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Kent B. Livezey

The University of Montana

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SOCIAL BEHAVIOR OF ROCKY MOUNTAIN ELK
AT THE NATIONAL BISON RANGE

By

Kent B. Livezey

B.S., Principia College, Elsah, Illinois, 1976

Presented in partial fulfillment of the requirements for the degree of
Master of Science
UNIVERSITY OF MONTANA
1979

Approved by:

[Signatures]

Chairman, Board of Examiners

Dean, Graduate School

[Date]

4/10/79

Date
An isolated elk herd, maximum of 20 individuals, was studied intensively from 1 April to 11 November 1977 at The National Bison Range, Moiese, Montana. Eleven elk of the cow-calf herd were individually identified from ear tags and physical characteristics. In addition, 14-22 bulls which associated with them were observed during the rut. The only individuals of this social herd observed more than a few hundred meters from other elk were calving cows, spikes during the rut, and a cow 16-18 years old. The herd’s home range was about 1,200 hectares. Elk were located in coniferous timber and timber-grassland edge between 27 May and 21 June more often than during any other period. This 26-day period corresponds with the dates of calving. Some of the cow-calf interactions from calving through weaning described and quantified were: hiding, following, social integration, duration and rate of suckles, and thief-suckles.

Over 500 aggressive acts were recorded and analyzed. Fifty-two behavioral acts were described. Analysis of over 22,500 bits of data from scan and instantaneous sampling showed differences in activity between sex-age classes and between different times of day.

Males older than spikes were observed with individuals of the isolated herd on only three occasions between 1 April and 30 August. Bulls were always present in the study area between 31 August and 11 November, dividing the herd into as many as three small harems. At least 10 bulls performed more than 1,800 repetitions of rutting behaviors such as bugling, spars, noses or licks to females, mounts, antler-thrashes, and wallows.

The presence of fences within the area provided observations of the disturbing conditions brought about by such unnatural boundaries.
ACKNOWLEDGEMENTS

I wish to thank the Montana Cooperative Wildlife Research Unit and the National Rifle Association of America for funding this research. The Montana Unit also provided vehicles and equipment. Dr. Donald Jenni initiated this research, assisted in datum presentation and thesis writing, and strove to improve the quality of the work presented. Milt Haderlie, Assistant Refuge Manager, and Marv Kashkie, Refuge Manager of the National Bison Range, encouraged the study and supplied information and guidance. Dr. Bart O'Gara provided help in the field and in thesis writing. My wife, Kim, assisted me in the field and drew the sketches of the behavioral displays. Drs. Les Marcum, Lin Irby, and David Kitchen advised me about quantification of the behaviors recorded and about the results obtainable from the activity data. Barb Von Gunten and Dr. Dale and Yvette McCullough furnished advice and elk observations. John Walkenbach wrote the computer programs required to analyze the activity data.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>ii</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>viii</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>x</td>
</tr>
</tbody>
</table>

## CHAPTER

I. INTRODUCTION .................................................. 1

II. DESCRIPTION OF THE STUDY AREA .................... 3

- Vegetation and Topography ................................. 3
- Tourist Impact ............................................... 5
- Mammalian Species .......................................... 5
- The Elk Herd .................................................. 6

III. MATERIALS AND METHODS ............................. 8

IV. RESULTS .................................................. 11

- Definitions of Behaviors ................................ 11
- Group Behavior and Possible Mother-offspring
  Relationships ............................................. 17
- Alert-alarm Behavior and Habituation to
  Disturbance ............................................... 19
- Vocalization ............................................... 23
- Interspecific Behavior ................................... 25
- Fence Behavior ........................................... 28
- Weather Effects .......................................... 33
- Play Behavior .............................................. 34
- Urination and Defecation ............................... 35
- Behavior of an Old Cow .................................. 36
Calving and Cow-calf Behavior ............................................ 37
Habitat Preference During Calving ............................. 37
Hiding Behavior .......................................................... 41
Cows Finding Hiding or Bedded Calves and Locating Calves After a Disturbance .............................................. 43
Cow Behavior When with Her Young Calf .......... 44
Following Behavior and Locomotive Development .............................................................. 45
Calf Mortality ............................................................ 46
Social Integration ....................................................... 48
Nursing Behavior ........................................................ 48
Suckle approach .......................................................... 48
Initiation and termination ........................................ 48
Frequency of nursing interactions ........................................... 49
Duration of nursing ..................................................... 50
Thief-suckle ............................................................... 51
Concurrent nursing behavior ........................................... 54
Disturbances .............................................................. 54
Nursing behavior preceded by bedding bouts .............. 54
Bunting ................................................................. 54
Bedding Behavior ....................................................... 55
Self-groom .................................................................. 56
Social-groom ............................................................ 56
Mutual-groom ............................................................ 57
Nose ........................................................................ 57
Nose-to-nose ............................................................. 58
Mount, Throat-place and Chest-bump by Elk Other than Rutting Males .................................................. 58
Head-up Twist ............................................................. 62
Aggressive Acts and Hierarchical Relationships .......................... 62
Head-high ................................................................. 62
Head-low .................................................................. 64
Kick .......................................................................... 66
Bite ......................................................................... 66
Antler Display ............................................................ 68
Head-push ................................................................. 68
Spar ......................................................................... 69
Sex-age Classes Comparison and Hierarchical Relationships ...................................................... 69
Displace and Supplant .................................................. 72
### Table of Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redirected Aggression</td>
<td>75</td>
</tr>
<tr>
<td>Head-off and Turn</td>
<td>75</td>
</tr>
<tr>
<td>Daily Activity Cycle</td>
<td>77</td>
</tr>
<tr>
<td>Behavior During the Rut</td>
<td>81</td>
</tr>
<tr>
<td>Harem Leadership Changes</td>
<td>83</td>
</tr>
<tr>
<td>Aggressive Acts</td>
<td>88</td>
</tr>
<tr>
<td>Rutting Bull Activity</td>
<td>90</td>
</tr>
<tr>
<td>Habitat Use</td>
<td>91</td>
</tr>
<tr>
<td>Herd and Herd-posture</td>
<td>92</td>
</tr>
<tr>
<td>Bugling</td>
<td>95</td>
</tr>
<tr>
<td>Chases of 5-point Bulls and Spikes by Harem Bulls</td>
<td>96</td>
</tr>
<tr>
<td>Sexual Approach</td>
<td>98</td>
</tr>
<tr>
<td>Nose and Lick</td>
<td>98</td>
</tr>
<tr>
<td>Nose-to-nose</td>
<td>100</td>
</tr>
<tr>
<td>Displace and Supplant</td>
<td>100</td>
</tr>
<tr>
<td>Throat-place</td>
<td>101</td>
</tr>
<tr>
<td>Mount and Mount-with-copulation</td>
<td>101</td>
</tr>
<tr>
<td>Wallow, Antler-rub, -scrape, and -thrash</td>
<td>103</td>
</tr>
<tr>
<td>Lowered Head Posture and Jaw</td>
<td>104</td>
</tr>
</tbody>
</table>

### V. DISCUSSION

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group Behavior</td>
<td>106</td>
</tr>
<tr>
<td>Alert-alarm Behavior</td>
<td>106</td>
</tr>
<tr>
<td>Vocalization</td>
<td>107</td>
</tr>
<tr>
<td>Urination and Defecation</td>
<td>107</td>
</tr>
<tr>
<td>Calving and Cow-calf Behavior</td>
<td>108</td>
</tr>
<tr>
<td>Habitat Preference During Calving</td>
<td>108</td>
</tr>
<tr>
<td>Hiding Behavior</td>
<td>108</td>
</tr>
<tr>
<td>Cow Behavior When with Her Young</td>
<td>109</td>
</tr>
<tr>
<td>Calf</td>
<td>109</td>
</tr>
<tr>
<td>Social Integration</td>
<td>109</td>
</tr>
<tr>
<td>Nursing Behavior</td>
<td>110</td>
</tr>
<tr>
<td>Bedding Behavior</td>
<td>113</td>
</tr>
<tr>
<td>Mutual-groom</td>
<td>113</td>
</tr>
<tr>
<td>Nose-to-nose</td>
<td>113</td>
</tr>
<tr>
<td>Mount, Throat-place, and Chest-bump by Elk</td>
<td>114</td>
</tr>
<tr>
<td>Elk other than Rutting Males</td>
<td>114</td>
</tr>
<tr>
<td>Head-up Twist</td>
<td>114</td>
</tr>
<tr>
<td>Topic</td>
<td>Page</td>
</tr>
<tr>
<td>-------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>Aggressive Behavior</td>
<td>114</td>
</tr>
<tr>
<td>Head-high</td>
<td>114</td>
</tr>
<tr>
<td>Bite and Kick</td>
<td>115</td>
</tr>
<tr>
<td>Antler Display</td>
<td>116</td>
</tr>
<tr>
<td>Head-push</td>
<td>116</td>
</tr>
<tr>
<td>Hierarchical Relationships</td>
<td>116</td>
</tr>
<tr>
<td>Daily Activity Cycle</td>
<td>117</td>
</tr>
<tr>
<td>Behavior During the Rut</td>
<td>118</td>
</tr>
<tr>
<td>Aggressive Acts</td>
<td>118</td>
</tr>
<tr>
<td>Habitat Use</td>
<td>118</td>
</tr>
<tr>
<td>Bugling</td>
<td>119</td>
</tr>
<tr>
<td>Mount-with-copulation</td>
<td>119</td>
</tr>
<tr>
<td>Wallow, Antler-rub, -scrape, and -thrash</td>
<td>120</td>
</tr>
<tr>
<td>Management Implications</td>
<td>121</td>
</tr>
<tr>
<td>VI. SUMMARY</td>
<td>124</td>
</tr>
<tr>
<td>REFERENCES CITED</td>
<td>128</td>
</tr>
<tr>
<td>APPENDIX</td>
<td></td>
</tr>
<tr>
<td>I. RESULTS AND DISCUSSION OF OBSERVATIONS</td>
<td>134</td>
</tr>
<tr>
<td>OF GROUP 3 ELK</td>
<td></td>
</tr>
<tr>
<td>II. WEIGHTS AND AGES OF CALVES WHEN</td>
<td>139</td>
</tr>
<tr>
<td>EARTAGGED AND EARTAG COLORS</td>
<td></td>
</tr>
<tr>
<td>III. NECROPSY REPORTS OF THE DEAD</td>
<td>140</td>
</tr>
<tr>
<td>CALVES</td>
<td></td>
</tr>
<tr>
<td>IV. GROWTH AND PELAGE CHANGE</td>
<td>141</td>
</tr>
<tr>
<td>V. EXAMPLES OF THE FIVE FACTORS THAT</td>
<td>143</td>
</tr>
<tr>
<td>EFFECTED HEAD-POSITION WHILE</td>
<td></td>
</tr>
<tr>
<td>PERFORMING A BITE</td>
<td></td>
</tr>
</tbody>
</table>

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# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Composition of the Group 1 elk herd, 1977</td>
<td>6</td>
</tr>
<tr>
<td>2. The 1977 Group 1 elk calves, dates of birth, dates eartagged, and dates of death</td>
<td>38</td>
</tr>
<tr>
<td>3. Frequency of suckles and suckle attempts over time. Interactions disturbed by humans, thief-suckles, attempts to thief-suckle, and nursing behavior of unhealthy calves (Calf 2 and Calf 6) are excluded</td>
<td>50</td>
</tr>
<tr>
<td>4. Duration of suckles over time. Interactions disturbed by humans, thief-suckles, attempts to thief-suckle, and nursing behavior of unhealthy calves (Calf 2 and Calf 6) are excluded</td>
<td>51</td>
</tr>
<tr>
<td>5. Frequency of thief-suckle attempts and thief-suckles over time</td>
<td>52</td>
</tr>
<tr>
<td>6. Number of aggressive encounters and aggressive acts by Group 1 elk (1 April-11 November) and rutting bulls (31 August-11 November)</td>
<td>63</td>
</tr>
<tr>
<td>7. The angle of the head during head-highs isolated from and in conjunction with other aggressive acts</td>
<td>64</td>
</tr>
<tr>
<td>8. Aggressive encounters of the sex-age classes of elk. The number of aggressive encounters won are arranged horizontally, and the number lost, vertically</td>
<td>70</td>
</tr>
<tr>
<td>9. Frequency of aggressive encounters within and between the sex-age classes</td>
<td>73</td>
</tr>
<tr>
<td>Table</td>
<td>Page</td>
</tr>
<tr>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td>10. Percentage of time calves spent bedded, feeding, and locomoting while not feeding</td>
<td>82</td>
</tr>
<tr>
<td>11. Percentage of time calves spent bedded with the head down</td>
<td>82</td>
</tr>
<tr>
<td>12. The bulls of the rut. Harem bulls are indicated with asterisks</td>
<td>85</td>
</tr>
<tr>
<td>13. Comparison of activities of bulls at different times of the rut (0848-1900 hours)</td>
<td>91</td>
</tr>
<tr>
<td>14. Number of noses and licks by rutting bulls and spikes toward females and calves</td>
<td>99</td>
</tr>
<tr>
<td>15. Number of nose-to-noses, throat-places, mounts, and mount-with-copulations by rutting bulls toward females and calves</td>
<td>100</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. The National Bison Range</td>
<td>4</td>
</tr>
<tr>
<td>2. Percentage of observations of elk in grassland or deciduous brush (clear areas) and in or within 200 m of coniferous timber (dotted areas) by 4-week periods. First calf born on 24 May; mean age of calves was 22 days on 21 June; rutting bulls in area from 31 August onward</td>
<td>39</td>
</tr>
<tr>
<td>3. A nose-to-nose between a cow and a female yearling</td>
<td>59</td>
</tr>
<tr>
<td>4. A female yearling approaches a cow and performs a mount</td>
<td>60</td>
</tr>
<tr>
<td>5. A cow performs a head-high to another cow, who responds with a head-high and a forefoot kick</td>
<td>65</td>
</tr>
<tr>
<td>6. A bite performed by a cow to a female yearling</td>
<td>67</td>
</tr>
<tr>
<td>7. A nose and a forefoot kick performed by a spike to a bedded female yearling before a displace</td>
<td>74</td>
</tr>
<tr>
<td>8. A head-off and a turn performed by a cow to another cow</td>
<td>76</td>
</tr>
<tr>
<td>9. Activity pattern, feeding and locomotion combined, for all elk during the summer (1 July-24 August). Sunrise times increased from 0445 on 1 July to 0545 on 24 August. The 2 September data are excluded, due to the probable changing in activity patterns brought about by a rutting bull</td>
<td>79</td>
</tr>
</tbody>
</table>

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10. Activity pattern for all elk during the summer (1 July-24 August). Solid lines = locomoting when not feeding. Dashed lines = feeding. Sunrise times increased from 0445 on 1 July to 0545 on 24 August. The 2 September data are excluded, due to the probable changing in activity brought about by a rutting bull.

11. The harem bulls of the rut. Solid lines indicate when the respective bulls possessed harems. Triangles indicate the presence of other rutting bulls. Observations were made infrequently from 22 October to 11 November.
CHAPTER I

INTRODUCTION

There are three surviving subspecies of elk (*Cervus elaphus*), or wapiti, in North America: tule elk (*C. e. nannodes*), reintroduced throughout central and southern California after declining to one pair in 1874 or 1875 (McCullough 1966); Roosevelt elk (*C. e. roosevelti*) of northern California, Oregon, and Washington; and Rocky Mountain elk (*C. e. nelsoni*) of the Rocky Mountains. McCullough (1966) described the probable evolution, historical distributions, and morphological differences of these subspecies. North American elk and European red deer comprise one species; they interbreed readily and intergrade morphologically (Guthrie 1966 in Kirsch and Greer 1968, McCullough 1966).


Of the few behavioral studies published, Darling's Herd of Red Deer (1937) is the classic. Other works include a comprehensive study of tule elk by McCullough (1966); studies of Roosevelt elk social behavior (Lieb 1973, Franklin et al. 1975), rutting behavior (Bowyer 1976), and activity (Bowyer in press); studies of Rocky Mountain elk rutting behavior (Struhsaker 1967), social behavior (Altmann 1952, 1956b, 1963), and many other facets of their behavior (Murie 1932, 1951). Reports of elk behavior are also included in works about other ungulates (Geist 1966, deVos et al. 1967, Fraser 1968).

The Rocky Mountain elk of the National Bison Range provide a unique opportunity to study a captive population in semi-wild conditions. The objectives of this study were to describe and quantify the social behavior of a cow herd and the rutting bulls which associated with them, to describe the behavioral displays, to discuss the possible functions of these displays, and to compare the behavior of Bison Range elk with the behavior of other elk as described in the literature.
CHAPTER II

DESCRIPTION OF THE STUDY AREA

Vegetation and Topography

The National Bison Range, a 7,503 ha National Wildlife Refuge, is located in Lake and Saunders counties of western Montana (Fig. 1). Common species in the Palousse Prairie grassland are bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), rough fescue (*F. scabrella*), and cheatgrass (*Bromus tectorum*). Shrubs and understory tree species include snowberry (*Symphoricarpos occidentalis*), Rocky Mountain maple (*Acer glabrum*), hawthorn (*Craetagus douglasii*), chokecherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), ninebark (*Physocarpus malvaceus*), and mockorange (*Philadelphus lewisii*) (Morris and Schwartz 1957). Forests dominated by Douglas fir (*Pseudotsuga menziesii*) on northern exposures and ponderosa pine (*Pinus ponderosa*) on southern exposures cover much of the higher elevations. About 25 percent of Upper South and Lower South ranges are forested.

Elevations range from about 792 m near Mission Creek and Jocko River to 1,489 m at the top of Red Sleep Mountain.
Fig. 1. The National Bison Range.
Tourist Impact

A 30 km road through the refuge was maintained by refuge personnel for public use during prescribed times of the day and year. Tourists were permitted in only the northernmost edge of the study region, and were not allowed to leave the areas near their cars. State Highway 200 passed 60 m from the southwest corner of Upper South Range. A pulloff point at the top of the hill above Ravalli, at the southeast corner of the refuge, allowed tourists to stop and look for wildlife. Human disturbances were frequent because tourists could observe, yell, whistle, "bugle," and blow their car horns at the elk in the area. Trespassers were found and told to leave on two occasions.

Mammalian Species

Populations of about 380 American bison (Bison bison), 113 pronghorn antelope (Antilocapra americana), 220 mule deer (Odocoileus hemionus), 175 white-tailed deer (O. virginianus), 55 bighorn sheep (Ovis canadensis), 16 mountain goats (Oreamnos americanus) (26 February 1977 count, Haderlie pers. comm.), and about 88 elk (Table 1 and Appendix I) were managed on the refuge. These populations were reduced regularly by Range personnel to hold them in check.

Potential predators of elk included a minimum of 30 coyotes
(Canis latrans) (Haderlie pers. comm.), some domestic dogs (C. familiaris) from nearby areas, and occasional bobcats (Lynx rufus) and black bears (Ursus americanus).

Table 1. Composition of the Group 1 elk herd, 1977.

<table>
<thead>
<tr>
<th>Cows</th>
<th>Calves</th>
<th>Yearlings</th>
<th>Yearlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cow 1</td>
<td>Calf 1</td>
<td>L♂, S♂</td>
<td>Five, none</td>
</tr>
<tr>
<td>Cow 2¹</td>
<td>Calf 2²</td>
<td></td>
<td>individually</td>
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<tr>
<td>Cow 3</td>
<td>Calf 3</td>
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<td>identified</td>
</tr>
<tr>
<td>Cow 4</td>
<td>Calf 4</td>
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</tr>
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<td>Cow 5</td>
<td>Calf 5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cow</td>
<td>Calf 6³</td>
<td></td>
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¹Cow 2 shot 4 August.
²Calf 2 died 10 June.
³Calf 6 died 17 June.

