

THE UNIVERSITY OF MANITOBA

SOCIAL ORGANIZATION OF WAPITI

AND WOODLAND CARIBOU

(Mammalia:Cervidae)

BY

MERLIN WENDELL SHOESMITH

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ABSTRACT

The social organization of wapiti (Cervus elaphus nelsoni Bailey) and woodland caribou [Rangifer tarandus caribou (Gmelin)] was examined through field studies conducted in Yellowstone National Park, Wyoming, and Reed Lake, Manitoba, respectively.

At least 40 percent of individually marked Yellowstone wapiti were found to be habitual in their use of summer range. Specific areas within a seasonal range (summer range, spring range) were also used habitually by some wapiti. Tests for intraspecific associations revealed that individually marked wapiti normally occurred together about as frequently as expected by chance. Groups of wapiti, regardless of size or time of year, appeared to be temporary aggregations of individuals or basic social units (cow-calf) deriving the benefits of grouping but maintaining their individual pattern of movement and use of an area. Group composition as revealed through marked wapiti could not be predicted.

The basic social unit of woodland caribou also appeared to be the cow-calf pair, with the possible association of off spring of the previous year. The social units in caribou were largely solitary from the spring seasonal shift to calving areas to winter. Occasionally two social units found in the same general area joined together for several days. Evidence for habitual use of seasonal range by woodland caribou was obtained from four transmitter-equipped females.

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Dorothy Ball typed the manuscript several times. Thanks to Mrs. V. Patrick for typing the final draft. I accept full responsibility for any errors left within the text.

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TABLE OF CONTENTS

	Page
ABSTRACT	i
ACKNOWLEDGEMENTS	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	ix
LIST OF PLATES	xi
I. INTRODUCTION	1
II. LITERATURE REVIEW	2
WAPITI	2
Social Behaviour	2
Movements and Home Range	5
CARIBOU	7
Social Behaviour	7
Movements and Home Range	9
SUMMARY	11
III. DESCRIPTION OF STUDY AREAS	12
MIRROR PLATEAU	12
Location and Physiography	12
Geology	15
Climate	17
Vegetation	18
Fire History	21
Resource Utilization	23
REED LAKE	23
Location and Physiography	23
Geology and Soils	25

	Page
Climate	26
Vegetation	26
Fire History	27
Resource Utilization	29
IV. METHODS AND MATERIALS	30
GENERAL	30
Intraspecific Association of Wapiti	30
Range Determination of Wapiti and Caribou	34
WAPITI	34
Live-capture and Marking	34
Field Observations	36
Aerial Observations	38
Biotelemetry	38
WOODLAND CARIBOU	38
Live-capture and Marking	38
Biotelemetry	42
Field and Aerial Observations	42
V. MOVEMENTS AND BEHAVIOUR OF WAPITI	45
MOVEMENTS	45
Periodic Distribution	45
Composite Distribution	51
Seasonal Movements	52
Seasonal and Aggregate Ranges	71
INTRASPECIFIC ASSOCIATION	75
Joint Occurrence	75
Coefficient of Association	79
GROUP BEHAVIOUR	88

	Page
Exchange of Marked Wapiti	88
Group Size	95
VI. MOVEMENTS AND BEHAVIOUR OF WOODLAND CARIBOU	103
MOVEMENTS	103
Periodic Distribution	103
Seasonal Movements	107
Home Range	115
Seasonal Ranges	119
GROUP BEHAVIOUR	125
Social Groupings.	125
Mean Group Size	130
VII. DISCUSSION AND CONCLUSIONS	133
VIII. SUMMARY	143
IX. LITERATURE CITED	147
X. APPENDIX	154
GLOSSARY OF TERMS	154

LIST OF TABLES

	Page
Table 1. Estimated area and composition of the vegetation on Mirror Plateau	19
Table 2. The number and monthly distribution of observations on 236 Mirror Plateau wapiti, 1963-69	35
Table 3. The composition and number of observations of woodland caribou at Reed Lake	43
Table 4. Seasonal and geographical distribution of Mirror wapiti, 1963-69	46
Table 5. Movement of individual Mirror wapiti from last summer location to first breeding location (north end of Mirror Plateau)	60
Table 6. Movement of Mirror wapiti from major wintering areas to northern Park boundary, 1963-67, and winter conditions . . .	65
Table 7. The winter-spring movement of Mirror wapiti from Specimen Ridge to Hellroaring Slopes (1966-1968)	67
Table 8. A comparison of winter conditions on Specimen Ridge and Hellroaring Slopes	69
Table 9. The number of Mirror cows observed in three general calving areas during 1, 2, or 3 calving periods, 1966-68	70
Table 10. Aggregate home range of nine Mirror females	72
Table 11. Seasonal range of seven Mirror wapiti	73
Table 12. Number and frequency of joint occurrences of 35 Mirror females, 1963-68	76
Table 13. Yearly, seasonal, and joint occurrence of marked pairs of Mirror cows (Nos. 88 and 183-3; Nos. 218 and 219-5)	77
Table 14. Number and frequency of joint occurrences of marked females summering on the southern end of Mirror Plateau, June 22-September 21, 1966-68	78
Table 15. Number and frequency of joint occurrences of 20 Mirror bulls from 1966-68	79

	Page
Table 16. Associations of potentially related wapiti marked and released at Little Buffalo Trap	80
Table 17. The association of family units trapped and released at Little Buffalo	81
Table 18. Association of Mirror Plateau wapiti during six periods . . .	84
Table 19. Changes in group composition and interchange of wapiti in groups containing a specific marked cow on Mirror Plateau, 1966-68.	89
Table 20. Group exchange of Mirror wapiti in the Hellroaring Slopes Area during winter and spring 1966	93
Table 21. Group exchange of Mirror cows during spring migration with individual cows that calved (A) on Hellroaring Slopes and (B) in the Crystal-Amethyst Creeks Area	94
Table 22. The spring association of Mirror cows which appeared in the same group in early summer on (A) Flint Creek and (B) Raven Creek	96
Table 23. Changes in social grouping of wapiti on Mirror Plateau from summer to breeding periods, 1966-68	100
Table 24. Number of bull, cow and harem groups observed on Mirror Plateau during the breeding periods, 1966-68	101
Table 25. Composition and mean group size of bull, cow and harem groups during the breeding periods, 1966-68	102
Table 26. The periodic distribution and seasonal range size of all transmitterd woodland caribou at Reed Lake	104
Table 27. The 1975 summer and fall range size of woodland caribou at Reed Lake (Km ²)	120
Table 28. Mean group size of woodland caribou at Reed Lake	131

LIST OF FIGURES

	Page
Fig. 1. The location of Mirror Plateau in Yellowstone National Park	13
Fig. 2. Major geologic deposits on Mirror Plateau and Mt. Norris-Saddle Mtn. summer ranges	16
Fig. 3. Distribution, date, and relative size of lightning-caused fires on Mirror Plateau	22
Fig. 4. The location of the Reed Lake study area in west-central Manitoba	24
Fig. 5. Distribution, date, and relative size of fires in Reed Lake area	28
Fig. 6. The distribution of Mirror wapiti during the summer and fall periods	47
Fig. 7. The distribution of Mirror wapiti during the winter to mid-spring periods	49
Fig. 8. The distribution of Mirror wapiti during the calving and spring migration periods	50
Fig. 9. Network of game trails and general migratory routes on Mirror Plateau	53
Fig. 10. The number and sex of marked wapiti observed one or more summers on Mirror Plateau	56
Fig. 11. The summer and fall movements of Raven in relation to the Mirror Plateau summer range	62
Fig. 12. Two major movement patterns of Mirror wapiti on the northern Yellowstone winter range.	66
Fig. 13. Seasonal areas occupied by Mirror cow 183-3 in 1967-68 . .	74
Fig. 14. The association of potentially related wapiti trapped at Little Buffalo Trap	82
Fig. 15. The association of adult cows from Mirror Plateau	86
Fig. 16. The association of marked wapiti with cow 183-3.	87
Fig. 17. Frequency of group size of Mirror wapiti on summer range	97

	Page
Fig. 18. Trends in mean group sizes of Mirror wapiti on summer and fall ranges	99
Fig. 19. The seasonal ranges and distribution of woodland caribou at Reed Lake	106
Fig. 20. The movements of Old Yella and Red from winter range to spring calving areas in 1975	109
Fig. 21. Candy's summer ranges in 1974 and 1975	111
Fig. 22. Old Yella's summer ranges in 1974 and 1975	112
Fig. 23. The 1974-75 seasonal ranges of Red	116
Fig. 24. The 1975 seasonal ranges of Candy	117
Fig. 25. The 1974-75 seasonal ranges of Old Yella	118
Fig. 26. Sundog's summer and fall ranges in 1975	122
Fig. 27. Flame's summer and fall ranges in 1975	123
Fig. 28. Bull's summer and fall ranges in 1975	124
Fig. 29. The 1975 summer ranges of three caribou social units . .	127
Fig. 30. The 1975 fall ranges of three caribou social units. . . .	129
Fig. 31. Monthly trend in mean group size of woodland caribou at Reed Lake	132
Fig. 32. A comparison of the concepts of group behaviour and related movement patterns as found in earlier studies (upper portion) and during this study (lower portion) . .	136

LIST OF PLATES

	Page
Plate I. Aerial photo of Mirror Plateau from Timothy Creek to Chalcedony Creek	14
Plate II. Radio-tracking wapiti cow 183-3 with portable receiver on winter range	39
Radio-transmitted wapiti cow 183-3 feeding in a small streambed on winter range	
Plate III. Old Yella resting along shore of small island.	41
Old Yella and Hornet just after release by tagging crew	41

I. INTRODUCTION

Numerous studies of social behaviour in ungulates and related forms have been conducted during the past 50 years. One of the earliest field studies in animal behaviour was the classic work on red deer (Cervus elaphus L.) in Scotland (Darling 1937). Until recently, however, most of the studies were descriptive and concentrated on basic behavioural acts (i.e. fixed action patterns) or specific aspects of social organization. Current attempts include the analysis of social organization at the family level. Most notable are studies of equids (Klingel 1974), bovids (Jarman 1974; Estes 1974), and suids (Frädrich 1974).

Altmann (1956b) was the first to compare social patterns of four ungulates which included two cervids, wapiti (Cervus elaphus nelsoni Bailey) and moose [Alces alces (L.)]. Pruitt (1960) added barren-ground caribou (Rangifer tarandus groenlandicus L.) to the list. Geist (1966) summarized his behavioural observations of four North American cervids and co-authored a review of cervid behaviour during the reproductive period (de Vos et al. 1967).

This study will examine aspects of social organization of two recent cervids, wapiti and woodland caribou [R. t. caribou (Gmelin)]. The hypothesis is that social organization is based at the family unit level and not at the group level even though some type of grouping may occur periodically. A group of wapiti or woodland caribou is thus a dynamic, temporary aggregation of individuals and family units in which associations of specific adult pairs cannot be predicted.

II. LITERATURE REVIEW

WAPITI

Social Behaviour

The social organization of wapiti and red deer has been studied largely by recording animal movements, group cohesion, mother-offspring relationships, and group size and structure as these relate to specific land areas. Animal to animal associations and movement patterns are basic parameters that must be measured and quantified in order to describe and understand social organization.

Darling (1937:74) related the movements of red deer to the "territory" of this species. His concept of a matriarchal system was, until recently, widely accepted and it was frequently assumed that wapiti had a similar social system. Darling described the social organization of red deer as follows:

"The outstanding feature of the hind group is its cohesion which, doubtless, is derived from the stability of the family. Maternal care is protracted in the red deer, extending to the third year of life of the offspring. Thus each hind may have two or three followers, and some of the other adult hinds may be the earlier offspring of a hind still in the group.

". . . There are hind territories carrying varying numbers of hinds from five to over two hundred. When the whole group is together orderliness is most apparent, but the sociality of the hinds is not so simple as that. The whole number of hinds on a territory is one group, though they are not usually all together. . . Let us imagine the Carn na Carnach hind territory. . . The total of 95 deer of the Carn includes between 40 and 45 adult hinds. These are divided into three main families. . . Under conditions of good weather and in daylight, at times of little herd movement, these three family groups may split up still further into individual families, so that the whole of the Carn is dotted with its deer. Any one of the hinds may wander anywhere on the territory, and as a group they

do so, but as families they have these preferences for particular parts of their territory. Each family group has its leader, but when the herd is together as one unit the family group leaders submit to the one leading hind of the herd.

" . . . In the course of the year there is constant rearrangement of grouping within the main hind group, but it is no random affair. There is a good reason for every change, and the point I want to emphasize is that the hind group still remains one 'city' even when subgroups of its members may be two miles apart. Orderliness is apparent throughout, and when the whole group assembles, from time to time, family discipline and leadership give way to that exercised by the leading hind of the territory."

Eygenraam (1963) supported Darling's theory on maternal care by quantitatively showing that complete independence of young from mother was not reached before the fourth year of life.

However, workers studying red deer populations containing marked individuals have found no group constancy. Schloeth (1961; 1966) recognized that the composition and association of red deer hind groups were not stable. Female offspring tended to occupy their mother's home range, but they spent most of their adult life independent of the maternal group (Schloeth and Burkhardt 1961).

Lowe (1966:222) presented evidence of inconstancy of groups in red deer. He stated:

"It is difficult to reconcile these observations with group territorial behaviour, postulated by Darling (1937, pp. 68-70), when the only relatively stable elements in each group appear to be the physically mature individuals with their established individual home ranges; and none of these has ever been observed to assume overall leadership.

"The present data do not suggest that there is any social organization extending beyond the family and the mother's home range."

Murie (1951) discussed the social habits of wapiti in general

terms. Altmann's (1952; 1956b) concept of social structure varied between publications but her main ideas seem aptly stated by de Vos, et al. (1967:392; 395):

"The basic social unit of elk is a family group consisting of 10-30 individuals, comprising several breeding hinds and their followers. The latter include the young-of-the year, 2-year-olds and some 3-year-olds (Altmann, 1956a). The group is led by an old hind (Altmann, op. cit.)."

"In the wintering areas the herds of elk constitute a loose assemblage of hinds, calves and bulls, and these herds differ from those on the summer ranges in which well-organized hind groups maintain their identity (Altmann, 1956a)."

McCullough (1966) recognized five small distinct herds of C. elaphus nannodes Merriam in the Owens valley. "The herding habit is strongly developed and herds are highly integrated and coordinated."

In these studies of unmarked wapiti, two main points are widely accepted:

- 1) The social unit is based on maternal lineage through the third year of an offspring's life.
- 2) Group cohesion is the general rule and the integrity of a herd in a specific area such as a summering population is maintained despite frequent breakdown of herds into subgroups and their subsequent re-aggregation.

Other evidence modified this concept. Harper (1964) discussed the dynamic interchange of individuals among groups of Roosevelt wapiti (C. e. roosevelti Merriam). Struhsaker (1967:81) described the social structure of wapiti during the rutting period as, ". . . a relatively dynamic society in which individuals apparently moved quite frequently from one group to another." In Jackson Hole, Martinka (1969) reported that prior

to the breeding season relatively distinct, sedentary female-calf groups occupied three areas, but group constancy was not evident among smaller group associations within each area. He found frequent exchange of yearlings among female-calf groups.

Knight (1970) attempted to quantify associations between marked female wapiti. ~~Although he did not~~ attach statistical significance to his association values, he concluded that there was no great attraction between particular animals (yearlings and older) in the population, seasonally or during successive years.

The literature suggests that the social unit of wapiti is based on individual adults and family units and not on the band (10-30 individuals). Although wapiti tend to occur in bands containing at least several adults, individual patterns of movement based on the traditional habits of each adult may be retained.

Movements and Home Range

Seasonal movements of wapiti were documented in Manitoba (Green 1933), Yellowstone Park (Skinner 1925; Murie 1951; Ellis 1965; Craighead et al. 1972; Craighead et al. 1973), Wyoming (Altmann 1952; Anderson 1958; Martinka 1969), Michigan (Moran 1968), California (McCullough 1966; Harper et al. 1967), Alaska (Troyer 1960; Batchelor 1965), Washington (Schwartz and Mitchell 1945), Montana (Brazda 1953; Picton 1960; Knight 1970) and Idaho (Dalke et al. 1965). These studies show that patterns of movement vary greatly with specific wapiti populations but do not show whether family ties or social structure influence the movement patterns.

