1). Number 1 was born at the time 0, and #2 was born 31 minutes later. The dashed line on the absissa indicated that no data was collected during that age interval.
SOCIALIZATION

Behavioral Interrelationships Between Mother and Young

Temporal and Spatial Relationships: The association between the tame doe and her fawns changed rapidly during the period immediately after parturition. The doe remained with her young constantly during the first 143 minutes for #1 and for the first 119 minutes for #2. When the male and female fawns of the tame doe were 11 and 10 minutes old respectively, they struggled toward their mother, although neither fawn walked. The male fawn moved on wrist and heel joints. Their first walking was also directed toward their mother. When #1 was 43 minutes old, it walked 6 feet away from and then back to its mother. Ninety-minute old #2 made a similar short trip.

At the start of the second observation period, which commenced 101 minutes after the end of the first one, the tame doe was 20 yards from her fawns. Fawn #2 made 10 trips away from and back to its mother when it was between 211 and 240 minutes old. The length of the trips ranged from 3 to 20 feet, and the average distance for 10 trips was 9 feet. When #1 was 269 minutes old, it ran 20 yards from the mother. The mother walked to her fawn. The fawns, with increasing age, tended to take longer trips from their mother.
Because wild fawns were captured as soon as possible after sighting, observations on wild animals were not as complete as those made on the tame doe's fawns. The mother of #10 and #11 was seen lying near her fawns shortly after dawn on the capture day. When the fawns were captured, their pelage was dry and they were able to run weakly. It is possible that the young were born during the night, and had remained with their mother after their birth.

At some time after parturition, the mother leaves her young. This was not directly observed during the study, but it occurred before the second day after birth. Mothers visited their young for intermittent short periods, defined as fawn-mother interaction periods, until their young were about three weeks of age. Eighteen observed fawn-mother interactions commenced in various ways. Mothers walked toward their lying fawns 10 times, and ran toward their fawns once. When the mothers approached the area of their lying fawns, they fed less often, although they continued to dip their heads. The mother of 5-day old #17 walked until she was 10 feet from her lying fawn before the fawn came to her. The 19-day old male fawn of the tame doe ran 50 yards to its mother. On four occasions fawns stood up and briefly remained in place before going to their mothers. Fawns ran to their mothers 12 times. Eight-day old #6 and #7 lowered their heads (Figure 3) when their mother approached and did not get up until their mother individually touched her nose.
to their noses. In two cases, fawns lay with lifted heads and looked directly toward their mothers before going to them. Similarly, on three occasions, mothers stared at their young before their fawns got up. The tame doe mewed before her 19-day old male fawn arose.

Although behavior of mother and young prior to fawn-mother interaction periods appeared quite variable, generally the mother walked into the area where her young were; the young stood up and ran to the mother; and finally the mother and young greeted. Mewing by the mother may occur before the fawns run to the mother.

The fawn-mother interaction periods lengthened toward the end of the first 3 weeks of fawn life. The average length of fawn-mother interaction periods was about 30 minutes from days 2 through 11 for 13 timed, complete periods. The length increased to 65 minutes from day 12 to day 16 for four timed periods. The greatest length of 74 minutes was observed on day 18 for fawns #8 and #9 (Figure 9). The length of time between fawn-mother periods was observed as 177 minutes on day 15 for #8 and #9 and their mother. Six hours and 43 minutes passed during which 14-day old #1 and #2 were separated from their mother.

Partial observations were made on 22 fawn-mother interaction period terminations. Just before leaving, 2-day old #11 and #17 approached their mother but were not greeted. The mother of #8 and #9 rejected nursing attempts.
just before her fawns left. Fawns walked on 13 occasions, ran once, and ran and walked twice. The distance that fawns moved away from their mother varied. The average of six observations was about 70 yards. Most of the distance was traversed at normal gaits, but the fawns walked with their heads close to the ground when choosing their bedding areas.

In general, fawn-mother interaction periods terminated when the fawns, which were subjected to maternal indifference, left their mothers. When nearing their bedding areas, the fawns walked with lowered heads. The mothers watched their departing fawns.

Fawns seemed to visit and follow their mothers more frequently when they first joined the herd than later in the summer. Does continued to nurse their fawns through the summer. The last record of nursing was made on 15 September.

During the breeding season, the fawns may be separated from their mothers. In 1965, two fawns were seen accompanying two yearling bucks during the rut. In 1966 fawn groups were observed which had few or no does with them during the rut.

Evidence for the following type of response was obtained on two occasions. The mother of fawns #6 and #7 became aware of the observer's presence just after or during parturition. When her older fawn (#7) was 62 minutes old, the mother walked a short distance from the fawn. The fawn
Figure 9. Length of complete fawn-mother interaction periods. The number of observations for each interval (from left to right on the absissa) were 11, 2, 4, 2. The data does not include day one, and the maximum length was 74 minutes.

Figure 10. Relative frequency of maternal grooming activities. The fawn-mother observation hours for each week of age (from left to right on the absissa) were: 18.3, 3.9, 5.7, 0.7, 15.3, 18.6, 24.2, 13.8. The maximum 1-week level was 14.8 activities per fawn observation hour.
walked to the mother. The mother and #7 made eight such trips in 63 minutes. Four of the trips were approximately 3 feet in length, and one trip was 10 yards long. At the termination of the last trip, #7 nursed. Fawn #6 did not interact with her mother during the above observations, but the mother ran off when I attempted to capture the fawn. The second observation of following was made when #12 followed its captors after being tagged less than one hour after its birth.

**Grooming:** Each of the six newborn fawns observed was groomed immediately after birth by its mother. The tame doe licked her first fawn's foreleg when #1 was 1 minute old. In the 30 minutes between the birth of her fawns, the tame doe licked #1, the male, 16 times, while she consumed the fetal sac and largely dried her young. The doe licked #2 17 times in the first 30 minutes after its birth and ate the birth membranes. Three times within 45 minutes after #1's birth, the doe also licked the ground where amniotic fluids had fallen. There appeared to be no pattern in the direction of the licking. Although the fawns appeared to be dry 30 minutes after birth, the mother continued licking occasionally.

When the male fawn was 127 minutes old, a specialized, stereotyped form of grooming appeared. The mother licked the young's rump. The fawn lowered its anterior trunk by bending its forelegs. The hind legs were brought forward
and held straight, and the tail held erect. When the fawn was in this position, the mother licked both the anal and urogenital areas of the fawn (Figure 6). This activity, "rump-licking," was first observed with the female fawn 108 minutes after her birth. During the observation period, the male and female fawns were rump-licked three times and four times respectively. The mother probably consumed fecal material, but no direct evidence was obtained. Fetal feces were present at the anus of the 79 minute-old male fawn. The tame doe licked her female fawn before it assumed the rump-licking position in the four observations. The male assumed the rump-licking posture before its mother licked in two or three observations.

Licking of a third type was observed in the tame doe when the female fawn approached its mother about 4 hours after birth. The mother turned her head and neck toward the fawn and licked its head. This activity, "greeting," was observed three times between the mother and male fawn, and four times between the mother and the female fawn during the observation periods on the first day. Nuzzling, in which a mother touches her young's body surface, was seen five times, all during week two.

Observations on grooming after birth in the wild does were far from complete. Each of the two does was observed for about one hour each after parturition. Both wild does licked their young and consumed the fetal membranes. Rump-
Figure 11. Relative frequency of "rump-licking" of fawns and does. The fawn-mother observation hours for each day of age (from left to right on the absissa) were: 10.0, 4.1, 1.1, 0.9, 0.0, 1.7, 0.5, 1.0, 0.0, 0.0, 0.0, 2.9, 2.7, 0.0, 0.0, 2.5, 0.0, 0.0, 0.0, 0.0, 0.1.

Figure 12. Average nursing bout lengths. The number of fawn-mother observation hours for each 5-day interval (from left to right on the absissa) were: 36, 29, 42, 0, 0, 6, 19, 15, 4, 2, 2, 3, 5, 2, 4. The dashed line on the absissa indicates no data was collected during that age interval. The maximum nursing bout length was 98 seconds.
licking was not observed in either of the does, but one mother licked the rump of her approximately 1-hour old fawn several times. Greeting was observed once in the first wild doe and her approximately 2-hour old male fawn.

As noted, mothers often groomed their newborn fawns. By the end of the young pronghorn's first 2 months, the relative frequency (observations per fawn-mother observation hour) of all types of grooming behavior dropped to nearly zero (Figure 10). The nature of the grooming changed from actual grooming to abbreviated motions which suggested grooming intentions. As Figure 11 shows, rump-licking all but disappeared by the end of the third week. The last record of rump-licking was on day 23. Nuzzling was seen only during week two. The relative frequencies of licking decreased rapidly with time, and was noted only occasionally after the third week. Although rump-licking was no longer seen, the does continued to investigate their fawns's rumps often through the fourth and fifth weeks. During the fifth week, a new behavior was noticed. On 14 occasions from weeks five to 10, does were observed to dip their heads briefly toward the rumps of their young (Table 2).

Rump-licking bout lengths averaged 27 seconds for 108 timed observations. The range was from 1 to a maximum of 245 seconds recorded for a 3-week old fawn and its mother.

The rump-licking posture was seen out of context.
when 40-day old #16 nuzzled its sibling's penial and inquinal areas. Fawn #17 assumed the rump-licking posture.

Table 2.—Relative frequencies and percent maximas for maximum 7-week periods for some grooming activities.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>18.3</td>
<td>6.2</td>
<td>100</td>
<td>0.5</td>
<td>26</td>
</tr>
<tr>
<td>2</td>
<td>3.9</td>
<td>1.3</td>
<td>21</td>
<td>1.3</td>
<td>100</td>
</tr>
<tr>
<td>3</td>
<td>5.7</td>
<td>0.5</td>
<td>8</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>0.7</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>15.3</td>
<td>0.1</td>
<td>2</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>18.6</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>24.2</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>13.8</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
<td>0</td>
</tr>
</tbody>
</table>

Greeting (Figure 4) was observed at the start of almost every fawn-mother interaction period. Greeting was particularly noticeable in the first three weeks of life, when fawns remained bedded down except during interaction periods. Greeting changed from actual licking of the young fawn's head by the mother to nose touching, and lastly to a nose toward nose gesture, as fawns became older. No quantitative data were obtained on this point.
Nursing: The most complete record of nursing by neonate pronghorns was of the tame doe's twins. A relationship between orientation of movements and "progress" toward nursing occurred in both fawns. Nine minutes after its birth, #1 attempted unsuccessfully to stand twice. One minute later #1 fell when it attempted to stand. Eleven-minute old #1 approached its mother on its wrist and ankle joints. The second fawn of the tame doe struggled prior to becoming free of the mother. Number 2 attempted but failed to stand when 5 minutes old. When #2 was 10 minutes old, it struggled toward its mother, but it was not yet walking. Both fawns moved toward the mother before they could walk.

As mentioned above, the mother licked the newborn fawns as they moved toward her. During this licking, the young gained their feet. Both #1 and #2 first walked when 24 minutes old. The fawns moved their heads up and under the mother. While the mother licked her fawns, the fawns mouthed their mother's ventral surface. Number One (#1) first mouthed the mother 25 minutes after birth. The doe slowly arched her back (Figure 5). This posture was seen at the start of every nursing bout observed during the study. When 44 minutes old, #1 mouthed inside one of its mother's hind legs. Four minutes later, it licked a teat, and when #1 was 61 minutes old, it nursed for the first time. The nursing bout lasted 5 seconds.

The second fawn first mouthed its mother's ventral
surface when it was 19 minutes old. Number 2 mouthed its mother's hind leg 122 minutes after birth, licked a teat, and first nursed when it was 130 minutes old. Fawn #2's first nursing bout lasted 45 seconds.

Although the second fawn took 2 hours and 10 minutes or more than twice as long to commence nursing as the first fawn, both fawns nursed less than 20 minutes after they first mouthed a hind leg of their mother (Table 3).