The Elk Herd

Three rather distinct groups of elk live on the Bison Range:

1) the 20 individuals of the Upper South and Lower South ranges (Table 1); 2) the five elk of the public display pasture; and 3) the "big herd" elk, usually of the ranges other than Upper South and Lower South. The elk of Group 1 are believed to be the progeny of three cows and two calves from the public display pasture that were released in Lower South Range on 2 May 1972 (Haderlie pers. comm.). In 1972, some
of these elk were so tame that they would take food from tourists' hands through the fences. Group 1 elk were more wild by 1977. Four Group 1 elk were shot between 1972 and 1977; a large bull and a cow were poached in July 1974, one very old cow was collected in January or February 1977, and another very old cow was collected on 4 August 1977 (Cow 2). The two old cows were probably two of the original cows released. It was decided to observe Group 1 elk almost exclusively due to their relative tameness, the supposed cohesiveness of the group, and the small amount of timber within their home range. All data and discussion in the following chapters are based on observations of Group 1 elk and, when noted, rutting bulls of Group 3 which associated with them. Observations of Group 3 elk are in Appendix I.
CHAPTER III

MATERIALS AND METHODS

Elk were observed during 691 of 962 hours spent in the field. The rest of the time was spent searching for elk or maneuvering into position to observe them. Viewing distances ranged from 15 m to 0.8 km, but most observations were from 100 to 400 m from the animals.

A four-wheel drive truck was used on the jeep trails and the graded dirt roads of the Range. Foot travel was frequently necessary. Observation and recording were done with a 15-60 power zoom telescope, two 10-power binoculars, two 35-mm cameras, and 55-, 300-, and 400-mm telephoto lenses.

Hiding elk calves were captured by slowly approaching and grabbing the calves or, if they stood and ran, chasing and carefully tackling them. Colored (white, red, blue), numbered eartags were inserted into holes made by piercing the calves' ears with a knife (Appendix II). The tags were then clamped together with a Dalton clamp. The calves were examined and usually weighed (Appendix II) to estimate date of birth (Johnson 1951). Human disturbance may cause cow moose (*Alces alces*) to abandon their calves (Ballard and
Taylor 1978). Cow elk may stay away from their calves for longer periods than usual, thus increasing the risk of predation (McCullough 1966). Consequently, we kept handling time at a minimum, left the area immediately after ear-tagging and examining the calves, and did not attempt to recapture calves for reweighing. A 50-pound (22.7-kg) scale proved inadequate to weigh Calf 3; thereafter, two 50-pound scales were carried. The plastic ear-tags (46 X 19 mm) were difficult or impossible to see from more than 200 m, and should have been at least twice as large. The red tags were difficult to distinguish from the reddish-brown ear hairs. The white tags were the most noticeable.

The yearling males, or spikes, were called Long-antlered Male (L♂) and Short-antlered Male (S♂). The spikes were differentiated by their pelage colors before their antlers grew. The bulls were named for the places they were first seen, their antlers, or their overall size. When referring to the unequal number of tines on a bull's rack, I ordered them the bull's (left, right)--(5,6), (8,7), and so on. Bulls with equal number of tines on each side were called 5-point bulls, 6-point bulls, etc.

Attempts were made to tranquilize 1976 calves with a Palmer CapChur gun for examination and ear-tagging during May. Dr. O'Gara helped for 13½ of the 18 hours spent in this activity. The attempts were terminated because of the time required and the increasing wariness of the elk caused by our close approaches.
Scan samples (as described in Altmann 1974) of the behaviors of from five to 17 individual Group 1 elk were recorded every 3 minutes on various dates from 1 July to 20 October. In addition, instantaneous samples (Altmann 1974) were recorded every minute for bulls during the rut (Brute, 6-9 September; Sym 2, 2 October). Activity classes included: bedding, browsing, grazing, feeding (if browsing or grazing could not be decided upon), standing, walking, trotting, and running. Standing or walking elk, which had temporarily ceased feeding for less than 6 seconds and usually continued chewing food at the 1- or 3-minute mark, were considered to be feeding, grazing, or browsing. In many cases, distinctions were made between positions and activities when bedded: head up and not ruminating, head up and ruminating, and head down and not ruminating. The hours of the day were sampled equally, although individuals sampled changed from day to day. Data sheets were prepared to increase efficiency in the field and allow easy transferral to data cards for computer analyzation.

In order to describe the positioning of the head, I estimated the degrees above (positive) and below (negative) the horizontal. An imaginary line from the middle of the posterior part of the skull to the tip of the nose was used as reference. An elk typically held its head at about -20° when standing.
CHAPTER IV

RESULTS

Definitions of Behaviors

Aggressive act: an antler-display, bite, head-high, head-push, kick, or spar

Aggressive encounter: an interaction between two individuals which includes one or more aggressive acts

Antler-display: quickly directing the antler tips at, and moving toward, another individual; performed by non-feeding males; head -70° to -45° (relative to the horizontal)

Antler-rub: rubbing the antlers back and forth on an inflexible part of a tree or shrub; performed by standing or bedded males

Antler-scrape: digging the ground with the antler tips; performed by non-feeding bulls who are standing or bedded

Antler-thrash: vigorously and repeatedly contacting the antlers on flexible plant growth such as bushes, small branches, small trees, or cattails; performed by standing or bedded bulls

Bite: orienting the mouth and quickly moving toward an individual with lips usually opened, head -45° to 80° (usually -45° to 45°), and ears at least half-way flattened; the mouth may contact the
other individual

Bounce: apparently unnecessary (when walking or trotting) or exaggerated (when running) raising and lowering of the head; when running, often coordinated with a greater than usual raising of the forefeet when the head is up, and raising of the hindfeet when the head is down

Buck: raising the hindquarters higher than usual and kicking the rear feet upward

Bunt (from Lent 1971): the upward pushing of the head by a suckling calf

Charge (from McCullough 1966): a bite given while locomoting at least 4 m toward another elk with the head lowered above level with the shoulders

Chase: the locomoting of one elk toward another which moves at least 5 m away from the first

Chest-bump: contacting the rump or hips of another elk with the chest; performed by elk other than rutting bulls

Displace: performing a behavior toward a bedded elk that causes the bedded elk to stand

Flail (from Bowyer 1976): performing rears by two individuals while facing one another and within 3 m of one another; one or both may perform forefoot kicks
Flehmen: extending and raising the upper lip, usually following a nose to the perineum, urine, or ground recently vacated by a cow, female yearling, or calf; performed by rutting males

Forefoot kick: stiffly striking one or both forefeet toward another elk

Head-high (from DeVos et al. 1967): quickly elevating (0° to 120°) and directing the muzzle toward an individual, usually with the ears at least half-way flattened, and usually performed while locomoting toward the individual

Head-low: approaching another individual and performing a kick or bite while holding the head at less than 0°

Head-off: displaying an aggressive act toward an individual who is attempting to locomote past

Head-push: contacting another elk with the dorsal or lateral surfaces of the head; performed by elk other than cow-calf pairs

Head-shake: lifting the nose (0° to 30°) and tossing the head backward and to one side while trotting or running; or lowering the nose (-45° to -90°) and turning the head from side to side while trotting or running

Head-up twist (from Bowyer 1976): tossing the muzzle upward and/or to one side, occasionally accompanied by flopping the ears; not directed at another individual

Herd: approaching one or more individuals of a harem in an apparent attempt to direct their movements; performed by bulls and spikes
Herd-posture: performing a herd with his head lowered approximately level with his shoulders and holding his nose about level with the ground (-20° to 20°) so his antlers lay horizontally alongside his back

Hide: lying so the ventral surface of the head is against the ground; the neck may curl to one side, allowing the side of the head to contact the body; performed by calves less than 4 weeks old

Jaw (from Struhsaker 1967): the rapid opening and closing of a female's mouth while she is in the lowered head posture

Jump-up: apparently unnecessary or exaggerated jumping

Kick: striking forward with the forefeet as in forefoot kick, flail, and rear

Lick: contacting a cow or female yearling with the tongue; performed by rutting bulls

Lowered head posture (from Struhsaker 1967): lowering the head close to the ground, and sometimes swinging it from side to side, in response to an approaching or contacting bull or spike; performed by females

Mount: raising the forefeet off the ground while the chest contacts the rump of another elk

Mount-with-copulation: the continuing of a mount so that the male moves forward, contacts his belly with the top of a female's rump, and jumps forward and upward as his penis enters her vagina
Mutual-groom: two elk performing social-grooms to one another

Nose: bringing the nose within about 3 dm of another's body without performing a suckle attempt, suckle, nose-to-nose, or social-groom

Nose-to-nose: bringing within about 3 dm of contact the noses of two elk

Nurse: contacting of a cow's udder to a calf's mouth for at least 7 seconds

Nursing behavior: suckles, nurses, and behaviors that relate directly to them

Nursing posture: the standing of a cow while watching her calf immediately preceding a suckle approach; the cow's rear legs may be spread wider than usual

Pace: locomoting along a fence line with the nose repeatedly directed over the fence and, if a non-bull, below the fence; mouth frequently held open

Rear: standing on the hindlegs so the dorsal surface of the body is approximately vertical while facing another elk less than 3 m away; usually preceded by a head-high; the individual may perform a forefoot kick

Self-groom: placing the tongue, and often the teeth, on one's own body
Sexual approach (from Struhsaker 1967): trotting or running by a rutting male toward a female with his head held high and nose held at usual angle (-30° to 0°), so that his antlers are directed upward; often moving his tongue in and out; usually locomoting directly toward her rump

Social-groom: placing the tongue, and often the teeth, on the body of another (other than suckles, licks, or bites)

Spar: bringing together the antlers of two males

Spin: running in a tight circle, as if chasing one's tail

Stamp: striking the ground very hard at the termination of a forefoot kick

Suckle: contacting of a calf's mouth to a cow's udder for at least 7 seconds

Suckle attempt: the moving of a calf toward a cow and orienting its nose toward her udder when less than 1 m from her; mouth to udder contact of 0-7 seconds

Suckle watch: directing the nose, and apparently the eyes, toward the udder of a nursing cow less than 2 m away

Supplant: performing a displace, then bedding on the place recently vacated by the displaced elk

Throat-place (from "placing throat over back," Struhsaker 1967): positioning the head over the rump of another elk
Turn: changing the direction of travel so the individual moves away from the displayer of a head-off

Urination posture (from Geist 1966): urinating with the rump lowered so the angle formed from backline to ground, relative to an imaginary line from the withers backward parallel to the ground, is $-15^\circ$ to $-25^\circ$

Wallow: bedding or rolling on water-soaked or urine-soaked ground; performed by rutting males

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**Group Behavior and Possible Mother-offspring Relationships**

The only individuals observed more than a few hundred meters from other elk were calving cows, a 16-18 year old cow (Cow 2) (see Behavior of an Old Cow), and spikes during the rut. The elk never were identified outside of Upper and Lower South ranges. The whole group remained together during most of the days from 29 April to 26 May 1977 and 11-25 July. During calving, 27 May -21 June, group numbers usually ranged from two to nine animals, with extremes of one and 15. From 22 June to 10 July, Cow 4, Calf 4, Cow 5, Calf 5, $S\sigma$, and a varying number of others usually stayed in Upper South while Cow 1, Calf 1, Cow 3, Calf 3, $L\sigma$, and the rest stayed in Lower South.

From 26 July to 11 November, the groupings were similar to the June-July period, except for the following changes: Cow 4 and
her calf switched pastures with Cow 3 and her calf, and Cow 5 disappeared. I last saw Cow 5 on 2 October, and first noticed her missing on 8 October. A "rather old cow, who had trouble keeping up with the others," a "mature bull," and "a few other elk" were herded up Trisky Creek, along with the bison, by refuge personnel during their annual roundup on 3-7 October (Haderlie, pers. comm.). Cow 5, the "old cow," was probably separated from the other elk, herded into a fenced pasture outside of Upper South, and then prohibited passage back into Upper South by gates closed after the bison roundup. Cow 5 may have died. Calf 5 stayed with Cow 3 and Calf 3 through 11 November. When I checked the group on 11 January 1978, the four calves (including Calf 5) and two spikes were with 10 females showing, I believe, that Cow 5 was still missing and that Calf 5 was doing well.

L♂ was not observed out of a group that included Cow 1 from immediately after calving, 22 June, through 11 November. Cow 1, Calf 1, and L♂ were occasionally the only members of a group. L♂ was probably Cow 1's calf of 1976. Almost 30 percent (8 of 27) of positively identified Cow 1 aggressive encounters took place between her and L♂, showing the agonistic capabilities possible between a cow and her yearling or the consequences of being together all the time.

Cow 5 seemed to be a younger version of Cow 2, both physically and behaviorally, and may have been Cow 2's offspring.
S♂ stayed with Cow 5 almost as consistently as L♂ stayed with Cow 1. If a strong criterion to prove a mother-yearling relationship is the degree to which the yearling stays with a cow, then S♂ was probably Cow 5's offspring.

**Alert-alarm Behavior and Habituation to Disturbance**

Elk usually reacted to an unidentified sight, sound, or smell by moving at least one step away from the disturbance. Elk usually moved directly uphill when alerted. If the disturbance were tangentially downhill from the elk, they would ascend the slope diagonally by moving uphill from the disturbance. Elk oriented their noses, ears, and eyes toward the cause of a disturbance. The nose was lifted above the horizontal, and the nostrils were alternately flared and relaxed, scent-testing the air. When alarmed, the elk usually bunched together, and the calves stayed especially close to other elk, usually their mothers. Bunching was displayed on two occasions even though the groups were separated by a fence.

The elk required positive identification of close human presence within the Range or, occasionally, close bison presence, before they would flee. While attempting to determine the presence of nearby humans within the Range, watching, listening, and scent-testing were often accompanied by walking more stiffly than usual, erecting the tail, locomoting or standing with the mouth open, and brief bursts
of running or trotting. The bunched group typically followed the lead of one or two cows, but any animal older than a calf who took flight was usually followed. Occasionally, one cow would leave the bunched group and trot as far as 100 m, apparently searching for the cause of disturbance. The cow usually stayed in view of the rest of the group. Once, however, when Cow 1 trotted over the top of several ridges, the group ran after her when she passed out of their view. Smell without sight identification tended to disturb the elk more than sight identification without smell, possibly because in the former circumstance the closeness of the disturbance could not be determined.

Fleeing elk never moved faster than a canter when in groups. Even small calves were able to keep up with the rest of the group. The ears were usually directed forward while fleeing. When crossing over a ridge, elk typically raised their heads high, enabling them to see more easily over the top. Distance of flight ranged from about 250 m to 4 km.

Most disturbances were identified quickly, and the elk soon resumed undisturbed activities or moved slowly from the area of disturbance. Examples of such disturbances were: mule deer or coyotes heard but not immediately seen or smelled; yelling or whistling tourists; car backfires; sonic booms; humans outside of the Range; and humans inside the Range but not "too close" (described below) to the elk. An elk walking from a disturbance may turn its head
from side to side, observing the area behind the elk with the peripheral vision of one eye, then the other.

Minimum safe viewing distances, ones that would at most mildly alert the elk if they located us, varied from 50 to 400 m, depending on the situation, place, and time of year. We often risked alarming the elk by watching them from closer than safe viewing distance. The conditions that influenced the degree of disturbance displayed were complex. Safe viewing distances were less in the noisier areas with human disturbance, such as the southeast corner of Lower South Range, than in quieter areas, such as the timber of Trisky and Elk creeks. The elk were habituated to vehicles on the dirt roads of the Range, and we could observe the animals from our vehicle at 50 m with little or no apparent change in their behavior. The distance had to be at least doubled if the observation vehicle were on one of the less travelled jeep roads. Elk often lifted the nose and flared the nostrils in our direction, as if they smelled us or the vehicle, but were not apparently bothered. Travel and observations on foot were quieter and necessary in many areas, but the elk were much more alerted if they located us. Humans identified on foot within the Range always alerted the elk to some degree. Humans upslope of elk generally alerted them more than humans level with or downhill from the elk did. Response was greater if a fence blocked the retreat route. People on foot were less disturbing when on the dirt roads
than when not on roads. Elk reacted differently to what appeared to be very similar instances of human presence. Either differing conditions were not noticed by us or the mood of the group and/or its leaders effected to what degree they were disturbed. Different individuals tended to be more disturbed than others. Cows reacted differently to disturbances immediately after, and for a few weeks following, parturition than they did during other times of the year. Weather also seemed to influence the degree of alarm behavior. On windy days, especially when wind direction was fluctuating, elk tended to show more alerting behavior than on calm days. This was probably due to decreased directional abilities of smelling and hearing on windy days.

Some habituation to our vehicle and to us on foot took place, and safe viewing distances decreased slightly. Calves habituated to howling coyotes. Total habituation to very loud sonic booms apparently takes at least a few years. Loud sonic booms elicited the most response from calves, yearlings showed less, and cows seldom responded. An example of this difference in response was seen on 25 July. A boom caused the four bedded calves to jump and run, while S $\gamma$, two female yearlings, and two cows stood and looked around. The remaining five cows did not stand. Bright lightning and very loud thunder on 16 September caused no apparent reaction from Curl, seven females, L $\delta$, 5pt, Calf 1, and Calf 5.
Vocalization

Calf vocalizations were quieter and less harsh than those of older elk, and had a distinctive squeaky quality. Calf 1, bedded with her head up, emitted at least five clear, high "caw's," about one every 3 seconds, on the day of her eartagging. She voiced at least 15 loud squeals as we handled her, and stopped squealing when we released her. Calf 3 and Calf 5 began squealing as they stood to run from us, and continued squealing until we released them after eartagging. One nearby cow approached within 6 m of me about 3 minutes after Calf 5's first squeal. I talked and moved my arms, and she trotted away. I continued weighing and examining the calf. About 2 minutes later, Cow 5 approached to within 6 m of me from the same direction the first cow had. She left after standing for about 10 seconds. The two tagged calves who died soon after birth did not vocalize when captured and tagged. Their lack of vocalization was probably related more to their very young ages when captured rather than to their health. Calf 2 was apparently healthy when born. Calf 1 and Calf 3 vocalized when I flushed them from hiding on 11 and 12 June, respectively.

Cows uttered a "chew!" call before nursing and calves gave "eaa" or "eau" calls before suckling. Two calves voiced at least five very quiet "eep" calls as I sat within 20 m of them, two cows, and five female yearlings for about 3 minutes. Soft "eau" calls, given by Calf 1 and/or Calf 3 as they followed the group, were audible on two
occasions from 100 m away.

L♂ uttered "eau" calls when his forefeet contacted the ground while he ran from a harem bull. I heard these calls from within 50 m of L♂ on two occasions.

Disturbances often elicited vocalizations from elk. Two bison cows and a calf kept Calf 5 separated from her mother for almost an hour. During, and immediately after the separation, 61 calls were heard between Cow 5 and Calf 5, and 17 calls were heard between the cow-calf pair and the 15 elk on the other side of the fence. I was about 200-300 m from them during this encounter. The cows' calls were harsher and airier than the calves', but both could be written "Weé-ah!" Cow 5's first calls during the separation caused the 15 elk, about 80 m away from her in brush, to run out of the brush and look around.

Individuals joining, or attempting to join, other elk vocalized frequently. Elk voiced 169 calls during the six instances of individuals vocalizing as they tried to get under a fence or through a gate to join other elk.

A cow saw me sitting in tall grass 160 m away from her on 20 April. She approached to within 100 m, barked 10 "oonk!" calls in 17 minutes, turned, and trotted away.

Other elk calls could be written, "Yeéoow!, " "Hunk," a flicker-like (Colaptes auratus) "Hcaar!," and "weéow-waýoo." These
were rarely heard.

**Interspecific Behavior**

Elk tended to interact with curiosity, play or aggression toward non-human animals smaller than themselves, and tended to react by avoidance and alerting behavior toward humans and animals larger than themselves.

Mule deer frequently grazed and bedded near elk. Disturbance by elk or any other cause usually stimulated deer to take flight with more alerting behavior than elk displayed. Pronghorns seemed more wary of elk than deer were, and often appeared to avoid elk. A female yearling elk chased a mule deer buck, another yearling chased a pronghorn buck, and a calf and female yearling chased a pronghorn doe. These encounters seemed to be in play.