Murie (1951) and Altmann (1956a) characterized the migrational movements of wapiti as traditional. Yet, quantitative data substantiating this have been spotty. Traditional use of summering areas by migratory wapiti was suggested by Bradza (1953), Picton (1960) and Geist (1966). The first quantitative data to support this view were obtained by Knight (1970). He reported that 32 percent of marked wapiti in a herd used the same summering areas for two summers. Craighead et al. (1972) demonstrated that individually marked wapiti of the Northern Yellowstone Herd returned to specific areas of the summer and winter ranges in successive years. Craighead et al. (1973) also showed that non-migratory wapiti of the Madison Drainage Herd in western Yellowstone Park used the same summering areas each year.

McCullough (1966), Geist (1966), Harper et al. (1967) and Struhsaker (1967) all obtained evidence that both sexes tend to move extensively during the breeding period. Whether this movement was to the same areas each fall in order to breed was not determined.

The ecology of a calving area has been described in general terms by Murie (1951) and in detail by Johnson (1951). Green (1933) and Anderson (1958) suggested repeated use of calving areas by specific females. However, movement patterns of females to specific calving sites were not quantitatively demonstrated.

Literature concerning concepts of home range and methods for deriving home ranges have been confined largely to studies of small mammals (Sanderson 1966). Concepts of home ranges for wapiti summering in Yellowstone National Park have been discussed in general terms by

Skinner (1925), Murie (1951) and Anderson (1958).

In Michigan, Moran (1968) described the home range of an adult female and a young bull each as 41.4 km². Craighead et al. (1973), the first to obtain biotelemetric data on home ranges of wapiti, defined the home range size of three non-migratory adult females in the western part of Yellowstone Park as 13.0, 25.9, and 30.6 km².

Patterns of movement directly influence size as well as shape of home and seasonal ranges. Craighead et al. (1972) suggested that the home range of wapiti of the Northern Yellowstone Herd consists of a migratory corridor with the size of seasonal segments of the home range (summer and winter ranges) greatly exceeding the size of these ranges for non-migratory wapiti. Variability in size of overlapping home ranges of several individuals would suggest independent patterns of movement. Whether such patterns are characteristic of a group of closely associated wapiti or of loosely associated individual wapiti was investigated in this study.

CARIBOU

Social Behaviour

Although Banfield (1962) conveniently revised all caribou and reindeer into one species, Rangifer tarandus, considerable variation in the behaviour of the resulting five subspecies still exists depending upon the environmental context in which they live. Most behavioural studies have been on behaviour of open habitat forms of caribou in subarctic Canada (Kelsall 1968; Miller 1974; Harper 1955; Banfield 1954; Pruitt 1960; de Vos 1960), Newfoundland (Bergerud 1974)

and Alaska (Skoog 1968; Lent 1965). However, little behavioural information is available on closed habitat or boreal forest forms, partially due to the difficulty of direct observation. What information is available (Freddy and Erickson 1975; Egorov 1967; Stardom 1975) suggests that the woodland forms may not be considered gregarious.

De Vos et al. (1967) described barren ground caribou as the most gregarious cervid. Their review aptly capsulated the results of field studies by Banfield (1954), Pruitt (1960), de Vos (1960), Harper (1955) and Lent (1965). Flerov (1952) and Egorov (1967) described the social organization of wild reindeer in tundra habitat across Eurasia in a similar manner. I have composed a scenario of social organization in tundra caribou and reindeer as follows:

Caribou occur in large herds of over 100 individuals at most times of the year. During spring migration, pregnant females are at the head of the migrating front and are the first to arrive at the calving grounds. They are followed by bands of barren cows, yearlings and bulls. The calving period is brief and females with their newborn soon aggregate into "nursery bands." The bulls remain in separate groups until late summer just prior to the breeding period. A loose organization is maintained by all groups when travelling or feeding. No social hierarchy is apparent except in test or confined situations. Bands of females are enlarged by groups of bulls as the rut begins. Harems are not formed in the strict sense since rutting occurs in groups containing all sex and age classes. Sex segregation occurs following the rut with mature bulls forming small wintering bands.

Newfoundland caribou were most gregarious during the calving and rutting periods and had smaller aggregations at other times of the year (Bergerud 1974). Miller (1974) and Miller et al. (1974) concluded that barren ground caribou were socially cohesive. This unity was maintained by the formation of postcalving aggregations in which family cohorts rejoined for the remainder of the year.

Bergerud (1974) and Lent (1966) concluded that social facilitation was an adequate description of group behaviour in caribou without invoking a rigid social structure. Bergerud (1974:582) stated:

"Social facilitation appears to be an important aspect of the ability of caribou to optimize patterns in time and space. Caribou groups show a degree of openness, permeability (Lent 1966a). Animals can join groups with ease. An animal can take advantage of a local food supply or insect-relief habitats located by others. Again animals frequently leave groups and groups separate. Lent (1966a) speaks of the temporary nature of a specific group and of the continued dynamic process of group formation. There is a strong following response among adults yet no lack of individuals to initiate action."

Movements and Home Range

The extensive migratory movements and seasonal shifts in home range have been well documented for barren-ground caribou (Parker 1972; Miller et al. 1972; Kelsall 1968), Alaska caribou (Lent 1965; Skoog 1968; Hemming 1971), Newfoundland caribou (Bergerud 1971), and reindeer (Flerov 1952; Egorov 1967). Much less is known of seasonal movements in woodland forms although an altitudinal migration does occur in some mountain populations (Freddy and Erickson 1975; Egorov 1967).

Miller et al. (1972) stated that migrational paths of caribou

are traditional and apparently learned by the animals when they associate with older members of their population. However, Skoog (1968) described R. t. granti Allen in Alaska as being nomadic with little emphasis on learned patterns of movements.

Bergerud (1973) stated that increased activity and mobility during the rut rather than migratory movements best described a "fall shuffle" in northern Quebec and Newfoundland caribou populations.

Barren-ground caribou in Alaska have exhibited circular patterns of movement prior to and after calving (Lent 1966). If pregnant females reach the calving ground prior to the calving period, they remain in the general area by moving in large circular patterns. Circular post-calving movements are probably related to plant phenology and summer diets.

As population densities increase, caribou move into peripheral areas of their home range. At high densities, movements become erratic with random mixing and splitting of herds (Kelsall 1968; Skoog 1968).

Seasonal movements and migrations (if they occur) appear to be characteristic of specific herds of woodland caribou. Simkin (1965) stated that most of the woodland caribou herds were migratory but such is not the case now, particularly in the southern part of their range. In Manitoba, Guymer (1957; 1958) reported northward movements of caribou in April in The Pas-Cranberry Portage area and southeast of Norway House. Carbyn (1968) indicated seasonal shifts of caribou in the Bloodvein River area.

SUMMARY

The mother-young unit is the type of social bonding which is characteristic of most mammals (Eisenberg 1966). In the foregoing literature review, it is not clear as to whether the basic social unit of wapiti is the mother-young unit or an assemblage of mother-young units forming a cohesive band, group or herd. Intensive field investigations have not been conducted on woodland caribou to verify its social organization which has been inferred from the results of studies of related forms such as barren ground and Newfoundland caribou.

Eisenberg (op. cit.) stressed that social organization affects how a species uses its environment. For example, gregarious forms of wapiti and caribou presumably would require larger area than solitary forms to meet their life requirements. Thus, the ecological significance of many aspects of social behaviour in both forms would be clarified by an investigation of their movements, seasonal habitat use and associated behaviour.

III. DESCRIPTION OF STUDY AREAS

MIRROR PLATEAU

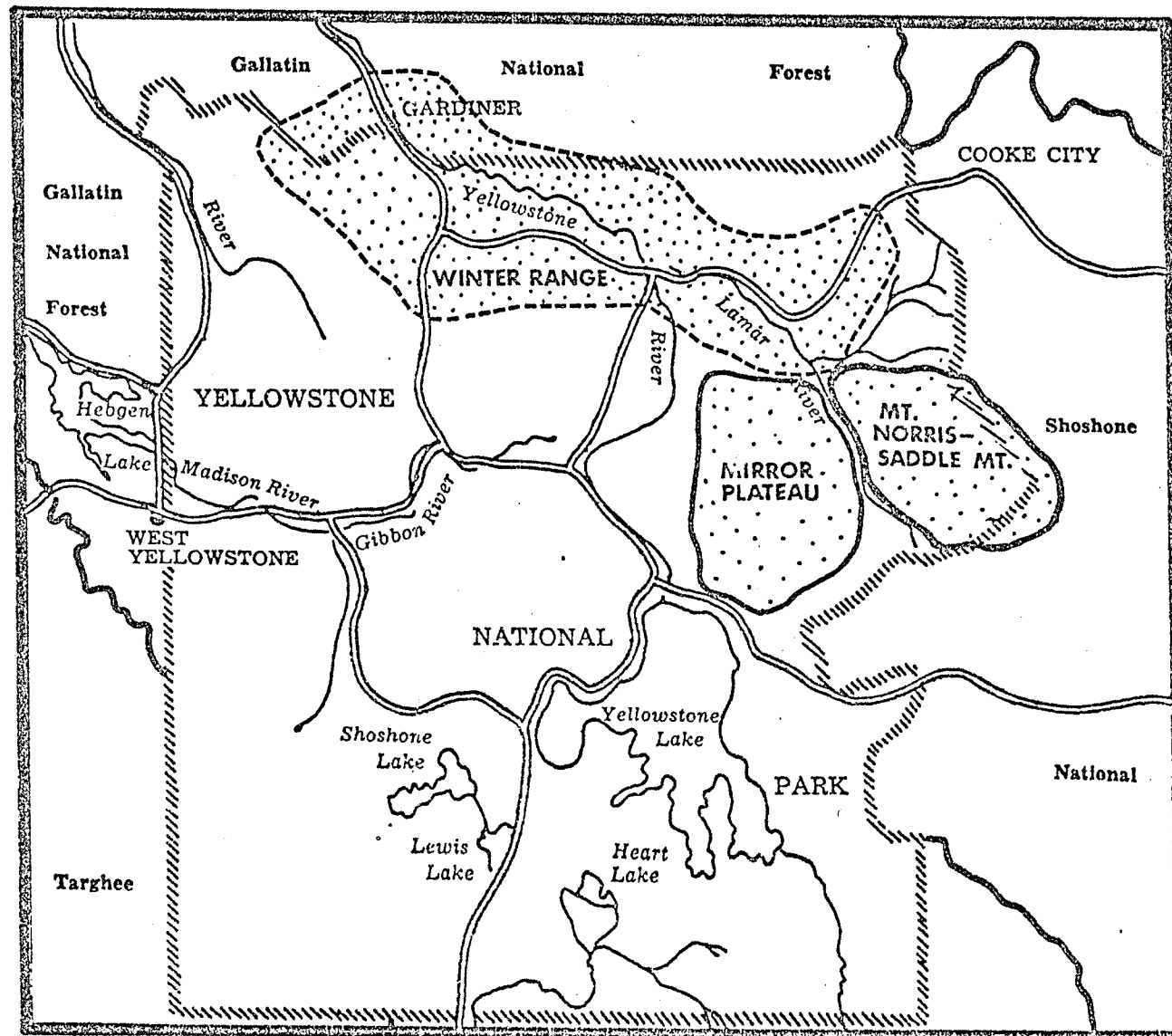
Location and Physiography

Mirror Plateau is situated in the northeast quarter of Yellowstone National Park (Fig. 1) at an elevation of 2,440-2,928 m. The Plateau is bounded on the north by Amethyst Mountain and the upper limits of the Northern Yellowstone Winter Range, to the east by the Lamar River, to the south by Mist Creek and Pelican Valley, and to the west by the Yellowstone River. The total area includes 400 square kilometers though most of my activities and observations were confined to 260 square kilometers.

Mirror Plateau is generally arcuate and oriented northwest to southeast (Plate I). The eastern side abruptly terminates as steep bluffs and slopes dropping over 600 m. to the Lamar River whereas the western side grades into a series of small knobs and long, low ridges which are heavily timbered with lodgepole pine (Pinus contorta Dougl. ex Loud). At the head of Mirror Fork lies Mirror Lake, a small shallow lake which is often used as a reference point for backcountry travel.

Numerous creeks drain the Plateau to the east and west. On the eastern side Opal, Flint and Timothy creeks are prominent among ten major creeks (two of which are unnamed but are called North Creek and South Creek in this study) of the Lamar watershed. To the west, Wrong, Broad, Shallow and Deep creeks flow into the Yellowstone River. Raven and Pelican creeks join in Pelican Valley and empty into Yellowstone Lake near Fishing Bridge.

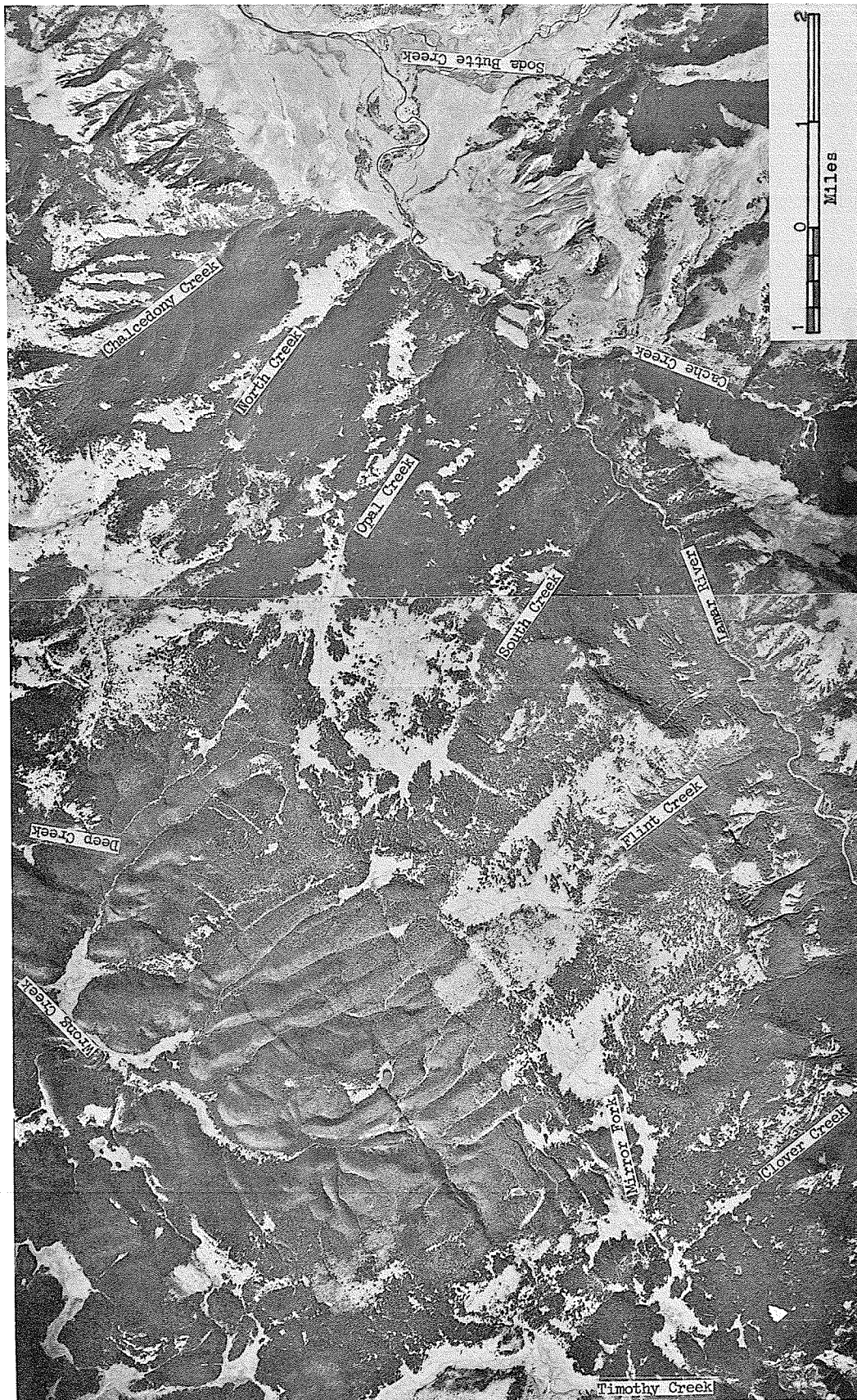
Figure 1. The location of Mirror Plateau in Yellowstone National Park.