Table 3.—Apparent stages in process leading to the first nursing of two pronghorn fawns.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Time 1</th>
<th>Time 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Approached mother.</td>
<td>11 minutes</td>
<td>10 minutes</td>
</tr>
<tr>
<td>2. Licked mother.</td>
<td>25 minutes</td>
<td>19 minutes</td>
</tr>
<tr>
<td>3. Licked inside of hind leg.</td>
<td>44 minutes</td>
<td>122 minutes</td>
</tr>
<tr>
<td>4. Licked a teat.</td>
<td>48 minutes</td>
<td>130 minutes</td>
</tr>
<tr>
<td>5. Nursed.</td>
<td>61 minutes</td>
<td>130 minutes</td>
</tr>
<tr>
<td>6. Length of time between stage 3 and stage 5.</td>
<td>17 minutes</td>
<td>8 minutes</td>
</tr>
</tbody>
</table>

*Time in minutes after birth.

In addition to observations of first nursings by the tame doe's fawns, one fawn of a wild doe nursed before it was 45 minutes old. Two other fawns (#12 and #13) were observed immediately after birth. One fawn was born 30 minutes before the other. Neither of the fawns nursed in the approximate observation time of 68 minutes for the oldest.
and 28 minutes for the youngest. Subsequent nursing attempts by the tame doe's fawns were more efficient. Two hours and three minutes after it first nursed, the tame doe's second fawn nursed about one minute after it moved its head up and under her abdomen.

Nursing was generally preceded by greeting when the fawn-mother interaction period commenced. As was noted above, the doe arched her back at the start of nursing. This was continued even when fawns became so large that they nursed while resting on their "wrists." The arched-back posture was gradually changed to a normal stance during the course of the nursing bout. Nursing and rump-licking often occurred concurrently during the first few weeks.

The relative frequency of successful and unsuccessful attempts by fawns to nurse their mothers, the relative frequency of attempts to nurse other does (does other than the fawn's mother), and the average length of nursing bouts in 5-day intervals were compiled, and the sum for each 5-day interval is expressed as a percent of the maximum 5-day period in Figures 12 and 13.

Fawns nursed through the summer and into the early fall. The last record was on 118-day old #8 and #9 which nursed for 28 seconds each on 15 September. The frequency of nursings markedly decreased when the young were between 10 and 30 days of age (Figure 13). As the frequency of nursing decreased, the length of time spent in the nursing
position increased to an average of 79 seconds for six nurs­
ings during the 5-day period ending on day 35 (Figure 12).
Five days after the average nursing bout length reached its
close, the relative frequency of unsuccessful attempts to
nurse reached a maximum level. Ten days later, the relative
frequency of fawns attempting to nurse other does reached a
peak. Fawns were seen nursing other does three times for
periods of 15, 10, and 10 seconds. The other does termin­
at ed the nursing by jumping away from the fawns. Although
fawns tended to avoid does which were not their mothers,
unrelated fawns occasionally approached such does when they
nursed their young.

Seven fawns between 7 and 18 days old were observed
mouthing vegetation. Fawns 3 weeks and older grazed
actively.

**Vocalization**: Vocalization is an integral part of
the doe-fawn relationship. Ten minutes after its birth,
the tame doe's first fawn uttered a low-pitched, mew-like
sound when it attempted to stand. The second fawn, which
had been breathing for at least 9 minutes before its birth,
mewed first during its last minute inside its mother. The
mother was silent until 18 minutes after the birth of #2
when she made a sound similar to her fawn's mew, but lower
in pitch. The doe's first vocalization occurred 39 minutes
after the first vocalization of her older fawn. Mewing oc­
curred in bouts of from one to several mews.
There were 19 bouts of mewing recorded for the mother, 18 bouts for #1 and 18 bouts for #2 during 135 minutes following the first observation of vocalization. During the 45 minute, second observation period, bouts totaled 11 for the mother, one for #1, and 16 for #2. Figure 8 illustrates rates of mewing for each individual. The mutual peaks for the doe and #2 reflects that on ten occasions in the first period and on three in the second, mewing by the mother or her young was followed immediately by vocalization by the other. Number 1 did not mew in the second period. Although the graph suggests that answering back and forth occurred, it also indicates that answering did not always occur.

Communication by vocalization accompanied two types of behaviors during both observation periods (Table 4). The first type included movements of the mother toward her young, of young toward their mother, and simultaneous movements toward each other. Mewing increased in both situations in the second observation period, which started 100 minutes after the first period's end. Type one increased 9.7% and type two increased 45.4%.

Vocalization by the tame doe was observed when her fawns were 19 days old. Number 1 watched its approaching mother, but did not leave its bed until the mother mewed. After its mother's mew, #1 ran to her, greeted, and nursed. After the male fawn left the mother and lay down, the mother walked 200 yards away from the fawn and then mewed 12
times. Her second fawn was found dead the next day.

Table 4.—Bouts of vocalization in relation to bouts of two categories of behaviors in the tame doe and her newborn fawns.

<table>
<thead>
<tr>
<th>Observation Period</th>
<th>Type I (Grooming, nursing, and attempting to nurse)</th>
<th>Type II (Movements of the mother toward her young, young towards its mother, and simultaneous movement of mother and young toward each other.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Period I (1616-1827):</strong></td>
<td>Relative frequency of the behavior type (occurrences/minute).</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>Relative frequency of vocalizations accompanying the behavior type.</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>Vocalizations per behavior type.</td>
<td>0.28</td>
</tr>
<tr>
<td><strong>Period II (2008-2045):</strong></td>
<td>Relative frequency of the behavior type (occurrences/minute).</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>Relative frequency of vocalizations accompanying the behavior type.</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Vocalization per behavior type.</td>
<td>0.34</td>
</tr>
<tr>
<td>Percent increase of vocalizations per behavior type.</td>
<td>9.70</td>
<td>45.40</td>
</tr>
</tbody>
</table>

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Figure 13. Relative frequency of nursing activities. Line a represents successful attempts to nurse mothers and its maximum 5-day level was 11.0 bouts per fawn observation hour. Line b represents successful attempts to nurse mothers and its maximum 5-day level was 13.0 bouts per fawn observation hour. Line c represents total attempts to nurse other does and its maximum 5-day level was 3.6 bouts per fawn observation hour. No data was collected from day 20 to day 25, from day 55 to day 60, and from day 70 to day 80. The number of fawn-mother observation hours for each 5-day age interval (from left to right on the absissa) were 17.1, 32, 5.6, 3.0, less than 0.5, 0.7, 9.6, 28.6, 18.5, 5.7, 13.8, less than 0.5, 1.6, 0.8, less than 0.5, less than 0.5, 1.7. The use of lines is merely to emphasize peak levels at different ages and does not necessarily reflect the true slope of the variables.

Figure 14. Relative frequency of other doe aggression toward fawns. The number of fawn-observation hours for each week (from left to right on the absissa) were: 18.4, 3.9, 6.7, 0.7, 11.0, 18.6, 31.1. The maximum 1-week level was 3.6 aggressions per fawn-observation hour.
A second kind of fawn vocalization, bleating, was observed when wild fawns were captured. While the captured fawns, which were from less than 1 to 7 days old, struggled, they emitted loud, high-pitched bleats, except for #12, who mewed. The bleating usually caused the mother to run to within a few hundred yards of the capture site.
BEHAVIORAL INTERACTIONS
BETWEEN FAWNS AND OTHER CLASSES OF CONSPECIFICS

Other Does: Interactions between fawns and does which were not their mothers began shortly after birth for #7, #12, and #13. When #7 was about 100 minutes old, a yearling female sniffed the fawn and then knocked it down. Twenty minutes later, a yearling doe sniffed #7. Fawns #12 and #13 were also sniffed by a doe within 90 minutes after birth.

After the day of birth, nearly all of the interactions between fawns and other does were agonistic (involving conflict [Scott, 1956]) in nature. On five occasions fawns less than 1 week old approached other does, which invariably moved away.

Aggressive behavior by other does toward fawns occurred from day one through to the end of the study. The different aggressive patterns and their percent occurrence in 94 observations are found in Table 5.

The relative frequency of aggression toward fawns by other does (aggressions/fawn-hour observation time) increased to maximum levels during weeks three and four. By week six the relative frequency of aggressive behavior dropped to the level observed for week one (Figure 14).
Table 5.—Aggressive patterns displayed to fawns by other does.

<table>
<thead>
<tr>
<th>Display</th>
<th>Percent occurrence in 94 observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apparently normal movement toward fawns</td>
<td>30</td>
</tr>
<tr>
<td>Rapid extension of head and neck toward fawns</td>
<td>23</td>
</tr>
<tr>
<td>Gentle butts or nudges</td>
<td>50</td>
</tr>
<tr>
<td>Hard butt attempts and hard butts</td>
<td>10</td>
</tr>
<tr>
<td>Chases</td>
<td>4</td>
</tr>
</tbody>
</table>

A relationship between aggression toward fawns by other does and the sex of the fawns was apparent after the fawns became integrated into the herd. The null hypothesis that other does displayed aggressive behaviors to fawns, regardless of the fawns' sex, was tested for the period after day 16, and rejected at the 0.05 level of significance ($X^2=18.92$). The test was based upon a population of five male fawns and three female fawns. Forty-eight of the 54 observed aggressive behaviors by other does were directed toward male fawns after day 16.

Usually fawns avoided other does. Fawns in their first week remained in their beds four times and lay down once when other does approached, and four of these fawns lowered their heads and necks to the ground. Remaining in the bed when other does approached was last seen in 15-day old #8.

In all other observations, fawns avoided does by
turning away, walking away, and running away from the does. After day 16, fawns avoided other does with less effort than before day 16 (Table 6). Before day 16, male fawns participated in 48% of 29 fawn-other doe agonistic interactions, but after day 16, male fawns participated in 81% of 31 interactions.

Table 6. Avoidance patterns displayed to other does by fawns.

<table>
<thead>
<tr>
<th>Display</th>
<th>Number of observations up to day 16</th>
<th>Number of observations after day 16</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turning away</td>
<td>2</td>
<td>20</td>
</tr>
<tr>
<td>Walking away</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>Running away</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

Other does avoided fawns in 12 observations. Does avoided fawns which ran toward them twice. (The record of a doe avoiding #11 is described above.) A standing, other doe jumped back when 45-day old #17 ran past her. Fawns older than 16 days were aggressive toward other does 10 times. Only male fawns were aggressive toward other does. Fawns nudged does three times. The preliminary movements of fighting (slow and simultaneous lowering of heads toward the ground as opponents stand facing each other about 1 foot apart) were observed seven times between other does and fawns 34 days old or older. Three times the fawns jumped,
turned, and moved away before contact. Head to head contact was made in the remaining four observations. In all six cases the fawns then moved and oriented away from the does.

**Bucks:** The first behavioral interactions between fawns and bucks were seen after the fawns joined the summer herds. Summer fawn-buck interactions usually involved aggressive behavior by bucks and flight behavior by fawns. Sexual behavior between bucks and fawns was observed during the pre-rut and rut. Buck orientation toward fawns, and approach toward fawns accounted for 84% of 19 buck aggressive behavior during the summer, and 81% of 16 buck aggressive behavior during the pre-rut and rut. Orientation toward fawns ranged from slight head turning to complete body turning toward fawns. Bucks attempted to butt fawns twice, once during the summer and once during the rut. A buck butted and chased #11 during the summer. Fawns were chased three times. Bucks ran an average of 20 yards in three chases, two of which were during the rut. All of the 19 aggressive actions directed toward fawns by bucks during the summer period were aimed at male fawns. Thirteen of 16 aggressive displays by bucks during the rut were directed toward male fawns.

Fawns generally avoided bucks. Fawn avoidance involved feeding, turning away, walking away, and running away from bucks. Avoidance displays were more brief during the rut than during the summer (Table 7).
In three of 35 fawn-buck interactions, fawns responded aggressively when they lowered their heads simultaneously with yearling bucks. Heads of the contestants met twice. The fawns terminated the encounters by facing away from the bucks.

The only observation of buck avoidance of fawns was made when an adult male avoided 49-day old #13, which ran toward the buck.