Young elk calves were of apparent interest to a band of pronghorn does and a group of mule deer bucks. The does walked past Cow 1 and Cow 5 and approached within 5 m of hiding Calf 1, while looking at the 6- or 7-day-old calf. Three mule deer bucks walked through a group of 10 bedded elk on 2 July. Calf 3 stood as one buck approached and extended its nose to within 0.3 m of the calf. These were the only instances of deer or pronghorn being obviously interested in individual elk.

The elk-mountain goat encounter I observed involved a cow

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with a calf and a nanny with a kid. The elk slowly walked past the standing goats at 10 m as the females watched one another.

Bighorn sheep showed no particular avoidance, attraction, or curiosity toward elk, and vice versa. White-tailed deer were observed in the study area only once, and elk were not in the area at that time.

Elk tended to avoid bison or at least be alerted by them. When a bison bull walked through a group of bedded elk, all 12 stood, a few ran, and two calves suckled. A bison cow stood on the trail between a group of elk and a water trough and pond. A cow walked through the brush in a 6 m radius semi-circle around her, and a female yearling failed to pass. On 16 July, Cow 5 stood when a group of bison grazed near her. As she trotted 100 m away from her calf, Calf 5, a bison calf chased Cow 5 for about 15 m. Two bison cows and the bison calf, approximately twice Calf 5's size, kept Calf 5 separated from Cow 5 for almost an hour by their presence and by repeatedly, probably playfully, herding Calf 5. Cow 5 and Calf 5 vocalized while facing one another at least 61 times during this interaction.

Coyotes were numerous on the Bison Range during this study. I heard or saw from one to six coyotes 43 times within the study area and six times out of the study area but within the Range or within hearing distance of the Range. Calves younger than about 2 months
tended to show more alerting behavior at the sight or sound of coyotes than did older elk. Coyotes passed within 4 m of elk. Elk typically stood and watched the coyotes as they went by, and stood and briefly listened to nearby howling coyotes. Noises from unobserved coyotes alerted the elk until they discovered the cause of the disturbance. Elk chased coyotes, but it was not clear whether these interactions were motivated by play, curiosity, or aggression. In one case, coyote chasing appeared to be motivated by calf protection. On 4 August, when the three calves present were from 4 to 6 weeks old, Cow 5 trotted toward four coyotes that approached to within 50 m of the group. The coyotes turned away from the elk, and she walked after them as they left. These large ungulates have little to fear, after the first couple weeks of life, from coyotes. Two observations of a mule deer doe with a fawn nearby chasing a coyote for at least 50 and 200 m were seen. A pronghorn doe, near her recently killed fawn, also chased a coyote.

Birds flying overhead were observed by the elk with apparently casual interest. Brewer's Blackbirds (*Euphagus cyanocephalus*) occasionally foraged near the elk. On two occasions individual elk repeatedly flushed blackbirds as the elk nosed the birds. The birds flew a meter or so, landed, and the elk approached again and again. One yearling tried to step on a blackbird with her forefoot. These birds were usually permitted to land and walk on the backs and heads.
of the elk; elk occasionally shook their heads to make the birds fly.

A group of 12 elk watched a porcupine (Erethizon dorsatum) for $6{\frac{1}{2}}$ minutes as it walked out of some brush, under a fence, and then, presumably, out of their view.

**Fence Behavior**

The National Bison Range was bounded by a 2.2-2.8 m tall fence, and was divided into eight bison rotation ranges by 1.2 m tall fences raised about 45 cm above the ground (Fig. 1). The bottom wires of the interior fences were raised as high as about 0.9 m above the ground in a few places between Lower South and Upper South ranges, which allowed all ungulates except bison older than about 6 months and antlered bull elk to pass under the fences.

The home range of Group 1 elk, Upper South and Lower South ranges, was bisected by a fence with nine gates. These gates were closed from 1 July to mid-October. Bison inhabited Upper South Range from 1 July to 28 September. In mid-October, Mr. Haderlie granted me permission to open the gates between Upper South and Lower South ranges; I opened three gates.

Elk crawled under fences in only five locations. The heights of the lowest wire of the fence were 48, 53, 65, 91, and 94 cm from the ground in these passageways. Some individuals crawled under fences with no apparent problems. Calves and female yearlings
usually crawled under easily. A female yearling, however, attempted to pass under a fence on 24 July and 14 October, but backed out again. Her shoulders were under the fence in one case before she retreated. Some repeated attempts were successful. A female yearling was the last of a group of six elk to pass under a fence on 5 July. For 5 minutes 15 seconds she ran, trotted, walked, looked over, under, and through the fence, and performed spins and bucks before she passed under it. There was no indication that cows, calves, female yearlings, or spikes ever jumped fences, probably because they could execute the apparently less risky crawling. Injuries or death could result from animals attempting to jump over fences. We found a dead bighorn ram hanging from a fence by his hindlegs, and we untangled the right rear leg of a yearling female bighorn from the upper two wires of a fence.

Cows varied in their ability to crawl under fences. Cow 1 used a passageway only once, although most elk frequently used them. This was the only time she was observed in Upper South Range while the gates were closed. Cow 1 trotted parallel to the fence with her mouth open and her tongue hanging limply through the diasteme on one side on another occasion after seven elk passed under a fence, but did not follow them.

The spikes' antlers made it difficult and sometimes impossible for them to crawl under fences. Bulls were not observed attempting to crawl under a fence. Many of the bulls in Upper South Range, and all
of the bulls in Lower South Range, must have jumped fences. Bulls were usually very hesitant to jump over fences (see below). Short5th, however, trotted to a fence line, paused for about 4 seconds, and jumped over it. This location had been used as a jump-over point. The top wires were pushed down and the fence top was only 1.3 m above the ground.

Fences thwarted many attempts by individuals or groups to get to water, join other elk, leave an area during a disturbance, and interact with other elk during the rut. Examples of these activities follow.

Twelve elk could not complete their apparent trip to the water trough north of Lower South Range on 16 September due to the closing of the gate on the preceding day.

Individuals separated from the rest of the herd sometimes spent hours performing paces along hundreds of meters of fence-line between them. Cow 5 and Calf 5 were separated from the other elk for about 2 weeks in July; Calf 5 frequently performed paces during this time.

Elk on different sides of a fence often moved, grazed, bedded, and alerted together.

Preference for Upper South or Lower South ranges was shown by certain individuals. Cow 1, Calf 1, and Lo were almost always in Lower South; Cow 5, Calf 5, and So were usually in Upper South.
Range after 1 July (the gate-closing day).

Noses and nose-to-noses usually accompanied the joining of two groups with a fence between them.

Elk who crossed under a fence usually behaved normally.
The elk left behind typically tried to join the ones who left them.

When disturbed or fleeing elk encountered a fence, at least one of the following occurrences took place: one or more elk crossed under a fence; the intensity of disturbed behavior apparently increased; the time required before cessation of disturbed behavior probably lengthened.

Smaller bulls possessed harems when larger bulls were unable to cross a fence. The Upper South-Lower South fence-line postponed interactions between Brute and Ridge, severely reduced contesting between Brute and Out, Brute and Curl, and TRight and Drop6th, and almost eliminated the herding ability of these bulls when cows were on the opposite side of a fence. Descriptions of these interactions follow.

Seven of the 11 elk present with Brute in Lower South Range crossed under a fence at 0730 on 12 September. Brute bugled at the seven, and moved parallel to them for about 300 m. There he continued bugling until 0825; he then followed Cow 1 and Calf 1 away from the others. 5pt and L♂ also remained in Lower South Range.

By 0945, Ridge was with the harem. Ridge was clearly a smaller bull...
than Brute, and when Brute approached the harem at 1851, after presumably jumping a fence, Ridge ran away.

A (5, 6) bull, named Out, jumped over the boundary fence on 26 February. From 31 August to 14 September, Out was frequently present along the east boundary fence line of Lower South Range while a bull and a harem were inside the refuge. Out performed an antler-thrash while urinating, a "spar" with 5pt, attempted a "spar" with Brute, performed a nose-to-nose with Cow 1, Calf 1, Lo', and Brute, and received a chase by Curl.

In through-the-fence encounters between Brute and Curl and between TRight and Drop6th, the larger bulls (Brute, TRight) were the aggressors. They performed paces and bugled along the fence line as the smaller bulls bugled or tended their own harems. Drop6th was apparently forced into a confrontation at 1930 on 13 October. Cow 1 and Calf 1 ran 100 m from their harem bull, Drop6th, and "joined" with TRight's harem, who were on the other side of the fence in Upper South Range. Drop6th followed until he was about 20 m from TRight, and then stopped. TRight trotted 10 m toward Drop6th and performed an antler-display as he stopped at the fence. Drop6th trotted away, leaving Cow 1 and Calf 1 to TRight.

By 0920 the following morning, TRight and Drop6th had switched fence sides, possessed different combinations of cows and calves, and were about 2.5 km west of their previous

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locations. This was the most shifting of individuals between fence sides observed during the rut. TRight bugled at Drop6th and/or the cows in Upper South Range, Cow 4 and Calf 4 crawled under the fence into Upper South Range, and a female yearling unsuccessfully tried to cross under the fence. I opened the gates in the area at 1830. By 0815 the next morning, TRight was in possession of both groups, and Drop6th was not seen.

**Weather Effects**

Wind speed and direction often appeared to determine where the elk bedded. If there were a strong west wind, the elk usually bedded on an east-facing slope. We used the knowledge of this tendency to our advantage when trying to locate the elk on foot in windy weather. Walking into the wind, we had a good chance of finding the elk lying or feeding within safe viewing distance on a hill facing us. During windy weather, especially if wind direction fluctuated, the elk were more apt to be alert, and were alarmed easier than during calm days. This change in alerting behavior correlated with their reduced directional abilities of smelling and hearing. The tendency to run and play in windy weather may be a consequence of their increased alertness.

Rain affected elk behavior very little, other than prompting many individuals to groom.
Elk often remained in the shade and avoided the hot summer sun. They moved to one of a few ponds and waded and splashed in the water as frequently as once a day during the summer. Both front and rear feet were used to stamp the water surface to splash themselves. They seemed to prefer to drink from the water troughs, rather than the duckweed-covered ponds, but drank from such ponds after kicking away the duckweed.

**Play Behavior**

Bounces, bucks, spins, jump-ups, and head-shakes differentiated play bouts from other activities. Play behavior also included chases, mounts, nose-to-noses, noses, aggressive acts, and runs or trots alone or in groups.

The younger the age group, after about 2 months of age, the greater the tendency to play. The calves displayed almost half of all play performances (43.0%; 34 of 79) while comprising less than one-fourth of the population. Calves were the only elk to display long individual bouts of play. Running around the other elk for as long as 9 minutes and throwing upward an uprooted plant with the mouth were two of the behaviors in these individual bouts of play. There seemed to be no difference between the male and female yearlings in play behavior, other than the possible increased tendency for \( \text{Ecf} \) to display aggressively. Cows played infrequently (6.3%; 5 of 79), and
bulls never played.

Moving downhill, joining another group of elk, and being in
or near water seemed, in many cases, to motivate elk to perform
bounces, bucks, spins, etc.

Aggressive acts were included in 16.4 percent (13 of 79) of
the observed bouts of play, totalling 10 head-highs, seven forefoot
kicks, four bites, three flails, three antler displays, and three
attempts to spar. No significant difference in use of aggressive
displays took place when comparing aggressive encounters which did
and did not include play ($p > 0.75$, $X^2 = 3.04$, 4 df). Aggressive acts
were exhibited between playing individuals, from players to non-
players, and vice versa.

**Urination and Defecation**

Elk defecated and urinated while standing or walking.
Disturbances tended to stimulate urination and, to a lesser degree,
defecation. Two definite and one possible occurrences of urination
postures were observed. On 28 July, two female yearlings urinated
as their rear feet contacted the ground directly below the posterior
portion of their rumps. Their rumps were lowered so the angle
formed from backline to ground, relative to an imaginary line from
the withers backward parallel to the ground, was -15° to -25°.
Calf 1 stood for 45 seconds on 24 June with her hocks flexed, back
humped, rump lowered, and nose lowered so that it almost touched the ground. Calf 1 was at least 300 m from us as she did this, so we could not determine whether or not she was urinating. If she were stretching, it was the only such stretch observed.

**Behavior of an Old Cow**

Cow 2 was probably one of the three cows brought to the Lower South Range on 2 May 1972. These cows came from the display pasture near refuge headquarters, and were habituated to humans. Cow 2 was the most tame individual of the Group 1 elk. Group 1 elk probably descended from these three cows.

Evidence of Cow 2's poor physical condition included stiff walking, erratic straightening of her rear legs while walking, stumbling, and poor hearing and seeing abilities. The first three symptoms appeared to worsen from the beginning of the field season through 4 August. She could be approached rather easily to within 25 m from behind and downwind. Her apparently healthy calf, born 2 June, died of starvation 8 days later. Cow 2 contracted mange by the end of July. Cow 2 spent from a few hours to a week alone on several occasions. No other individual, other than calving cows and spikes during the rut, were ever more than a few hundred meters from another elk.

Cow 2 sometimes led the group grazing and walking. On
22 July, the other 14 elk with her stood and followed her as she grazed away from them.

Cow 2's aggressive behavior seemed to correspond less with the actions and closeness of others than did the aggressive acts of other elk, as if her physical problems prompted her to act aggressively. Cow 1 was the only individual to win an aggressive encounter with Cow 2.

Because of Cow 2's worsening physical problems, tendency to be alone, and the probability that if she calved in 1978 that calf would also starve, she was shot on 4 August as part of the regular reduction program of the refuge. Her lower jaw indicated that she was 16-18 years old. Cartilaginous "mice," about 1-1 1/2 cm (3/8-1 1/2 inch) in diameter were lodged in both knees; such "mice" in humans cause extreme pain. Examinations of scrapings positively identified the mites of sarcoptic mange that covered her sides and rear legs (O'Gara pers. comm.).

**Calving and Cow-calf Behavior**

**Habitat Preference During Calving**

Seven cows were present during calving. Five of the six known calves were located when young enough for us to capture and eartag them. I first saw the other calf, Calf 4, on 8 June. He and eight other elk began running from me when 100 m away, and easily
eluded me in the timber of lower Elk Creek. The six calves were born within a 22- or 23-day period (Table 2).

Table 2. The 1977 Group 1 elk calves, dates of birth, dates eartagged, and dates of death.

<table>
<thead>
<tr>
<th>Calf</th>
<th>Date of birth</th>
<th>Date eartagged</th>
<th>Date of death</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calf 1</td>
<td>24-25 May</td>
<td>26 May</td>
<td>---</td>
</tr>
<tr>
<td>Calf 2</td>
<td>1 June</td>
<td>2 June</td>
<td>10 June</td>
</tr>
<tr>
<td>Calf 3</td>
<td>29-31 May</td>
<td>5 June</td>
<td>---</td>
</tr>
<tr>
<td>Calf 4</td>
<td>1 June or before</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Calf 5</td>
<td>7-9 June</td>
<td>11 June</td>
<td>---</td>
</tr>
<tr>
<td>Calf 6</td>
<td>15 June</td>
<td>15 June</td>
<td>17 June</td>
</tr>
</tbody>
</table>

Elk were often found in or within 200 m of coniferous timber during the 26-day period of 27 May to 21 June (Fig. 2). This period corresponds with the dates of calving. Elk were usually in more open habitats during the 45 days before calving and during the 70 days between the end of calving and the beginning of the rut.

Calf 1 was born earlier, on 24 or 25 May. We located and tagged her on 26 May in one of the few areas of brush in the eastern half of Lower South Range. This small (20 X 80 m) but dense stand of mixed deciduous growth, with its own spring, often concealed as many as 10 elk from our view. Such a draw provides adequate cover for a calving cow.

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Fig. 2. Percentage of observations of elk in grassland or deciduous brush (clear areas) and in or within 200 m of coniferous timber (dotted areas) by 4-week periods. First calf born on 24 May; mean age of calves was 22 days on 21 June; rutting bulls in area from 31 August onward.
Two cow-calf pairs moved from grassland toward timbered areas within a few days after parturition. During the 5 days following the eartagging of Calf 1, Cow 1 and Calf 1 slowly made their way from the northeast section of Lower South Range to the small stand of timber south of Sheep Mountain, about 3 km to the southwest. The disturbance of eartagging may have motivated the pair to move from the area. They arrived at the dense timber of lower Trisky Creek by 4 June. Every time we observed Cow 1 or Calf 1 from 31 May to 21 June, they were either in timber (8 times) or within 200 m of timber (2 times). Cow 2 also calved in the relatively treeless area of the southeast corner of Lower South Range. Cow 2 and Calf 2 moved westward for about 1.5 km on 6 June. The calf died on 10 June, while they were still away from timber but they had moved away from tourist observations and highway noise.

Calf 6 was born on the timbered, east-facing slope of lower Trisky Creek. The birth locations of Calf 3, Calf 4, and Calf 5 were not determined.

Possibly, although not necessarily, all seven cows calved (Harper et al. 1967, Bowyer 1976). We never saw the seventh calf and did not see the seventh cow for about 2 weeks during the calving period, although we spent many hours trying to find her. She was probably in timber or out of the study area.

A cow who had recently given birth was located at 1020 on
15 June. The following description of her behavior excludes interactions with her calf, Calf 6, who remained within 3 m of the cow throughout the period of observation. Observations of the calf are described below in "Calf Mortality." The cow groomed her sides, shoulders, and front legs from 1020-1028 and from 1050-1058. The afterbirth was hanging from her vaginal opening to about 10 cm below her hocks. At 1130, she walked 2 m and began eating the amnion, which was lying on or near some loose rocks. The amnion was about 1 m long, and seemed to be about 4 l of material. She finished eating the amnion at 1118, walked 1 m, turned, expelled the hanging afterbirth and about 2 l of material. She turned and began eating the afterbirth. She lifted and shook the afterbirth, and bit off a piece at a time. The afterbirth fell to the ground after most bites. She consumed most of the afterbirth by 1139, after swallowing the second cotyledon. She searched the ground and consumed small bits of material from 1140-1150.

Hiding Behavior

Calves tended to hide beside objects at least as large as themselves, such as large grass or forb clumps, rocks, small cliffs, and fallen or standing trees. Calves moved slowly and held their noses close to the ground before hiding or standing between hides. Cows remained within about 200 m of their hiding calves. Hiding
calves remained motionless for long periods of time. Calf 2 stood on all fours three times and on wrists and rear toes twice, for a total standing time of less than 2 minutes, during the 5 3/4 hours of observation of him before ear tagging. The calf stretched during these movements and changed his hiding position after at least four of these. His head rested motionlessly on the ground about 95 percent of the time; he also performed noses to the ground, scent-tested the air, looked around, and yawned. Frequent ear movement accompanied bedding with the head up or down.

Individual hiding calves were observed on eight occasions. Very young calves could be approached more closely than could older calves. Approaches as close as 2, 2.5, 6, 11, and 11 m were permitted in the five cases in which the calves (2-4, 13-14, 6-7, 11-12, and 17-18 days old, respectively) stood and ran. We observed Calf 1 hiding when she was 2 or 3 days old, from 6.5 m away, without her taking flight, but when she was 11 or 12 days old, she flushed at 11 m. We tagged, weighed, and examined Calf 2, when 1 day old, and Calf 6, when less than 1 day old, without their vocalizing or struggling. Calf 6 was probably in poor health during handling.

Human disturbance was the apparent cause of hiding only once of the eight times hiding calves were located. In this case, Calf 3 followed his cow away from us after I alerted the 11 elk in Trisky Woods on 5 June. This 6- to 8-day-old calf and his cow
travelled about 100 m before passing out of our view. I saw the cow about 5 minutes later as she trotted away from us. We found Calf 3 almost 1 hour later hiding along the cow's probable path.

Young calves hid during most of the day. Rocky, grassy areas in timber (five sightings), open grassland (two), and brush (one) were used.