SCALE 5 4 3 2 1 0 5 10

PLATE I

Aerial photo of Mirror Plateau from Timothy Creek to Chalcedony Creek



Rush (1932), Ellis (1965), Craighead et al. (1972), Barmore (1967) and Pengelly (1963) described the ecology of the Northern Yellowstone Winter Range, its history of game abundance, general range conditions and changes in ungulate and predator populations. Since this report is concerned with a summer range and its wapiti population, the reader should refer to the above literature for particular aspects of the winter range.

Geology

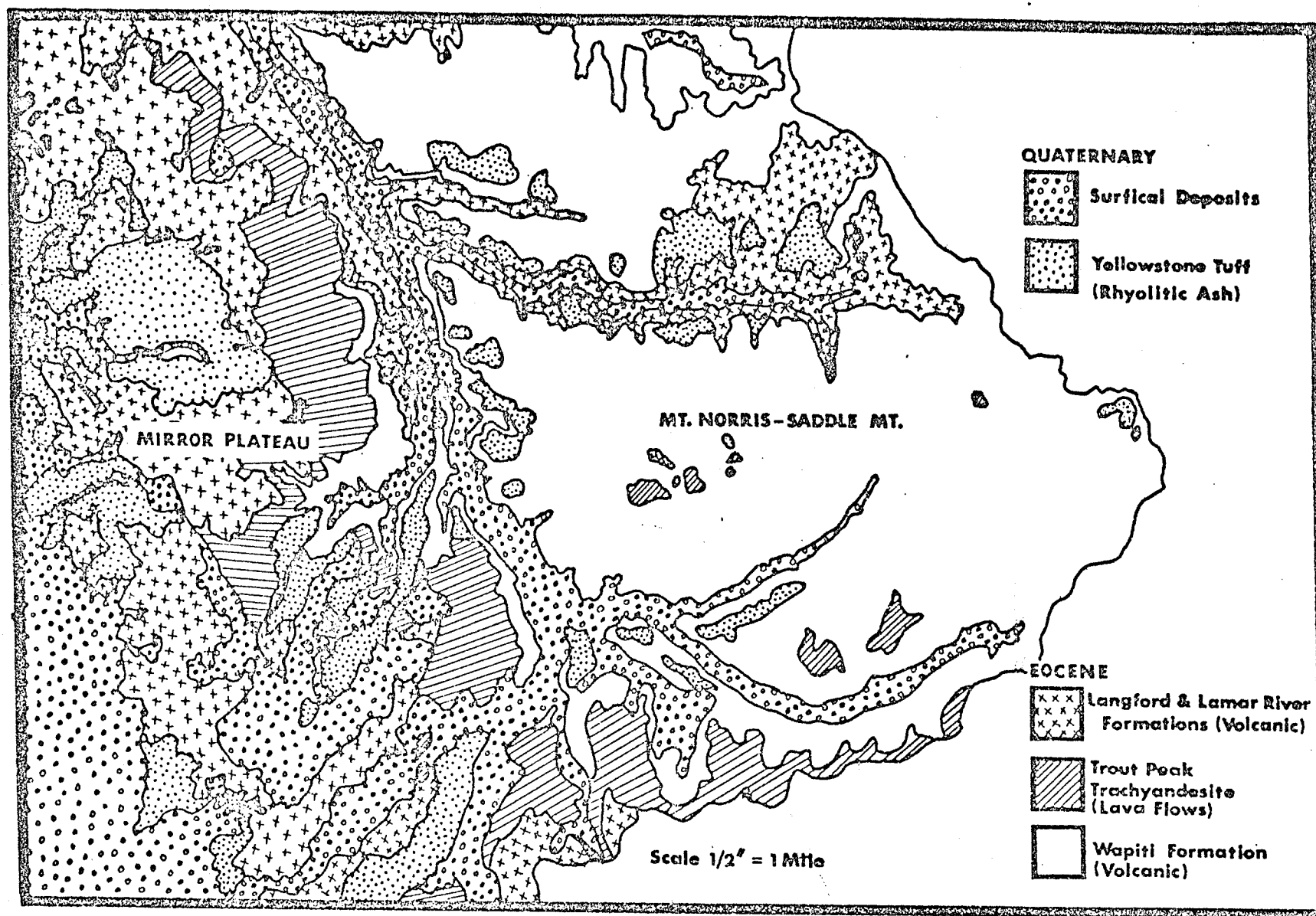
Dr. Harold J. Prostka, U.S. Geological Survey, recently completed a detailed geologic mapping of northeastern Yellowstone Park. He depicted the geologic features of Mirror Plateau as falling into two broad categories (Fig. 2):

- 1) The Absaroka Volcanics of the Eocene (about 50 million years old).
- 2) Much younger rocks and deposits of the Quaternary (less than 2 million years old).

Both types of deposits are characteristic of Mirror Plateau. Light-to-medium-gray volcanic sandstones and conglomerates of the Eocene extend across much of the Plateau. At the headwaters of Opal Creek this type is mainly conglomerate but as it extends to the southeast, it becomes interlayered with volcanic sandstone and flinty beds of indurated volcanic ash. Resistant ledge- and bench-forming lava flows of potassium-rich basalt (trachybasalt) are responsible for the high rolling surface and precipitous east and southeast sides, e.g., upper Flint Creek.

The Quaternary rocks on Mirror are Yellowstone tuff and

Figure 2. Major geologic deposits on Mirror Plateau and Mt. Norris-Saddle Mtn. summer ranges.



surficial deposits. Patches of Yellowstone tuff are erosional remnants of a formerly continuous blanket of rhyolitic ash flows. Tuff forms benches and ledges capped by a thin, well-drained soil that is favored by open lodgepole pine forest and huckleberries (Vaccinium sp.). This type is found at the headwaters of Opal, Flint, Wrong, and Pelican creeks.

Surficial deposits are found along Wrong, Pelican, Raven and Willow creeks and in Pelican Valley. These deposits may occur as landslides and talus deposits along steep slopes, alluvium along streams and gullies, and swampy, poorly drained ancient lake beds in the Pelican Creek and Raven Creek drainages.

Fault scarps are numerous on Mirror. They parallel its long axis forming abrupt benches which give a two-layered appearance to some of the meadows (mid-Mirror Fork).

Climate

Climatological records were maintained at the Pelican Cone Lookout Station, a fire guard tower situated on the south end of the Plateau at 2,941 m. Weather data were recorded daily at 3:00 P.M. The information reflected the general summer range conditions for the entire area from 1966-68, but it should not be construed to represent the microclimatic conditions, such as wind direction or dew point, locally prevailing in each drainage.

From 1966-68, mean maximum and minimum summer temperatures were 17.4°C and 4.7°C, respectively. There was a decline in maximum and minimum temperatures from early July through early September.

The dew point was generally below the minimum temperature during any one year, which suggested that condensation was not an influence on wapiti activity during dry periods. This was true of high ridges such as the one on which the Pelican Lookout Station was situated, but not of the lower and protected meadows. Dew usually formed on the vegetation as water droplets or frost, in all of the meadows throughout the summer.

Wind direction was generally west-southwest during the summer except for occasional days when major storm systems passed through the area. This seemed to be a diurnal direction since at night campfire smoke often drifted west.

Total summer precipitation was 82.8 mm in 1966, 70.3 mm in 1967 and 127.8 mm in 1968. Sleet and hail accompanied thunder-showers throughout the summer. Major storm systems included rain mixed with wet snow during late June, mid-August and early September. In August 1968, 95.8 mm of precipitation was received and 203 mm of wet snow fell during one storm system.

Winter snow depths on Mirror Plateau were assumed to be similar to those of the Mt. Norris-Saddle Mountain Area. On April 1, 1967, a snow gauge located at 2,928 m just northwest of Parker Peak was checked by Park rangers. They recorded an average depth of 2,921 mm of snow which had a water content of 1,270 mm.

Vegetation

The estimated area and percent of the vegetative cover of the various plant communities on Mirror Plateau are presented in Table 1. A brief description of each type is included here.

TABLE 1
ESTIMATED AREA AND COMPOSITION OF THE VEGETATION
ON MIRROR PLATEAU

Plant Community ^a	Area		Percent
	Hectares	Km ²	
Lodgepole pine	16,128	163	41
Spruce-fir	8,192	83	20
Whitebark pine	2,560	26	7
Coniferous Forest	26,880	272	68
Sedge-hairgrass	8,704	88	22
Wet meadow	2,304	23	6
Fescue-bluegrass	1,536	16	4
Subalpine Meadows	12,544	127	32
Total Area	39,424	399	100

^aOutline based on plant communities described for northwestern Wyoming by Beetle (1961) and Johnson (1962).

Coniferous Forest

Lodgepole pine occurs in extensive stands that may either be a climax stage on certain geologic deposits or a subclimax type in burned areas of spruce-fir. Beetle (1961) noted the association of lodgepole with volcanic rhyolitic flows of the Tertiary in southern Yellowstone Park and northern Teton County, Wyoming. He suggested that lodgepole has dominated these areas since the Tertiary.

On the Flint and Timothy-Pelican burn areas, Quaternary rhyolitic deposits (not Tertiary rhyolite as stated by Beetle, op. cit.)

are dominated by lodgepole pine. Tertiary volcanic deposits contain the spruce-fir climax in which lodgepole appears to be a subclimax species. At the head of Flint Creek, a clear block in the forest is interrupted by a narrow lighter band (fault line) which then grades into scattered timber and meadow. The fault line separates the Quaternary rhyolitic tuff (the clear block) from the Tertiary volcanic sandstone and ash (scattered timber and meadow). This aerial photo taken in 1954 does not show the reproduction of lodgepole in both areas. Lodgepole occurs as a dense thicket of saplings in the clear block but only as scattered individuals mixed with spruce saplings in the dispersed timber area.

Similarly, Tertiary deposits underlie the burned area at the head of Timothy Creek which contains a thin stand of young lodgepole and spruce. Another burned area at the head of Pelican Creek is underlain by Quaternary rhyolitic ash. Young lodgepole trees cover most of this area.

The spruce-fir [Picea engelmannii Parry ex Engelm.-Abies lasiocarpa (Hook.) Nutt] stands were found on northern exposures and on mesic sites on the Plateau. This type is the forest climax at high elevations despite the invasion of lodgepole pine in burned areas. The areas of "tree clumps" around the large meadows in Plate I are spruce-fir whereas the closed timber areas are predominantly lodgepole pine. Understory was either absent or characterized by an aspectual dominant, Arnica cordifolia Hook.

Whitebark pine (Pinus albicaulis Engelm.) is a common associate

of spruce-fir on the ridgetops and knobs above 2,800 m. It occurs as individual trees or small stands scattered throughout the fescue-bluegrass or at timber-meadow margins.

Subalpine Meadows

The sedge-hairgrass community occupied most of the meadow area on Mirror Plateau. Dominants were hairgrass [Deschampsia caespitosa (L.) Beauv.], Carex phaeocephala Piper, C. hepburnii Boott, C. epipilosa Mack. and C. saxatilis L. Varileaf cinquefoil (Potentilla diversifolia Lehm) and field chickweed (Cerastium arvense L.) were prominent forbs.

The wet meadow type comprised a large portion of the meadow area on upper Pelican and Willow Creeks. Important sedges found there were Carex aquatilis Wahl., C. raynoldsii Dewey and C. rostrata Stokes. Dense patches of marsh reedgrass [Calamagrostis canadensis (Michx.) Beauv.] occurred intermittently. A narrow band of Salix planifolia Pursh. grew along the streambanks.

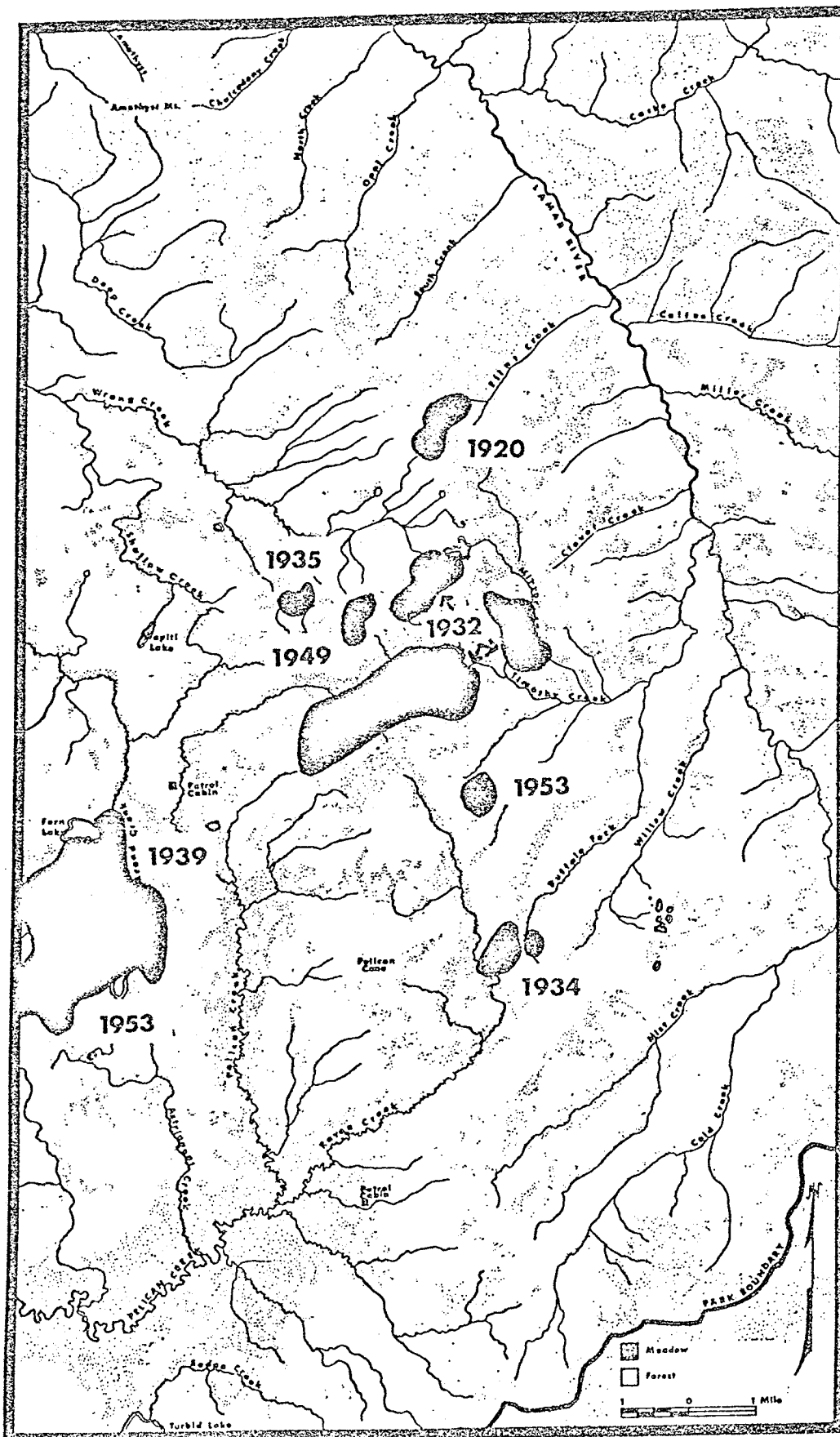
The drier sites near the forest edges, dry ridgetops and knobs were dominated by Idaho fescue (Festuca idahoensis Elmer) and several species of bluegrass (Poa reflexa Vasey & Scribn., P. interior Rydb., P. epilis Scribn. and P. leptocoma Trin.).

A transitional community which included dominants of both the sedge-hairgrass and fescue-bluegrass types was found in many areas.

Fire History

The occurrence of fires in Yellowstone National Park has been recorded by Park officials since 1930. All fires occurring in the Mirror Plateau area were lightning caused (Fig. 3). No major fires

Figure 3. Distribution, date, and relative size of lightning-caused fires on Mirror Plateau.



have been extinguished there since 1961. Undoubtedly the Park's fire control program prevented more burning of the area.

Resource Utilization

Wilderness hiking, camping and fishing are the only recreational uses of the Mirror Plateau. Even at that, few people were known to have traveled across this subalpine region other than myself and two assistants.

No hunting is allowed within the park. However, a wapiti herd reduction program during this study (live-capture and removal from winter range) undoubtedly resulted in the removal of some wapiti that summered on Mirror Plateau. The possible influence of this "harvest" of wapiti on group behaviour is discussed after the presentation of results.