Bucks displayed sexual behavior toward fawns during the rut. Yearling bucks accounted for 77% of 60 bouts. Bucks displayed to female fawns in 82% of the 60 bouts. Copulation between bucks and fawns was not observed. Buck sexual displays and the number of times seen are listed below (Table 8). The displays will be more thoroughly described in a future paper.

Fawns almost always avoided buck sexual approaches. Apparent avoidance displays were: turning away, walking
away, and running away from displaying bucks; feeding; and lying down (Table 9). Fawn avoidance often included more than one of the above actions, such as walking away and feeding or lying down.

Table 8.—Sexual patterns displayed by bucks to fawns.

<table>
<thead>
<tr>
<th>Display</th>
<th>Number of times seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approach with head held high</td>
<td>10</td>
</tr>
<tr>
<td>Approach with head held high and waved laterally</td>
<td>45</td>
</tr>
<tr>
<td>Approach with mane and sacral hair erections</td>
<td>28</td>
</tr>
<tr>
<td>Touching the fawn's rump with the chest</td>
<td>19</td>
</tr>
<tr>
<td>Mounting attempts</td>
<td>54</td>
</tr>
<tr>
<td>Mountings</td>
<td>11</td>
</tr>
</tbody>
</table>

Table 9.—Fawn avoidance patterns displayed to sexually-displaying bucks.

<table>
<thead>
<tr>
<th>Fawn displays</th>
<th>Number of times seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turning away</td>
<td>5</td>
</tr>
<tr>
<td>Walking away</td>
<td>84</td>
</tr>
<tr>
<td>Running away</td>
<td>13</td>
</tr>
<tr>
<td>Feeding</td>
<td>17</td>
</tr>
<tr>
<td>Lying down</td>
<td>10</td>
</tr>
</tbody>
</table>

Although most of the buck displays resulted in fawn avoidance, 16 observations of apparent female sexual behavior were observed in female fawns. Female fawns were seen to stand when the buck approached four times; to stand with their hind legs held back and slightly spread (lordosis) six
An unusual behavior of an unmarked female fawn was witnessed on 13 July 1966. The fawn chewed on the horn tip of a sleeping adult buck. The buck moved its head slowly toward the fawn, and the fawn moved 3 feet away. The fawn then moved back to the buck and chewed on the horn tip again. The entire sequence occupied 3 to 5 minutes.

**Peer-Peer Relationships:**

1. **Temporal and spacial relationships:** The degree of association between fawns increased rapidly with age. At and shortly after their birth, fawns of the tame doe and of the two wild does (fawns #6, 7, 12, 13) had little contact and less interaction. The female fawn of the tame doe licked its sibling prior to her first nursing, but the male made no visible response. Prior to capture, #6 and #7 were 3 feet apart when they were approached for capture. Fawns #8, #9, #10, and #11, all approximately 1-day old at capture, were observed to have common fawn-mother interaction periods, but each fawn independently selected its own bedding site on the capture day. No bouts of agonistic, sexual, or play behaviors were observed between these two pairs of siblings on the capture day.

Three pairs of fawns were observed on days two, three, and five. Not only did each of the six fawns bed down independently, but each interacted with its mother independently of the other. On day six the first record of mutual
play behavior was recorded. All three sets of twins observed on day six had common fawn-mother interaction periods. In one set of twins, the siblings left their mother independently, while in the other two sets of twins, the siblings left their mother together. These two sets broke up when actual bed-seeking took place, and each fawn lay down 30 feet from its sibling. The trend noted on day six was further emphasized as the days passed, and siblings became more or less unified in their movements. From day 12 through the first month, the greatest distance observed between bedded siblings was 10 yards, and the usual distance between bedded fawns was 5 feet or less (Figure 15). Siblings were cared for together, as a rule, from day six on.

Interactions between non-siblings were first recorded on day 15. From day 21 to day 30, 50% of fawn-fawn agonistic, sexual, and play interactions were between non-siblings. From day 31 to day 40 agonistic, sexual, and play interactions between non-siblings were more frequently observed than interactions between siblings. This relationship continued through the rest of the study period, except from day 61 to day 70 when five out of nine observed agonistic, sexual, and play interactions were between siblings (Figure 16).

When fawns integrated into the herd, fawn groups developed. From day 30 on these groups were together, except during fawn-mother interaction periods and occasionally
Figure 15. Average distance between bedded siblings. The number of observations for each 3-day interval (from left to right on the absissa) were $3, 3, 2, 1, 3, 1, 0, 2$. The maximum 3-day average distance was 330 feet.

Figure 16. Proportion of total fawn-fawn interaction observed between siblings, and between unfamiliar fawns. The number of observations for each 10-day interval (from left to right on the absissa) were: $2, 19, 38, 65, 79, 61, 9, 18, 10$. 

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during grazing. Within the main fawn group, sibling pairs persisted. The unity of the fawn group was retained through the rut, even though the structure of the doe herd was disrupted.

2. **Agonistic Behavior**: Interactions between one fawn and another were often agonistic in nature. Agonistic behaviors between fawns were first observed on day 15 and last observed on day 122. The relative frequency of agonistic bouts of behavior was highest for week five (2.7 bouts per fawn-fawn observation hour), and weeks five through nine were characterized by frequent bouts of agonistic behavior (Figure 17).

Aggressive displays by fawns toward other fawns were: approach; nudging; sparring; butt attempts and butts; driving; and displacement. Sparring between fawns which faced each other involved simultaneous lowering of heads, slow moving of heads until they touched, and pushing. Driving occurred when one fawn walked or ran behind another fawn. Displacement, the process of taking another fawn's bed by approaching and nudging the other fawn, occurred occasionally but it was not recorded (Table 10).

Flight patterns displayed by fawns to other fawns were turning away, walking away, and running away from other fawns (Table 11).

Although the relative frequency of agonistic behaviors remained quite high from week five until week nine,
the nature of the behaviors noted in conflict situations changed. Prior to day 40, sparring was observed in 31% of all fawn-fawn agonistic bouts, while after day 40 sparring was seen in 9.6% of the agonistic bouts. Conversely, the proportions of the other aggressive behaviors increased after day 40.

Table 10.---Aggressive patterns displayed by fawns to other fawns.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Number of times seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approach</td>
<td>97</td>
</tr>
<tr>
<td>Nudging</td>
<td>97</td>
</tr>
<tr>
<td>Sparring</td>
<td>57</td>
</tr>
<tr>
<td>Butt attempts and butts</td>
<td>11</td>
</tr>
<tr>
<td>Driving</td>
<td>32</td>
</tr>
</tbody>
</table>

Table 11.---Flight patterns displayed by fawns to other fawns.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Number of times seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turning away</td>
<td>44</td>
</tr>
<tr>
<td>Walking away</td>
<td>46</td>
</tr>
<tr>
<td>Running away</td>
<td>13</td>
</tr>
</tbody>
</table>

The frequencies of the three flight behaviors also changed with time. Turning and running away dropped from 19.2% to 10.4% of the observed flight behaviors after day 40. The proportion of turning and walking away remained
Figure 17. Relative frequency of agonistic fawn-fawn interaction. The number of observations for each week (from left to right on the absissa) were: 4.4, 5.5, 8.3, 9.7, 13.1, 31.7, 42.4, 34.4, 5.7, 12.9. The maximum 1-week level was 2.7 bouts per fawn-fawn observation hour.

Figure 18. Relative frequency of fawn play. The number of fawn-observation hours (from left to right on the absissa) were: 9.9, 18.0, 44.8, 76.8, 18.6. The maximum 2-week level was one bout per fawn-observation hour.
about the same. Orientation away from aggressive fawns increased from 34.6% before day 40 to 45.4% after day 40.

3. **Sexual Behavior**: Fawns occasionally exhibited behavior patterns similar to adult behavior patterns. Sexual displays seen in fawn-fawn interactions included: following directly behind another fawn; standing directly behind another fawn; investigating a leading fawn's rump; holding the head above a leading fawn's rump or back; placing a foreleg on a leading fawn's rump; raising up on the hind legs behind another fawn without touching the other fawn; and mounting a leading fawn, which included contact of the mounter's forelegs with the mounted's back (Table 12).

Table 12.—Sexual patterns displayed by fawns to other fawns.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Number of times seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Following directly behind.</td>
<td>17</td>
</tr>
<tr>
<td>Standing behind</td>
<td>14</td>
</tr>
<tr>
<td>Investigating a leading fawn's rump.</td>
<td>14</td>
</tr>
<tr>
<td>Holding the head above a leading fawn's rump or back.</td>
<td>11</td>
</tr>
<tr>
<td>Placing a foreleg on a leading fawn's rump.</td>
<td>1</td>
</tr>
<tr>
<td>Raising up of the hind legs behind another fawn without touching the other fawn.</td>
<td>17</td>
</tr>
<tr>
<td>Mounting.</td>
<td>7</td>
</tr>
</tbody>
</table>

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Thirty-six bouts of one or more sexual displays were observed. Fourteen of the bouts immediately preceded or followed agonistic behavior. Dominant fawns displayed to subordinant fawns in 80.6% of 36 sexual behavior bouts.

A relationship between the sex of the fawns and sexual behavior was noted. Male fawns exhibited 97.2% of the observed sexual behavior. The sole observation of sexual behavior by females occurred when a female fawn followed and raised up on her hind legs behind 69-day old male #17. Males directed sexual behavior patterns toward females 18 times, and toward males 17 times. The marked fawn herd was composed of three females and five males. The hypothesis that male fawns did not distinguish between sexes when displaying sexual behavior is significant at the 0.05 level ($X^2=1.05$).

4. Play: The term play refers to certain fawn activities which served no apparent purpose other than exercise. Play of single fawns and play between fawns will be described. Fourteen of the 16 records of single fawn play were made on or before day 18.

Fawn #8 was observed to jump, kick out with its hind legs, and change its body axis orientation 45° a total of three times on days 15 and 18. The other 13 records of single fawn play involved running. The fawns ran around the mother 12 times, and around the herd once. Fawns ran in circles or ellipses six times and back and forth on nearly
straight line courses seven times. The greatest distance from the starting point of the run ranged from 35 feet to 300 yards for eight runs. Three bouts of single fawn running were 2, 2, and 6 minutes long. The rump rosettes were erected on four of the 13 single fawn runs. Runs involving two fawns were observed 17 times, and nine times with siblings. Two were preceded by sexual behavior. Six runs were either preceded or followed by sexual behavior. The only record of more than two fawns running together was of fawns #12, #13, and an unmarked fawn.

Play behavior was seen most frequently during the first 2 weeks of fawn life (one bout per fawn-fawn observation hour). During the following 2 weeks, fawn play was seen less often, and no fawn play was seen after day 53 (Figure 18).

5. **Hierarchy:** By the age of 6 weeks, the most frequently observed group of six tagged fawns had established a dominance hierarchy. Siblings #10 and #11 integrated into the group during the following week. The number of times each tagged fawn was dominant or subordinate to each of the other fawns is shown in Table 13. The fawns are arranged with the most dominant #8 in the upper left-hand corner of the chart. For example, #8 dominated #12 seven times, #13 twice, etc., and was subordinated to #12 once and to #13 once, etc. The hierarchial arrangement of the eight tagged fawns is based on the results of 130
Table 13.—Dominance relationships between members of the fawn group.

<table>
<thead>
<tr>
<th>Number of encounters: Fawns subordinate. (Read across)</th>
<th>Number of encounters; fawns dominant. (Read down.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8</td>
</tr>
<tr>
<td>8</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>7</td>
</tr>
<tr>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>16</td>
<td>13</td>
</tr>
<tr>
<td>17</td>
<td>10</td>
</tr>
<tr>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Sum</td>
<td>38</td>
</tr>
</tbody>
</table>
agonistic or conflict interactions between them. The fawn which displayed a flight behavior at the termination of the interaction was judged subordinate.

Each of the five male fawns was dominant over the three females. Dominance status was closely associated with age. Fawn #8 was the oldest of the group and the highest in the hierarchy; fawn #17 was one of the youngest fawns and was the lowest male. Fawns #12 and #13 were intermediate in age and in position among the males (Table 1).

Hierarchial position and sexual behavior appeared to be related, because dominant fawns commonly directed sexual behaviors toward subordinate fawns (see above).