Cows Finding Hiding or Bedded Calves and Locating Calves After a Disturbance

Two cows were observed apparently calf-searching. Cow 2 stood and began walking back and forth between two ravines at 2210 on 3 June. She walked almost continually for most of the next 50 minutes with her head directed downward at about -30°. Darkness prohibited my witnessing her finding her calf. Cow 5 appeared at the site of her calf's ear-tagging within a few minutes of my releasing Calf 5. She walked and trotted back and forth, cross-slope and downhill, with her nose about 0.3 to 0.9 m above the ground and her ears forward. Cow 5 crossed the path Calf 5 had taken with no apparent response. She passed out of my view after about 10 minutes of searching.

Calves 1, 2, 3, and 5 reunited with their cows after ear-tagging. Calf 3 ran 100 m downhill before we caught him on 5 June. After release, he travelled at least 100 m further away from where his cow had left him. A few minutes before we tagged Calf 1, a cow
flushed from the brush near the calf and ran away from us.

Hiding or bedded calves, when approached closely by their mothers, occasionally stood and moved to the cows.

Cow Behavior When with Her Young Calf

The presence and behavior of cows facilitated our finding their calves. Cows with very young calves displayed a unique reluctance to leave an area, and allowed us to approach as close as 50-100 m on at least two occasions involving a total of 11 individuals. Cow 1, Cow 3, and the seven yearlings saw or heard me at least four times from 0900-1315 on 5 June as we observed the group and I searched the Lower Trisky Woods for calves. They alerted a few times, ran short distances, then stood. Any one of these disturbances would usually have caused them to leave the area. They finally ran out of the timber and down the valley after seeing me less than 50 m from them. Both Calf 1 and Calf 3 were hiding in the area. On 11 June, Cow 5 grazed, lay down, and seemed to be unaware of my presence when I was 100 m away in clear view. Her calf and Calf 1 were hiding about 180 and 200 m, respectively, from her. The only other time this reluctance to leave was exhibited was on 29 May. A cow and the yearlings allowed me to approach within 35 m for over 30 minutes. I believe a calf was hiding in the area and I simply failed to find it. In all three cases, the yearlings with the cow(s) were
typically alerted; they moved away, stopped, and then returned to the apparently undisturbed cows.

The cows lost their reluctance to leave the area of their calves after the calves reached about 2 weeks of age. The cows then showed an increased tendency for flight during a disturbance.

Cows stood for long periods of time near their bedded calves. Cow 1 stood, without locomoting, for about 4½ hours of the 5½ hours of observation of her and Calf 1 on 31 May. Calf 6's mother displayed similar behavior on the day of calving and on the following day. The occasional lifting of a foot, as if to relax tired muscles, accompanied these hours of almost motionless standing.

Following Behavior and Locomotive Development

Healthy calves stood weakly with a humped-back appearance when 1 day old. It is probable that they stood earlier. By 3 to 4 days, they were more sturdy and erect (pers. obs. and Johnson 1951), but locomoted with slightly arched backs and bobbing heads. Calf 1 moved more than 2 km when she was 2 to 3 days old. She and Cow 1 moved at least 1.5 km more during the next 3 days. Calves 5 to 7 days old moved strongly and quickly. Much of our success at catching Calf 3, estimated to be 6 to 8 days old, was due to the following: he was hiding under the hot sun for almost an hour before he stood and ran; we prevented his initial attempt to run uphill; and he tripped and fell.
twice during the 100 m downhill chase. Calf 1 and Calf 3 flushed from hiding when about 12 days old. They ran strongly and very quickly, with heads level and backs nearly straight.

Improved vision coincided with increased locomotive ability. Calf 1 and Calf 5 apparently did not notice me as close as 1 and 3 m, respectively, on their tagdays. Their vision greatly improved during their first few weeks of life.

Calves less than a few weeks old usually followed within 4 m of their cows. Two observations of a calf less than 1 week old indicate that younger calves may typically follow their mothers as close as 2 m. Older calves often followed at greater distances.

Calf Mortality

Two of the five ear-tagged calves died shortly after birth and were necropsied by Dr. O'Gara, Assistant Leader of the Montana Cooperative Wildlife Research Unit.

Calf 2 attempted to suckle 14 times and suckled eight times from 1000 to 1203 on 6 June. Cow 2 terminated most bouts of suckling by stumbling sideways (see Behavior of an Old Cow). The calf terminated three of the eight bouts, although he frequently attempted to suckle. This suggested that he was receiving an insufficient amount of milk. Von Gunten found the dead calf 4 days later in the same area. The calf probably died of starvation. Its
stomach contained a small amount of curdled milk, dried grass, and gravel. A mass of clay and sand blocked the posterior end of the colon (O'Gara pers. comm.) (Appendix III).

Calf 6's cow was located shortly after calving. The calf was apparently too weak to locomote to her mother standing nearby. Calf 6 stood 14 times during the 5 3/4 hours of undisturbed observation on 15 June. In most cases, she was able to stand for only a few seconds before falling or lying down. A few times she crawled forward on her wrists and rear toes. Four times she fell and rolled as far as 1 m downhill. A fallen tree stopped her downward rolling in at least two instances. The following evening, she stood and lay down at least four times. She never stood for longer than 2 minutes or stood on her front toes. The cow was within 10 m of her calf for all but 1 hour of the 8 3/4 hours of undisturbed observations of them on 15 and 16 June. She groomed the calf at least four times. She was more than 100 m from Calf 6 from 0950-1440 on 17 June; she then walked out of view and presumably left the area. About 3 1/2 hours later, I approached Calf 6 and found the calf dead, facing downhill against a fallen log. Due to the calf's undersized lymphatic system, the absence of a cardiac thymus, and the small size and weakness of the calf, the cow probably had had a high fever during pregnancy (O'Gara pers. comm.) (Appendix III).

The seven yearlings present with the seven cows suggests
that all seven cows successfully calved in 1976. The seventh calf of 1977 was not discovered. This calf may have died, although all elk cows do not necessarily calve each spring (Harper et al. 1967, Bowyer 1976).

**Social Integration**

The calves' integration into the herd began when they were very young. Calf 1 was only 4 to 5 days old when she, Cow 1, and Cow 5 were joined by a third cow and the seven yearlings. Calf 1 was out of view from the time of joining, 2130, until darkness 1 hour later, so I could not observe her interactions with the others. Calf 3 and Calf 5 were with 10 and at least five other elk, respectively, on the days they were cartagged.

**Nursing Behavior**

**Suckle approach.** Calves walked, trotted, or ran during suckle approaches. Trotting was the most common means of locomotion (74.6%; 44 of 59 approaches described in detail). Suckle approaches ranged from walking 1 m to running over 50 m. The usual distance was 3-7 m.

**Initiation and termination.** Calves apparently initiated most nursing interactions (39.9%; 106 of 122 suckles and suckle attempts in which initiation was observed).
Cows initiated the remainder of the nursing interactions (13.1%; 16 of 122). Cow 1, Cow 3, and Cow 4 assumed nurse postures five, three, and three times, respectively, before their calves performed suckle approaches. Cows stood with their rear legs spread about 15 and 30 cm further apart than usual during two of these nurse postures. The most active cow-initiated nursing interaction was on 21 August. Cow 4 looked around with her ears up and nostrils flared, and called "Eaw!" at least nine times as she moved downhill toward her bedded calf 100 m away on the other side of a fence. She crawled under the fence, walked toward her calf, and assumed the nurse posture. Calf 4 stood, trotted the 9 m between them, and suckled.

Vocalizations before suckles were heard on five occasions. Cows prohibited suckles (caused suckle attempts) and terminated suckles by walking forward, backward, or to the side. Calves stopped suckles by pulling away from the standing cow. Cows stopped suckles in 90.0 percent of the cases in which termination was determined (81 of 90). Calf 1 was responsible for eight of the nine calf-ended suckles when she was 4-7 days old. About 3-5 seconds before the end of a suckle, a cow would typically turn her head to the side, nose the calf, and walk forward as she directed her head anteriorly.

Frequency of nursing interactions. The frequency of suckles
and suckle attempts decreased as the calves aged (Table 3). Assuming elk maintained periods of activity and inactivity throughout the day and night (this study, McCullough 1966, Stehn 1973), the number of suckles per 24 hours for calves up to 1 month, 1 month, 2-, 3-, and 4-months old would be 4.1, 3.6, 3.6, 1.9, and 2.4, respectively.

Table 3. Frequency of suckles and suckle attempts over time. Interactions disturbed by humans, thief-suckles, attempts to thief-suckle, and nursing behavior of unhealthy calves (Calf 2 and Calf 6) are excluded.

<table>
<thead>
<tr>
<th>Age of calves in months</th>
<th>Hours of observation</th>
<th>Number of suckles or attempts per hour (no. of observations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 1</td>
<td>107.25</td>
<td>.17 (18) .20 (21) .36 (39)</td>
</tr>
<tr>
<td>1</td>
<td>190.00</td>
<td>.15 (29) .15 (28) .30 (57)</td>
</tr>
<tr>
<td>2</td>
<td>129.00</td>
<td>.15 (19) .12 (15) .26 (34)</td>
</tr>
<tr>
<td>3</td>
<td>375.25</td>
<td>.08 (29) .07 (27) .15 (56)</td>
</tr>
<tr>
<td>4</td>
<td>20.50</td>
<td>.10 (2) .05 (1) .15 (3)</td>
</tr>
</tbody>
</table>

1 Based on the earliest estimated birth dates.

Duration of nursing. The duration of suckles decreased as the calves aged (Table 4). The two longest suckles recorded, both 9 min. 15 sec., were performed by Calf 1 when she was 6-7 days old; Calf 1's third suckle within 1 1/2 hours was at least 1 min. in duration.

Cow 5 was separated from her calf between 3 and 7 October when Calf 5 was about 17 weeks old (see Group Behavior and Possible
Mother-offspring Relationships). Calf 5 remained with the elk throughout 11 November, and was still apparently healthy on 11 January. Cow 5 was still missing at that time. Calf 5 was not observed performing a thief-suckle.

Table 4. Duration of suckles over time. Interactions disturbed by humans, thief-suckles, attempts to thief-suckle, and nursing behavior of unhealthy calves (Calf 2 and Calf 6) are excluded.

<table>
<thead>
<tr>
<th>Age of calves in months</th>
<th>Mean suckle times (number of suckles)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Calf 1</td>
</tr>
<tr>
<td>&lt;1</td>
<td>171.6 (10)</td>
</tr>
<tr>
<td>1</td>
<td>45.6 (14)</td>
</tr>
<tr>
<td>2</td>
<td>43.5 (8)</td>
</tr>
<tr>
<td>3</td>
<td>32.8 (13)</td>
</tr>
<tr>
<td>4</td>
<td>---</td>
</tr>
</tbody>
</table>

1Based on the earliest estimated birth dates.

Thief-suckle. A female and a calf that was not her own were involved in 7.0 percent of all suckles and suckle attempts (21 of 198). The frequency of thief-suckles and thief-suckle attempts decreased over time (Table 5). Four thief-suckles were observed. Calf 3 suckled Cow 1 twice, for 31 and 36 seconds, on 5 July. Calf 4 suckled Cow 1 for 15 and 10 seconds, on 31 August and 15 September, respectively. Calf 1 concurrently suckled Cow 1 in all four instances, and began before the "thieves" in three cases. The calves assumed
Table 5. Frequency of thief-suckle attempts and thief-suckles over time.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Hours of observation</th>
<th>Unsuccessful attempts to thief-suckle cows</th>
<th>Unsuccessful attempts to thief-suckle ? yearlings</th>
<th>Successful thief-suckles to cows</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>104.25</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>July</td>
<td>203.75</td>
<td>0.064 (13)</td>
<td>0.004 (1)</td>
<td>0.010 (2)</td>
<td>0.078 (16)</td>
</tr>
<tr>
<td>Aug</td>
<td>166.00</td>
<td>0.006 (1)</td>
<td>0 (0)</td>
<td>0.006 (1)</td>
<td>0.012 (2)</td>
</tr>
<tr>
<td>Sept</td>
<td>322.50</td>
<td>0.003 (1)</td>
<td>0.003 (1)</td>
<td>0.003 (1)</td>
<td>0.009 (3)</td>
</tr>
<tr>
<td>Oct</td>
<td>39.50</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>

1Number of hours of observation of one or both individuals of a cow-calf pair.
reverse parallel positions; twice they were on opposite sides. Cow 1 was apparently aware that both calves were suckling, but was not aggressive toward the thieves.

Calf 3, Calf 4, Calf 1, and an unidentified calf attempted thief-suckles seven, five, four times, and once, respectively. Calves' attempts began after a cow's offspring had started suckling in four cases; the cow then terminated the suckle. Calf 4 attempted suckles to one or two female yearlings. Once, the yearling did not noticeably respond, then followed Calf 4 to his cow and performed a suckle watch. In the other case, the yearling responded with a bite.

Calves were significantly more successful when attempting to suckle from their mothers than from females other than their mothers ($p < 0.001$, $X^2 = 12.7$, 1 df).

Female yearlings performed noses to the udders of cows on three occasions (not considered to be suckle attempts). When a yearling performed a nose to Cow 5's udder on 15 May, the cow made no apparent response, but when a different yearling did so to a cow on the same day, the cow flattened her ears and performed a forefoot kick.

Suckle approaches and suckle watches also occurred between a cow and non-1977 offspring. Calves ran or trotted 2 to 6 m to cows other than their mothers, then stopped and turned away, on 10 June and 1 and 28 September. Calf 3, Calf 4, and a female yearling performed suckle watches.
Concurrent nursing behavior. All observed thief-suckles and four attempts to thief-suckle occurred as a cow and her calf were nursing. Calves apparently were motivated to suckle from their mother when a nearby calf was suckling. Some undisturbed suckles and suckle attempts by healthy calves were done within 10 minutes of another pair's doing so (9.4%; 28 of 298). Concurrent nursing behavior by two cow-calf pairs was observed on six occasions.

Disturbances. Disturbances apparently caused calves to display nursing behavior in some cases. Twenty-four suckle attempts and four suckles took place during 11 human and one bison disturbances. A very significant increase in suckle attempts over successful suckles was displayed in disturbed compared to undisturbed situations (<.001, $\chi^2 = 16.79$, 2 df). Two suckles took place while a bison bull walked through the alerted group.

Nursing behavior preceded by bedding bouts. Many suckles and suckle attempts were performed within 10 minutes of the end of the calves' bedding bout (27.4%; 60 of 219 suckles, suckle attempts, or series of these. Bouts possibly initiated by human disturbances were excluded. The percentage reported may be too low, for I was unaware of this tendency early in the field season and failed to note calf bedding times consistently.).

Bunting. Bunting seemed to be painful to the cow when the calf's hitting moved her upward and to the side. The cow would then
terminate the nurse. During the 4½ hours after such an interaction, Cow 5 did not permit Calf 5 to suckle the two times she tried to do so.

**Bedding Behavior**

Elk often bedded as a group. Less than 30 minutes typically passed between the times the first and last individuals of a group bedded.

Twenty-two diagrams of groups of bedded elk were drawn so that arrows represented each individual present. One mm-wide lines extending forward from the tips of the arrows, the directions the elk faced, were later drawn to determine the degree to which they faced one another. Elk did not face directly toward another individual in most cases (72.6%; 167 of 230). Elk were face-to-face in only 7.0 percent of the instances (16 of 230). Calves displayed the tendency to face away from other elk less than the older elk; one-third of the instances of individuals facing another elk were calves (33.3%; 21 of 63). Two female yearlings lay facing one another with their noses less than 1 m apart on two occasions.

Elk commonly bedded as one group even though a fence separated them. Calves often bedded close together. Scraping the ground with one or both forefeet rarely preceded bedding. One female yearling scraped the ground four times with her right forefoot, four with her left, three with her right, and then four with her left before
bedding.

**Self-groom**

Self-grooms were performed on areas other than the head, upper neck, and dorsal sides of the neck and shoulders. Nipping and licking the body surfaces were the methods used. Scratching was done with the antlers, rear toes, and the sides of the head. Self-grooms of the flanks or rectal area frequently followed bedding bouts. An apparently disturbing itch prompted bedded individuals to stand and scratch. Most self-grooms lasted about 5-15 seconds, many lasted up to 1 minute, and few took more than 1 minute to complete. Brute's grooming two cows apparently stimulated them to perform long self-grooms of their posterior back and sides (3 min. 20 sec., 4 min. 15 sec.). Wetting of the pelage in the ponds or from rainfall often led to self-grooms.

**Social-groom**

Social-grooms usually were directed to areas not covered by self-grooms (listed above). The recipient of a social-groom usually stood almost motionless, but sometimes nosed the other elk if it was temporarily performing some other activity (usually a self-groom).

Most social-grooms were between cows and their 1977 calves (73.4%; 47 of 64). Suckle's or suckle attempts closely preceded or followed cow-calf social-grooms in most cases (74.4%; 32 of 43,
exclusive of Calf 6 who was groomed by her mother but performed no suckle attempts). The inguinal regions of suckling calves occasionally received social-grooms.

Most of the social-grooms that were not between a cow and her 1977 calf were between a cow and a female yearling (70.6%; 12 of 17). The yearlings were probably the offspring of these cows. A yearling displayed social-grooms to a cow twice.

The other social-grooms were between two cows, two female yearlings, and L♂ and a female yearling. Cow 2 performing a social-groom to Cow 5 may have been another cow to offspring social-groom (see Group Behavior and Possible Mother-offspring Relationships).

Social-grooms ranged from 3 seconds to 22 minutes 44 seconds ($\bar{X}=2\text{min }18\text{ s, } n=50$). Non cow-calf social-grooms did not significantly differ in length compared to cow-calf social-grooms (Mann-Whitney Test; $<0.90, n=14, m=32$).

**Mutual-groom**

The length of time calves received social-grooms from their cows during the three cases of mutual-grooms observed were significantly longer than cow to calf social-grooms (Mann-Whitney Test; $<0.05, n=3, m=32$).

**Nose**

An individual usually displayed a nose and then moved away...
without any apparent reaction from the other elk (60.0%; 15 of 25). Noses sometimes led to aggressive acts by the recipient of the nose (24.0%; 6 of 25). The dominant animal displayed aggressively toward the subdominant elk in these cases. Noses infrequently led to mutual-grooms and, when performed to bedded calves, displacements (both 8.0%; 2 of 25).

**Nose-to-nose**

Aggressive acts followed nose-to-noses less frequently than they followed noses (3.3%; 8 of 96) (Fig. 3). Apparently a nose-to-nose was used as a form of aggression as Cow 2 initiated this behavior toward a bedded female yearling with the cow's ears flattened. The yearling stood, and the cow soon lay in her place (a supplant). Aggressive encounters twice followed nose-to-noses.

Non cow-calf pair nose-to-noses were usually terminated by one or both participants quickly moving away. Apparent attempts to perform a nose-to-nose were thwarted by one individual moving its nose away from the other elk.

**Mount, Throat-place and Chest-bump by Elk Other than Rutting Males**

Mounts and throat-places (each 44.4%; 20 of 45) were more common than chest-bumps (11.1%; 5 of 45) in the 45 performances of these behaviors within 33 encounters (Fig. 4).
Fig. 3. A nose-to-nose between a cow and a female yearling.
Fig. 4. A female yearling approaches a cow and performs a mount.
Mounts, throat-places, and chest-bumps were performed in several contexts and in association with a variety of other displays. Elk of the same sex-age class performed one or more of these behaviors to one another (36.4%; 12 of 33 encounters), subdominant elk performed to dominant elk (36.4%; 12 of 33), and dominant elk performed to subdominant elk (27.3%; 9 of 33). Frequently one or more of these three displays were executed without other displays (42.4%; 14 of 33).

Aggressive acts (24.3%; 8 of 33), noses (12.1%; 4 of 33), playful acts (9.1%; 3 of 33), nose-to-noses, displaces (both 6.1%; 2 of 33), and a groom (3.0%; 1 of 33) were performed in encounters that also included mounts, throat-places, or chest-bumps.