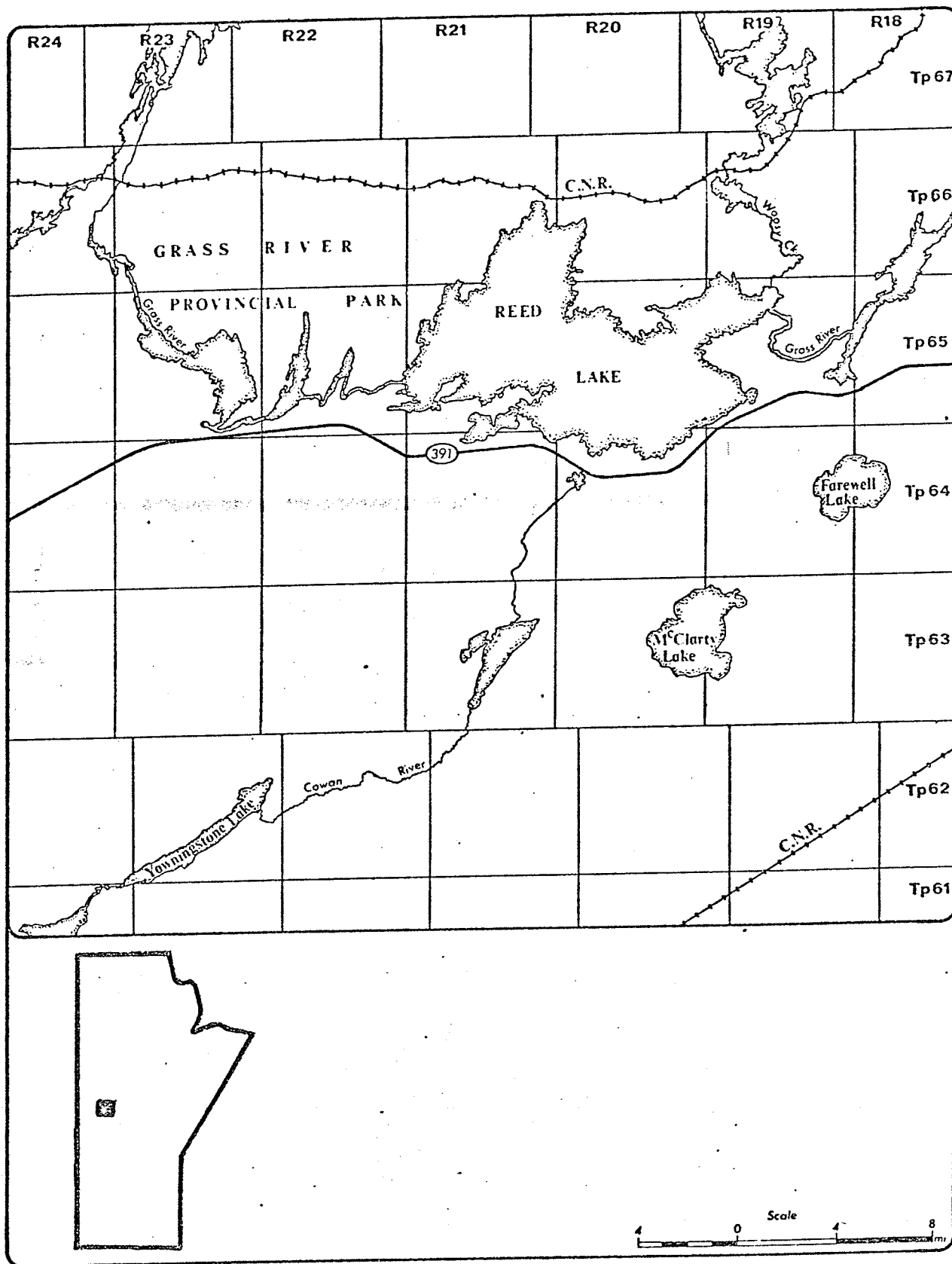
REED LAKE

Location and Physiography

Reed Lake is situated about 160 kilometers northeast of The Pas, Manitoba (Fig. 4). It occupies the eastern half of the Grass River Provincial Park. Provincial Road 391 divides the total study area on a north-south basis with Reed Lake in the northern half.

While the Reed Lake area (200 square kilometers) was the focal point of field investigations, the total area used by caribou from Reed Lake was 1,700 square kilometers. It was bounded to the west by Iskwasum Lake, to the north by the Chisel Subline of the Canadian National Railroad to Snow Lake, to the east by Tramping Lake and to the south by Mitchell and Cormorant lakes. The geographical limits are approximately 54° 15' N to 54° N and 100° 00' W to 101° 15' W.

Figure 4. The location of the Reed Lake study area in west-central
Manitoba.



Reed Lake is a part of the Nelson River Drainage Basin. A major tributary, the Grass River, forms a chain of large lakes connected by short stretches of river. Reed Lake is situated about midway in this river-lake chain.

The southern portion of the study area drains into the Saskatchewan River Basin through small creeks emptying into Cormorant Lake. The central area dividing the two drainages is composed chiefly of black spruce [Picea mariana (Mill.) BSP.] bog. The elevation through the entire area ranges from 275 to 313 m.

Reed Lake has numerous small islands of one square kilometer or less on the northern and western sides. Only one of the six large islands is officially named and appropriately called Fourmile Island.

Geology and Soils

The northern portion of the study area is Precambrian Shield consisting of granite or granitic gneisses (Weir 1960). The oldest Precambrian rocks consist of a volcanic-sedimentary sequence of basic volcanic flows, pyroclastic rocks and sedimentary rocks. The three units are interbedded and form a northeasterly trending belt across Reed Lake.

Shoreline areas around Reed Lake, particularly to the west, also have volcanic rock upheavals and ledges of rhyolite and basalt. Copper deposits are known on Fourmile Island.

This northern portion is an ice-scoured upland that is rolling to hilly with abundant rocky outcrops and pockets of peat bog. Surface deposits are glacial drift mixed with granitic material. The thin soils are gray-wooded podzolic.

Flat-lying beds of dolomite limestone overlie the Precambrian

rocks in the southern half. These beds comprise the Stonewall Formation of the upper Ordovician and consist of dolomite, shale and quartzose sandstone. The area is an ice-scoured lowland that is undulating with rocky outcrops surrounded by extensive marsh, swamp or bog areas. The soils are a degraded rendzina with peaty meadows and half bogs.

Rousell (1970:1) adequately summarized the geologic features:

"The southern part of the area underlain by Ordovician rocks is nearly flat. The northern part of the area is underlain by rocks of Precambrian age. Exposure of these rocks is quite extensive, especially in those areas underlain by metagabbro and granitic rocks. Low ground between rock exposures is occupied by swamps, muskeg, lakes or forest cover. The greatest relief is made by cliffs of Ordovician limestone at the northernmost limit of these rocks. The cliffs rise as much as 60 feet (18.3 m) above lake level.

"Glacial deposits appear to be rather thin; in fact the only good exposures of drift occur along the railway tracks. The railway crosses a sand plain at the easternmost edge of the area. Some of the islands in Reed Lake contain heaps of large boulders, apparently deposited by glacial ice."

Climate

The study area lies within the moist fringe of the "Dry Subhumid" region (Weir 1960). Annual precipitation is approximately 430 to 460 mm with nearly half occurring as summer rainfall. Annual snowfall ranges from 1,143 to 1,270 mm. The mean maximum July and January temperatures are 18°C and -22°C, respectively. The frost free season is 100 days. The mean date of freeze-over of rivers is November 1. Mean date of initial breakup of ice in lakes and rivers is May 10.

Vegetation

The Boreal Coniferous Forest is the major vegetative formation

in the study area with black spruce and spruce-balsam communities dominating (Shelford 1963). Dominant trees include black spruce, larch [Larix laricina (DuRoi) K. Koch] in poorly drained areas, white spruce [Picea glauca (Moench) Voss], balsam fir [Abies balsamea (L.) Mill.], trembling aspen (Populus tremuloides Michx.), white birch (Betula papyrifera Marsh.) and balsam poplar (Populus balsamifera L.). Jack pine (Pinus banksiana Lamb.) is present on well-drained ridges and recently burned areas. There are many swampy and peat bog areas.

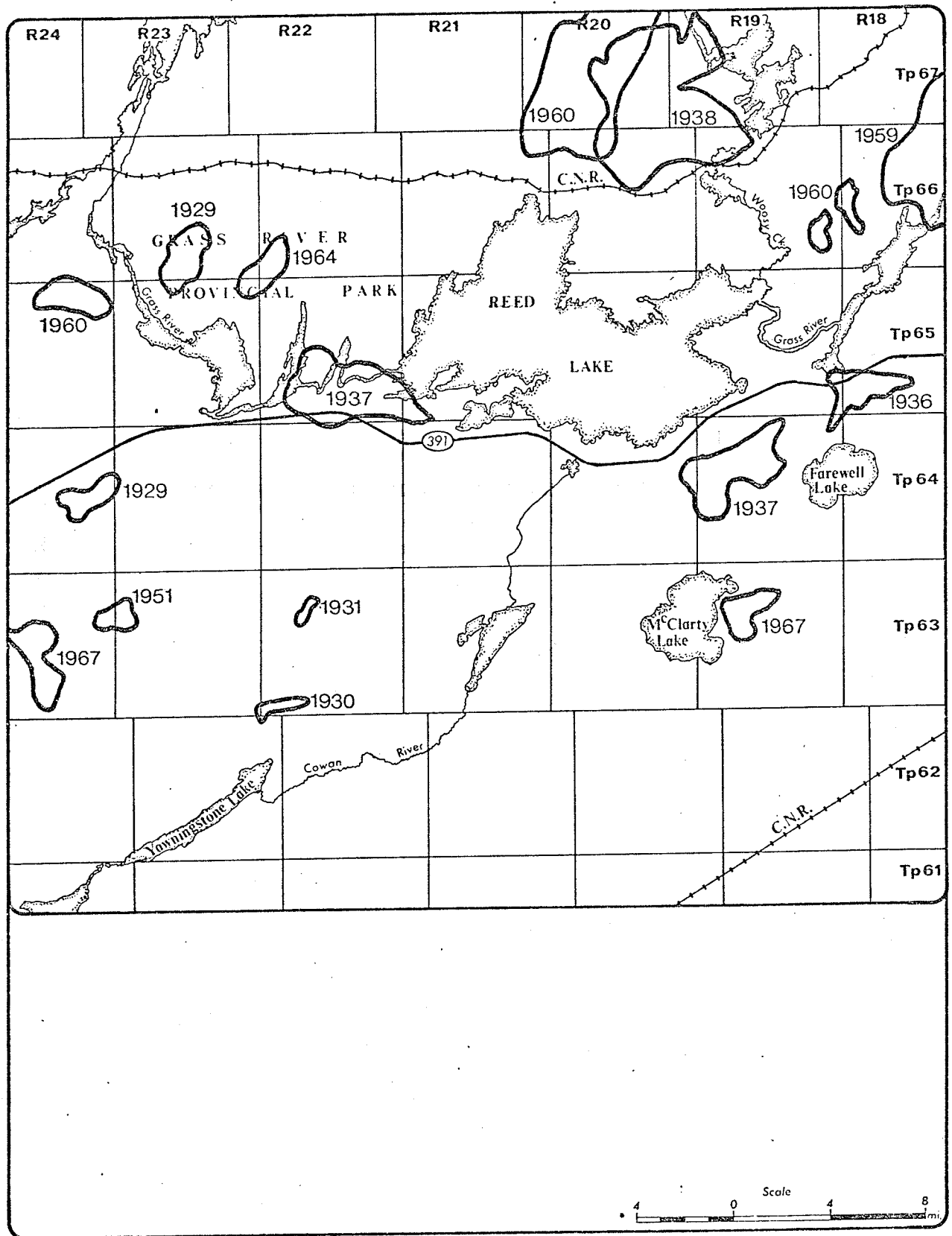
The principal shrubs include speckled alder [Alnus rugosa (DuRoi) Spreng.], Labrador-tea (Ledum groenlandicum Oeder), bunchberry (Cornus canadensis L.), bilberry (Vaccinium sp.), and mountain ash (Sorbus americana Marsh.).

Fire History

The distribution of fires in the Reed Lake area has been recorded by the forest protection staff of the Department of Renewable Resources and Transportation Services since 1929 (Fig. 5). A major fire in 1937 burned most of the area along the Grass River from Loucks Lake to Reed Lake. From 1936-38, other major fires occurred north of McClarty Lake, south of Tramping Lake and southwest of Woosey Lake.

From 1958-60, major fires occurred near Chisel Lake, Morton and File lakes, northeast of Tramping Lake, east of Woosey Creek and east of Wedge Lake. Since then, small fires have burned near Reed Lake, McClarty Lake, and Loucks Lake. It is likely that recent distributions of caribou near Reed Lake have significantly been affected by fires only since 1960.

Figure 5. Distribution, date, and relative size of fires in Reed Lake area.



Resource Utilization

Fishing, camping and hunting are the major recreational uses of the study area. Two private lodges and a provincial park campground provide tourist facilities, largely for fishermen. Some moose and caribou hunting is done during the fall season. Few waterfowl and grouse hunters use the area.

Timber cutting for pulp and lumber continues in the Mitchell Lake-Yawingstone Lake Area at the south end of the study area. Registered traplines are operated throughout the area. Some mineral exploration for copper and zinc continues.

IV. METHODS AND MATERIALS

GENERAL

Intraspecific Association of Wapiti

Coefficients and indices for quantitative measurement of interspecific association are numerous in the biological literature. Dice (1945) proposed an index of association which he adapted from a coefficient described by Forbes (1907). Dice (op. cit.) also proposed a coincidence index which differs from the index of association in that the amount of association does not change depending on which species was used as a base. McMillan (1953) used the coincidence and association indices to express the joint occurrence of wapiti and moose in Yellowstone Park.

Cole (1949) reviewed the various methods proposed to express interspecific association. He objected to Dice's indices because they gave no indication whether the association was random or whether it expressed strong interaction. Also, values for the coincidence index were dependent on sample size.

Cole (1949) described a coefficient of association (C_7) to measure the degree to which two species' joint occurrence was more or less frequent than was to be expected on the basis of chance. Plant ecologists (Bray 1956; Cook and Hurst 1963; Beaman and Andresen 1966; Smith and Cottam 1967) and animal ecologists (Macan 1954; Maguire 1963) have used C_7 to express interspecific association. Knight (1970) expressed intraspecific association between individual wapiti with a formula which he called Cole's C_7 but which was actually Dice's

coincidence index.

Four important characteristics of C_7 are:

- 1) It is an expression of joint occurrence and its deviation from chance alone.
- 2) It does not measure the degree to which two species occur jointly.
- 3) It is independent of sample size.
- 4) It is biased in terms of frequency of occurrence of each species.

Hurlbert (1969) suggested C_8 to minimize the influence of species frequencies. However, I decided to use the C_7 formula since he concluded:

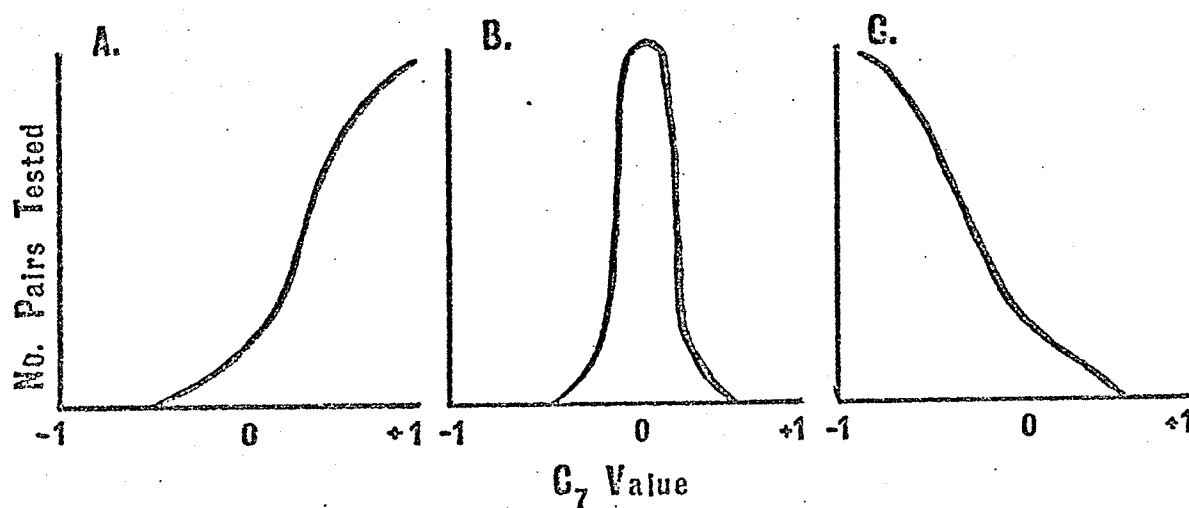
"If one is concerned only with the presence or absence of association between two particular species in a given area, C_8 is superfluous; one can simply calculate C_7 and determine (from χ^2) its statistical significance."