Fawn Integration Into Herd Activities

Fawn integration into summer herds which included adult and yearling does and occasional bucks began when the fawns were about 3 weeks old. Fawns acted as part of the herd and were usually observed to rest when the herd rested, to feed when the herd fed, and to move with the herd.

A definite pattern of herd flight was observed in both 1965 and in 1966. Eleven out of 19 recorded herd flight orders were led each time by an adult doe followed by a compact fawn group, and then by a doe group. On six occasions an adult buck trailed the herd. Four flight orders were nearly typical with groups of two, three, or four does leading in four cases, and with one fawn accompanying
the trailing doe group once. Of the atypical flight orders, two were led by fawn groups; one was led by an adult doe, which was followed by three fawns, a buck, three fawns, and a doe in that order; and one fleeing herd was apparently without order.

The organization of the herd into the typical flight order was observed four times, once in detail. On 7 July 1966 at 0830, the mother of #16 and #17 and their mother started to run. Another doe and her fawns, #10 and #11, also ran. At 0840 #10 and #11 ran after #16 and #17 who were following their mother. A second doe, not certainly identified as the one accompanying #10 and #11, was running. Fawns #8 and #9 ran behind a third doe. All the pronghorns in sight were running, but they appeared disorganized. The herd stopped after traversing 30 feet, and the fawns clumped together. The does surrounded the fawns. At 0845 a doe snorted and ran 10 feet. The herd then ran in the following order: one adult doe, a group of five fawns, and a group of five does and one fawn. Shortly after the herd started running, the trailing fawn joined the fawn group.

The organization of another typical flight order, observed on 29 June 1966, occurred after the herd had run a short distance. On 25 July 1966, the organization process took 5 minutes when a herd was scared by a human 1/4 mile away. Earlier that day, the herd had been startled from only 50 feet and no organization was noted.
Fawns apparently were integrated into the summer herd when they were 3 weeks of age. The fawns were subordinate to all other age classes of the summer herd. Fawn subordination to unfamiliar does and to bucks is described above. By the end of the summer, the fawns had established a group within the herd. With the onset of the rut, the unified summer doe-fawn herds changed. The groups separated, but the fawn groups remained intact.

Evidence for a Critical Period for Primary Socialization

The concept of a critical period, during which the newborn supposedly learns to recognize its own species, is a debated subject (see Discussion). Nevertheless, observations made on six newborn pronghorns suggests that a critical period for the development of species recognition exists in this precocial species.

When the tame doe's male fawn was 41 minutes old it approached a man and mewed. Just 51 minutes later, a man approached the fawn, but the fawn lay down, with his head and neck on the ground and ears laid back in the "head-low" posture (Figure 3). The male fawn's younger sibling was not observed to assume this posture on its birth day. Similar observations were made on the neo-natal offspring of the two wild does. Number 7, the older twin of one wild doe, assumed the head-low posture when it was approached by two men. Its possible age range at the time was 171 to 200 minutes. Its
sibling, #6, which was at least 20 minutes younger, did not assume the head-low posture when approached but moved toward its captors. This fawn had not been licked as thoroughly as it sibling by the time of its capture. Fawns #12 and #13, the approximately 60 and 84-minute old young of the second doe, were lying 3 feet apart when approached. Number 13 assumed the head-low posture when its captors were 20 yards away. When #12 was restrained, #13 got up and feebly ran about 32 feet before lying down in the head-low posture. Number 12 mewed three or four times and sucked on an offered finger after it was measured and tagged. Number 12 followed its captors, as they approached its lying sibling. Number 13 retained the head-low posture when captured, and its muscles were limp. When #13 was measured and tagged, it bleated. The less-than-104-minute old #12 apparently responded to the bleats of its sibling, and wandered off approximately 10 yards before it lay down in the head-low posture.

Three of the six newborn pronghorns assumed the head-low posture upon the approach of men, and fourth exhibited the posture during the tagging of its sibling. The average, approximate age for the four fawns exhibiting the behavior was 114 minutes, and the range was from 84 to 176 minutes. This head-low behavior was not observed in two of the fawns, #6 and the tame doe's second fawn, whose ages were between 151 to 181 minutes and from birth to 110 minutes, respec-
tively. All the 1-day old or older fawns approached during capturing attempts assumed the head-low posture. Thus a critical period for the development of head-low posture in response to the approach of another species, man, may exist in the pronghorn fawn.

Territoriality

Observations made during the rut of 1965 suggested that mature bucks were territorial on the National Bison Range. However, proof of territoriality was not obtained until the rut of 1966, when the position and behavior of seven, large, naturally marked bucks were observed for 102.6 hours on 25 days from 1 September to 7 October. These seven bucks were usually the only large males seen on the study area, although at least two others were occasionally observed. Similar records were kept on three smaller, naturally-marked bucks.

During the rut, the mature bucks were located, in two-thirds of the distribution records, in specific, non-overlapping areas (Figure 19). The two-thirds distribution areas were based on the following total position records for each buck: A, 27; B, 48; C, 32; D, 30; E, 33; F, 32; and G, 25. These areas ranged from approximately 3/16 square miles for bucks E and F to 1/8 square miles for buck B (Table 14). One-hundred-percent distribution areas were constructed with straight lines (Figures 20-26).
Table 14.—Approximate areas (square miles) inhabited by mature bucks

<table>
<thead>
<tr>
<th>Buck</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>Two-thirds area</td>
<td>1/16</td>
<td>1/16</td>
<td>1/8</td>
<td>1/12</td>
<td>1/16</td>
<td>1/16</td>
<td>1/16</td>
</tr>
<tr>
<td>Total area</td>
<td>1/2</td>
<td>3/4</td>
<td>1/3</td>
<td>1/3</td>
<td>1/4</td>
<td>1/4</td>
<td>1/2</td>
</tr>
</tbody>
</table>

Each buck's 100% distribution area overlapped with one or more of the other bucks' 67% and/or 100% distribution areas. Overlap occurred in three of four possible ways. The 100% distribution areas of some bucks overlapped the 67% areas of other bucks and vice-versa in 26.2% of 42 possible cases. The average percent of distribution points included in the overlapped two-thirds distribution was 5.5%. Mutual overlap of 100% areas occurred in 46.5% of 42 possible combinations. The average percent of distribution points included in mutual distribution area overlap was 19.6%. The two-thirds distribution areas did not overlap each other (Tables 15 and 16).

Bucks on their territories displayed aggressively to any buck who looked toward them, or exposed the side of his body to the territorial buck. Although variations in the following order occurred, the typical, progressive series of aggressive displays by territorial males were: 1) looking toward the challenging buck; 2) walking or running toward the buck; 3) lowering the ears and neck to a nearly
Table 15.—Percent overlap between 67% and 100% buck distribution areas.

<table>
<thead>
<tr>
<th>Overlapped Bucks 100% distribution areas</th>
<th>Overlapping bucks and their 67% distribution areas</th>
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<tr>
<td></td>
<td>A</td>
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<tr>
<td>A</td>
<td>---</td>
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<tr>
<td>B</td>
<td>4.2</td>
</tr>
<tr>
<td>C</td>
<td>0.0</td>
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<tr>
<td>D</td>
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<td>E</td>
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<td>F</td>
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<tr>
<td>G</td>
<td>0.0</td>
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</tbody>
</table>

Table 16.—Percent overlap between 100% buck distribution areas.

<table>
<thead>
<tr>
<th>Overlapped bucks 100% distribution areas</th>
<th>Overlapping bucks and their 100% distribution areas</th>
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horizontal level, while approaching the opponent; 4) walking slowly in the posture mentioned above in #3 so that the territorial buck's side was exposed to the opponent; 5) slowly turning the horizontally-held head toward the opponent; 6) facing and approaching the opponent, followed by lowering of the head to near the ground; and 7) vigorous fighting after slowly making horn to horn contact with the opponent. Fighting occurred if the opponent failed to display subordination to the displaying, territorial buck. The displays of adult pronghorns will be more thoroughly described in a future paper.

Through these ritualized displays, territorial bucks defended their territories in all 131 observed agonistic encounters with yearling bucks and in 94.5% of 73 similar encounters with adult bucks. Bucks who displayed subordination were tolerated on the territories. Only four battles between territorial males were observed. One fight occurred when both bucks were away from their territories. The remaining three fights occurred on the territories. The defending territorial bucks retained their dominance in two of the three fights.

The one buck who subordinated after a territorial battle retained his territory, because the victor left the area immediately after the fight. Territorial males were observed to subordinate to challenging males twice without battles. In one of these observations, the newly dominant
male, B, left the area and was seen later that day on his regular territory. Later, Buck B lost his territory to an unrecognized buck for 1 day, but B was on his territory and dominant to other males the following day.

Males probably marked their territories in three ways. First, the males were visible to other males, because the vegetation height was not great enough to conceal a standing buck on any of the territories. A second probable means of marking was by scent. According to McLean (1944), pronghorns possess postmandibular scent glands. Bucks probably utilized these glands for marking and were often observed rubbing the angles of their jaws on tall vegetation, especially on Verbascum blattaria spires. A third possible form of marking was auditory, through a special vocalization of males, which Gregg (1955) termed the "laugh." This vocalization was typically a series of about eight sneeze-like notes which descended in pitch. Territorial males gave the male vocalization when other males approached in 22 of 204 agonistic encounters.
Figure 19. Territories of seven naturally marked mature bucks. The territory represents two-thirds of the position records for each buck. Each grid square equals 1/16 square miles. The dashed line represents the study area boundary.
Figure 20. The position records for Buck A. The solid line connects the outermost points in the two-thirds distribution area. The dashed line connects the outermost points of the 100% distribution area.

Figure 21. The position records for Buck B. Explanation as in Figure 20.
Figure 22. The position records for Buck C. Explanation as in Figure 20.

Figure 23. The position records for Buck D. Explanation as in Figure 20.
Figure 24. The position records for Buck E. Explanation as in Figure 20.

Figure 25. (Lower Left) The position records for Buck F. Explanation as in Figure 20.

Figure 26. (Lower Right) The position records for Buck G. Explanation as in Figure 20.
DISCUSSION

Behavior Before and During Parturition

Records of parturition in and behavior during parturition in wild, North American ungulates are restricted to five of the 12 species. Behavior during parturition has been reported twice in bison (McHugh, 1958); once in mule deer (Miller, 1965); four times in white-tailed deer (Haugen and Davenport, 1950; Michael, 1964; Sevringhaus and Cheatum, 1956); six times in barren-ground caribou, once by deVos (1960) and five times by Pruitt (1960); and seven times in pronghorn (Autenrieth, 1966; Buechner, 1950; Hoover et al., 1959; Howard, 1966; McLean, 1944; Prenzlow, 1964). Darling (1964) reported parturition in Scotland's red deer. Some behavioral aspects of parturition in Grant's and Thompson's gazelles have been reported (Estes, 1967).

**Pregnancy:** Prenzlow (1965) recognized pregnant does 2 to 3 weeks before parturition by their abdominal swelling and increase in nervousness. In the tame doe, noticeable abdominal swelling appeared about 1 month before parturition, and she appeared nervous to Bison Range personnel about 1 week before parturition. Her udder was distended 5 days before parturition.

Prenzlow (1964) stated that pregnant does, between
12 and 24 hours prior to parturition, may be recognized by lateral and posterior abdominal distension, which indicated that fetuses had entered the birth canal. In addition to marked abdominal distension at this time, the tame doe's udder was noticeably dark and swollen such that skin was visible between the hairs on the day prior to parturition. A third sign of approaching parturition in the tame doe was slight difficulty in walking.

It has been stated that near-term pronghorns leave the doe herds (Einarsen, 1948; McLean, 1944; Prenzlow, 1964). Prenzlow (1964) noted one doe within a 100 square yard area for 4 days before parturition. Autenrieth (1966) observed parturition in a lone doe. One wild doe, observed on the Bison Range, apparently attempted to leave her herd several times before she gave birth, but was followed to her birth-site by three yearling does. A second wild doe was herded by a buck and followed by several does before she gave birth within 100 yards of other pronghorns. Buechner (1950) noted a doe which gave birth in the same locale as eight does and a buck. Howard (1966) recorded parturition in a doe which had just previously been in a herd. The doe reported by Howard (op. cit.) gave birth 100 yards from another doe. According to the above sources, other pronghorns near does giving birth paid little attention to them. The variation in reported relationships between parturient does and other pronghorns suggests that the presence or absence
of conspecifics has little effect on birth-site selection.