Female yearlings performed mounts to other yearlings eight times, to cows four times, and to L♂ once. Two female yearlings alternately performed mounts and noses to one another. Spikes performed chest-bumps and mounts to one another, throat-places and mounts to female yearlings, and chest-bumps and mount to cows. Calf 3 and Calf 4 performed mounts to their mothers three times, and Calf 4 once performed a throat-place to his mother. A cow once performed a throat-place to S♂ after displaying six head-highs and a forefoot kick.

During the rut, 5pt performed mounts to L♂ three times—once alone, once before a spar, and once after a spar.
Head-up Twist

Elk performed head-up twists when pestered by insects, alerted by humans or human noise, thwarted in attempts to cross under a fence, displayed aggressively toward by a dominant individual (see Redirected Aggression for an example), or when receiving a sexual approach.

Aggressive Acts and Hierarchical Relationships

Aggressive acts were important in maintaining individual distances, establishing hierarchical relationships, and enabling bulls to hold harems. The closer two individuals were, the more likely an aggressive act would occur between them. When the heads of two individuals (not a cow-calf pair) were closer than about 1 m, usually one or both elk quickly moved away or displayed aggressively. Most aggressive acts resulted in one or both elk quickly moving away. Some aggressive acts, such as charges and antler displays, were initiated when the participants were as far apart as 5 and 20 m, respectively. Aggressive encounters included from one to eight aggressive acts. More than one type of act (antler display, bite, kick, etc.) were exhibited in some encounters (10.7%; 20 of 187).

Head-high

Head-highs temporally isolated from other aggressive acts comprised about one-third of all aggressive acts (33.5%) (Table 6).
Table 6. Number of aggressive encounters and aggressive acts by Group 1 elk (1 April-11 November) and rutting bulls (31 August-11 November).

<table>
<thead>
<tr>
<th>Display</th>
<th>Group 1 elk</th>
<th>Rutting bulls and Group 1 elk with rutting bulls</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Encounters</td>
<td>Acts</td>
</tr>
<tr>
<td>Head-high</td>
<td>91</td>
<td>122</td>
</tr>
<tr>
<td>Kick</td>
<td>87</td>
<td>122</td>
</tr>
<tr>
<td>Forefoot</td>
<td>68</td>
<td>35</td>
</tr>
<tr>
<td>Flail</td>
<td>9</td>
<td>26</td>
</tr>
<tr>
<td>Rear</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>Bite</td>
<td>69</td>
<td>90</td>
</tr>
<tr>
<td>Antler display</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>Head-push</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Spar</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Total</td>
<td>187</td>
<td>364</td>
</tr>
</tbody>
</table>

\(^1\)Performed by cows or Calf 1.

\(^2\)Performed by rutting bulls.

\(^3\)33 of 106 performed by S♂ or L♂.
Head-highs in combination with other aggressive acts were considered conservatively as part of the other displays (Fig. 5). Head-highs were the only aggressive act performed in 40.1 percent of the aggressive encounters (75 of 187). Cows, female yearlings, spikes, and calves executed head-highs. The elevation of the muzzle generally coordinated with the stance of the displayer and whether or not the display was combined with other aggressive acts (Table 7). The ears were flattened at least half-way during most head-highs (83.7%; 36 of 43 recorded).

Table 7. The angle of the head during head-highs isolated from and in conjunction with other aggressive acts.

<table>
<thead>
<tr>
<th>Head-highs</th>
<th>$\bar{X}$ (degrees)</th>
<th>s (degrees)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>While bedded</td>
<td>81.25</td>
<td>25.60</td>
<td>8</td>
</tr>
<tr>
<td>While standing</td>
<td>37.06</td>
<td>25.05</td>
<td>53</td>
</tr>
<tr>
<td>While standing and accompanied with</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forefoot kick</td>
<td>22.78</td>
<td>19.54</td>
<td>9</td>
</tr>
<tr>
<td>Bite</td>
<td>42.04</td>
<td>27.24</td>
<td>22</td>
</tr>
<tr>
<td>Flail</td>
<td>64.33</td>
<td>23.21</td>
<td>8</td>
</tr>
<tr>
<td>Rear</td>
<td>70.00</td>
<td>8.67</td>
<td>3</td>
</tr>
</tbody>
</table>

Head-low

Head-lows accompanied by forefoot kicks were observed four
Fig. 5. A cow performs a head-high to another cow, who responds with a head-high and a forefoot kick.
times. The elk kicked both forefeet forward simultaneously in two of these displays. Approaches with the head low without a forefoot kick were recorded as bites or charges.

**Kick**

Kicks comprised about one-third of all aggressive acts (33.5%), and almost half of all aggressive encounters included kicks (46.5%; 87 of 187) (Fig. 5). Most kicks were forefoot kicks, flails and rears were less common.

The forefoot usually reached no higher than about 0.5 m during a forefoot kick, or about 45° above the horizontal. The highest forefoot kick observed reached the shoulder-height of the display. Both forefeet were kicked forward simultaneously on several occasions. Once three such "double-kicks" were delivered in rapid succession. Stamps were a variation of the forefoot kick. Head-highs frequently were combined with forefoot kicks (32.8%; 40 of 122).

Cows, female yearlings, spikes, and calves performed kicks, but actually contacted the other individuals on only four occasions.

**Bite**

Almost one-fourth of all aggressive acts were bites (24.7%), and more than one-third of all aggressive encounters included this act (Fig. 6).

Head-position while performing a bite (-45° to 80°) depended
Fig. 6. A bite performed by a cow to a female yearling.
on five factors: the relative locations of the individuals, the relative sizes of them, the part of the body at which the bite was directed, whether the nose was directed slightly away from the other individual, and whether the displayer performed a charge (Appendix V).

Cows, female yearlings, and, occasionally, spikes performed bites. The displayer contacted the individual during a bite only once.

**Antler Display**

L♂'s and S♀'s occasional exhibition of antler displays comprised 6.0 percent of all aggressive acts. Antler displays were often performed during bouts of play. Most displays were shallow head bobbing without contact with another individual. L♂ once contacted a cow's face with his antlers, and he once lowered his nose almost to the ground while bobbing his head. The spikes performed antler displays toward female yearlings, cows, and calves, but were not observed performing this display to one another.

**Head-push**

Head-pushes occurred rarely, but comprised over half of the physical contacts occurring during aggressive acts (57.1%; 8 of 14). Bedded individuals were displaced by head-pushes on four occasions. Males executed most head-pushes (72.7%; 8 of 11); the rest were performed by a cow, a female yearling, and Calf 1. Head-pushes were directed against heads, necks, and rumps.
Spar

Although Lɔ and Sɔ did not perform spars with each other, they executed spars with bulls during the rut. During a play bout on 30 April, the spikes, then without antlers, leaned their heads downward facing one another and each bobbed his head several times during each of two "spars."

Sex-age Classes Comparison and Hierarchical Relationships

The frequency of use of head-highs, bites, and forefoot kicks displayed by spikes, cows, and female yearlings was not significantly different \((p<0.10, \chi^2 = 7.86, 4 \text{ df})\). Spikes also differed from the female yearlings and cows in their use of antler displays and their more frequent performance of head-pushes. Calves infrequently displayed aggressively.

An individual won an aggressive encounter by causing another elk to face away first and, usually, by delivering the final aggressive act. If the elk which faced away first was not recorded, the participant which last displayed aggressively was considered the winner.

The hierarchy for the sex-age classes was deduced from the numbers of encounters won and lost between groups (Table 8) and the proportion of encounters won relative to the encounters engaged in. The proportion of encounters won/engaged in for cows, spikes, female
yearlings, and calves were 0.95, 0.39, 0.18, and 0.06, respectively. Cows almost invariably won cow to non-cow aggressive encounters; spikes often won, female yearlings infrequently won, and calves rarely won (or took part in) encounters with elk not of their sex-age class. The hierarchy was, from most to least dominant: cows, spikes, female yearlings, and calves. The dominance of spikes over female yearlings increased between April and October. The spikes won aggressive encounters with cows when the spikes were smaller than the cows and, in three of the four cases, without antler displays. Calves and female yearlings never displayed aggressively toward cows.

Table 8. Aggressive encounters of the sex-age classes of elk. The number of aggressive encounters won are arranged horizontally, and the number lost, vertically.

<table>
<thead>
<tr>
<th>Losers</th>
<th>Cows</th>
<th>Male yearlings</th>
<th>Female yearlings</th>
<th>Calves</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cows</td>
<td>--</td>
<td>36</td>
<td>38</td>
<td>9</td>
<td>33</td>
</tr>
<tr>
<td>Male yearlings</td>
<td>4</td>
<td>--</td>
<td>23</td>
<td>2</td>
<td>29</td>
</tr>
<tr>
<td>Female yearlings</td>
<td>0</td>
<td>9</td>
<td>--</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>Calves</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>--</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>4</td>
<td>45</td>
<td>62</td>
<td>16</td>
<td>--</td>
</tr>
</tbody>
</table>

A calf won only one encounter with a non-calf; a female yearling turned and walked from Calf 1 after the calf performed a head-high. Amongst the calves, Calf 1 was clearly dominant. Calf 1's
confidence was shown by her running 3 m toward 1A, a large harem bull, and directing a head-high at him. Other than Calf 1, nothing can be stated about the individual hierarchy because: most cow-cow interactions were between elk not identified at the time of the encounter (70.0%; 14 of 20); the female yearling data were grouped; the spikes rarely displayed aggressively toward one another; and the calves infrequently displayed aggressively.

Only three encounters including aggressive acts took place between L and S during the hundreds of hours of observation of them within the same group. One of these, on 30 April, took place during a play bout. The other two encounters were single head-highs displayed by L. During one of these head-highs, S was looking away. The spikes frequently grazed, browsed, bedded, and travelled near one another.

Two-year-old bulls were apparently subdominant to cows, but 2 1/2-year-old bulls both won and lost encounters with cows during the rut. A 4-point bull entered a group of four cows, two calves, and the seven yearlings on 24 April. Cow 1 and at least one other cow displayed aggressively toward him six times, for a total of five head-highs, three bites, and two forefoot kicks, during the 2 hours he was in the group. On 16 September, a cow walked 6 m to 5pt and displayed an 80° head-high for about 4 seconds. The cow and 5pt performed flails. She then chased the bull six trotting steps. The
few aggressive acts cows directed toward 6-point bulls appeared
defensive in nature. Five-point bulls controlled harems poorly. Bulls
3½ years old and older were clearly dominant over younger bulls,
cows, yearlings, and calves.

To compare the frequency of aggressive encounters within
and between the sex-age classes, the number of aggressive encounters
were divided by the number of individuals within each sex-age class
or by the number of individuals in each pair of classes being compared
(Table 9). These data show: 1) cows more often displayed aggres-
sively toward yearlings than to cows; 2) spikes frequently displayed
aggressively to females but infrequently to one another; 3) female
yearlings were more often involved in aggressive encounters with
other yearlings (male or female) than with cows; 4) calves were more
often involved in encounters within their own class than between
classes, and older elk generally did not display aggressively toward
calves.

Displace and Supplant

Elk usually performed displaces and supplants to individuals
of a subdominant sex-age class (64.7%; 11 of 17) (Fig. 7). Displaces
were more common than supplants (88.2%; 15 of 17). Most displaces
and supplants included aggressive behavior (forefoot kicks, forefoot
stamps, head-highs, antler-displays, head-pushes) (82.4%; 14 of 17),
Table 9. Frequency of aggressive encounters within and between the sex-age classes.

<table>
<thead>
<tr>
<th>Rank from most to least frequent</th>
<th>Sex-age classes</th>
<th>Number of aggressive encounters/number of elk</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>spikes and ♀ yearlings</td>
<td>4.6 (32/7)</td>
</tr>
<tr>
<td>2</td>
<td>spikes and cows</td>
<td>4.4 (40/9)</td>
</tr>
<tr>
<td>3</td>
<td>♀ yearlings</td>
<td>4.2 (21/5)</td>
</tr>
<tr>
<td>4</td>
<td>calves</td>
<td>3.8 (15/4)</td>
</tr>
<tr>
<td>5</td>
<td>cows and ♀ yearlings</td>
<td>3.2 (38/12)</td>
</tr>
<tr>
<td>6</td>
<td>cows</td>
<td>2.9 (20/7)</td>
</tr>
<tr>
<td>7</td>
<td>spikes</td>
<td>1.5 (3/2)</td>
</tr>
<tr>
<td>8</td>
<td>cows and calves</td>
<td>0.8 (9/11)</td>
</tr>
<tr>
<td>9</td>
<td>♀ yearlings and calves</td>
<td>0.7 (6/9)</td>
</tr>
<tr>
<td>10</td>
<td>spikes and calves</td>
<td>0.3 (2/6)</td>
</tr>
</tbody>
</table>
Fig. 7. A nose and a forefoot kick performed by a spike to a bedded female yearling before a displace.
some of which included contact (35.7%; 5 of 14).

Cows, female yearlings, spikes, and Calf 1 performed displaces or supplants. Individuals received noses before standing in three cases. Standing beside a bedded elk caused it to stand on two occasions. Bedded elk performed 10 head-highs to standing elk and were not displaced.

Redirected Aggression

One instance of apparent redirected aggression was observed. On 31 July, Cow 1 performed a head-high, followed by a forefoot kick (with contact) to a standing cow. The cow ran 6 m, and groomed the side hit by Cow 1. The cow then turned to a nearby female yearling and performed three head-highs, causing the yearling to move away. The cow and the yearling each performed at least two head-up twists.

Head-off and Turn

Head-offs included forefoot kicks, bites, and head-highs. In some cases, the displayer increased her speed from a walk to a trot in order to overtake the other individual(s) (Fig. 3). In response to receiving a head-off, the individual(s) stopped locomoting, turned away while locomoting, continued on their way apparently uninter rupted, or locomoted faster. One cow stopped four elk from running, and another cow stopped four elk from trotting by moving ahead of the group, quickly turning around to face them, and displaying a head-high.
Fig. 8. A head-off and a turn performed by a cow to another cow.
Repeated head-offs were performed in a few cases. Two individuals trotting alongside another in apparent attempts to get ahead of the other, occurred four times.

L. chased Cow 3 on 11 July for 30 seconds, displaying two head-offs. She performed a jaw as the second head-off stopped her running. L. then performed a chase and a head-off to a female yearling.

A unique occurrence of two individuals performing head-offs to a third elk took place on 29 April. As four cows trotted downhill, one cow performed a head-off to the cow to her left and displayed a head-high. The second cow veered to her left and continued trotting downhill. A third cow, on the second cow's left side, displayed a head-off and a forefoot kick, stopping the cow.

**Daily Activity Cycle**

Daily activity data were obtained for Group 1 elk. A total of 22,503 bits of data were recorded at 2,258 3-minute intervals from 1 July to 2 September. Because calves were most easily obscured by brush and tall grass, less activity data are available for them than for the other groups. If these data had been recorded in addition to the 10,069 active bits actually recorded, active data for all elk would be increased from about 45 to 53 percent. Some inequalities of sampling elk groups in active and non-active times of day appeared, in some
cases, to contribute to or to detract from differences between the
groups. The data, however, are consistent with my subjective
impressions after observing these animals.

A diurnal pattern of activity was apparent (Fig. 9). Elk
almost always locomoted and fed during the 1st-2nd hours and 15th-
18th hours after sunrise. Midday temperatures frequently rose to
about 32°C. Elk locomoted much less than they fed during the early
morning and evening periods; they locomoted and fed more equally
during the midday active period (Fig. 10).

The percentage of time spikes, female yearlings, and cows
bedded, grazed, browsed, and locomoted were very similar (approxi-
mately 52%, 25%, 3%, and 16%, respectively).

Individuals and sex-age classes differed in frequency of some
activities. Calves bedded significantly more and fed less than spikes
\( p < 0.0001, \chi^2 = 180.4, 1 \text{ df} \), female yearlings \( p < 0.0001, \chi^2 = 286.8, 1 \text{ df} \), and cows (excluding Cow 2) \( p < 0.0001, \chi^2 = 225.7, 1 \text{ df} \), but
locomoted when not feeding in very similar proportions to these
groups. The four calves ran more than all other elk combined (20 vs.
19 instances). Cow 2 (see Behavior of an Old Cow) significantly
bedded more, fed less, and locomoted less than the other cows
\( p < 0.0001, \chi^2 = 54.7, 2 \text{ df} \), female yearlings \( p < 0.0001, \chi^2 = 60.2, 2 \text{ df} \), and spikes \( p < 0.0001, \chi^2 = 55.3, 2 \text{ df} \). Cow 2 bedded more, fed
more, and locomoted less than the calves \( p < 0.0001, \chi^2 = 48.1, 2 \text{ df} \).
Fig. 9. Activity pattern, feeding and locomotion combined, for all elk during the summer (1 July-24 August). Sunrise times increased from 0445 on 1 July to 0545 on 24 August. The 2 September data are excluded, due to the probable changing in activity patterns brought about by a rutting bull.
Fig. 10. Activity pattern for all elk during the summer (1 July-24 August). Solid lines = locomoting when not feeding. Dashed lines = feeding. Sunrise times increased from 0445 on 1 July to 0545 on 24 August. The 2 September data are excluded, due to the probable changing in activity brought about by a rutting bull.
Cow 2 locomoted when not feeding about half as often as the other elk.

Cows with calves ruminated more than all other sex-age groups (13.2% of time). They ruminated more than all cows together (10.6%), spikes (9.1%), female yearlings (7.0%), and calves (2.6%). Cow 2 ruminated more than any other individual or group (24.1%).

As calves aged, they bedded less, grazed and browsed more, and locomoted less when not feeding (Table 10). An increase in rumination must have accompanied this increase in feeding, but the data did not show this, probably due to the difficulty in observing rumination in smaller individuals at the usual viewing distances.

The tendency of calves to bed with the head down (14.4%) decreased as they aged (Table 11). Spikes (6.0%), female yearlings (3.2%), and cows (1.4%) also bedded with the head down. Some individual differences, such as Calf 3 bedding with his head down 22.0 percent of the time, were displayed within each activity.

When elk fed, they grazed 83.3 percent and browsed 11.7 percent of the time.

Elk rarely stood while ruminating (0.02%), and stood in water or drank water rarely (0.02%).

**Behavior During the Rut**

A rutting bull in the cow herd caused a marked change in their behavior. The cows which had dominated most or all of the
Table 10. Percentage of time calves spent bedded, feeding, and locomoting while not feeding.

<table>
<thead>
<tr>
<th>Age of calf (in weeks)</th>
<th>Percentage of time in activity</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bedded</td>
<td>Feeding</td>
</tr>
<tr>
<td>0-1</td>
<td>68.2</td>
<td>11.7</td>
</tr>
<tr>
<td>2-3</td>
<td>70.1</td>
<td>16.6</td>
</tr>
<tr>
<td>4-5</td>
<td>56.0</td>
<td>29.8</td>
</tr>
</tbody>
</table>

Table 11. Percentage of time calves spent bedded with the head down.

<table>
<thead>
<tr>
<th>Age of calf (in weeks)</th>
<th>Percentage of time calves spent bedded with the head down</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Calf 1</td>
<td>Calf 3</td>
</tr>
<tr>
<td>0-1</td>
<td>19.3</td>
<td>26.9</td>
</tr>
<tr>
<td>2-3</td>
<td>10.7</td>
<td>15.5</td>
</tr>
<tr>
<td>4-5</td>
<td>8.5</td>
<td>14.4</td>
</tr>
</tbody>
</table>
other elk and travelled, fed, and bedded whenever and wherever they chose, became, along with the female yearlings, recipients of aggressive acts, herds, and sexual approaches. The spikes received aggressive acts and chases by the newcomer, and the calves received chases and herds.

A successful harem bull displayed aggressive acts and herds to the group often enough to keep them bunched together, but not so often that they took flight. His aggressive acts were mixed with less disturbing behaviors and females allowed noses and mounts.