Values of C_7 range between -1 and +1 depending on the relative magnitude of a, b, c, and d values in a 2 X 2 contingency table, an example of which is shown below (assuming the sample size (n) equals 100):

No. 156

		Present	Absent	Totals
No. 183-3	Present	a 2	b 45	a + b 47
	Absent	c 22	d 31	c + d 53
Totals		a + c 24	b + d 76	n 100

If two wapiti occurred together as many times as they possibly could have, this positive association or C_7 value would be +1. A number of marked wapiti pairs with a significantly positive association would appear as in A below and theoretically reflect Darling's (1937) concept of wapiti sociality quoted on page 2. If all of the pairs of wapiti tested were clustered around 0, the histogram curve as in B suggests that wapiti occur together about as expected by chance alone. The curve in C indicates that wapiti occur together less frequently than by chance alone. The importance of C_7 is that it indicates whether wapiti occur together more or less frequently than by chance alone. It is not a measure of degree of joint association.



N refers to the number of groups containing at least one of the marked wapiti used in a particular test. Once one marked individual was present in a group, it was assumed that if wapiti are closely associated, the occurrence of a second marked wapiti was equally likely.

Cole (1949) proposed three formulas for calculating C_7 :

$$1) \text{ When } ad \geq bc, \quad C_7 = \frac{ad}{(a+b)} - \frac{bc}{(b+d)}$$

$$2) \text{ When } ad < bc, \text{ and } a \leq d, \quad C_7 = \frac{ad}{(a+b)} - \frac{bc}{(a+c)}$$

$$3) \text{ When } ad < bc, \text{ and } a > d, \quad C_7 = \frac{ab}{(b+d)} - \frac{bc}{(c+d)}$$

In order to minimize a bias of small expected frequencies, Cochran (1954) recommended the Chi-square test corrected for continuity when n is greater than 40. The formula is:

$$\chi^2 = \frac{n \left(\frac{|ad - bc|}{(a+b)(c+d)} - n/2 \right)^2}{(a+c)(b+d)}$$

Thus, I used Cole's C_7 analysis and Cochran's corrected Chi-square test in the analysis of wapiti associations. The data were tested at 0.05 and 0.01 levels of significance.

Range Determination of Wapiti and Caribou

Aggregate and seasonal ranges (See Appendix for definition of terms) were determined for wapiti and caribou by plotting all observations acquired on each marked individual during the study and connecting the outermost observation points with boundary lines. Seasonal ranges were based on the calendar year and on the activity of the animal. For example, early and late summer are those periods when wapiti utilized specific geographic portions of summer range. The breeding period is based on the animal's behaviour; this period extends from the first observation of a breeding group to the time when females were last observed. The calving period was based on the first and last calving dates from personal observations and pertinent literature.

A planimeter was used to determine the area of each range by following the boundary lines on a map with a scale of 1/2 inch = 1 Km. This minimum area method was similar to that described by Dalke (1942) and Mohr (1947).

WAPITI

Live-capture and Marking

From 1962-68, 6,865 wapiti were live-trapped on the Northern Yellowstone Winter Range at seven locations. Many of these wapiti were transplanted from the Park but 1,507 received coloured neckbands and were released for further observation. Of these, 236 marked wapiti (180 females, 56 males) were observed at least once on Mirror Plateau from 1963-69. Over 7,200 observations of marked wapiti were accumulated, 2,269 were of Mirror wapiti (Table 2).

TABLE 2

THE NUMBER AND MONTHLY DISTRIBUTION OF OBSERVATIONS ON 236
MIRROR PLATEAU WAPITI, 1963-69

Month	Year							TOTAL
	1963	1964	1965	1966	1967	1968	1969	
180 FEMALES								
January	8	87	33	83	47	28	0	286
February	42	80	18	47	14	37	2	240
March	0	48	1	27	15	67	4	162
April	4	8	3	83	0	48	0	146
May	10	0	0	182	0	91	0	283
June	7	27	1	28	45	49	0	157
July	0	45	35	50	74	59	29	292
August	0	16	8	21	5	17	0	67
September	1	0	0	40	18	39	1	99
October	2	0	1	0	20	43	0	66
November	2	0	0	3	8	2	0	15
December	15	25	22	48	14	0	0	124
TOTAL	91	336	122	612	260	480	36	1937
56 MALES								
January	4	20	16	14	9	3	0	66
February	1	14	2	8	2	2	0	29
March	1	8	0	8	4	0	0	21
April	2	0	1	13	0	2	0	18
May	0	0	1	28	0	8	0	37
June	1	6	1	6	6	3	0	23
July	0	11	14	9	11	17	1	63
August	0	2	3	6	1	11	0	23
September	0	0	0	8	6	3	0	17
October	0	0	0	0	1	2	0	3
November	0	0	1	1	2	5	0	9
December	5	1	11	6	0	0	0	23
TOTAL	14	62	50	107	42	56	1	332

The marking system and the type of neckband developed were described by Craighead et al. (1969) with one exception. Some marked wapiti were assigned the same pendant number during different years of the marking program. For example, five different cows received pendant number 31 during successive years of trapping. The pendant number was coded as -1, -2, etc., according to the year the individual was marked in the following scheme:

<u>Pendant Number</u>	<u>Winter Period</u>
31-1	1962-63
31-2	1963-64
31-3	1964-65
31-4	1965-66
31-5	1966-67 and 1967-68

Whenever the dash and code number is dropped in the list or in the text, there was only one Mirror wapiti with pendant 31. Any non-Mirror wapiti referred to in tables or text will always have the dash and code number. All marked bulls are indicated with an M following the pendant number.

Field Observations

A number of biologists observed and recorded marked wapiti in Yellowstone National Park from 1963 through 1969. Winter and spring movements of marked wapiti, some of which summered on Mirror Plateau, were recorded by Ellis (1965) in 1963 and 1964 and by Richard Blott in 1966. From 1963-65, movement data of wapiti on Mirror Plateau were collected by Craighead et al. (1972). I gathered data on the movement of Mirror wapiti for 22 months during 1966, 1967 and 1968.

I made a special effort to observe marked wapiti during the summer periods, logging 4,056 man-hours on Mirror Plateau. Two summer

assistants, Jim Claar and Rand Bradley, provided an estimated 900 man-hours of additional observation time. We made our observations during the following periods:

June 16-September 24, 1966

June 22-October 16, 1967

June 19-October 9, 1968

July 28-31, 1969

We operated from a base camp near the forks of Opal Creek and also occupied temporary camps at strategic observation points overlooking the large meadows on Flint, Mirror Fork, Timothy and Raven Creeks. These camps were located in the timber to minimize the influence of our activities on the behaviour of the wapiti.

Biweekly surveys of distribution, numbers and sex-age ratios of wapiti and the location of marked wapiti were conducted between North Creek and upper Pelican-Raven Creeks. These surveys resulted in essentially unduplicated observations taken within a 2-3 day period. The total number of ground observations on unmarked and marked wapiti was 4,378.

About 80 percent of the marked wapiti seen were identified as individuals with the aid of a 15 X 60 variable power spotting scope. Group size, composition, location and general activity for each individual were recorded on field data cards. A portable tape recorder and three types of form sheets were used to record data on group behaviour and associations of recognizable individuals.

Aerial Observations

In 1968, observations obtained from six flights over summer ranges supplemented my ground observations. These flights were made in a Super Cub flown at 105 km.p.h. and an altitude of 150 m. The same flight pattern was followed each time beginning on Mirror 15-30 minutes after sunrise. All of the large meadows were flown in 0.8 km. transects until wapiti were seen. The group was then circled until all observations were recorded on tape. During these flights, 2,516 wapiti were classified as to sex and age. Only groups which were completely classified were used in the analysis.

Biotelemetry

A 3-6 year old Mirror female (No. 183-3) was instrumented with a radio transmitter while on the winter range. During a 122-day period she was radio-tracked (Plate II) until the battery-powered transmitter ceased operation. Fifty-one fixes and 23 direct observations were recorded. After the transmitter failed, she was identified an additional 24 times by the color-coded transmitter collar for a total of 90 observations.

A yearling male was instrumented on Raven Creek on July 11, 1968, and monitored until the transmitter was removed on November 17, 1968. Twenty-three fixes and seven direct observations revealed an interesting movement pattern. Since this male was not identified by a pendant number, he was named Raven.

WOODLAND CARIBOU

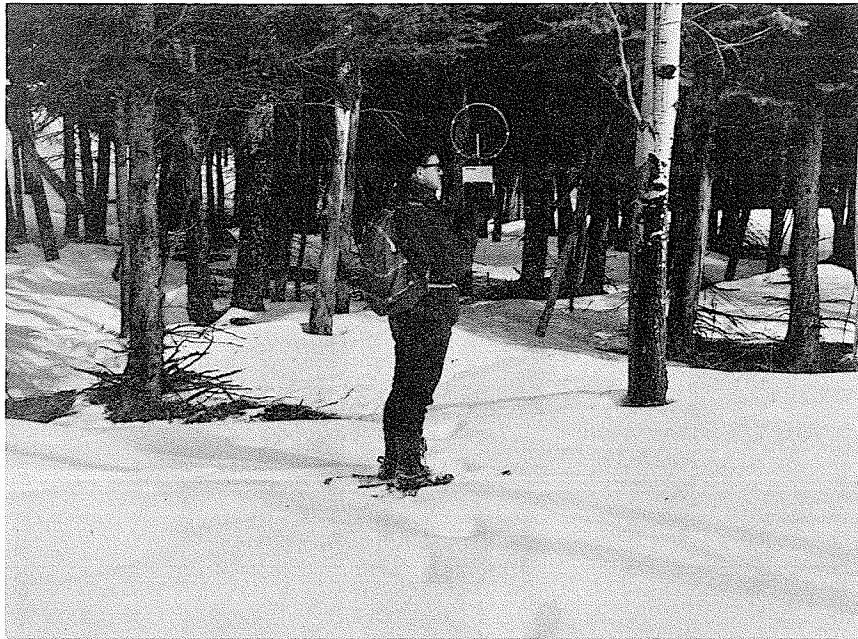
Live-capture and Marking

Regional staff of the Department of Renewable Resources and

PLATE II

Radio-tracking wapiti female 183-3 with portable receiver on winter range

Radio-transmitted wapiti female 183-3 feeding in a small stream bed on winter range



Transportation Services began marking woodland caribou on Reed Lake in June, 1973. The general technique used for capturing caribou in the summer was developed by Miller and Robertson (1967) during barren ground caribou investigations in northern Manitoba.

Woodland caribou were driven off small islands in the lake and marked while swimming to adjacent islands or the mainland. A 4-man tagging crew (two people in each of two boats) were stationed some distance from two opposite sides of the island after 1-5 drivers and 1-2 dogs were left on one end. The drivers and dogs walked across the island in a line often in visual contact with each other while the tagging crew maintained contact by way of short-range transceivers. Once a caribou was driven into the water, the two boats would converge on the animal and maneuver it away from shore while one person in the boats tried to hook the caribou around the neck with a "shepherd's crook" and draw it to the side of the boat. There, it was held against the side of the boat and marked with eartags, streamers, and a neckband. If calves were present, they were taken on board for marking. Upon release, the calf and mother were herded together and headed for the nearest island or mainland (Plate III).

Approximately 15 woodland caribou per year were live-captured, marked, and released on Reed Lake by this method from 1973-75. A majority of the caribou driven off the islands were successfully captured.

The marking material consisted of yellow or blue cattle eartags with yellow streamers that were 10 cm. long. Canvas neckbands with an outer

PLATE III

Old Yella resting along shore of small island

Old Yella and Hornet just after release by tagging crew



orange vinyl webbing were slipped over the head.

Biotelemetry

The radio telemetry equipment used in this study was developed by AVM Instrument Company, Champaign, Illinois. The basic components were purchased and assembled by an electronics consultant. The transmitters, which operate at 150-151 MHz, were constructed as collars which could either be slipped over the head of an antlerless caribou or opened up, placed around the neck and snapped together on adult bulls or females with growing antlers. Each collar was wrapped with black electrician tape and coloured coded with plastic tape.

Biotelemetry equipment was initially placed on woodland caribou at Reed Lake in June 1974 when two adult females (Old Yella and Candy) with young calves were caught and instrumented. One of the females (Old Yella) had been earmarked the previous year.

Only one of the transmitters placed on 11 caribou failed to operate for a full year. One inoperative transmitter was mistakenly placed on an adult female.

Field and Aerial Observations

Since June 1974, 910 caribou observations have been made (Table 3). Few other caribou were observed except during the breeding period and winter aerial observations. Even then, the groups were relatively small and difficult to see in the closed forest canopy.

Routine field observations were obtained by Peter Hildebrand in 1974 and Doug Storey in 1975 when I was unable to be there. Attempts to locate marked caribou were made on a daily basis or as

TABLE 3

THE SEX-AGE COMPOSITION AND NUMBER OF OBSERVATIONS OF
INDIVIDUAL WOODLAND CARIBOU WITH RADIO
TRANSMITTERS AT REED LAKE

Name	Date		Length of Period (days)	No. of Observations
	Initial Capture	Last Observation		
<u>Females</u>				
Old Yella	June 25, 1974	December 31, 1975*	546	201
Candy	July 3, 1974	December 31, 1975*	537	207
Flame	June 17, 1975	December 31, 1975*	198	100
Red	July 31, 1974	April 23, 1975	274	53
Blue	June 17, 1975	July 19, 1975	33	28
Rainbow	August 2, 1975	October 11, 1975	70	3**
<u>Calves</u>				
Sundog	June 18, 1975	December 31, 1975*	197	114
Hornet	July 8, 1975	December 31, 1975*	176	92
Tiny	July 4, 1975	July 5, 1975	2	3
<u>Males</u>				
Bull	July 16, 1975	November 16, 1975*	124	78
Devil	August 6, 1975	November 16, 1975*	102	31
Total			2,259	910

*Individual still is being monitored beyond last observation included in this study.

**Individual received an inoperative transmitter and was observed twice in 70 days after initial capture.

weather permitted. The intensive field seasons involving over 3,000 man-hours extended from July 1 to October 15, 1974, and May 29 to November 17, 1975.

Winter aerial flights were conducted at 2-3 week intervals with a twin-antenna-equipped Beaver aircraft. Direct observations of radio-equipped caribou were attempted, but often the individual was not seen although its location could be pin-pointed. When caribou were observed, location, group composition and size, habitat features and general behaviour were recorded.

V. MOVEMENTS AND BEHAVIOUR OF WAPITI

MOVEMENTS

Periodic Distribution

The periodic distribution of the marked wapiti of the Mirror Plateau (Mirror wapiti) is summarized in Table 4 and Figs. 6-8. Only some of the 236 marked wapiti (180 females, 56 males) were observed during any one period. For example, only 90 Mirror wapiti were observed 230 times during the early fall (breeding) period.

Summer

From July 1-15, Mirror wapiti were distributed from Pelican Valley to North Creek. Areas most frequented were the meadows at the headwaters of Opal, Flint and Timothy Creeks. From July 16-August 20, marked wapiti were found throughout Mirror Plateau but mostly in the Timothy-Raven-Pelican Creeks Areas. Many females moved from northern to southern Mirror between July 1 and August 20.