Darling (1964) reported that red deer females leave the herd a few days before they give birth. Single parturient females have been observed in mule deer once (Miller, 1965), and probably in white-tailed deer once (Michael, 1964). However, Michael (1964) observed a second doe who gave birth within sight of a buck. Altmann (1963) reported that cow elk give birth in the herd area. Pruitt (1960) observed parturient barren-ground caribou, and Grant's and Thomson's gazelles are reported (Pruitt, 1960; Estes, 1967) to walk a short distance from their herd before giving birth. Cow bison give birth either in or out of their herd according to McHugh (1958).

Parturient pronghorns are thought to give birth in certain habitats. Einarsen (1948) stated that parturient does preferred basins surrounded by low ridges which contained vegetation from 12 to 18 inches in height. McLean (1944) felt that parturient does usually picked an open area with high brush. Hoover (et al., 1959) stated that does used an area with low vegetation. Two does gave birth in small depressions in open areas on the Bison Range, where vegetation height did not exceed 18 inches. Howard (1966) reported a doe which gave birth in a shallow swale. Autenrieth (1966) observed a doe give birth in a ravine. O'Gara (pers. comm.) observed a parturient doe in a steep-sided, flat-bottomed gulley with sparse vegetation.
Most of the reported parturition sites afforded limited visibility to both the parturient doe and to any potential terrestrial predator, such as a coyote. Such a predator might capture the doe or, later, her newborn fawns. Therefore, it seems reasonable that does would select areas affording limited visibility for birth-sites.

Selection of birth sites in other ungulates is less well documented. Miller (1965) reported a mule deer doe which gave birth in a previously-used bed, which was surrounded by fairly dense cover on all sides. Michael (1964) observed one white-tailed deer, with a fawn hanging from her vulva, walk into a dense thicket. A second white-tailed doe gave birth near the base of a shrub in a more or less open area (Michael, 1964). Although these cervids show a tendency toward giving birth near cover, barren-ground caribou, reported by Pruitt (1960), apparently did not. Maternity bands composed of pregnant female barren-ground caribou apparently avoid brushy, rocky, or swampy areas, and "...frequent rolling rugged uplands..." (Pruitt, 1960). Pruitt stated that the parturient doe usually walked a few meters from its maternity band and lay down on a snow-free area. Grant's and Thomson's gazelles, according to Estes (1967), usually select areas of medium to long grass. These observations suggest that ungulates, except possibly barren-ground caribou, are likely to select secluded parturition sites.
Labor: The first sign of labor in the pronghorns observed on the National Bison Range was the tail-up. A tail-up was observed nearly 9 hours before parturition in the tame doe, but frequent tail-ups were not seen until about 6 hours later (Figure 7). Tail-ups in two other does were recorded 2 hours and 40 minutes and 3 hours and 20 minutes pre-partum. Prenzlow (1964) reported that a doe occasionally raised her tail about 1/2 hour pre-partum. Howard (pers. comm.) observed a doe which held her tail erect for short periods while standing, walking, or stretching. The tail-up indicates imminent parturition, and because of its easy detection, the movement is invaluable to workers on parturition and socialization in the pronghorn. Tail erection has been reported in parturient barren-ground caribou (deVos, 1960) and white-tailed deer (Haugen and Davenport, 1950; Sevringhaus and Cheatum, 1956).

Details of labor postures of parturient pronghorns appear to vary considerably. However, four wild does (Autenrieth, 1966; Buechner, 1950; Howard, 1966; Prenzlow, 1964) and the tame doe struggled while lying and were apparently subject to strong labor contractions.

Miller (1965) observed rocking motions in a lying, parturating mule deer. Visible straining was recorded for two white-tailed deer (Sevringhaus and Cheatum, 1956), while little or no difficulty was observed in three other white-tailed does (Haugen and Davenport, 1950; Michael,
1964). Devos (1960) reported no visible labor contractions in a parturient barren-ground caribou. Although the cervids seem less affected by labor contractions than the pronghorns, the effect of previous births on the degree of apparent labor has not been taken into account.

**Parturition:** Einarsen (1948) observed that parturition in the pronghorn generally took less than 1 hour, and that a doe usually gave birth to two fawns. Observation on twin births in the tame doe and in two other does agree with Einarsen's time estimate (Autenrieth, 1966; Howard, 1966; Prenzlow, 1964). The period between the births of twins was 31 minutes for the tame doe's young, and about 30 minutes for one wild doe's twins. Other records of this period were 31 minutes (Autenrieth, 1966), 26 minutes (Prenzlow, 1964), and 9 minutes (Howard, 1966). During this time gap, the mothers licked their first fawns while laboring with their second fawns.

Prenzlow (1964) observed a doe which stood when she gave birth to both of her fawns and suggested that the shock of striking ground caused commencement of fawn breathing. Delivery of six fawns observed on the Bison Range occurred while their mothers were lying for five fawns and standing for one fawn. Autenrieth (1966) and Howard (1966) each observed a doe give birth while lying. Moreover, the tame doe's second fawn breathed before being free of its mother. These data clearly support Autenrieth's (op. cit.) opinion that
shock of striking the ground at birth does not cause commencement of breathing as suggested previously by Prenzlau (1964).

Other female ungulates lie while giving birth (deVos, 1960; Haugen and Davenport, 1950; McHugh, 1958; Miller, 1965; Pruitt, 1960; Sevringhaus and Cheatum, 1956). Birth of the single fawn caribou generally lasts about 15 minutes (Pruitt, 1960), although deVos (1960) reported a doe that gave birth 65 minutes after her young was present at her vulva. Haugen and Davenport (1960) reported that a two-year or older white-tailed doe gave birth with little difficulty to one fawn in 12 minutes, while another white-tailed doe, reported by Sevringhaus and Cheatum (1956), gave birth to twins in 92 minutes. A mule deer doe delivered one fawn in 7 minutes (Miller, 1965). The cow bison gave birth to their single calves in 20 and 27 minutes (McHugh, 1958).

Much of the above variation in parturition length may be related to the number of previous births given by the females. It is well-known that primiparous cattle have considerably more difficulty giving birth than do multiparous females.

Socialization

The development of social behavior in the pronghorn fawn from its birth to 5 months of age is marked by gradual
but distinct changes in fawn behavior patterns and interrelationships between the fawn and other pronghorns, as well as between the fawn and its herd as a group. By summer's end, fawns are difficult to distinguish behaviorally from herd adults and have become integrated parts of summer herds.

The development of social behavior in the fawn will be considered in four periods; immediate post-partum; first day through third week; fourth week through third month; and fourth month.

**Immediate post-partum:** A generalized account of typical interactions between pronghorn mother and her newborn fawn follows. Because there appears to be little interaction between newborn siblings, the account concerns only member of the usual pair of newborn fawns.

The fawn's first social interaction is with its mother. While the mother licks and eats her fawn's fetal sac and then licks her fawn's wet body surface, the fawn becomes mobile and begins mewing. The vocalizing fawn moves toward its mother, even before it stands. The mother continues to lick, as her fawn stands and approaches her. The mother adds her deeper-pitched mews to the fawn's. The fawn moves head up and under its mother's ventral surface; it gradually approaches its mother's udder, and then nurses for the first time. When the fawn moves under its mother's abdomen, the doe arches her back and slightly spreads her hind
legs. With each successive nursing attempt, the fawn becomes more efficient.

As the fawn nurses, lies or stands near its mother, moves with its mother, or returns from short trips, its mother licks it less often, but in two additional patterns. At some point in her generalized licking, the mother strokes the fawn's inguinal area; the fawn lowers its anterior trunk, holds its hind legs straight, and erects its tail, and rump-licking commences. With increasing age and mobility, the fawn takes longer trips from its mother. When the fawn returns from these trips, the fawn and its mother exhibit greeting by extending their heads toward each other, and by the mother's licking of her fawn's head. A few hours after its birth, the fawn lies down in an area of its own selection, and its mother wanders off.

1. **Licking**: Female ungulates of the following 11 species have been reported to lick their newborn young; domestic cattle (Hafez, 1962); domestic sheep (*Ovis aries*) (Hafez and Scott, 1962); domestic goat (*Capra hircus*) (Collias, 1956); barren-ground caribou (Pruitt, 1960); eik (Altmann, 1952); red deer (Darling, 1964); white-tailed deer (Haugen and Davenport, 1950; Sevringhaus and Cheatum, 1956); mule deer (Miller, 1965); moose (Altmann, 1963); bison (McHugh, 1958); and pronghorn (Autenrieth, 1966; Prenzlow, 1964; Howard, 1966). The sow (*Sus domesticus*)
reportedly does not lick off her newborn (Hafez et al., 1962).

There are at least three possible functions of maternal licking of newborn young. First, licking may decrease neonatal mortality due to excessive evaporative heat loss. Licking by the pronghorn mother reduces the amount of fluid adhering to her fawn's coat and probably increases the insulative quality of her fawn's coat by ruffling it. Cold, wet springs have been linked directly to newborn mortality in pronghorn (Einarsen, 1948) and in sheep (Alexander et al., 1959). McHugh (1958) reported that a calf buffalo was licked dry within 30 minutes after its birth.

Maternal licking may reduce the newborn's odor, which would decrease a mammalian predator's chances of finding it.

A sort of "maternal imprinting" (Klopfer et al., 1964), may occur when the ungulate mother licks off her newborn. As pointed out by Klopfer and Gamble (1966), such a maternal-filial bond would be important in mammals whose young are capable of leaving their mothers shortly after their birth. Collias (1956) estimated that the mother goat bonded herself to each of her individual newborn kids within 2 hours after parturition. Later work by Klopfer (1964) indicated that mother goats learned the identity of their young within 5 to 19 minutes after parturition. Smith et al. (1966) reported that sheep mothers "imprint" the identity of their young on themselves during a 20 to 30 minute period.
Collias (1956) observed that presence of birth membranes and fluids enhanced but were not essential for acceptance in sheep and goats. Smith et al. (1966) suggested that maternal imprinting was due to a "...gustatory or olfactory impression..." Recent work confirmed Collias's (1956) view that olfaction was probably not the only stimulus mode utilized by the mother for identification of her newborn (Klopfer and Gamble, 1966).

Prenzlow (1964:6) utilized the maternal imprinting concept to explain abandonment of newborn pronghorn. At least three and perhaps five out of 13 fawns he captured during the first study period were abandoned, and "All 5 of these animals, when handled, were only a few hours old since birth fluids still adhered to the pelage of the young animals." Prenzlow then waited "...until the socialization or 'imprinting' period was well under way," before capturing fawns during the next spring, and none of these fawns were subsequently abandoned. Prenzlow thus concluded that the critical period for maternal imprinting was 6 hours.

However, observations made at the Bison Range suggest that fawns a few hours old should have little or no birth fluids on their coats, because maternal licking and environmental drying. Thus, Prenzlow's five fawns may have been close to 1-hour old when he handled them. Furthermore, two fawns captured on the Bison Range when about 60 to 84 minutes old and two 3-hour old fawns were not aband-
oned, which suggests that their maternal-filial bond had already formed.

2. Initial Fawn Movements: Under wild conditions, the pronghorn fawn's first movements are probably made toward its mother. Both of the tame doe's fawns struggled toward her before they first stood. After they stood, they continued to direct their movements toward their mother. Autenrieth (1966) made similar observations on a newborn pair of pronghorns.

The tame doe's male fawn approached a man 3 minutes before it first nursed. Young sheep and goats, who had not yet nursed, followed a man who stood near them and then moved slowly away (Collias, 1956). Collias (1956) stated that the newborn's "...tendency to go toward a large moving object helps bring the young one in contact with the mother." This tendency in newborn sheep and goats has also been mentioned by Hersher et al. (1963). Hess (1959) stated that movement toward the first large, moving object encountered by the newborn is present in all animals which have mobile newborn young.