**Harem Leadership Changes**

Males from Group 3 were observed with Group 1 elk on only two occasions from 1 April to 30 August. Bulls were always present in the study area between 31 August and the end of observation on 11 November (Fig. 11). They divided the herd into as many as three small harems. Between 10 and 12 bulls possessed harems at some time during the rut (Table 12). Far viewing distances and similarity between bulls possibly caused some confusion. Between four and 10 other bulls were also observed in Upper South and Lower South ranges during the rut.

Nine encounters between 6-point bulls in possession of a harem and other 6-point bulls were observed. Bulls did not contact one another during any of these encounters. Three of these interactions
Fig. 11. The harem bulls of the rut. Solid lines indicate when the respective bulls possessed harems. Triangles indicate the presence of other rutting bulls. Observations were made infrequently from 22 October to 11 November.
Table 12. The bulls of the rut. Harem bulls are indicated with asterisks.

<table>
<thead>
<tr>
<th>Name of bull</th>
<th>Other names possibly given to same bull</th>
<th>Antler tines (left, right)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bench</td>
<td>Curl, Long, Ridge, Short5th, 6pt, Sym, Thin, Top, Trisky (or their other names)</td>
<td>(6,6)</td>
</tr>
<tr>
<td>Brute*</td>
<td>BA</td>
<td>(6,6)</td>
</tr>
<tr>
<td>Curl*</td>
<td></td>
<td>(6,6)</td>
</tr>
<tr>
<td>Drop*</td>
<td>Drop6th*</td>
<td>(6,6)</td>
</tr>
<tr>
<td>5pt</td>
<td></td>
<td>(5,5)</td>
</tr>
<tr>
<td>5Tel*</td>
<td>5T</td>
<td>(5,5)</td>
</tr>
<tr>
<td>Long</td>
<td></td>
<td>(6,6)</td>
</tr>
<tr>
<td>1A*</td>
<td></td>
<td>(0,7)</td>
</tr>
<tr>
<td>Ridge*</td>
<td></td>
<td>(6,6)</td>
</tr>
<tr>
<td>Short5th</td>
<td>Short5th2nd</td>
<td>(6,6)</td>
</tr>
<tr>
<td>6pt</td>
<td>Bench (or his other names), 6pt2</td>
<td>(6,6)</td>
</tr>
<tr>
<td>Sym*</td>
<td>Sym2*</td>
<td>(6,6)</td>
</tr>
<tr>
<td>Thin*</td>
<td></td>
<td>(6,6)</td>
</tr>
<tr>
<td>Top</td>
<td>Top2, Top3</td>
<td>(6,6)</td>
</tr>
<tr>
<td>TRight*</td>
<td></td>
<td>(6,6)</td>
</tr>
<tr>
<td>Trisky*</td>
<td>Arched</td>
<td>(6,6)</td>
</tr>
</tbody>
</table>
are described elsewhere (Brute-Trisky in "Bugling"; Brute-Ridge and TRight-Drop6th in "Fence Behavior"). The other encounters are described below.

Ridge and Brute confronted each other in the morning following their first observed encounter. Brute left his harem in the Upper South Range at least 300 m behind as he paced the fence line and bugled at the rest of the herd who were with Curl in the Lower South Range. Ridge trotted to Brute's harem. Brute turned, apparently noticed Ridge, and walked back to his harem. Ridge bugled five times, and approached 9 m toward the oncoming Brute. Brute walked for about 10 m with his head parallel to the ground and lowered below his shoulders. This was the only time such a stance was observed. Ridge trotted away when Brute approached within 10 m of him.

Curl, 5pt, and L J kept within 200 m of 1A's harem of seven females, Calf I, and Calf 4 on 23 September in Lower Trisky Woods. When 1A walked away from his harem, bugling at the nearby males, Bowl walked into the harem and bugled once. L J also trotted into the group. 1A bugled, limpingly walked back to the harem, bugled again, and Bowl and L J retreated. The bulls were never closer than 15 m. 1A had only one antler (0, 7), and had an obvious limp in his right rear leg which restricted him to a walk. 1A caused an apparently healthy, although seemingly lighter and younger, 6-point bull to leave the area.
Brute approached to within 20 m of Short5th2nd and 35 m of Top on 24 September, 300 m of Arched on 26 September, and 25 m of Top3 2 days later, before these other bulls retreated from him. Brute performed an antler-thrash, urinated, scraped his forefeet, and lay down as Top3 watched.

Interactions between Brute and Curl were limited to bugling. Brute frequently paced the fence separating them and bugled toward Curl or Curl's harem. Curl maintained a distance of at least 100 m, and at most bugled back at Brute. Brute was apparently the superior bull.

A bull was observed leaving his harem although unprovoked by another bull. A small 6-point bull, Thin, stood and left his small harem, consisting of Cow 4, Calf 4, and Calf 5, at 1135 on 19 October. Thin walked at least 300 m from his group, and then disappeared into the Upper Trisky Woods. At least four elk, including a (3, 6) bull, were later found in those woods. 5Tel, a 5-point bull, was bedded about 15 m from the small harem. Within 5 minutes of Thin's departure, 5Tel stood and vigorously performed herds and noses to the cow and two calves. These four individuals were together 6 1/2 hours later.

Brute was last observed with a harem on 8 October. Five days later (the next field day), Brute, I believe, approached to within 75 m of TRight's harem and lay down. The left main beam of this bull
was broken off at the base of the 5th tine, and one-half of the right 5th tine was absent. (The bull was named BA—Broken Antler.) BA's chest heaved as he breathed for 30 minutes after he bedded. BA bugled twice toward the TRight harem as the harem grazed away from him. TRight bugled and performed an antler-thrash as he and his harem moved away from BA.

At least 5 days after 1A lost his harem to TRight, 1A was observed about 250 m from TRight's harem.

When bulls lost harems, they did not regain a harem in Upper South or Lower South ranges. The only possible exceptions to this are the fence-related disturbance of Brute's harem on 12 September, and the Brute-Trisky encounter of 22 September in which it was not determined whether Trisky did assume leadership.

**Aggressive Acts**

Differences between the aggressive behavior displayed by rutting bulls and Group 1 elk were obvious (Table 6). A significant difference was exhibited in the use of antler displays, spars, head-highs, bites, and kicks between the spikes and the rutting bulls ($p < 0.001$, $X^2 = 34.05$, 4 df), because bulls did not perform head-highs or bites, and they displayed spars and forefoot kicks more frequently than spikes did. Harem members rarely displayed aggressively toward rutting bulls. Harem members never performed forefoot kicks.
to bulls, but bulls frequently performed this display to harem members. All aggressive acts by the bulls, except spars, were done while chasing males or herding harem members. Antler displays by bulls were usually quick, strong lowerings of the antlers while approaching another individual.

All observed spars in Upper South and Lower South ranges involved males of different age classes (86.5%; 45 of 52) and/or males with a fence between them (13.5%; 7 of 52). In the first case, the larger male always won easily; in the second case, usually little was resolved. Spars between males of different age classes appeared to be playful activities for the 1½ and 2½ year olds. The larger bulls easily showed their superior strength either by standing as the smaller bull or spike pushed, or by walking forward as the smaller male stepped backward. After losing spars to 5pt on 9 and 12 September, L♂ cantered backward for at least 60 and 15 m, respectively, with his head lowered (-90°), as 5pt walked toward him. There was no relation between bull size and tendency to initiate or terminate spars. L♂ contacted 5pt's antlers with difficulty, due to the lack of tines on the spike's antlers. 5Tel and L♂ interrupted their brief spars with soft rubbing of each other's heads, necks, and antlers for 5 minutes 30 seconds on 23 September. No apparent injuries resulted from the spars observed, although fatal bull spars have been observed in past years (O'Gara pers. comm.).
Rutting Bull Activity

Instantaneous sample data were obtained for two rutting bulls, Brute during the peak of rutting behavior, and Sym2 later in the season. Brute's activities were recorded every minute for a total of two daylight "days" during 6-9 September (1045-2046, 0630-1044, 1515-2041, 0615-1514, respectively). Sym2's activities were similarly recorded on 29 October (0848-1900). Brute's harem consisted of four cows, two calves, two female yearlings, and one cow or female yearling (LJ was nearby 6-9 September; 5pt was nearby on 7 September). Sym2's harem was comprised of four cows, two calves, five female yearlings. (LS', SJS, and 5Tel were nearby.) The difference in percentage of time spent in various activities between Brute during the peak of the rut and Sym2 at the end of the rut is shown in Table 13. Brute clearly was active more than Sym2. By restricting comparison to similar times of day (0848-1900), a more consistent look at the bulls' activities was obtained because the active morning and evening periods for Brute are deleted. With this restriction, the amount of time spent bedded, standing, feeding, and locomoting was significantly different between Brute and Sym2 ($p<0.001$, $X^2 = 103.38$, 3 df). The amount of time spent bedded and not bedded when comparing these two bulls was also significantly different ($p<0.01$, $X^2 = 6.89$, 1 df), due to Brute's increased tendency to locomote and stand rather than eat.
Table 13. Comparison of activities of bulls at different times of the rut (0848-1900 hours).

<table>
<thead>
<tr>
<th>Date</th>
<th>Bull</th>
<th>Bed</th>
<th>Feed</th>
<th>Stand</th>
<th>Walk, trot</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>6-9 Sept</td>
<td>Brute</td>
<td>50.5</td>
<td>10.1</td>
<td>32.4</td>
<td>7.2</td>
<td>1,159</td>
</tr>
<tr>
<td>29 Oct</td>
<td>Sym2</td>
<td>57.1</td>
<td>23.6</td>
<td>17.6</td>
<td>1.8</td>
<td>581</td>
</tr>
</tbody>
</table>

The rutting activities, spars, herds, noses to females, etc., displayed at each 1 minute interval were also recorded. Brute displayed rutting behaviors 10.3 percent of the time (119 of 1,159 data points) from 0848-1900, and 11.4 percent (191 of 1,676) of all data points recorded. Sym2 displayed such behaviors only 7.2 percent of the time (42 of 581 data points), again showing the higher activity level for Brute during early September compared to Sym2 during the end of October.

The time Brute and Sym2 spent bedded, feeding, and locomoting was significantly different from Group 1 elk (excluding calves and the old cow, Cow 2) \( (p<0.0001, \chi^2 = 513.93, 2 \text{ df} \) and \( p<0.0001, \chi^2 = 19.13, 2 \text{ df} \), respectively).

**Habitat Use**

Elk frequently used areas of coniferous timber during the rut, but spent most of the time before calving and between calving and the
rut in grassland or brush (Fig. 2).

**Herd and Herd-posture**

Performing herds, herd-postures, and aggressive acts toward one or more individuals of a harem tended to keep the harem bunched. A bunched harem was more easily controlled by the bull.

Herd-postures were displayed during most herds (97.1%; 643 of 662). Bulls oriented their bodies and necks so the neck-side was approximately broadside to the harem's direction of movement. This neck-side presentation was also displayed by Brute to Out, Brute to L, and Out to 5pt; in these cases, the males displayed toward moved away.

Most herd-postures were displayed while walking (75.4%; 485 of 643). Trotting (17.1%; 110 of 643), running (7.0%; 45 of 643), and standing (0.5%; 3 of 643) also accompanied herd-postures. The only stot observed for any elk was on 6 September when Brute stotted five strides after displaying a herd-posture. Individuals varied in their use of different locomotions while herding. Brute performed herd-postures while standing or walking in significantly higher proportions than when trotting or running when compared with Curl ($p < 0.005, \chi^2 = 10.33, 1 \text{ df}$). Most herd-postures recorded were displayed by Brute (69.9%; 448 of 643); Curl was second (20.1%; 129 of 643). Bulls locomoted as much as 10 running strides and 30 trotting strides.
while displaying a herd-posture. The head was usually held higher when running than when walking or trotting.

A response from one or more harem members was elicited by almost all herd-postures (93.8%; 603 of 643). Responses ranged from running from the bull to flattening the ears and turning away from him. Most herd-postures not responded to were displayed as the harem members happened to be looking away from the bull. Herd-postures typically lasted from about 4 to 8 seconds (maximum of 20 seconds).

Stamping a forefoot (1.2%; 8 of 643) and antler displays (0.8%; 5 of 643) infrequently terminated herd-postures. The bull's penis rarely palpitated while he displayed a herd-posture (0.9%; 6 of 643); the difficulty of observing this behavior at least partially accounts for its rarity in the data. Females seldom performed jaws in response to a herd-posture (0.8%; 5 of 643).

Bulls often performed herds to move their harems away from spikes and other bulls, rather than display chases to the intruding males. On 17 September, I attempted to quantify the degree Curl displayed herd-postures in order to keep his harem away from L♂ and 5pt. Imagining a large square bounding the group, more than half of Curl's herd-postures were displayed on the side where 5pt or L♂ were situated (53.6%; 22 of 41). Rates of herd-postures per active (non-bedded) hour ranged from 0 to 28.
5pt and 5Tel, the two 5-point bulls, and L♂ poorly controlled the movement of females. 5pt's two herd-postures were apparently ignored by Calf 1, and three of L♂'s five herd-postures elicited no response. One female trotted away from L♂ after a herd-posture, shaking her head as if bothered by him. L♂ weakly executed herd-postures; his head lowered little from normal, and his nose remained at about -20°.

Performing a herd without a herd-posture was usually done while trotting or running, and was often displayed when a bull brought back a female who had strayed more than about 50 m from the group. One herd displayed by Brute to Cow 1 lasted 3 minutes; most herds lasted less than about 15 seconds. Females driven away from the harem by the bull circled back and joined the group.

Bulls occasionally allowed their harems to stray as far as 100 m from them. Bulls usually were situated within or along the periphery of their harems. When not performing herds, bulls usually followed the lead of the rest of the group. One female strayed as far as 200 m from Brute's harem on 24 September. Top soon appeared and grazed near her until Brute drove him away. Brute permitted her to stay out of the harem, and allowed a female to graze as far as 50 m from his harem 1 1/2 days later.
Bugling

Only rutting bulls were heard bugling (204 instances). Bugling usually, possibly always, was directed at another bull, a spike, or a harem. Cows and calves showed little or no response to bugling. Spikes usually moved away from a bugling bull.

A bugling dialogue caused Brute to leave his harem on 22 September when the intruding bull, Trisky, was in timber and at least 65 m from the harem. Bugling also accompanied encounters between Brute and Ridge, TRight and Drop6th, 1A and Bowl, and a through-the-fence encounter between Brute and Curl. Intruding bulls and harem activity apparently exerted greater effect on bugling frequency than did any inherent daily cycle of bugling. Bulls usually stood or walked while bugling, although BA, TR, and Brute bugled three times, three times, and once, respectively, while bedded. On two occasions, TR distinctly double-bugled by vocalizing two of the long calls followed by a series of grunts. Buglings ended with from two to seven grunts. Pitch and length of buglings varied.

Buglings were distorted by distance and were very directional. A few buglings were heard from as far away as 0.5 km. On 23 September, I heard 1A bugle at Bowl while I was 40 m away. This vocalization was very loud, low, and beautiful, with a two-toned quality. Much of the musically pleasing qualities of buglings were lost in distance, and the vocalizations sounded more like "whistles,"
as they are often called. A bugling heard from 100 m away, given by a bull with his head turned at a 45° angle from the observer, could sound no louder than one given by a bull directly facing the observer 250 m away. Wind direction and velocity also determined what was heard. Barely audible buglings often sounded like, "Eeeee-yu-yu-yu-yu!"

Brute's and TR's penises palpitated once as they bugled on 23 September and 2 October, respectively.

The 30 calls Brute gave as he paced and watched most of his harem on the other side of a fence (see the Brute-Ridge encounter in "Fence Behavior") were one-syllable, airy vocalizations that sounded like the first 1/2-second of a full bugle.

**Chases of 5-point Bulls and Spikes by Harem Bulls**

Harem bulls repeatedly chased L♂, S♂, 5pt, and 5Tel away from the harems. The spikes were difficult to keep away from the groups they had lived with all their lives. They frequently circled back into the group when the bull stopped the chase, or tried to join the harem soon thereafter. The 5-point bulls were easier to exclude from the harems than the spikes were. Much repetition was necessary to keep the spikes and 5-point bulls away from the harems. Chases were performed by Brute to L♂, S♂, or 5pt 88 times; Curl to L♂ or 5pt 24 times; TRight to L♂ five times; 1A to L♂ or 5pt four
times; Sym2 to L♂ and S♂ twice and 5Tel three times; Drop to L♂ twice; and Ridge to L♂ once. Bulls usually trotted or ran during chases.

Most chases took place during the first few weeks of the rut. During the first 2 weeks of the rut, L♂ spent much of his time trying to get past Brute back into the harem. Over 94 percent of all recorded chases by Brute took place from 31 August to 13 September (94.3%; 83 of 88), during only 35 percent of the days he possessed a harem. By mid-September, the spikes and 5-point bulls seemed to accept the situation. They frequently approached to within 100 to 400 m of the harems, and they generally kept in sight of their harem. The spikes and 2½-year-old bulls often joined a harem when the harem bull was bedded, performing a wallow, or away from the harem. The spikes and 5-point bulls were occasionally permitted to move and bed with a harem.

Temporary dyadic associations were formed between pairs of non-harem bulls and spikes; L♂ with 5pt, 5Tel, 6pt, or Bench; Out "with" L♂ or 5pt; Short5th with 5pt. The tendency for males to be together was observed as early as 24 June after the cows displayed aggressively toward a transient 4-point bull, causing him to leave the area. S♂ followed the bull for at least 400 m before he returned to the group.

Other aggressive acts were associated with chases
infrequently. Only three forefoot kicks (2.3%; 3 of 129) and two antler displays (1.6%; 2 of 129) accompanied chases.

**Sexual Approach**

Sexual approaches initiated many encounters between bulls and females. Females occasionally moved away from an approaching bull before contact. Sexual approaches and other approaches usually led to noses, licks, nose-to-noses, throat-places, and mounts. An average of 2.1 of such behaviors per bull-harem member encounter were recorded (692 in 332 encounters). The females and calves almost invariably moved away from the bull during these behaviors.

**Nose and Lick**

Noses and licks were displayed frequently (Table 14). Rumps or inguinal regions received the majority of noses or licks (84.4%; 433 of 513). Females' and calves' heads, necks, sides, and backs also received noses or licks (15.6%; 80 of 513). Standing harem members received noses or licks more frequently than did bedded elk (77.6%; 398 of 513). Bulls' penises palpitated during rump licks on a few occasions.

Most Flehmens occurred shortly after a bull performed noses or licks to a female's rump (57.3%; 63 of 110). Bulls frequently exhibited a Flehmen after performing a nose or, in a few cases, a lick to the ground on which a female or calf had bedded or
Table 14. Number of noses and licks by rutting bulls and spikes toward females and calves.

<table>
<thead>
<tr>
<th>Bulls</th>
<th>To rumps or inguinal regions</th>
<th>To areas other than rumps or inguinal regions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>To standing individuals</td>
<td>To bedded individuals</td>
</tr>
<tr>
<td>Brute</td>
<td>275</td>
<td>38</td>
</tr>
<tr>
<td>Curl</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>5pt</td>
<td>14</td>
<td>--</td>
</tr>
<tr>
<td>5Tel</td>
<td>3</td>
<td>--</td>
</tr>
<tr>
<td>L♂</td>
<td>21</td>
<td>--</td>
</tr>
<tr>
<td>1A</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Ridge</td>
<td>11</td>
<td>--</td>
</tr>
<tr>
<td>S♂</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>Short5th2nd</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>Sym2</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>TRight</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>373</td>
<td>60</td>
</tr>
</tbody>
</table>
urinated (38.2%; 42 of 110). Bulls also performed a nose to the ground recently vacated by a female without displaying a Flehmen (18 instances). Flehmens ranged from 3 to 41 seconds ($\bar{X}=20.0$ s, n = 97).

**Nose-to-nose**

Nose-to-noses were displayed infrequently between harem bulls and harem members (Table 15).