Fall

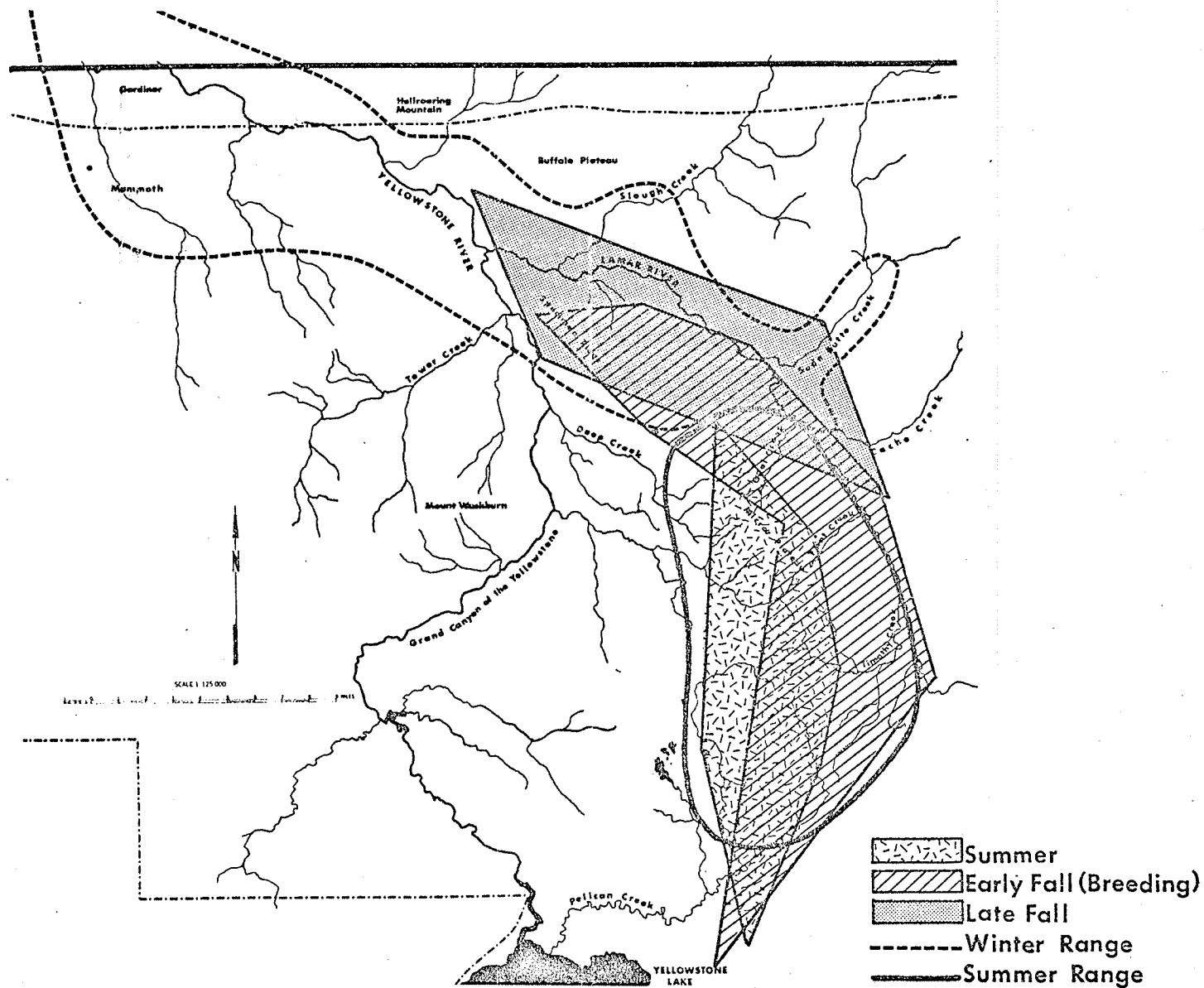
During the early fall or breeding period, most of the marked wapiti were found in the Chalcedony-South Creeks Area (northern Mirror Plateau). They moved north and east on the Plateau from summering to breeding areas (Fig. 6). This movement was supported by aerial observations of herd movements in 1966 and 1968. The large groups observed on southern Mirror in midsummer dwindled to single bulls and an occasional harem by late September. Conversely, both harems and single bulls were numerous on the eastern ridges and slopes above the Lamar River and on northern Mirror Plateau from Chalcedony to South Creeks.

TABLE 4

SEASONAL AND GEOGRAPHICAL DISTRIBUTION
OF MIRROR WAPITI 1963 - 1969

Period	Time Interval	No. Observed	No. of Observations	Areas of Frequent Observations
Summer				
Early (On the summer range)	July 1-15	112	158	North Mirror Plateau
Late	July 16-Aug. 20	133	238	Mirror Plateau
Fall				
Early (Breeding)	Aug. 21-Oct. 31	90	230	North Mirror Plateau
Late (Migration)		112	157	Specimen Ridge Lamar Valley
Winter				
Early (On the winter range)	Dec. 21-Jan. 31	201	361	Lamar Valley
Late	Feb. 1-March 20	179	395	Specimen Ridge Hellroaring Slopes Deckard Flats
Spring				
Early	March 21-Apr. 30	110	214	Hellroaring Slopes Specimen Ridge
Mid (Pre-calving)	May 1-20	110	203	Hellroaring Slopes Lamar Valley
Late (Calving)	May 21-June 10	96	164	Hellroaring Slopes Lamar Valley
(Spring Migration)	June 11-30	98	149	Hellroaring Slopes North Mirror Plateau Pelican Valley

Figure 6. The distribution of Mirror wapiti during the summer and fall periods.



In late fall, Mirror wapiti drifted down the upper Lamar River Valley and Specimen Ridge as cold weather and accumulating snow drove them to lower elevations. Thus, following breeding, Mirror wapiti were distributed throughout the Lamar Valley Area on the upper half of their winter range.

Winter

In early winter, Mirror wapiti were predominantly found on the upper portion of their winter range (Lamar Valley), but some movement to the lower half of the winter range had occurred (Fig. 7). Three Mirror cows were observed in the Gardiner-Mammoth Area by late January.

In late winter, Mirror wapiti were widely distributed throughout their winter range in the Lamar Valley, on Specimen Ridge, on Hellroaring Slopes and in the Gardiner-Deckard Flats Area.

Spring

By early spring, few Mirror wapiti were observed in the lower Yellowstone River Valley or near the Park boundary. They were concentrated in the central part of the winter range on Hellroaring Slopes, Specimen Ridge and in the Lamar Valley (Fig. 8). From March 21 to April 30, Mirror wapiti were frequently recorded in the Crystal-Amethyst Creeks Area (a calving area in the Lamar Valley). Fewer were observed on Specimen Ridge in early spring than during late winter. This early spring distribution remained relatively unchanged through the pre-calving and calving periods; however, a shift from Hellroaring Slopes to Little Buffalo-Slough Creeks Area (1.6-4.8 km distant) occurred during the calving period.

Figure 7. The distribution of Mirror wapiti during the winter to mid-spring periods.

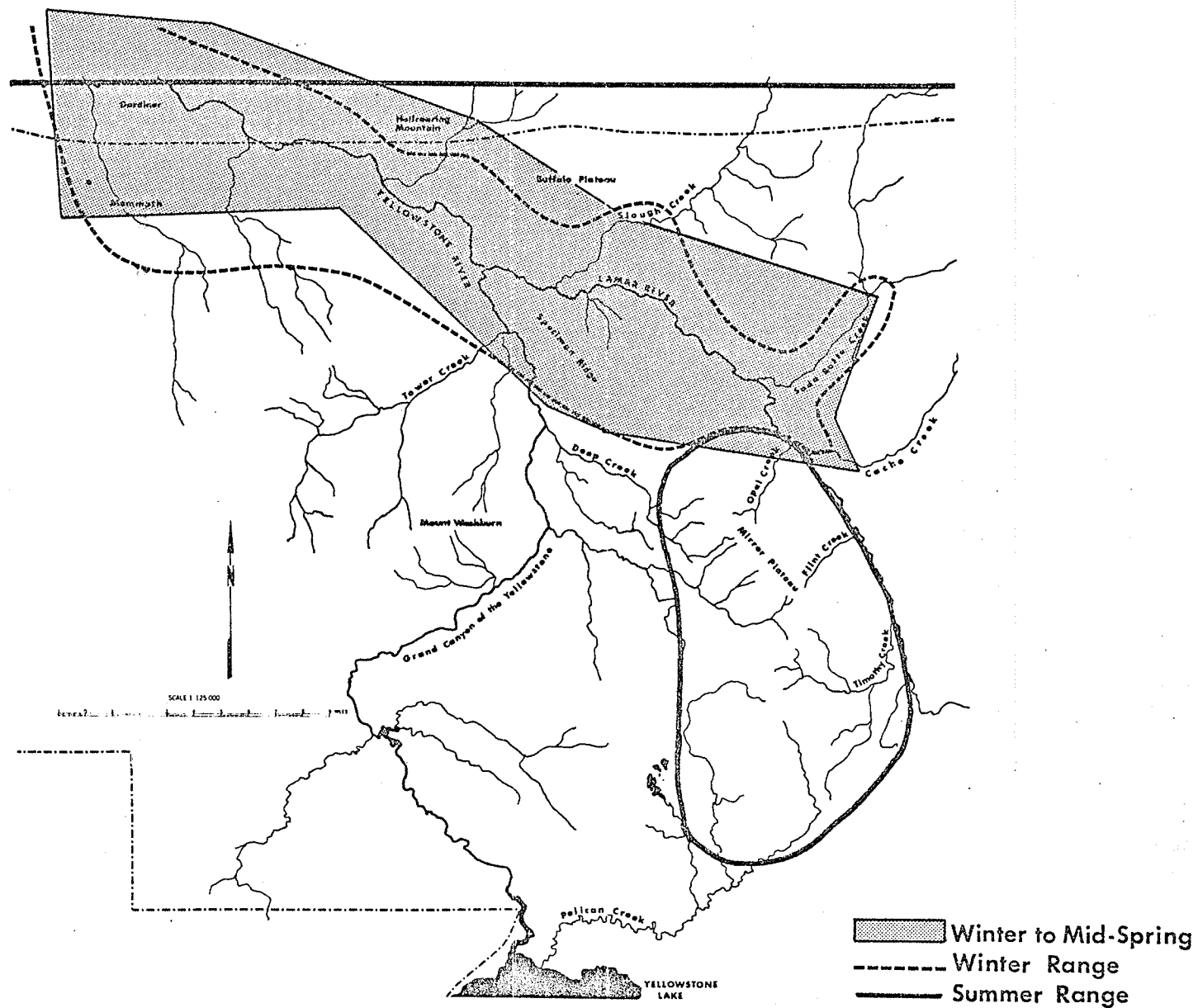
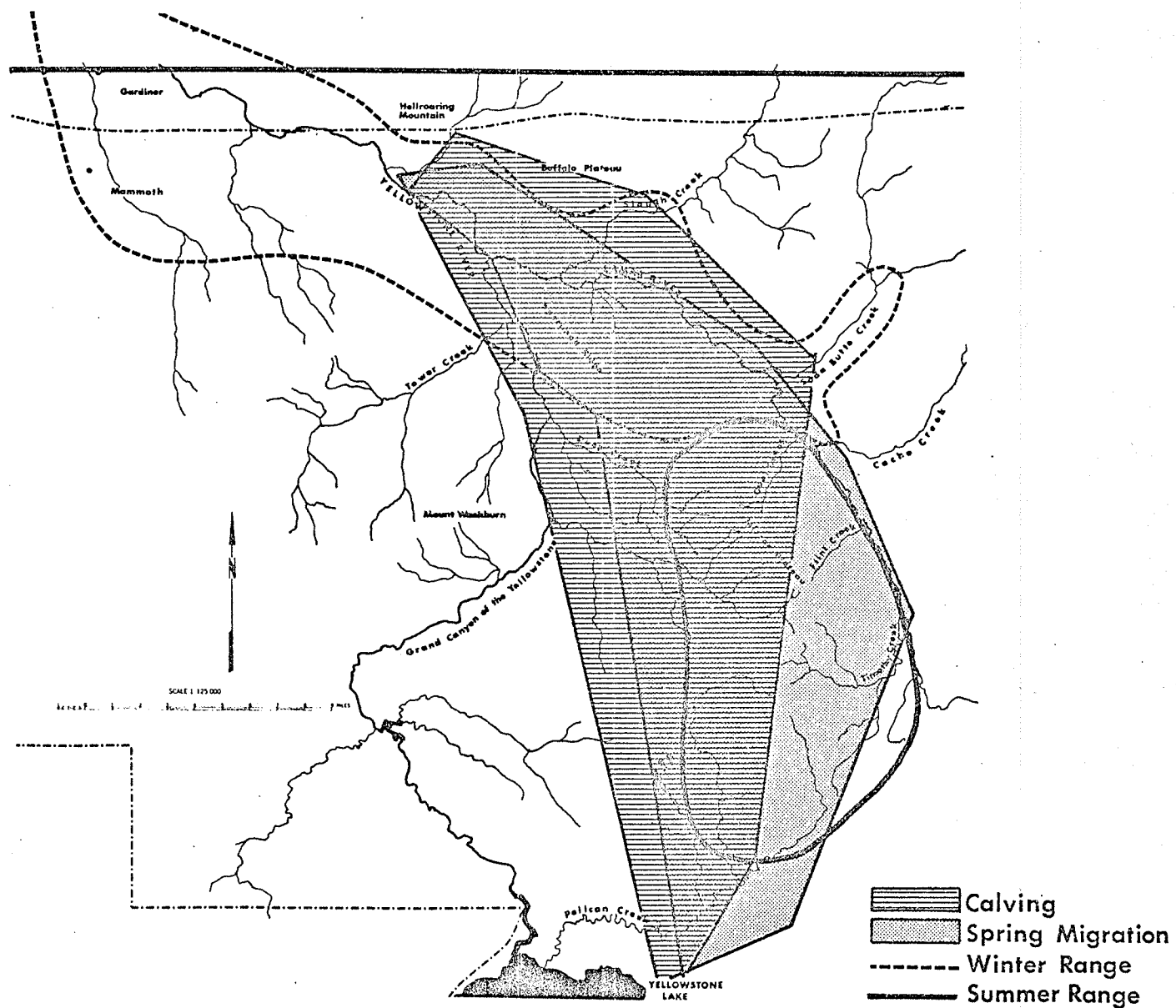


Figure 8. The distribution of Mirror wapiti during the calving and spring migration periods.



Most of the Mirror wapiti observed during the calving period were females. Although some females apparently calve as far south as Pelican Valley during their migration to summer range, most of them calve on Hellroaring Slopes and in the Lamar Valley.

Following calving, Mirror wapiti were distributed over a large area from Hellroaring Slopes to Pelican Valley with the greatest concentrations on northern Mirror and the upper Lamar Valley. This distribution is the result of spring migratory movements from winter range and calving areas to summer range. By June 30, many wapiti had reached their summer ranges while others still remained in the calving areas at lower elevations.

Composite Distribution

Periodic distribution shows that Mirror wapiti occupy a northwest-southeast arc of approximately $1,350 \text{ km}^2$ lying between Pelican Valley and Gardiner, Montana. The extremities of this area are 80 km apart. Most of the Northern Yellowstone winter range lies within the arc.

Some Mirror wapiti remained on the upper portion of the Northern Yellowstone Winter Range as late as June and others were seen there in late August. Thus the winter range was occupied by some portion of the Mirror population for over 80 percent of the year. The area occupied in spring was essentially the upper portion of their winter range.

As shown in Figs. 6 and 8, Mirror wapiti were more widely distributed during the spring than during the fall period. This was due largely to calving and to differences in seasonal migratory movements which are discussed later.

Seasonal Movements

Spring Migration

Spring migratory routes are shown in Fig. 9. Lateral trails connect the four major routes in an east-west direction on Mirror Plateau.