3. Vocalization: There is a striking similarity between the vocalizations of young pronghorns and those of sheep and goats of the same age. The young pronghorn fawn is capable of at least two kinds of vocalization, a "mew" and a distress cry or "bleat." The first type was heard within a few minutes before or after birth, while the
second type was observed in fawns more than 1 hour old. Both of the tame doe's fawns vocalized (mewed) before they stood, but their mother did not commence mewing until 18 minutes after her second fawn's birth. While a ewe reported by Collias (1956) vocalized immediately after her lamb's first vocalization, a mother goat first vocalized 6 minutes after her second kid's birth. Altmann (1958) reported that neonatal calf moose vocalize. Similar mother-young communication has been reported in bison (McHugh, 1958), barren-ground caribou (Pruitt, 1960), elk (Altmann, 1952; Murie, 1951), and red deer (Darling, 1964), but it is not known when this behavior in these species.

Collias (1956) stated that newborn sheep and goats vocalized when they heard their mother's call, or when their nearby mothers moved. Vocalization by either the newborn or the mother was increased by separating them (Collias, 1956). Although observations made at the Bison Range indicate that answering between the tame doe and her fawns occurred, answers were not always made (Figure 9).

Collias (1956) stated that the function of these initial vocalizations in sheep and goats is to bring the mother and her newborn together. If a fawn pronghorn were born at night, and if there is a short critical period for maternal acceptance of the newborn, the survival value of immediate vocalization would be great indeed.

Utilizing Scott's (1956) classification of behavior
patterns, Altmann (1959) interpreted the calf moose's vocalizations as being an et-epimeletic or care-seeking behavior. This classification suggests that the calf-moose vocalizes with the intention of receiving care. Perhaps this is true, but there is no way of eliminating the possibility that the calf moose merely responds to stimuli, without contemplation of a goal. Thus, I feel that Scott's (1956) classification of behavior is not justifiable because of its teleological basis.

Distress cries of young sheep and goats and subsequent bleats by their mothers can be induced shortly after birth by placing the young in a stressful situation (Collias, 1956). Similar long, high-pitched bleats in struggling, captured pronghorn fawns have been reported, but bleats by does have not been noted (Einarsen, 1948; Hoover et al., 1959). On the Bison Range, a fawn approximately 60 minutes old did not bleat when captured, but its 84-minute old sibling and two other 3-hour old fawns did when they each were captured. Mothers of bleating pronghorn fawns, captured on the Bison Range and elsewhere (Einarsen, 1948; Hoover et al., 1959), ran to the capture areas. Cow elk are reported to respond similarly to bleats from their handled calves (Murie, 1951). Presumably, the mother, upon hearing her fawn's bleat would run to the area and chase a predator away from her young. McLean
(1944) reported two incidences of single does chasing coyotes and one observation of a doe striking at a golden eagle, when young fawns were nearby.

4. Nursing: Newborn ungulates usually commence nursing within a few hours after their birth. Alexander et al. (1959) reported that in 99 lambs, which survived for at least 72 hours after their birth, the average age at first nursing was 93 minutes. Collias (1956) observed first suckling in a 56-minute old goat kid. A mule deer fawn was observed to suckle 53 minutes after its birth (Miller, 1965). Three pronghorn fawns observed on the Bison Range first nursed when they were 45, 61, and 130 minutes old. (The fawn who took 130 minutes died when 14 days old.) Autenrieth (1966) observed a 58-minute old pronghorn fawn nursing for its first time. Domestic cattle calves are reported to first nurse when they are from 2 to 5 hours old (Hafez and Schein, 1962).

The behavior of the mother and young prior to nursing is remarkably similar among ungulates. As noted above, the newborn ungulate's initial movements typically are directed toward its mother. Upon reaching the dam, the young kid or lamb thrusts its head up and under its mother's ventral surface, sucks her hair and protuberances, and after a number of such movements, finds and sucks the teat (Alexander and Williams, 1966; Collias, 1956; Hersher et al.,

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McHugh (1958) reported that calf bison moved their heads up and between their mother's forelegs before their first nursing. Altmann (1952) noted a newborn elk who "...pushed upwards and had to work hard to get milk." Observations made at the Bison Range and in Idaho (Autenrieth, 1966) indicate that the course leading to the pronghorn fawn's first nursing is not noticeably different from that followed by newborn sheep and goats.

While the newborn sheep and goat move under their mother's abdomen, the mother arches her back, which makes her udder more accessible to her young (Collias, 1956; Hafez and Scott, 1962). The tame doe arched her back when her newborn fawns were moving under her abdomen (Figure 5). Autenrieth (1966) also observed a doe which "...hunched down..." when one of her newborn fawns nursed. Altmann (1963) observed that "...mother moose may squat or even lie down for nursing during the first few attempts."

Subsequent nursing attempts by the tame doe's fawns were more efficient than first attempts. Hafez and Scott (1962) remarked that within a few days after birth, the lamb "...runs directly to the udder and begins to suckle immediately."

5. Rump Licking: Rump-licking is a stereotyped behavior which appears between pronghorn mothers and their fawns (Figure 6). The posture of fawns during the first rump-licking observed between the tame doe and 108 and
127-minute old fawns, was not noticeably different from the last recorded posture, seen in a 23-day old fawn.

The tame doe licked her female fawn before each of four rump-lickings on the fawn's birth day. The tame doe's male fawn assumed the rump-licking posture once after, and twice before it was licked. Prenzlow (1965a) caused captive fawns to assume the rump-licking posture and to urinate and defecate by wiping their inguinal areas with a wet, warm cloth. Apparently, assumption of the rump-licking posture can be autonomous or can be caused by physical stroking of the inguinal area.

There are at least two possible functions of rump-licking. Perhaps inguinal stimulation is necessary for defecation and urination in the young fawn. Estes (1967) reported that fawn Grant's and Thomson's gazelles must be licked before they can urinate or defecate. Altmann (1963) suggested that the cow moose's licking and nudging stimulated her calf to eliminate. A second source of survival value might be reduction of fawn odor, and therefore reduction of the probability that the bedded fawn will be detected by an olfactory predator, such as the coyote.

6. Greeting: The young pronghorn fawn usually is greeted when it approaches its mother (Figure 4). The mother and fawn extend their heads toward each other, and the mother licks her fawn's head. This behavior was observed seven times between the tame doe and her two fawns when they
were about 4 hours old and older on their day of birth. Autenrieth (1966) observed a greeting between a doe and her approximately 3-and 1/2-hours old fawn. A similar behavior has been reported in barren-ground caribou does and fawns (Pruitt, 1960).

As will be discussed below, greeting behavior in the pronghorn changes with time. The function of greeting is unclear, although it may be involved with maternal identification of individual young.

7. The Mother Leaving Her Fawns: Pronghorn does have been reported to leave their fawns 126 minutes (Prenzlow, 1964) and 155 minutes (Autenrieth, 1966) after their birth. One wild doe observed on the Bison Range was apparently leaving her 3-hour old fawns. Altmann (1963) reported that elk mothers leave their young after the first nursing. Collias (1956) noted that newborn sheep and goats lie down and sleep after they have nursed, and that their mothers then wander off and graze near the area. Pruitt (1960) reported that barren-ground caribou does do not leave their newborn fawns. Cow moose also do not leave their newborn young (Altmann, 1959).

Prenzlow (1964) observed a doe which led her fawns away from the birth site before leaving them, and felt that the doe was conditioning her fawns to follow her. This is apparently not a typical behavior, because neither the tame
doe, nor the doe observed by Autenrieth (1966) led their fawns away from the birth area before leaving them. One wild doe observed on the Bison Range did lead one of her approximately 3-hour old fawns away from its birth-site, but the presence of two observers probably influenced her behavior.

Although conditioning newborn young to follow their mother apparently is not typical in sheep and goats (Collias, 1956), it is important in barren-ground caribou (Pruitt, 1960). Pruitt (op. cit.) stated that within an hour after the fawn's birth, it is conditioned to approach its mother, which bobs her head up and down in a stereotyped manner. It would be interesting to study cow-calf bison behavior in this light.

8. Species recognition: If newborn elk, pronghorns, or goats continue to approach large, moving objects after their mothers leave them, they could be captured with ease by any predator. Thus it seems likely that the development of species recognition occurs shortly after birth in these species, and that attachment of the young to other species should not happen after this period. Autenrieth (1966) claimed that species recognition developed when the pronghorn fawn was less than 6 hours old.

Hess (1959) theorized that the initial approach response of mammals was analogous to imprinting in birds. He defined imprinting as "An effect of early experience."
which...determines later social behavior..." Finally, Hess (op. cit.) postulated that the critical period for imprinting, which terminates with the development of a fear response to strange, large, moving objects, should be present in all precocial animals.

Avoidance reactions to the approach of men were observed in known-aged fawns at the Bison Range. When the tame doe's male fawn was 41 minutes old, it approached a man, but when it was 92 minutes old, it assumed the head-low posture (Figure 3) when a man approached it. In one set of wild captured twins, one fawn, whose possible age range was 171 to 200 minutes, assumed the head-low posture when approached by two men, while its sibling, which was at least 20 minutes younger, and which had interacted little with its mother after its initial licking, struggled toward its captors. A similar observation was made on two other wild, caught fawns, which were 60 and 84 minutes old. One of the pair approached and followed its captors, but its sibling assumed the head-low posture when approached by two men.

Postures similar to the head-low posture have been reported in elk (Altmann, 1952; Murie, 1951); bison (McHugh, 1958); Grant's and Thomson's gazelles (Estes, 1967); and goats (Collias, 1956), but are reportedly absent in sheep (Collias, op. cit.), barren-ground caribou (Pruitt, 1960), and moose (Altmann, 1963). Species whose young show avoidance postures when approached by men have mothers which
normally leave their newborn young for grazing.

The problem remains; is the development of the avoidance posture a manifestation of matured species recognition? Observations by Altmann (1952) suggest that there are two processes involved in avoidance behavior. She reported that several elk calves less than a few days old rose from their beds and approached her in response to her slow approach. A 1-day old calf bison persistantly followed a horse and rider. Because species recognition has such great survival value, there should be intensive examination of this behavior and its development.

The First Day Through the Third Week:

1. Fawn-mother Relationships: During this age interval, mothers visited their fawns for brief periods throughout the day. As Figure 9 shows, the lengths of these fawn-mother interaction periods increased to more than 1 hour before the fawns remained continually near their mothers. Autenrieth (1966) observed two does who visited their less-than-3-day old fawns four to five times daily. Foree (1960) stated that does visited their fawns at dawn and every 2 to 3 hours through the day until the fawns were about 1 week old. The length of time between two fawn-mother interaction periods for two 15-day old fawns observed on the Bison Range was 177 minutes.

A fawn-mother interaction period commenced, according to Prenzlow (1965a) after the does ran to their fawns' bed-
ding area. They then "...began walking slowly, in search of their kids, often giving semantic display of their rump-patch." (Prenzlow, op. cit.) Doe pronghorns on the Bison Range were observed running to the area of their lying fawns once, and walking to the area 10 times. Gregg (1955) observed that the doe usually feeds intermittently or stands motionless in her fawns' bedding area. Forcee (1960) noted that the doe approached her lying fawns with her head lowered. When does on the Bison Range approached their lying fawns, they fed less often, but continues to raise and lower their heads. Although this head-bobbing is apparently associated with bringing the pronghorn fawns to their mother, it is probably not homologous to head-bobbing in doe barren-ground caribou, described by Pruitt (1960), which is a fully formed behavior within an hour after the doe gives birth.

The mother pronghorn can call her fawns to her. The doe's low-pitched vocalization and the subsequent approach of her fawns has been observed by myself, Buechner (1950), Hoover et al. (1959), and McLean (1944). The tame doe's call sounded similar to her mewings heard shortly after her second fawn's birth. Collias (1956) reported that a mother goat bleated before her kid came to her. Estes (1967) stated that mother Grant's and Thomson's gazelles call their lying fawns. One doe pronghorn nosed her two lying fawns before they got up, which suggests that does either do not always call or that their calls do not always succeed in attracting...
their fawns.