<table>
<thead>
<tr>
<th>Bulls</th>
<th>Nose-to-nose</th>
<th>Throat-place</th>
<th>Mount</th>
<th>Mount-with-copulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brute</td>
<td>18</td>
<td>119</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Curl</td>
<td>1</td>
<td>8</td>
<td>2</td>
<td>--</td>
</tr>
<tr>
<td>5pt</td>
<td>6</td>
<td>2</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Ridge</td>
<td>1</td>
<td>1</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Short5th2nd</td>
<td>--</td>
<td>1</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Sym2</td>
<td>--</td>
<td>9</td>
<td>2</td>
<td>--</td>
</tr>
<tr>
<td>TRight</td>
<td>1</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

**Displace and Supplant**

Most of the displaces and supplants observed from 1 April to 11 November were performed by rutting bulls (78.2%; 61 of 68). Bulls caused females and calves to stand by performing sexual approaches, noses, licks, grooms, or by standing near them. Females usually stood before 15 seconds of a nose, lick, or groom took place. The
longest groom lasted 6 minutes. The bulls usually performed noses or licks to the standing female or noses to the ground she vacated after a displace. Three supplants were performed.

**Throat-place**

Throat-places preceded mounts, but most females who remained standing during a throat-place did not receive a mount. Rump noses or licks often preceded or followed one or more throat-places. Although bulls frequently displayed noses and licks to male and female calves, the 6-point bulls never performed a throat-place to a calf. 5pt, however, performed five throat-places to Calf 4 on 17 September.

**Mount and Mount-with-copulation**

Bulls rarely performed mounts and mount-with-copulations (Table 15).

Curl and Sym2 performed mounts. Three times Curl performed sexual approaches, throat-places, and licks to a female on 15 September. He lifted his forefeet off the ground as mounts during the second and third throat-places. She withdrew each time. On 29 October, Sym2 stood, performed a sexual approach and then a nose to the rump of a bedded female. She stood and trotted away from him. Sym2 followed, performed two throat-places, and lifted his forefeet from the ground during a mount. She withdrew. He followed,
performed three throat-places and another mount. She withdrew, and he no longer followed her.

Brute copulated with a female yearling at 0758 on 9 September. The mount-with-copulation was preceded by four rump noses, two throat-places, two grooms to her back, and five mounts. His penis unsheathed during the third mount, and he raised onto his hindlegs and contacted his chest to her rump on the fourth mount. He then performed a lick to her back while standing directly behind her, raised onto his hindlegs, positioned his unsheathed penis, moved slightly forward, and leaped forward and upward as copulation occurred. Brute's leap sent her forward about 1 m. After he backed off of her, she stood with her back arched for 15 seconds, and remained standing for 3 minutes 45 seconds. She excreted some liquid after copulation. Brute faced the yearling, who was 2 m away, from 0758 to 0810. Brute nosed the ground below where her rump was positioned during copulation and displayed a 22 second-long Flehmen at 0813. She began browsing at 0804, then bedded at 0813. He performed a nose to her 1 minute later, causing her to stand. He then performed a nose to the ground she vacated, but did not display a Flehmen. She bedded again at 0816.

Brute attempted to copulate with another female yearling from 1359 to 1552 later that day. This yearling showed that cooperation is necessary to effect copulation in elk. She continually moved away from his sexual approaches and contacts. Brute performed 55 noses or licks...
to her rump and 5 licks to her back as she stood, 16 noses or licks as she bedded, 50 throat-places, two mounts, and two Flehmens. His penis partly unshched during one throat-place. The rest of the group then stood, and the harem grazed. Brute resumed typical herding behavior and did not approach the yearling again for at least 15 minutes.

Females standing with rear legs spread apparently stimulated bulls to perform sexual approaches to them, probably because the females appeared to be standing to receive a mount. Bulls performed sexual approaches to nursing cows 13 times, and to females, standing with rear legs spread while stretching or self-grooming twice.

Wallow, Antler-rub, -scrape, and -thrash

Wallows, antler-rubs, antler-scrapes, and antler-thrashes occurred commonly from 1 September to 29 October (the last lengthy observations of a rutting bull). The polished-antlered bulls apparently had performed antler-rubs and antler-thrashes before 1 September (see Growth and Pelage Change).

Antler-thrashes were more frequent (73.1%; 49 of 67) than antler-scrapes (23.9%; 16 of 67) or antler-rubs (3.0%; 2 of 67). Plants contacted during thrashes ranged in size from 0.3 m tall snowberry (Symphoricarpos), 1 m tall cattails (Typha), 2 m tall Ponderosa pine, and 4 m tall deciduous trees. Sym2 rubbed one side of his head against some brush during an antler-thrash on 29 October. Thrashes
ranged from 10 seconds to 17 minutes 24 seconds ($\bar{X} = 5$ min., 22.7 sec.,
$n = 34$).

The antler-thrashes that preceded wallows (24.5%; 12 of 49
wallows) were usually performed in one of the several cattail ponds.
After lying down, bulls often rolled onto their sides, dug with their
antlers, and performed thrashes with the cattails. Bedding bouts after
antler-thrashes lasted from 1 minute to several hours. After a wallow,
bulls were often black with mud and had some vegetation, usually
cattails, hanging from their antlers. A few antler-thrashes included
digging or stamping with the forefeet (8.2%; 4 of 49). A bull's penis
palpitated during an antler-thrash in at least one instance.

Most antler-scrapes were performed while urinating onto the
ground or body (75.0%; 12 of 16). A bull urinated onto his body when
not performing an antler-scraper on two occasions. Bulls urinated onto
their bellies, forelegs, and, with the head lowered close to the ground,
the ventral surface of their necks. The bull lay on the scrape-urinated
spot on five occasions. Once a bull pawed the ground with a forefoot
while displaying an antler-scraper.

**Lowered Head Posture and Jaw**

Females frequently displayed lowered head postures and jaws
in response to sexual approaches, noses, licks, throat-places, and
mounts. Most lowered head postures occurred while moving or
standing (77.5%; 62 of 80). In most of these instances, the female performed a jaw while in the lowered head posture and locomoted away from the bull (77.4%; 48 of 62). A bull approaching from as far away as 6 m stimulated females to perform jaws, but in most cases contact was made before a female performed a jaw. Females occasionally moved their heads from side to side while retreating in the lowered head posture. They usually opened and closed their mouths 5-10 times per jaw. One female opened and closed her mouth 30 times as Brute closely approached her. Another female did so 78 times as Brute walked beside her on the other side of a fence. One cow displayed a nose to Brute's inguinal region, without contact, then turned and performed a lowered head posture and a jaw as she withdrew.

Bedded females occasionally displayed lowered head postures and jaws when a bull performed a sexual approach or contacted them. The only instance of a female performing a jaw when not assuming a lowered head posture was displayed by bedded Cow 1 as she lifted her nose to about 70° eight times while opening and closing her mouth as 1A stood beside her.
CHAPTER V

DISCUSSION

Group Behavior

The social regimes of cow and bull groups of the elk of the National Bison Range were similar to those of red deer as described by Darling (1937):

The sociality of red deer is matriarchal, and the apparent modification of this structure for a short season of the year does not break up the matriarchy and establish a patriarchy.

The stag company is a number of egocentric males and is a very loose organization. There is no apparent leader, though one animal may be in a position to bully the rest, which is quite a different thing.

Alert-alarm Behavior

Tourists and biologists observed that the elk of Upper South and Lower South ranges became wilder since the five original individuals of this group were released in 1972. It seems likely that this trend toward wildness will continue, until they become about as wild as Group 3 elk. With this change may come a shifting in use of the Range--less use of the humanly disturbed areas and more use of the undisturbed regions. It is impossible to predict whether elk from Groups 1 and 3 will frequently associate out of the rut in the near future.
Holding the mouth open during disturbing conditions, displayed by Rocky Mountain elk on the Bison Range and by tule elk (McCullough 1966), was not performed by Roosevelt elk (Bowyer 1976). The elk subspecies may react to similar conditions with different displays.

**Vocalization**

There are probable functions to all vocalizations by elk. Calves squealing when disturbed, which attracted cows' attention and brought them to the scene of a disturbance, would often benefit the calf. Cow 5 chased a group of coyotes when three calves were nearby, and cows sometimes fight predators in defense of their young (Seton 1929, Murie 1951, Altmann 1952, McCullough 1966). Cows calling their calves before sucklings could increase the amount of milk ingested by the calves, and so help their growth. Cows and calves vocalized to one another frequently when not in nursing activities. A continuous dialogue between cows and calves may help to keep the animals together (Murie 1932, Altmann 1956b), and an interruption in the callings may communicate danger or warning (Altmann 1963). However, cows vocalizing during a disturbance appeared to alert the group members to the situation and probably assisted in cohesive action. Cows nearing parturition were not observed bugling, as reported elsewhere (Murie 1932, 1951, Altmann 1952, 1956a, 1963).

**Urination and Defecation**

Urinating and defecating in response to a disturbance may serve as alerting signals to the rest of the group (Geist 1966). It may
be advantageous for elk to void themselves of waste before possibly taking flight. At least two occurrences of urination postures were observed, but one author reported that elk display no conspicuous urination posture (Geist 1966).

**Calving and Cow-calf Behavior**

**Habitat Preference During Calving**

Elk stayed in coniferous timber and timber-grassland edge more often during, and up to 3 weeks following, parturition than during any other time from April through November. Some Rocky Mountain elk cows seem to seek a safe place for calving (this study, Johnson 1951, Altmann 1963, Fraser 1968); however, other cows seem to show no such behavior (Murie 1951). Tule elk apparently calved away from areas used frequently by elk throughout the year (McCullough 1966). Red deer generally do not seek especially safe calving areas (Darling 1937).

**Hiding Behavior**

Elk calves moved slowly and held their noses close to the ground before hiding or while standing between hides. Pronghorn fawns moved to hiding locations and hid very similarly to elk calves when executing the "move to lie secluded" (Autenrieth and Fichter 1975). Hiding behavior has been described for red deer (Darling 1937, Bubenik 1965 in Lent 1971) and wapiti (Murie 1951, Altmann 1952, de Vos et al. 1967). Hiding behavior functions "as a strategy for avoiding predation and as a means of gradually introducing the infant
into a closed social group" (Lent 1971).

Some Bison Range cows returned to their young, hiding calves during both the day and night. Tule elk cows apparently did not return to their calves during the day (McCullough 1966).

**Cow Behavior When with Her Young Calf**

Cows appeared reluctant to leave areas during a disturbance when their young calves were hiding nearby, but tended to take flight when their calves were older. There are probable selective advantages for a cow to stay near her very young, hiding calf during a potentially dangerous situation, and to run from such a disturbance when the calf is older and strong enough to follow quickly. Cows stood almost motionlessly for hours as their young calves bedded nearby. Such behavior would make the cow less conspicuous to predators, permit the cow to guard the calf from, and alert the calf to, predators, and allow the cow-calf pair to observe one another and to perform nursings, social-grooms, etc. more easily.

**Social Integration**

Cows and calves of the Bison Range joined other elk when the calves were less than 1 week old. The young ages at which calves and their cows joined the rest of the elk, compared to Rocky Mountain elk at other locations (Harper et al. 1967, Altmann 1963) and Roosevelt elk (Lieb 1973) could be due to either the herd's cohesiveness and small size or to the "considerable variation in this period" (Altmann 1952).
Nursing behavior in Roosevelt elk was usually initiated by a call from the cow (Bowyer 1976). Such calls were rarely heard from Range elk. McCullough's (1966) description of nursing initiation in tule elk is confusing. He stated that nursing was usually initiated by the cow by some signal, probably auditory, and that the calf was "never rejected." But calves attempting to initiate nursing were "only occasionally successful." Since he did not determine the identity of the signal, it seems impossible to differentiate between cow- and calf-initiated suckles and attempts to suckle.

Vocalizations before suckles were heard on five occasions. Reasons for this infrequency include long viewing distances, highway noise, the probable directiveness of the calls, and, I believe, the common absence of vocal solicitation.

Eight of the nine calf-ended suckles were by Calf 1 when she was 4-7 days old, indicating a selective advantage for cows to permit their very young calves to suckle as long as they want. Cows almost always terminated sucklings when their calves were older than 1 week. Such a change in termination of nurses has been described for other ungulates (Lent 1971).

The rate of nurses per 24 hours for each month for Bison Range calves were less than for red deer, which suckled six times per day in the first 3-4 weeks, but the Bison Range calves suckled more
frequently than the 3 times per day noted for 2-month red deer (Bubenik 1965 in Lent 1971). If Bubenik's (1965) definition of "day" was "daylight hours," my findings would be much less than his for the young calves, but similar to his for the 2-month-old calves. Other populations of Rocky Mountain calves suckled five to six times per day (Harper et al. 1967). The frequency of suckles of very young Calf 1 is similar to other Rocky Mountain elk, who tended to suckle most frequently right after birth (Altmann 1963). All species of cervids studied by one author displayed "a marked decrease in frequency of nursing... as the offspring age" (Lent 1971). Weaning, initiated by the decrease in rate and duration of suckles as the calves aged, took place in October. Rocky Mountain elk calves are reported to be weaned by November (Harper et al. 1967), but may still suckle in December (Johnson 1951) and January (Murie 1951). If a red deer cow's ability to give milk wanes or if she dies in the fall, "there is little hope of the calf surviving" (Darling 1937). Calf 5, however, survived her mother's disappearance when the calf was 17 weeks old. The frequency and duration of nurses in Roosevelt elk were virtually constant from August through October (Bowyer 1976). Both frequency and duration of suckles declined from June through October in Range elk. This decrease in nursing behavior was coupled with an increase in grazing and browsing.

Two Bison Range elk calves performed two thief-suckles each,
all while the cow was nursing her own calf. Thief-suckles were performed once by a tule elk calf (McCullough 1966), once by a Roosevelt elk calf (Bowyer 1976), and twice in several hundred observations of caribou (Rangifer tarandus) nursings (Lent 1971).

The significant increase of suckle attempts over successful suckles, in disturbed compared to undisturbed situations, showed that cows tended to prohibit suckles under troubled conditions. Ungulate young of many species attempt to suckle during a disturbance, and these alerted mothers also tend to prohibit nursing (Lent 1971). Cows were evidently less alerted by bison than by humans, indicated by the two suckles permitted during a bison bull disturbance (and other alarming situations).

"Nursery group" (Altmann 1952) or creche formation was not observed. Studies of other Rocky Mountain elk (Struhsaker 1967) and tule elk (McCullough 1966) made no mention of such behavior, and a Roosevelt elk study "found nothing to indicate" (Bowyer 1976) the presence of "'elk-calf-pools' with one or two caretaking cows in charge" of from four to 70 calves (Altmann 1952). Other Roosevelt elk studies, however, observed groups of three to eight calves with one or more cows or female yearlings (Lieb 1973, Franklin et al. 1975). The existence of nursery groups could be due to the calves' tendency to travel, graze, and bed together rather than the cows intending to take care of the many calves of the group. Temporary
grouping of elk during and following a disturbance could cause an observer to assume a group of calves to be under the supervision of a lesser number of cows.

**Bedding Behavior**

Elk usually bedded so they did not face directly toward another elk. Possible functions of this behavior are to avoid aggressive behavior, to use favored bedding spots, to orient themselves comfortably on slopes, to utilize solar radiation correctly at different times of day, to avoid strong winds, and to maximize the collective observation of their surroundings.

**Mutual-groom**

Mutual-grooms between a cow and her calf were significantly longer than simple cow to calf social-grooms. Since grooms clean the pelage, there may be a selective advantage for calves to social-groom their cows and so lengthen the grooms received.

**Nose-to-nose**

Dominant Group 1 elk occasionally initiated nose-to-noses with subdominant individuals. Nose-to-noses in Roosevelt elk ("presents"), however, were performed as subordinate individuals "cautiously approached a dominant one" (Bowyer 1976). Nose-to-noses may serve as greetings or individual identifications, evidenced by their exhibition before suckles or suckle attempts (3.0%; 19 of 298...
suckles or attempts), during the joining of two groups of elk (5 instances), and before cow-calf social-grooms (0.9%; 4 of 43 social-grooms). Aggressive acts less frequently followed nose-to-noses than noses, probably due to the more cooperative nature of this behavior.

Mount, Throat-place, and Chest-bump by Elk other than Rutting Males

Classifying mounts, throat-places, and chest-bumps by elk other than rutting males as dominance displays, which has been done for Roosevelt elk (Lieb 1973, Bowyer 1976), bison (Lott 1974), and pronghorn (Kitchen 1974), would be too subjective for the data collected in this study, because these behaviors were displayed in several contexts and along with a variety of non-aggressive displays.

Head-up Twist

An elk displaying a head-up twist was apparently aggravated or disturbed. This display was called "fly-chasing behavior" in McCullough (1966).

Aggressive Behavior

Head-high

Head-highs executed with unflattened ears possibly indicated low intensity aggressive behavior because ear flattening almost always accompanied the apparently more aggressive displays.
Bite and Kick

Bites and forefoot kicks by Roosevelt were similar to those of Range elk, but Roosevelt elk much more frequently contacted other individuals when performing these aggressive acts (Lieb 1973, Bowyer 1976). Forefoot kicks by tule elk almost never resulted in contact (McCullough 1966), as was true for Range elk. While performing a forefoot kick, some Rocky Mountain elk held the nose "nearly horizontal" (Struhsaker 1967). Bison Range elk, however, held the nose about 20° above the horizontal.

Other Rocky Mountain elk may perform head-highs coupled with bites as Range elk did. Struhsaker (1967) stated: "Elevating the muzzle was sometimes followed by kicking with a stiff foreleg or by the extended-head threat." The "extended-head threat" was similar to the herd-posture of my study, but Struhsaker (1967) described cows displaying this gesture "in its simplest form." The extended-head threat for cows was apparently a bite, judging from his description of this display for cows, and his lack of describing bites. Geist (1966) described an "open-mouth, head-up display as a biting threat." Displays similar to head-highs, but not noted to be in conjunction with bites, were reported for tule elk (McCullough 1966) and Roosevelt elk (Bowyer 1976).
**Antler Display**

The only instance of two unantlered elk directing their foreheads toward one another involved L♀ and S♀ on 30 April. Antler displays may be fixed action patterns that can be exhibited before antler growth.

**Head-push**

Head-pushes were performed most often by males, indicating a similarity between antler use and forehead use in aggressive behavior.

**Hierarchical Relationships**

The aggressors in non-contact aggressive encounters in Struhsaker's (1966) study were always the same age or older than the elk displayed toward (with possible exceptions of cows and bulls older than 3½ years). However, spikes of the Range infrequently initiated aggressive encounters with cows. The lack of aggressive behavior between L♀ and S♀ could have been due to one of the spikes being so dominant that contests were unnecessary. If that were true, the dominance had been established before they were 10 months old. If neither of these similarly sized spikes were dominant, they were apparently comfortable with the arrangement. In tule elk, cows usually were dominant over 2½-year-old bulls until the bulls "developed sexually to the stage where they are adequately aggressive and initiate
encounters with cows based on an antler threat" (McCullough 1966). Limited observations suggest that this is true for Range elk also.

Roosevelt elk displayed a higher frequency of aggression between sex-age groups than within groups, other than the calves (Lieb 1973). This was generally true for Group 1 elk, except female yearlings took part in aggressive encounters with other female yearlings more often than with cows.

Daily Activity Cycle

The diurnal pattern of activity strongly indicated that elk feed during the night. The differences in feeding and locomoting percentages when active appeared to show that the early morning and evening periods serve mainly as feeding times, and the midday active period serves both movement and feeding. Crepuscular increases in activity have been reported for Roosevelt elk (Bowyer in press), tule elk (McCullough 1966), and Rocky Mountain elk (Mackie 1970, Stehn 1973). The Rocky Mountain elk of the Bison Range were less active than Roosevelt elk in midday, and began evening activities later than Roosevelt elk (Bowyer in press). Bison Range elk grazed when feeding less than Roosevelt elk did (88% vs. about 96%; Bowyer in press). Brute, Sym2, and probably the other rutting bulls were less active than Roosevelt bulls during the rut (50% and 43% vs. 58%; Bowyer in press).
Behavior During the Rut

Aggressive Acts

Bulls did not contact each other during the nine encounters between 6+-point harem bulls and other 6-point bulls, suggesting that the bull hierarchy was established before rutting activities began in Upper South and Lower South ranges.