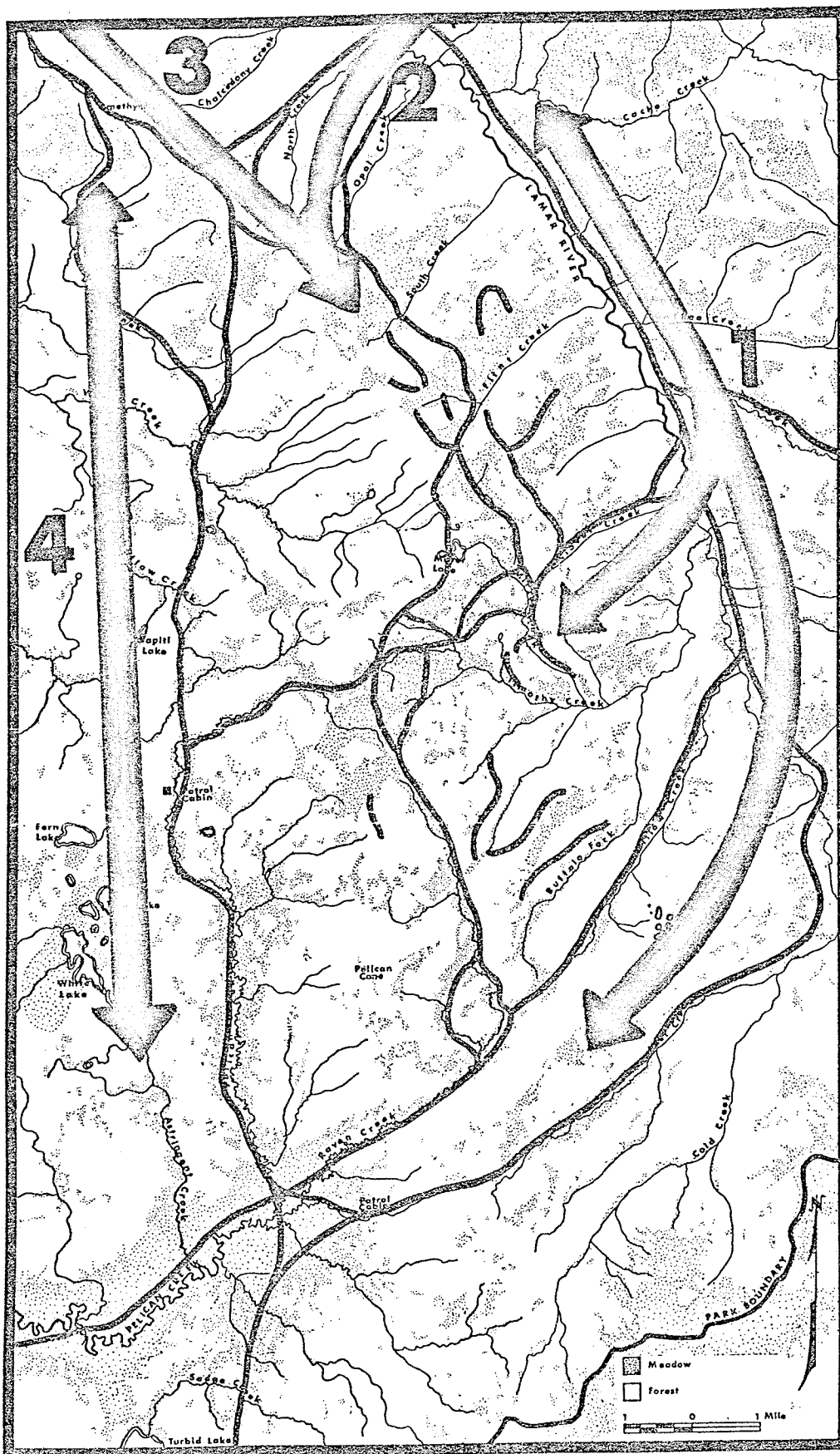
Migratory Route No. 1 follows the Lamar River to Clover, Timothy and Willow creeks. Wapiti move up these lateral drainages to the south end of Mirror Plateau. This route extends to Pelican Valley along another maintained Park trail between Willow creek and Mist creek. According to Skinner (1925), this route was the main migratory route of that segment of the Northern Yellowstone Herd that summers on the east side of Yellowstone Lake. Observations of marked wapiti by Craighead et al. (1972) support Skinner's observations. During this study, many wapiti using the Mt. Norris-Saddle Mtn. summer range also used Route No. 1 during migration.

Route No. 2 follows the upper Lamar Valley, continues up the ridge between North and Opal creeks, and terminates at the north end of Mirror Plateau. Skinner (1925) believed that this was the major migratory route to and from Mirror Plateau.

Migratory Route Nos. 1 and 2 were used by Mirror females that had left Hellroaring Slopes by mid-May, migrated to the Lamar Valley to calve, then moved to Mirror Plateau by late June. Those Mirror wapiti which had remained in the Lamar Valley Area throughout the spring period also used Routes 1 and 2.

Route No. 3 follows Specimen Ridge to the top of Amethyst

Figure 9. Network of game trials and general migratory routes on Mirror Plateau.



Mountain and terminates at the north end of Mirror Plateau. This route was used by Mirror wapiti that had remained on Hellroaring Slopes through mid-June and moved to Mirror Plateau by late June.

Route No. 4 follows Specimen Ridge over Amethyst Mountain and continues along the west side of Mirror Plateau to Pelican Valley. It curves north along Raven Creek to the southern end of Mirror Plateau.

Skinner (1925) did not mention Route No. 4 but it was noted by Craighead et al. (1972). Although I observed no Mirror wapiti along Route No. 4, marked females were observed on Specimen Ridge in May and in Pelican Valley in late June and early July of 1966. They were re-observed on southern Mirror later in July. The top of Mirror Plateau, with an average altitude of 2,790 m., would appear to be an ideal travel route to Pelican Valley. However, aerial observations of the area in early June revealed that the top of Mirror Plateau was covered with 3 m snow drifts in timbered areas and snow thicknesses of 1 m in open meadows. Migratory Route No. 4 was relatively snowfree. No wapiti or their tracks were observed on Mirror but Route No. 4 was well worn with many tracks in snow-covered portions. Sixty-three and 88 wapiti were observed from the air at the beginning and the end of this trail, respectively. Thus, wapiti appeared to move to Pelican Valley from Specimen Ridge over Route No. 4 early in the season when the top of Mirror Plateau was still snow-covered.

Return to Summer Range

The cohesiveness of a summer population of wapiti was examined by observing the frequency of return of marked wapiti to Mirror Plateau. Of 236 marked individuals observed on Mirror Plateau in 7 summers,

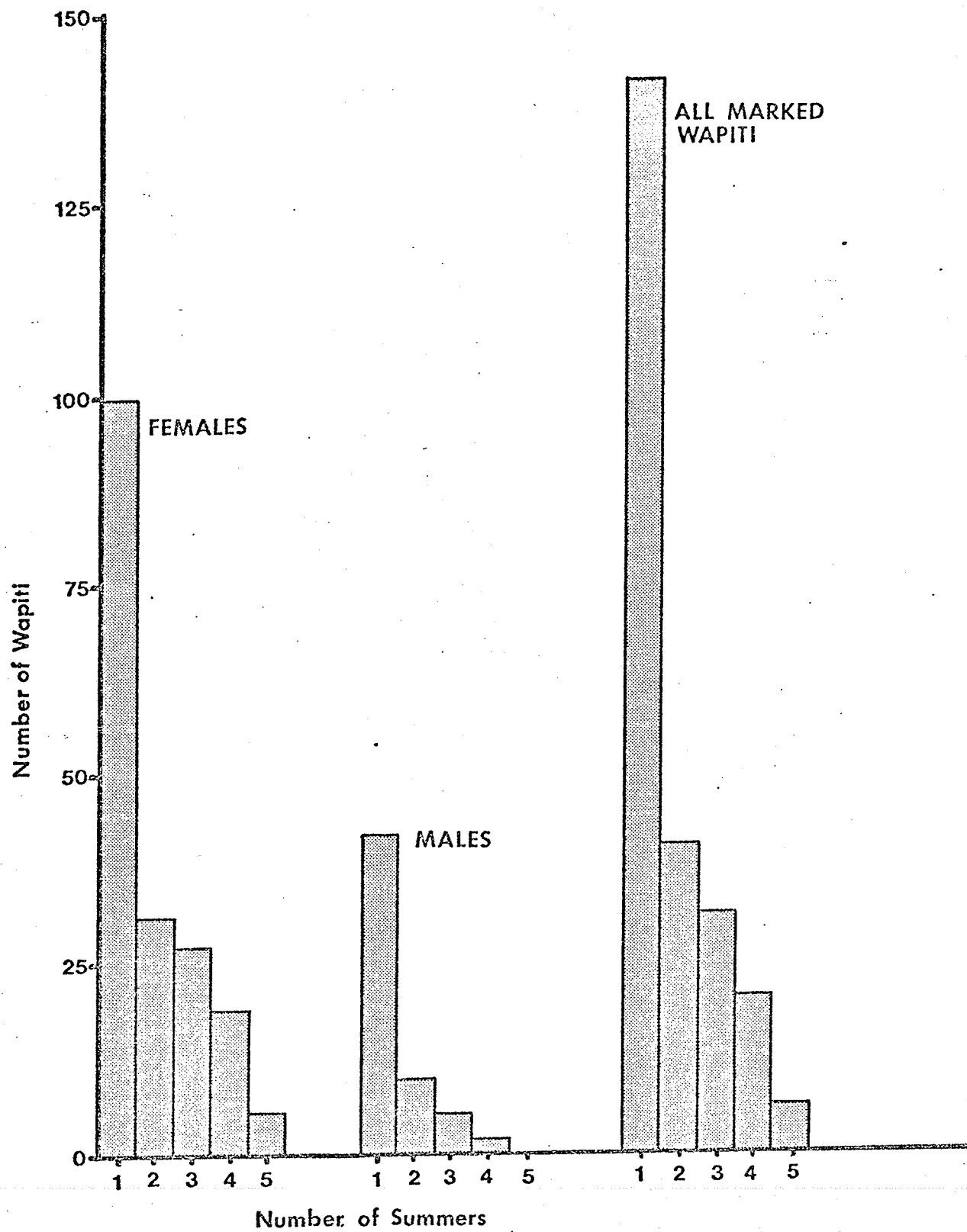
141 (60%) were observed there only one summer. Five cows returned 5 of 7 years and one bull returned 4 of 7 (Fig. 10). Traditional use of summer range was indicated by the 24 marked wapiti which returned to Mirror Plateau 4-5 summers. This supports the findings of Knight (1970) and Craighead et al. (1972) that wapiti may exhibit traditional use of a summer range.

The ratio of marked bulls to marked cows in the Mirror population was 1:3. One marked bull returned to Mirror Plateau for every six females that did so. Thus, females returned to a summer range more consistently than did males ($P < 0.05$).

The percentages of wapiti that were recorded as returning to Mirror Plateau in summer are minimal values because of observational difficulties. Marked wapiti observed in only one of six-seven summers could have been present more than one summer but not observed. For example, cow 74-5, marked in February 1963, was observed on Mirror in 1964 and 1966; she was not observed there in 1963 and 1965 and was shot outside the Park boundary in February 1967. This cow was observed on Mirror 2 of the 4 years she was known to be alive.

The influence of mortality on repeated use of summer range and calving areas (p. 72) by Mirror wapiti was difficult to assess. Trap mortality was negligible (two Mirror females were gored by antlers in traps). All marked wapiti that were retrapped were released and not transplanted from Yellowstone. Of the 236 Mirror wapiti, at least 11 percent (27 wapiti; 19 females and 8 males) died of natural or unknown causes during field investigations. This is a minimum natural mortality factor since more undoubtedly died but were never found. Fifteen of the 27 wapiti

Figure 10. The number and sex of marked wapiti observed one or more summers on Mirror Plateau.



died within the first year of marking and had no opportunity to occur on Mirror Plateau more than once. This mortality means that some Mirror wapiti did not have the opportunity to return more than once. Hence, the data in Fig. 10 represent a minimum estimate of returns to the summer range.

Of 95 Mirror wapiti that returned 2 or more summers to the same summer range, 39 returned to specific areas. Female 84 not only returned to Mirror Plateau 5 of 7 summers but also returned each summer to Timothy Creek on the southern end of Mirror. Cow 48-3 returned to central Mirror 4 summers. During 3 summers, bull 208 returned to Raven Creek (southern Mirror) and bulls 89M and 493M returned to northern Mirror.

The return of 40 percent of Mirror wapiti to summer range over a 7 year period and the return of some wapiti four or five times was in agreement with suggestions of site tenacity by Brazda (1953), Picton (1960), and Geist (1966) and confirmed the conclusions of Knight (1970) and Craighead *et al.* (1972). That females return to the same summer range more frequently than males has not been previously reported. The return of wapiti to specific areas or drainages of the summer range, particularly adult females, suggests a movement pattern that is both traditional and precise.

Movements on Summer Range

Wapiti on Mirror Plateau exhibited individualistic movements but conformed to generalized long-term movement patterns. For example, 20 Mirror females migrated to southern Mirror in early July, remained there through late July, and then moved to northern Mirror by

late August. While this pattern was generally the same for all 20, the movement of each female in the pattern was individualistic and unrelated to the movement of other females. Few of the marked females were observed in the same group or even on the same drainage at the same time. The observations of adult Mirror females 271 and 219-5 illustrate this. In 1968, they were observed on Mirror Plateau as follows:

<u>DATE</u>	<u>LOCATION OF MARKED COWS</u>	
	<u>No. 271</u>	<u>No. 219-5</u>
June 19	Not seen	Opal Creek
July 11	Timothy Creek	Timothy Creek
August 1	Timothy Creek	Not seen
August 22	South Creek	Not seen
August 28	Not seen	North Creek
August 29	Not seen	North Creek
September 26	Opal Creek	Not seen

On July 11, these females were 2.5 km apart when seen on Timothy Creek. The two females were never observed in the same group although they occurred in the same general areas throughout the summer and breeding periods.

Other marked cows remained on the northern and central portions of Mirror Plateau from late June through August, but in early September they moved to undetermined areas, presumably to breed. Females 48-3 and 129-3 were found in the South-Flint creeks area throughout the summer, but they were never observed within a kilometre of each other nor were they observed in the South-Flint creeks area or elsewhere during

the breeding period.

While most patterns of movement were probably dictated by feeding, breeding and insects, each individual apparently maintained its own pattern of movement. Craighead et al. (1973) found highly individualistic activity patterns among females in the Madison Drainage Herd.

Movements to Northern Mirror Plateau

From 1966-68, about one-third of all the marked wapiti observed on summer range were later observed on northern Mirror during the breeding period. The remaining two-thirds were presumed to breed elsewhere on the Plateau or in the upper Specimen Ridge Area.

Observations made from 1966-68 showed that many of the marked wapiti found on northern Mirror during the breeding period had moved there from southern Mirror. This movement is best illustrated by data on eight wapiti observed in 1966-68 (Table 5). The exact nature of this movement could not be determined from the observations but it appeared that the animals gradually drifted northward to the breeding areas with most of the movement occurring in August, although some cows (Nos. 60-5, 107, 566) could have moved during September. The bulls moved between late July and September 1. No. 23M moved in the shortest time--16 days. The time intervals suggest when the movements occurred and reflect the difficulties of re-observing the same individual.

Other wapiti identified on southern Mirror in mid-summer were not observed on northern Mirror during the breeding period. Four cows moved north to the central portion of Mirror while seven remained on

TABLE 5

MOVEMENT OF INDIVIDUAL MIRROR WAPITI FROM LAST
SUMMER LOCATION TO FIRST BREEDING LOCATION
(NORTH END OF MIRROR PLATEAU)

Pendant no. of indivi- dual	Date last observed in summering area	Date first observed in breeding area	Time interval (days)	Distance moved (km)
21	July 27	Sept. 11	46	9.0
23M	July 21	Aug. 6	16	9.8
235	July 25	Aug. 29	35	9.0
60-5	Aug. 24	Sept. 25	32	25.6
107	Aug. 7	Oct. 8	62	13.6
115M-4	July 25	Aug. 28	34	14.4
271-4	Aug. 1	Aug. 22	21	9.0
566	July 30	Sept. 26	58	9.0
Range (16-62)				9.0-25.6

the southern end.

From 1966 to 1968, 11 cows and four bulls that summered on northern Mirror were not found there during the breeding period. They were presumed to have moved to other unidentified areas for breeding. The evidence for movement presented in Table 5 and less precise data on similar movements by 31 other Mirror wapiti suggest a well-defined movement from summering areas to breeding areas during mid and late summer.

During three breeding periods (1966-68), a total of 58 marked wapiti were observed at the north end of Mirror Plateau. Twelve of these Mirror wapiti, 10 females and two males, were found on northern Mirror during two or three breeding periods, suggesting that individual

wapiti return to the same general area to breed each year.

Northern Mirror Plateau is undoubtedly an important breeding area for wapiti summering on the Plateau. Many of the wapiti which bred there came from southern Mirror while wapiti which inhabited northern Mirror during July and August left there by September presumably for a breeding area or areas not discovered in this study. This tendency for wapiti to return to the same breeding area each year was also found by Craighead et al. (1973).