The fawn-mother interaction periods observed on the Bison Range typically began when the fawn ran to its mother and greeted her. Prenzlow (1964) noted that fawns licked their muzzles while they ran to their mothers. Although the mother licked her fawn's head at first, this pattern soon changed to a simple nose-toward-nose gesture. Autenrieth (1966) and Gregg (1955) also observed that greeting usually occurred when fawns approached their mother.

Nursing usually commenced immediately after greeting. Prenzlow (1965a) noted that the doe stands motionless just before her fawns nurse and suggested that this signaled her fawns to nurse. Does arched their backs when their fawns started to nurse, also noted by Gregg (1955) and Prenzlow (1965a). The arched-back nursing position gradually was changed to a normal standing position when the nursing bout neared its end. Fawns 1 week old or less usually nursed several times during each fawn-mother interaction period. Prenzlow (1964) noted that during the first few days after their birth, fawns terminated the nursing period (and were, according to Prenzlow, apparently satiated), but that after the first few days, the doe terminated nursing periods by moving away from her nursing fawn. Toward the end of their third week, fawns were observed to nurse only once or twice per fawn-mother interaction period.

After nursing commenced, the does on the Bison Range
and elsewhere (Autenrieth, 1966; Gregg, 1955; Prenzlow, 1965a), usually rump-licked their fawns. This activity, according to Gregg (1955), may last several minutes, but the average duration of 108 rump-licking bouts times on the Bison Range was 27 seconds.

By the end of the fawn's third week, the observed frequency of total fawn grooming by mothers decreased to 40% of the first week's level (Table 3). During the first 3 weeks, rump-licking all but disappeared (Figure 11), non-specific licking dropped to 8% of its week-one frequency, and nuzzling appeared and disappeared (Table 2).

After the initial nursing and rump-licking, fawns on the Bison Range usually followed their grazing mother. They also interacted with their siblings, played alone, interacted with other pronghorns, or grazed during the remainder of the fawn-mother interaction period. Autenrieth (1966) observed that fawns exercised while they were with their mothers. Similarly, Gregg (1955) observed that "very young fawns were seen playing and scampering about the doe only after feeding." As mentioned above, fawns 2 weeks old and younger typically participated in nursing and rump-licking several times during an interaction period.

Fawn-mother interaction periods observed on the Bison Range usually terminated when the doe became indifferent to her fawns' approaches. The fawns then alternately walked and ran about 70 yards away from their mother, and with lowered

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heads, selected a bedding site. Similarly, Gregg (1955) and Prenzlow (1964) observed that fawns found their own bedding area. Young fawn Grant's and Thomson's gazelles leave their mothers for bedding sites (Estes, 1967). According to Folker (1956) very young pronghorn fawns lie with their heads down, and older fawns lay with their heads up. Observations by Autenrieth (op. cit.) and myself indicate that bedded fawns may lie with their heads either up or down from their first day.

At about the end of the third week of fawn-life, the fawn ceases to leave its mother and remains with her and other does and fawns of the summer, doe-fawn herd. Autenrieth (1966) observed that fawns enter doe-fawn herds when they are from 3 to 5 weeks old. Altmann (1952) observed that calf elk usually remain near their mothers from 3 weeks of age on.

2. **Sibling-sibling Relationships**: Pronghorn fawns usually do not interact with their siblings until they are several days old. Two pairs of 1-day old siblings were observed together, but no interactions were recorded. Six fawns, 2, 3, and 5 days old were not observed to share either bedding areas or fawn-mother interaction periods with their siblings. Three sets of 6-day old twins were observed together during fawn-mother interaction periods, but signs of their solitary life were apparent. Two of the fawns left their mother independently of each other. In the other two
sets of twins, the siblings left their mother together but sought individual bedding sites. Prenzlow (1964) observed two does who first nursed their twin fawns together 3 days after the fawns' birth. Siblings more than 6 days old usually were seen together (Figure 15). Siblings remained together throughout the rest of the summer and fall.

3. Interactions between Fawns and Other Pronghorns:
During their first week of life fawns made little contact with pronghorns other than their mothers. Occasionally an other doe walked near bedded fawns, but the fawns assumed head-low postures, avoiding the does. As indicated by Figure 14, aggressive behavior by other does toward fawns was observed from the first day of fawn life on, and reached its peak level during the third week of fawn life. With the longer fawn-mother interaction periods, more fawn-other doe interactions occurred. These interactions typically resulted in fawn avoidance of aggressive does. Fawns in their third week interacted with more unfamiliar does than before, they also interacted with more other (unrelated) fawns. These interactions included agonistic, play and sexual behaviors (Figure 17).

4. This Period's Significance: From its first day until the end of its third week, the fawn pronghorn interacts largely with its mother and siblings. During this period, according to Collias (1962), one would expect the

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family to shape the fawn's social behavior "...to a considerable degree..."

As described above, fawns interact mainly with their mothers until they are about 1 week old, even though they may be near their siblings. This behavior may have at least two functions. If young fawns remain separate, the chances of a predator killing both fawns may be reduced. Secondly, it may take the fawn pronghorn several days to develop species recognition (see above) and to distinguish its mother from other does. Pruitt (1960) suggested that caribou fawns at 1 week of age had not developed individual recognition. Hafez and Schein (1962) state that domestic cattle calves develop strong ties to their mothers several days after their birth. An apparently orphaned 1-week old bighorn (Ovis canadensis) lamb captured by Forrester and Hoffman (1963) seemed to "adopt" its captors, but the lamb's bond to humans was not irreversible, for the lamb later was seen with a herd of bighorn sheep. The length of time this lamb had spent with its mother prior to its capture was not reported. Altmann (1958) stated that the cow moose actually prevents other moose from interacting with her calf until the calf is about 60 days old.

The significance of the sibling-sibling bond is not clear, but perhaps interactions between siblings and the subsequent establishment of their social bond facilitates their later integration into the herd.
From the Fourth Week Through the Third Month:

1. **Fawn-Mother Relationships:** After the siblings joined the herd, they spent progressively less time with their mothers. Changes in behavior associated with nursing accompanied the bond reduction (Figure 13). When the fawns first joined the herd, the frequency of observed nursing bouts increased (Figure 12). The relative frequency of the mother's rejection of nursing attempts by her fawns increased until the fawns' sixth week of life, and then the frequency of maternal rejection dropped quite rapidly. This suggests that either the fawns had learned that their mothers determined nursing times, or the fawns' hunger for milk was substantially reduced.

Contrary to Gregg's (1955) observation, the arched-back posture was seen at the commencement of every nursing bout observed at the Bison Range. It occurred even when the fawns were so large that they nursed while on their wrist joints.

Although rump-licking had nearly ceased when the fawns joined the herd (Figure 11), the mothers were seen to dip their heads toward their fawns' rumps. Does persisted in making these incomplete grooming movements until their fawns were about 8 weeks old (Figure 10).

Frequencies of both maternal nursing and grooming activities decreased to a relatively low level by the time the fawns were 2 months old. These reductions suggest that
a major reduction of the maternal-filial bond's strength takes place between fawn ages of 3 weeks and 2 months. However, fawns older than 2 months nursed (Figure 13) and occasionally followed their mothers, which agrees with Autenrieth's (1966) observations.

2. Fawn-Other Doe Relationships: When the fawns entered the herd, they often interacted agonistically with does which were not their mothers. Similar observations have been made in pronghorns (Autenrieth, 1966) and in sheep (Scott, 1945). The observed frequency of aggressive behaviors by other does toward fawns was highest during the third and fourth week of the fawns' lives. When the fawns reached 6 weeks of age, the level of other doe aggression toward them dropped to the level observed during their first week (Figure 14). These observations clearly indicate that the fawns learned their subordinate status with respect to other does in about 2 weeks after they joined the herd.

Prior to joining the herd, male and female fawns were subject to about equal amounts of other doe aggressive behavior, but after the fawns joined the herd, 89% of other doe aggressive behavior was directed toward male fawns. In seven observations, male fawns displayed sparring intention movements toward other does, and actual sparring was seen four times. Autenrieth (1966) observed buck fawns which sparred with yearling does. These observations indicate that male fawns are more aggressive than female fawns, and
that male fawns are closer than female fawns to other does in the dominance hierarchy.

In addition to being herd members, other does were a potential milk source. Fawn attempts to nurse other does were most often seen when the fawns were about 8 weeks old, and were almost always unsuccessful. The peak level of observed fawn attempts to nurse other does followed the peak level of unsuccessful fawn attempts to nurse their mothers (Figure 13). The subsequent sharp drop in the observed frequency of fawn attempts to nurse other does indicates that the fawns either learned that their attempts were futile, or that they were less hungry for milk. It seems reasonable that the fawns, which had been grazing for more than a month by this time, had less hunger for milk, and that they learned to nurse only in response to their mothers' indicated willingness to nurse them.

3. Sibling-Sibling Relationships: As mentioned above, the siblings were regularly seen together throughout the study. Siblings continued to interact agonistically, sexually, and playfully with each other (Figure 16), and the changes in the nature of these interactions is discussed below.

4. Fawn-Other Fawn Relationships: After the fawns passed their third week, their agonistic, play, and sexual interactions were with unrelated fawns, in all but one apparently trial 10-day exception (Figure 16).
The frequency of fawn-fawn agonistic interaction rose sharply from the beginning of the fawns' second week to their fifth week (Figure 17). During their second and third weeks, the dominance status between siblings probably was established. Dominance relationships between members of the fawn group (Table 13) probably were established by the fawns' sixth week (except for #’s 10 and 11, which joined the herd during their sixth week), for this includes: 1) an increasing level of fawn-fawn agonistic interaction from the third through the fifth week (Figure 17); 2) a simultaneous high level of fawn-other fawn interaction (Figure 16); 3) a distinct drop in fawn-fawn agonistic interaction level during the sixth week (Figure 17); and 4) the observations that sparring between fawns occurred three times more often before they were 40 days old than after this age, while mere turning away from aggressive fawns occurred twice as often after than before their fortieth day. Autenrieth (1966) felt that fawns did not establish a hierarchy, but he observed unmarked fawns.

The fairly high level of agonistic behavior observed from weeks six to nine (Figure 17) suggests that the fawn continually tested their dominance relationships, although no reversals were observed.

The dominance status of a fawn, in the fawn group observed on the Bison Range, was not a random property. The males were more aggressive and dominated the females with-
out exception (Table 13). Autenrieth (1966) and Buechner (1950) made similar observations. Robinson (1962) reported that male white-tailed deer fawns usually dominated the female fawns. The order of the male fawns was directly correlated with their age (Table 1).

Behavior apparently associated with the tendency to attack and the tendency to flee was often observed in fawns (Figure 17). Aggressive behaviors included: apparently normal movement toward another fawn, nudging; simultaneous lowering of heads by two fawns in head-on position, without contact; sparring; butt attempts and butts; driving another fawn by walking or running behind it; and displacement of a lying fawn.

Sparring between pronghorn fawns has been previously observed by Autenrieth (1966), Buechner (1966), Gregg (1955), and Prenzlow (1964). Sparring among the young of other ungulates has been observed in sheep (Scott, 1945) and in bison (McHugh, 1958). Autenrieth (1966) and Gregg (1955) described displacement of lying fawns. As had been described in the "Results" section on territoriality, the adult repertoire of aggressive behaviors includes threat displays as well as the patterns described in fawns.

In addition to the aggressive behaviors typical of adults, fawns exhibited typical flight behaviors, which were turning away, walking away, and running away from dominant animals. Autenrieth (1966) described fawn avoidance behav-
Sexual behavior observed between fawns included: standing directly behind another fawn; investigating a leading fawn's rump; holding the head above the rump of a leading fawn; raising up on the hind legs behind another fawn without touching the other fawn; and mounting which included contact of the mounter's forelegs with the mounted fawn's back. Neither Autenrieth (1966) nor I recorded penile erections, pelvic thrusts, or copulation. Gregg (1955) and Prenzlow (1964) also observed fawns mounting other fawns.