Roosevelt elk bulls performed a "post-spar present" as they turned their forequarters away from their opponents after a spar (Bowyer 1976). Some Rocky Mountain bulls performed a similar display, a "present-threat," as they walked or trotted beside one another, in a "parallel march" before a spar (Geist 1966). Bison Range elk did not perform such displays before or after any of the 57 spars observed. However, the three neck-side presentations by rutting bulls toward other males were similar to these displays described for other elk. The frequency of aggressive acts increased during the peak of the rut for tule elk (McCullough 1966), but no such trend was evident for Range elk. There appeared to be a reduced rate of aggressive behavior during initial rutting activity which increased to the usual non-rut level during the peak of the rut.

Habitat Use

Elk frequently used areas of coniferous timber during the rut, and other elk in Montana also preferred regions of heavy timber at that
time (Janson 1974, Lonner 1974, Joslin 1975, Smith 1978). By comparing use of habitats by cow, bull, and bull-cow groups, the females of the harems proved to be responsible for this habitat use change in one area (Joslin 1975). Roosevelt elk, however, preferred the open coastal prairie during the rut rather than semi-open and thick alder (Alnus sp.) groves or redwood (Sequoia sempervirens) forests (Bowyer in press).

**Bugling**

Murie's (1932) description of bugling of Rocky Mountain elk bulls well fitted the typical bugle heard at the Bison Range:

The call begins on a low note, slides upward until it reaches high, clear, bugle-like notes, which are prolonged, then drops quickly to a final grunt, the call frequently being followed by a series of grunts. The call may be roughly represented thus: "A-a-a-a-ai-e-eeeeeeeeee-ough! e-uh! e-uh! e-uh! e-uh!"

McCullough (1966) and Bowyer (1976) described in detail the possible functions of bugling.

**Mount-with-copulation**

Mount-with-copulations may have taken place mainly at dawn and dusk, as in some areas (Murie 1951), which would partially account for my seeing only one copulation. It seemed, however, that bulls were ready to copulate whenever given the opportunity. Copulation was observed during the day in other studies, and no mention was made of diurnal copulatory cycles (McCullough 1966, Struhsaker 1967, Bowyer...
1976). The yearling Brute copulated with on 9 September stood with her back humped after being bred, as did tule elk females after being bred (McCullough 1966).

Wallow, Antler-rub, -scrape, and -thrash

Antler-thrashes and antler-scrapes with urination may advertise the bull's physical condition and scent-mark the lower backs of copulated females (McCullough 1966). When Sym2 rubbed one side of his head against brush during an antler-thrash on 29 October, he may have deposited pheromones from his preorbital glands (Fraser 1968) as a type of sign-post marking (Graf 1956). Wallowing is done by bulls at least 3½ years old and, occasionally, by 2½-year-old bulls (Murie 1951). Generally, this was true for Bison Range males, except 5pt, a 2½-year-old bull, wallowed six times and L♂, a 1½-year-old male, wallowed once. Wallowing may serve to soothe the "rutting fever," cool the body, and act as a release for energy (Murie 1951). Moose may wallow in urinated pits in order to transfer the scent to their body (Geist 1963), and this may also be true for elk. The distinctive appearance of a mud-covered bull may aid one rutting bull in locating another rutting bull (Struhsaker 1967). By wallowing and scraping the ground with the forefeet, bulls may be claiming occupancy, although only temporarily, which could have an intimidating effect on challengers (Walther 1971). Two bulls simultaneously marking nearby
areas could be communicating a challenge (Walther 1971). Such functions and communications could also be true for antler-rubs, -scrapes, and -thrashes.

Management Implications

Human disturbances were infrequent, other than the almost continual flow of human noise from U.S. Highway 93. The elk usually were able to leave areas of disturbance if they chose, which undoubtedly lessened the alert-alarm behavior displayed.

The elk of the Range lived with a minimum of interspecific strife.

The boundary fences, about 2.6 m high, prohibited most, though not all, elk from jumping over. Fences with the bottom wire less than about 40 cm from the ground prohibited elk movement; bottom wires at least 48 cm from the ground permitted most non-antlered elk to crawl under. Bulls were hesitant to, but capable of, jumping over fences 1.7 m tall. The interior fences caused many unnatural and disturbing conditions by permitting young, small bulls to control harems, by separating individuals which attempted to stay together, and by adding to troubled situations by blocking flight during a disturbance.

The tendency for cows to seek dense cover during, and for up to 3 weeks following, parturition, suggests that such habitats must be
available during that critical time.

Calf 5 was only 17 weeks old when her mother was separated from her for at least $3\frac{1}{2}$ months. The calf stayed with other elk, seemed to remain healthy, and apparently did not thiefsuckle. A calf 17 or more weeks old, whose cow is killed, dies, or experiences a lessened ability to give milk, may remain healthy.

The amount of time spent feeding could indicate the food quality and/or quantity in an area, assuming elk feed no more than is necessary.

Concern has been expressed for the "suppression" of rutting activity and mating due to the hunting of bulls during the rut (Altmann 1956a). The argument has been proposed that removal of the "trophy" males from an ungulate population could lead to negative changes in social structure, reduced productivity, and degredation of genetic quality. For such reasons, the bull-only bugling season for elk was ended in Montana in 1975. My observations of rutting behavior at the Range indicate that if all 6-point or better bulls were removed before the rut, the 5-point or less bulls and many of the spikes would take over as harem bulls. These males were less able to control harems, and, assuming they had smaller fat reserves, probably would be less able than large bulls to maintain high degrees of energy output. These inabilities could permit less "organized" leadership of harems and encourage more aggressive behavior between males and between harem
males and harem members. The obvious readiness of 5-point bulls to mate, coupled with the recurrent estrus of the cows (Morrison et al. 1959), would probably insure similar productivity. Shooting bulls during the rut would add human disturbance to the apparently stressing situation, causing flight behavior and changes in harem ownership.
CHAPTER VI

SUMMARY

A herd of Rocky Mountain elk (*Cervus elaphus nelsoni*), maximum of 20 individuals, was studied intensively from 1 April to 11 November 1977 on The National Bison Range, Moiese, Montana. Eleven elk were individually identified. In addition, 14-22 bulls which associated with them were observed during the rut. The objectives were to describe and quantify the social behavior of these elk, describe behavioral displays and discuss their possible functions, and compare this group's behavior to that of elk in other studies.

The Range was divided into eight bison ranges. In addition to the cows, calves, and yearlings who remained in Upper South and Lower South ranges (Group 1), five elk in the public display pasture (Group 2) and about 66 elk of other parts of the Range (Group 3) also lived on the Bison Range. Females and calves of Group 3 were never observed with Group 1.

Descriptions of 52 behavioral acts allowed more efficient analysis of behavior, facilitated comparisons with elk of other areas, and will permit other workers to compare their observations with the Bison Range data.
Elk vocalized a variety of sounds. Disturbances and attempts to join other elk apparently elicited vocalizations. Individuals varied in their abilities to crawl under interior fences at five passageways 48-94 cm high. The fences caused many unnatural and disturbing situations by blocking flight paths during disturbances, separating individuals which attempted to stay together, and permitting young, small bulls to control harems.

A 16-18 year old cow suffered from many physical problems, and behaved differently from other elk. Her apparently healthy calf died of starvation when 8 days old.

Elk were more often found in or within 200 m of coniferous timber from 27 May to 21 June, the dates of calving, than during any other time. Calves less than 2 weeks old frequently hid during the day, but also moved as much as 0.5 km per 24-hours with their dams. Cows were reluctant to leave an area when their young, hiding calves were nearby. The social integration of calves began within their first week of life. Calves initiated most nursing interactions. Cows terminated most sucklings of calves over 1 week old. The frequency of suckles and suckle attempts and the duration of suckles decreased as calves aged. Calves were observed thief-suckling four times and attempting to thief-suckle 17 times. The frequency of thief-suckle behavior decreased as calves aged. Calves appeared to be motivated to suckle from their mothers when a nearby calf was suckling as well.
as during disturbances. A 17-week-old calf, permanently separated from her mother, apparently remained healthy.

Most social-grooms and all mutual-grooms were performed by cows and their calves.

Mounts, throat-places, and chest-bumps were performed in several contexts and in association with a variety of other displays.

Aggressive acts were important in maintaining individual distances, establishing hierarchical relationships, and enabling bulls to hold harems. Group 1 elk performed head-highs, kicks, bites, antler-displays, head-pushes, and spars 364 observed times.

Examinations of instantaneous sample data showed a diurnal pattern of elk activity and significant differences in amount of time individuals and sex-age classes spent in certain activities.

Males from Group 3 were observed with Group 1 elk on only three occasions from 1 April to 30 August. Bulls were always present in the study area between 31 August and 11 November. Ten to 12 bulls possessed harems at some time during the rut, and four to 10 other bulls were also observed in the study area during the rut. Harem bulls did not contact each other during the nine encounters between 6-plus-point harem bulls and other 6-point bulls, suggesting that the bull hierarchy was established before rutting activities began in Upper South and Lower South ranges. Antler-displays, bugles, or mere presence of bulls were sufficient to cause bulls to forfeit their harems.
to other bulls. Rutting bulls and Group 1 spikes differed significantly in their use of aggressive displays. The activity of a harem bull during the peak of rutting behavior differed significantly from the activity of another bull later in the season and from the activity of Group 1 elk. Bulls performed more than 1,800 observed repetitions of rutting behaviors such as bugling, spars, noses or licks to females, mounts, antler-thrashes, and wallows. One copulation was observed.

Some of the behaviors displayed by Bison Range elk were not described in other elk studies; other behaviors showed similarities with or differences from behaviors displayed by other elk. Possible functions of some behaviors included young calves vocalizing during a disturbance to bring their cows to the scene, and suckle frequency and duration lessening to gradually wean the calves.
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APPENDIX I

RESULTS AND DISCUSSION OF OBSERVATIONS OF GROUP 3 ELK

The Population

Approximately 31 cows and female yearlings, 10 calves, six spikes, 6 2\frac{1}{2}-year-old bulls, and 13 older bulls comprised the Group 3 elk herd (pers. obs. and Haderlie pers. comm.).

Group Behavior

None of the estimated 47 female, calf, and spike elk of Group 3 were observed in Upper South and Lower South ranges. Group 3 males were observed with Group 1 elk on only three occasions before the rut. A 5-point bull and a (2,1) bull were with Group 1 elk on 15-16 April and 16 and 20 April, respectively. A 4-point bull joined 13 elk of Group 1 for about 2 hours on 24 April. He left them after the cows directed many aggressive acts at him (see Hierarchical Relationships).

Alert-alarm Behavior

Group 3 elk were more easily alerted by humans than Group 1 elk were. By the time tourists were permitted on the tour road each morning, most or all elk had moved away from the road, although they

134
often watered at Pauline and Elk creeks during the night or early morning. When we disturbed 43 elk at 0630 on 28 August in lower Pauline Creek, they ran west and south for about 2 km before stopping. At 0625 the following morning, 38 elk disturbed by my vehicle at 250 m, left the area, and ran, trotted, then walked 2 km to the same area as on the preceding day. Other observations of smaller groups also showed the wilder behavior of these elk. During 1977, Group 3 elk were hunted monthly as part of the refuge reduction program.

The most extreme example of alerting behavior known during 1977 concerned a (5,6) bull we later named "Out" (Haderlie pers. comm.). Several people approached to within about 400 m of Out during the annual big game census on 26 February. The bull took flight, and was later seen by three of four people from at least 800 m away. Out travelled from the southern ridge of Red Sleep Mountain south about 3.5 km to mid Trisky Creek, then east, probably jumping the interior fence between Upper South and Lower South ranges before jumping the boundary fence. The top wire of the boundary fence over which he apparently jumped was pulled down, and on it was attached a 5 X 20 cm strip of hide. He interacted with many individuals of Group 1 through the boundary fence before he was shot on 12 October (Haderlie pers. comm.).
Vocalization

A wind shift allowed at least 10 elk to smell me when I was 15-20 m from them in coniferous timber on 29 August. They crashed through some brush for about 30 seconds while taking flight. Elk voiced at least 35 "eau" calls within the following minutes as they apparently regrouped.

Bulls and Antler Growth

The 6-point or better bulls were out of velvet by about mid-August. The 5-point bulls took from about 1 to 3 weeks longer. Age differences in velvet-shedding times were reported by Murie (1951). It is believed that increased levels of testosterone cause the shedding of velvet (Wislocki 1943 in McCullough 1966, Turner 1959 in Struhsaker 1967, Robinson et al. 1965 in McCullough 1966). It is possible that the 2½-year-old bulls develop their highest level of testosterone 1 or 2 weeks later than the older bulls (Struhsaker 1967). Some spikes of the Refuge never lost their velvet, while others, like Lσ and Sσ, had polished antlers by 1 September. Rocky Mountain elk spikes in some areas are reported to retain their velvet (Kirsch and Greer 1968). Shedding of velvet by tule elk spikes varied between years (McCullough 1966).

Most bulls had symmetric antlers with the same number of tines on each antler. Bulls with unequal tine numbers were a (3,2),
a (5, 6) (Out), a (6, 5), two (8, 7)'s, a (3, 6), and a (0, 7) (1A) with no left antler. The (3, 6) bull's left antler had only brow and bez tines. The left main beam swept lower than the right, and then curved upward to the height of the base of the fifth right tine. 1A ("One Antler") was observed on 1 and 10 June before he acquired a harem in the study area on 18 September. His one antler had only four tines in June, and he limped conspicuously then as well as during the rut.

**Aggressive Behavior**

**Antler-display**

Antler-displays per encounter were more numerous when a fence separated the individuals than when no fence was involved. When fences separated the individuals, 2.25 antler-displays were performed per encounter (9 in 4 encounters), but when no fence was between the elk, 1.20 displays were performed (18 in 15 encounters). The fences evidently lessened the effectiveness of the antler-displays.

**Spar**

Three spars involving Group 3 bulls were observed. Two 5-point bulls sparsed at 0715 on 4 September. A 5-point and a 4-point bull sparsed at 0715 and 0720 on 15 September for 16 seconds and 1 minute 45 seconds, respectively, with apparently strenuous leg-pushing and head-twisting. The 4-point retreated. A 7-point and a 6-point bull sparsed at 0723 and 0724 on 15 September for 18 seconds.
and 5 seconds, respectively, with apparently strenuous leg-pushing and head-twisting. The 6-point retreated.

**Harem Observations**

Three Group 3 harems were observed. A 6-point bull was seen with 46 elk including 10 calves on 4 September from 0735-0829. A 6-point and a (6, 5) bull were seen with 32 elk (17 females, eight calves, five spikes, two smaller bulls) on 8 September from 0740 to 1000. An (8, 7) bull was observed with 14 elk (seven females, four calves, one spike, two $2\frac{1}{2}$-year-old bulls) on 24 September from 0845 to 0907.
### APPENDIX II

**WEIGHTS AND AGES OF CALVES WHEN EARTAGGED AND EARTAG COLORS**

<table>
<thead>
<tr>
<th>Calf</th>
<th>Weight (kg)</th>
<th>Age when eartagged</th>
<th>Eartag colors (left, right)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>---</td>
<td>1-2 days</td>
<td>white, white</td>
</tr>
<tr>
<td>Calf 2</td>
<td>18.6</td>
<td>1 day</td>
<td>blue, blue</td>
</tr>
<tr>
<td>Calf 3</td>
<td>22.7+</td>
<td>6-8 days</td>
<td>red, red</td>
</tr>
<tr>
<td>Calf 5</td>
<td>20.0</td>
<td>2-4 days</td>
<td>blue, blue</td>
</tr>
<tr>
<td>Calf 6</td>
<td>15.4</td>
<td>½ day</td>
<td>white, blue</td>
</tr>
</tbody>
</table>
APPENDIX III

NECROPSY REPORTS OF THE DEAD CALVES

1. Calf 2

The male weighed 46 lbs. (20.0 kg). The apparent cause of death was starvation. The animal had curds in its stomach from about a tablespoon of milk along with about a half cup of gravel and dry grass. The rest of the digestive track was completely empty except for a large mass, at the posterior end of the colon, about 2" in diameter and 5" long. This mass was formed entirely of clay and sand and probably would have been an effective block to passage of anything through the intestine. Apparently the calf simply was not getting enough milk and tried to feed getting mostly dirt and debris.

2. Calf 6

The female was not weighed, but it was exceedingly small and thin. There was no evidence that the calf had ever fed. The only gross abnormality was the lack of a cardiac thymus. A small amount of thymal tissue was present in the cervical region. The entire lymphatic system was undersized. Since the carcass had been frozen, we could not culture anything from it; but it appeared that either it or its mother had had a high fever. The chances are greater that it was the mother since the calf was obviously undersized and weak at birth. A high fever in a pregnant female often causes regression of the thymus.

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1B. W. O'Gara.
GROWTH AND PELAGE CHANGE

The change from winter to summer pelages for the cows and yearlings began during the last week of April and the first week of May, respectively. The yearlings took longer to acquire the summer coat than the cows did. The completed pelage change for all elk and much of the spikes' antler growth took place during calving, when the animals were often in timber and difficult to observe. Four cows, whom we could tell apart through pelage characteristics under favorable conditions before calving, lost their identity to us during that time.

The calves were tan with light spots when first observed. Placement of spots could be used to differentiate calves at close range. The spots completely disappeared from the coats of Calf 1, Calf 4, and Calf 5 on 28 August, 3 and 11 September, respectively. These dates closely correspond to the relative ages of the calves (Table 2). The relative sizes of the calves also indicated their ages. Calf 1 was probably the heaviest calf of the four. Calf 3 and Calf 4 were similar in size. Calf 5 was the smallest calf of the group. These size differences persisted until at least mid-October.
L♂ and S♀ acquired the light coloration of a bull by 7 August, and were then the two lightest elk of the herd. The two male calves, Calf 3 and Calf 4, were much lighter than the female calves by mid-September.

Differentiation between cows and female yearlings was difficult or impossible as early as mid-August. Individual differences in size caused an overlapping of sizes between these two groups. At least two female yearlings were much heavier than Cow 4 by 1 September. This cow noticeably decreased in weight from 1 July to 1 September.

Group 1 calves molted their calf coat when about 3 months old, from late August through mid-September, which may have been later than Rocky Mountain calves of other areas whose pelage changes occurred "by August" (Kirsch and Greer 1968). Tule elk calves molted when approximately 4 months old (McCullough 1966). Cow and female yearling Bison Range elk, as well as tule elk (McCullough 1966), could not be easily differentiated by midsummer.
APPENDIX V

EXAMPLES OF THE FIVE FACTORS THAT EFFECTED HEAD-POSITION WHILE PERFORMING A BITE

Head-positions were estimated by the degree above (positive) and below (negative) the horizontal. An imaginary line from the middle of the posterior part of the skull to the tip of the nose was used as reference. An elk typically held its head at about -20° when standing.

1. The relative locations of the individuals
   a. Displayer uphill of other elk (negative)
   b. Displayer downhill of other elk (positive)
   c. Bedded cow to standing Brute (45°)

2. The relative sizes of the individuals
   a. Cow to calf (-20°)

3. The part of the body at which the bite was directed
   a. Cow to Sće's lowered head (-20° to 0°)
   b. Cow to cow's head held at shoulder level (0°)
   c. Two female yearlings displaying bites at one another's raised mouths (80°)

4. Whether the nose was directed slightly away from the other individual
   a. Cow 2 to female yearling bite directed above the yearling's head (80°)

5. Whether or not the displayer performed a charge
   a. When performing a charge, the head was held about level with the shoulders (-15° to 25°, usually 0°)