Fawns continued to play or chase one another after they joined the herd, but the observed frequency of play behaviors rapidly decreased with increased fawn age (Figure 18).

5. Fawn-buck Relationships: Fawns were not observed to interact with bucks until after the fawns entered the herd. During the summer, all interactions recorded were agonistic, and typically involved buck aggression and fawn flight. All 19 observations of buck aggression were directed toward male fawns. The subordination of fawns to bucks was observed by Gregg (1955) and suggested by Autenrieth (1966). Scott (1954) noted that male sheep were dominant over lambs.

Relationships Between Fawns and Groups of Pronghorns: Fawns became members of a sub-group within the herd. The fawns gathered together and were seen with each other more
often when they grew older, while the bond strength between them and their mothers decreased. Autenrieth (1966) also observed the fawn sub-group. Similar groupings of young bison have been reported by McHugh (1958). Behavioral observations by Autenrieth (op. cit.), McHugh (op. cit.) and myself included sexual, agonistic and play interactions between the young. I concur with Autenrieth (op. cit.) who felt that a function was to facilitate development of social behavior through frequent fawn-fawn interaction.

The summer doe-fawn pronghorn herd observed at the Bison Range exhibited a hierarchial structure. The buck, when present, dominated the does, and the does dominated the fawns. Gregg (1955) felt that bucks dominated does, and that the does were arranged hierarchically. The fawns observed at the Bison Range established a hierarchy amongst themselves and apparently learned their status with respect to does by the age of 6 weeks. Browman and Hudson (1957) reported that in a group of penned mule deer, the buck dominated the does and that the does and fawns were organized into a "kick-order."

When the doe-fawn herd took flight, another structure was observed. Einarsen (1948) observed that fleeing pronghorns display their white rump rosettes. Buechner (1950) noted that alerted pronghorns form a compact group; that an adult doe led the herd in flight, while an adult buck followed the rest of the herd; and that the fleeing herd tended
to string out. Gregg (1955) essentially confirmed Buechner's (op. cit.) observations and added that snorts, usually given by nursing does, alarm the herd; that the fleeing herd often stopped and started a few times during flight; and that the herd typically was shaped elliptically during flight, with the long axis pointed in the direction of flight. My observations agree with Buechner's (op. cit.) and Gregg's (op. cit.) and extend the description of herd flight to include, if the herd has sufficient time to organize, the following order: A lead doe, a fawn group, a doe group, and a trailing buck. This exact herd order was observed in 11 out of 19 fleeing herds, and in four other observations the flight was nearly typical.

If flight order were an adaption to predation, one would expect to find the most expendable herd members closest to the predator(s). As we have seen, the buck, which frequently accompanies the doe-fawn herd, apparently is not as important to the herd social structure as are the does and fawns. A buck's life is not as valuable to the breeding population as a doe's because one buck probably can breed several does. The buck is clearly the least valuable member of the herd; therefore, the trailing buck should be and is probably the most vulnerable to predation.

The next most expendable member of the summer herd is probably one of the doe group. Some of the does are usually nulliparous yearlings. Their death would not impair the
survival of the herd's young.

By mid-summer, even the mother may not be essential for fawn survival. The fact that two siblings who were orphaned when they were 7 weeks old survived at least most of their first winter on the Bison Range indicated that surprisingly young fawns can survive without their mother (Bromley and O'Gara), in press).

Thus, it seems that members of the doe group would be more expendable than the young themselves, but what of the lead doe? The lead doe would be more important (presumably) to the surviving fawns than one of the doe group because of her previously acquired knowledge. At least the lead doe, an adult, would be able to recognize distant sources of danger, know the local habitat, and display "typical" social behavior to the surviving fawns.

In addition, the herd member best able to defend itself should be the first to encounter the predator(s). Having much larger horns and greater weight than the doe, the buck should face the predator(s) first. The does should be between the buck and the fawns. The lead doe would be needed for the reasons suggested above.

Obviously, group selection (Wynne-Edwards, 1962) is assumed in the above explanations of the pronghorn doe-fawn herd flight order.

Between the ages of 3 weeks and 3 months, the fawn's social behavior changes to adult-like. The fawn establishes
dominance relationships with its peers and with other herd members. The herd behaves as a unit, with the fawn an integral part of it. Although the fawn has many adult behavioral characteristics when it reaches its third month, it still retains its bond to its sibling, and to its mother, but this maternal-filial bond has weakened. In short, by this period's end, the pronghorn fawn's social behavior has matured from dependence to dependence on its herd. According to Collias (1962:272), "The principal end of social development among animals is to enable acceptance and effective functioning of an individual as a member of an organized group." It appears that the pronghorn fawn reaches this point by the end of its third month.

The Fourth Month: When the fawns were about 4 months old, they were weaned, prepared for possible separation from their mothers, male sexual displays, and disruption of the doe-fawn summer herd.

Prenzlow (1964) noted that complete weaning occurred when the rut commenced. Buechner (1950) felt that fawns were self-sufficient when the rut began, but that they frequently accompanied their mothers through the fall and winter. The last nursing observed on the Bison Range occurred at the onset of the rut. Two fawns, which were orphaned when they were 7 weeks old, survived at least through most of their first winter. Therefore, other fawns could prob-
ably survive without their mothers when the rut commenced. Buechner (1950) stated that fawns tend to follow their mothers during the winter, but that during the rut, the fawns may be separate from their mothers. Observations made during the rut on the Bison Range of intact fawn groups without does and of fawns with bachelor herds, also suggests that the fawns are capable of nutritional and social independence from their mothers at this time.

Fawn avoidance of buck sexual displays was not different in form from fawn subordinance displayed to other pronghorns. The absence of abnormal fawn behavior displays suggests that trauma was not too great. Furthermore, disruption of the doe-fawn summer herd apparently did not disrupt the fawn group.

The apparent "normalcy" among pronghorn fawns during the rut suggests that their independence from their mothers is matched by their dependence on their herd. This is not to say that the development of social behavior ceases, but it strongly suggests that the 5-month old pronghorn has achieved the main goal of social development, according to Collias (1962).

Territoriality

The current concept of territoriality, according to Leuthold (1966:229), "...is the defense of a given area by its occupant against other individuals of the same species."
An earlier concept, expressed by Noble (1931) as "any defended area" and accepted by Burt (1943), left room for ambiguous use of the term. Territory could mean defense of a specific area, or of an area which moved with the animal, such as has been postulated by Altmann (1958) for the area around a calf moose protected by its mother. The territories described below for rutting pronghorn bucks were definite areas which were defended by their occupants against rival bucks.

Buechner (1950), Folker (1956) and Gregg (1955) did not detect territoriality in the pronghorn and claimed that the bucks defended harems. Gregg (op. cit.) specifically denied the possibility of territoriality in Wyoming pronghorns. Cole (1956:43) cited evidence that three, individually known, male pronghorns in central Montana were confined to definite areas, one of which was occupied from 23 July to 22 September, 1953. Later, Cole and Wilkins (1958:23) found that mature bucks were located in specific areas, and stated that the bucks defended these areas against other males. During the height of the rut, according to Cole and Wilkins (op. cit.) males often left their territories while pursuing single does.

Seven territories were found on the National Bison Range during the rut of 1966 (Figure 19). Although the exact territory boundaries were not determined, two-thirds of their occupants' position records were located in relatively
small, non-overlapping areas, suggesting that these 67% distribution areas approximated their territories (Figures 19-26). The separation of the 67% distribution areas can be inferred from the fact that although 46.5% of the 100% areas overlapped, only 26.2% of the 100% and 67% areas overlapped. Approximately four times more position records were in 100%-100% areas of overlap, than were in the 67%-100% areas of overlap (Tables 15 and 16).

Using ritualized displays, the territorial males defended their territories from all other males which did not show subordination by turning and facing away when the territorial males looked toward them. In all 131 agonistic encounters between territorial and yearling males, the yearling males were subordinated. In 94.5% of 73 similar encounters between territorial and other adult bucks, the territorial males dominated. Bucks which displayed subordination were often tolerated on the territories.

A visual, territorial marking system, other than the buck's presence was not detected. Auditory marking may have been the function of the 22 male vocalizations recorded when other bucks approached the territory. Gregg (1955) described the male vocalization and linked it to the rut. Buck pronghorns probably marked their territories by rubbing scent from their postmandibular glands on vegetation and by urinating and defecating on their territories. Signpost production by vegetation rubbing was considered by Gregg (op. cit.).
but, because he ruled out territoriality, he suggested no function for this behavior.

Manifestations of territoriality in other ungulates range from the specific, highly-sought-after territories of the Uganda kob (Buechner, 1961, 1963; Leuthold, 1966), to, according to Estes (1967:202) "...languid..." territorial defense in Grant's gazelle, and to apparently none in North American moose (Geist, 1963).

Territorial boundaries have been variously described. Buechner (1961, 1963; and Leuthold (1966) described Uganda kob territories as usually having common boundaries with several other territories. Kiley-Worthington (1965) noted that territory boundaries in waterbuck were most distinct near a river front and least distinct in the arid land some distance away from the river. DeVos (1965) described overlapping territorial boundaries in puku, but added that no two males were in the same area simultaneously. The pronghorn territories studied at the National Bison Range apparently had mutual borders in one case. Darling (1964) reported non-bordering territories in red deer.

All described territorial species defend their areas with ritualized displays. That others males may be tolerated on occupied territories has been stated by Leuthold (op. cit.) in Uganda kob, DeVos and Dowsett (op. cit.) in puku, lechwe, and waterbuck, and by Estes (op. cit.) in Grant's and Thomson's gazelles. Observations by DeVos and Dowsett
on lechwe indicated that bucks who did not display sexually to does may be tolerated, even when lying near the does. Territorial pronghorns observed on the National Bison Range did not allow other bucks to lie near does.

Territory marking also varies greatly between the studied species. Leuthold (op. cit.) found no visual marking system, other than the buck's presence, and could not detect an olfactory marking system in Uganda kob. However, he did not consider the male kob's whistle as a possible advertisement. Graf (1956) claimed Roosvelt elk marked territories by shaving stakes and placing scent on these stakes. Wynne-Edwards (1962) noted indications of similar behavior in the related red deer. Estes (1967) found that buck Thomson's gazelles olfactorily marked their territories by rubbing scent from preorbital glands on vegetation and by urination and defecation, whereas Grant's gazelles used only urination and defecation.
CONCLUSIONS

1. Parturient does did not seek seclusion from other herd members.
2. Parturient does displayed the tail-up (elevated their tails for short periods) at least 3 hours before they gave birth.
3. Does licked their newborn immediately after its birth, and consumed both the amnion and placenta.
4. Doe and fawn pronghorns communicated by vocalization (mewing).
5. Newborn fawns approached close, large, moving objects.
6. Fawns avoided similar large, moving objects before they were 1 day old.
7. Does arched their backs at the start of every nursing.
8. The fawn posture during rump-licking (inguinal licking of the fawn by its mother) was stereotyped, and can be caused by inguinal rubbing or can be autonomous.
9. Pronghorn does could call their fawns by vocalizing.
10. Fawns selected their own bedding locations from their first day.
11. Fawns remained solitary, except for short interaction periods with their mothers, until they were about 6 days old.
12. Fawns developed sibling-sibling, as well as maternal-filial social bonds before they joined summer herds.

13. Fawns typically avoided other yearling and adult pronghorns in the summer herd, and were the lowest group in the herd hierarchy.

14. Fawn avoidance patterns were not different from similar adult patterns.

15. Fawn aggressive displays were similar but fewer in number than adult displays.

16. Fawn sexual displays were similar but fewer in number than adult displays.

17. The members of the fawn group were arranged hierarchically by the age of 6 weeks.

18. Fawns were functional members of the herd by their sixth week.

19. Fawns were capable of nutritional and social dependence from their mothers by their fourth month.

20. The summer herd exhibited the following flight order (from the first to the last): lead doe; fawn group; doe group; and buck.

21. Fawns usually were not involved in the excited activity of the rut although they were displayed to by yearling and adult bucks.

22. Mature bucks on the study area were territorial.
LITERATURE CITED