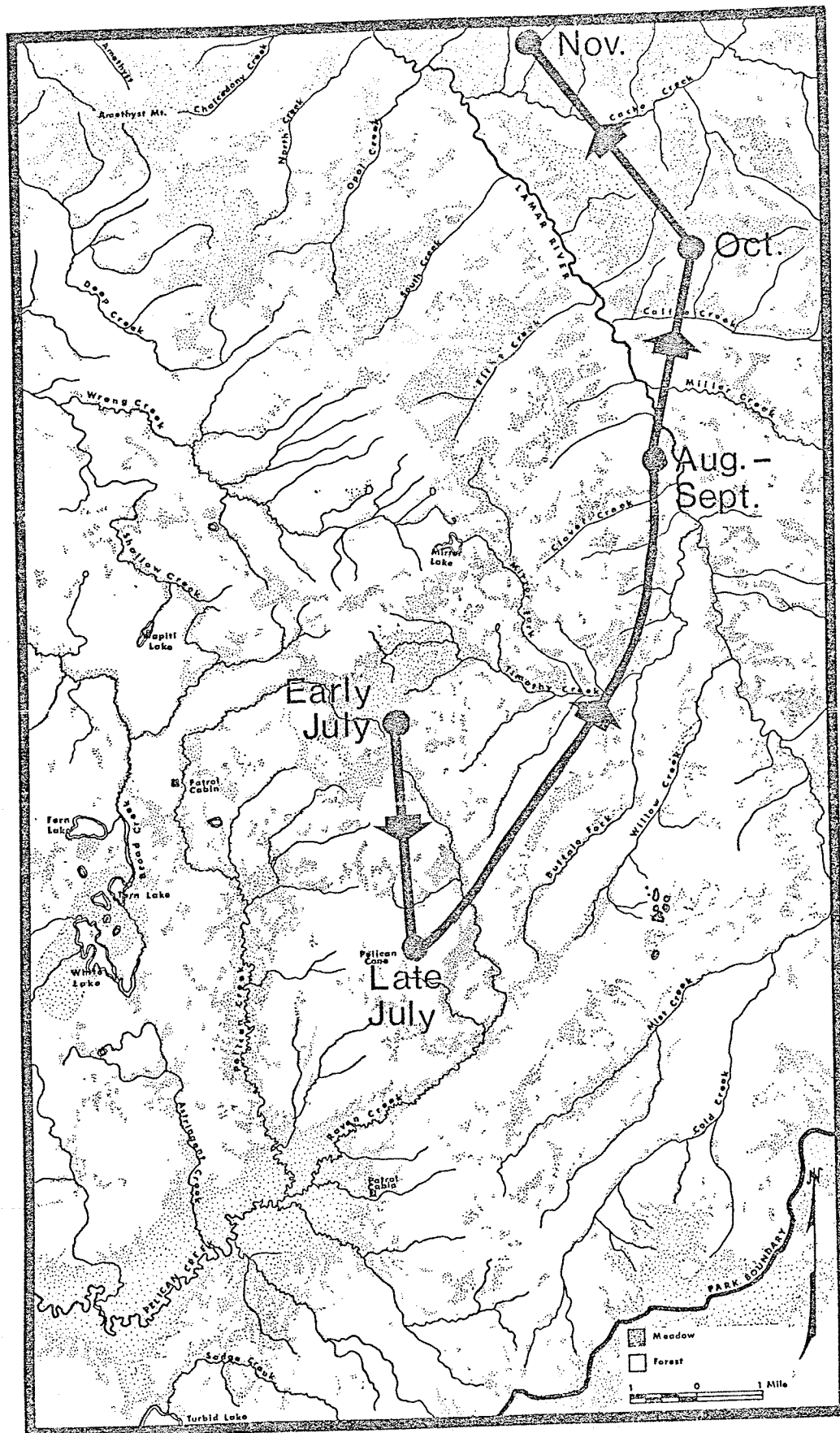
Summer-Fall Movements of Raven

In 1968, information on the summer and fall movements of a yearling male (Raven) further indicated that Mirror wapiti move from summering areas to breeding areas (Fig. 11). Following instrumentation on July 11, Raven remained in the Timothy-Raven creeks area at 2,600 m for the rest of July. He was observed once on July 29 in a band of six cows and two calves. Two days later, he was still in the same area but was with two adult bulls.

Raven left the Timothy-Raven area soon after August 1. Technical difficulties with the receiving equipment prevented relocation until August 25th at which time Raven was near the mouth of Flint Creek at 2,230m. This was 15.2 km from the August 1 location on Pelican Cone. During the rest of August and September he remained in the Flint Creek area at elevations of 2,230-2,480 m. When observed, Raven was either solitary or with another yearling male. Fresh droppings and tracks indicated that other wapiti were in the area.

Raven shed his velvet about October 1. In early October he

Figure 11. The summer and fall movements of Raven in relation to the Mirror Plateau summer range.



crossed the Lamar Valley and joined harem groups on the lower Cache-Calfee creeks ridge. On October 21 Raven was found in a group of 27 animals--one harem bull, two yearling bulls, 20 cows (seven marked) and a minimum of four calves. The seven marked wapiti were all cows that had been observed on the Mt. Norris-Saddle Mtn. summer range about 16 km distant.

During November, Raven was found among small groups of unmarked cows. On November 17, when the transmitter was removed, he was on the southwestern exposures of Mt. Norris, approximately 6.4 km from his breeding area. Thus by mid-November, Raven was on the winter range near Cache Creek.

Raven was associated with both female and male groups in late July. His movement from summer range in August to a breeding area was characteristic of other Mirror wapiti. As indicated earlier, there is other evidence that some Mirror wapiti leave the Plateau entirely as Raven did during the breeding period. In this instance, Raven joined harems from another summer range.

Movements to Winter Range

Mirror wapiti used the same migratory trails in fall as in spring (Fig. 9). Eighteen Mirror cows moved north over Amethyst Mountain to Specimen Ridge (Route No. 3); eight used the North-Opal creeks route (No. 2). Two (Nos. 29-5 and 80) were observed along the Lamar River Trail near the Cold Creek Patrol Cabin suggesting that they moved from the south end of Mirror and down the Lamar River Trail to winter range (Route No. 1). Craighead et al. (1972) recorded considerable movement

of wapiti over Mirror Plateau to Specimen Ridge and on to the winter range.

Although adult females used the same migration trails in fall as in spring, individual animals exhibited considerable variability in the specific trails they followed. For example, adult females used Routes 1 and 3 (Fig. 9) to return to the winter range. However, cow No. 271-4 used route No. 3 in 1966 and No. 1 in 1968, and No. 96.4 used Trail No. 3 in 2 consecutive years--1966 and 1967.

Some marked wapiti used one migratory route in fall and a different route in spring. No. 183-3 moved in a circular pattern up the Lamar River Trail (Route No. 1) in spring to southern Mirror. She then crossed the top of Mirror to a breeding area at the north end. In the fall she moved down Opal-North creeks (Route No. 2). Other Mirror wapiti migrated along the same route during both spring and fall.

Movements on Winter Range

Some Mirror wapiti migrated as far as the Mammoth-Gardiner-Deckard Flats Area regardless of the severity of the winter. However, more wapiti moved during moderate to severe winters than during mild winters (Table 6). To determine the general distribution of Mirror wapiti on the winter range of the Northern Herd, I grouped my observations as to whether they were recorded on the upper, mid or lower third of the range. From 1964-68, 15 percent of the Mirror wapiti observed were on the lower one-third near the Park boundary. Nearly half were found on the lower two-thirds of the winter range. Thus, Mirror wapiti occupied most of the northern Yellowstone winter range and it would be

TABLE 6

MOVEMENT OF MIRROR WAPITI FROM MAJOR WINTERING
AREAS TO NORTHERN PARK BOUNDARY, 1963-67,
AND WINTER CONDITIONS

<u>Winter</u>	Severity of winter ^a	Numbers of Mirror wapiti moving to or outside of Park boundary
1963-64	Moderate	15
1964-65	Severe	7
1965-66	Mild	1
1966-67	Moderate	<u>9</u> 32

^aDescribed by Greer (1966).

difficult to divide the area according to migratory and non-migratory segments of the Northern Herd as suggested by Cole (1970).

Two major movement patterns were recorded for Mirror wapiti on their winter range. One of these was an extensive movement to the northern Park boundary. This movement normally occurred between mid-January and March 21 (Fig. 12) with most of the elk moving in February. No. 235 traveled 29 km leaving Crystal Creek on January 23 and arriving on Deckard Flats February 3. Five Mirror cows observed near the Park boundary during one winter were also seen there a second winter.

The second movement pattern was from Specimen Ridge to Hell-roaring Slopes (Fig. 12). Movement that occurred in late winter and early spring of 1966 and 1968 is shown in Table 7. In 1966 this movement occurred from April to early May. No. 15M traveled the 14 km in 1 day and seven other wapiti took 15 or fewer days.

In 1968 a similar type of movement occurred in mid-March.

Figure 12. Two major movement patterns of Mirror wapiti on the northern Yellowstone winter range.

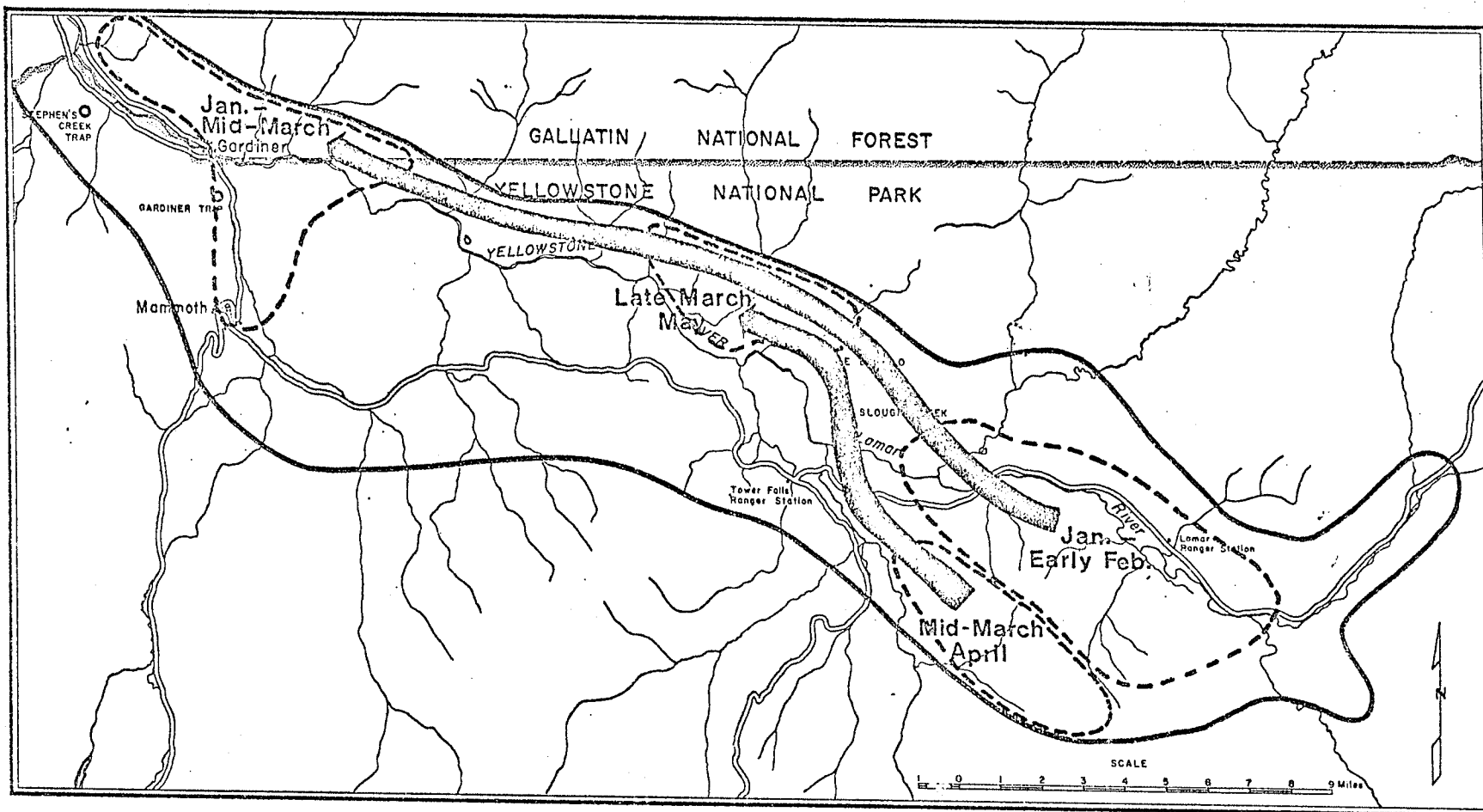


TABLE 7

THE WINTER-SPRING MOVEMENT OF MIRROR WAPITI FROM SPECIMEN
RIDGE TO HELLROARING SLOPES (1966 and 1968)

<u>Pendant No.</u>	<u>Date Last Observed on Specimen Ridge</u>	<u>Date First Observed on Hellroaring Slopes</u>	<u>Time Interval (Days)</u>
A. Mirror wapiti which moved in 1966			
13	April 28	May 4	6
15M	May 1	May 2	1
23M	April 19	May 2	13
62 ^a	March 14	May 5	52
67	May 1	May 5	4
72	March 31	April 20	20
83M	April 23	May 4	11
84	April 19	May 4	15
91-5 ^a	March 14	May 21	68
96-4 ^a	March 31	May 21	51
113	May 1	May 4	3
134-3 ^a	May 12	May 20	8
236-4 ^a	March 14	May 2	49
563	April 14	May 2	18
B. Mirror wapiti which moved in 1968			
61-5	Feb. 19	March 16	25
62 ^a	March 12	March 27	15
91-5 ^a	March 12	March 27	15
96-4 ^a	Feb. 1	March 5	32
134-3 ^a	Jan. 31	March 16	44
183-3	Feb. 22	March 5	11
212-1	March 12	March 27	15
236-4 ^a	March 12	April 14	33

^aObserved in both years.

On March 12, 203 wapiti were counted on Specimen Ridge. On March 21, only 63 were observed. A fresh trail in the snow led from upper Specimen Ridge to the Hellroaring Slopes. On March 16, 234 wapiti were counted on Hellroaring Slopes. On March 27 and April 8, 300 and 325 wapiti, respectively, were observed there. This change in relative numbers of wapiti, the occurrence of the same marked wapiti in both areas, and the snow trail between the two areas suggested a movement of nearly 100 wapiti from Specimen Ridge to Hellroaring Slopes.

The winter movements of No. 183-3 typified this mid-winter shift. This radio-transmitted cow spent late January and the first week of February at the heads of Crystal and Jasper creeks. Snow thicknesses there varied from 30-60 cm. under forest canopy to more than 90 cm. in openings.

On February 8 and 9, 183-3 was located on Specimen Ridge. On February 15 she was observed on upper Quartz Creek and 5 days later was found on the extreme northern end of Specimen Ridge. Another 5 days later, she had moved north of Junction Butte and the mouth of the Lamar River. On March 5 she was located near the Hellroaring Patrol Cabin on Hellroaring Slopes having moved 14 km from Specimen Ridge to Hellroaring Creek in 12 days. It is difficult to explain the movements of 183-3 in terms of what is known concerning wapiti behaviour. She traveled in midwinter through deep snow expending considerable energy to negotiate 16-24 km at a time when forage was least available. Food did not appear to be an incentive since this movement occurred nearly a month before spring greenup began on Hellroaring Slopes.

In late winter there were major environmental differences between

Specimen Ridge and Hellroaring Slopes (Table 8). Conditions on Specimen Ridge were generally more severe than those on Hellroaring Slopes.

TABLE 8

A COMPARISON OF WINTER CONDITIONS ON SPECIMEN
RIDGE AND HELLROARING SLOPES

<u>Characteristic</u>	<u>Specimen Ridge</u>	<u>Hellroaring Slopes</u>
Exposure	West-northwest	Southwest
Range in elevation	2100-2480 m.	1860-2450 m.
Dominant vegetation	fir; spruce-fir big sage-grass	Douglas fir big sage-grass
Approximate date of spring greenup	April 15	April 1
Areas occupied in winter	Wind-swept ridges; protected knobs and ridges above Yellow- stone River	Open slopes to timbered areas along streams
Winter snow depths	0-127 cm	25-102 cm

Dalke et al. (1965) reported a movement of Idaho wapiti to lower elevations during spring greenup. There was no conclusive evidence that spring forage induced the movement in Yellowstone. Normally spring greenup began about April 1 on Hellroaring Slopes and April 15 on Specimen Ridge. The winter of 1965-66 was generally mild. Greenup may have begun even earlier though no specific observations were recorded. Nevertheless the movement in 1966 occurred from April to early May when spring greenup had already begun in other areas. In 1968 the movement occurred in mid-March at the end of a moderate winter but nearly 2 weeks prior to greenup on Hellroaring Slopes. The data suggest a traditional movement poorly timed with spring greenup.

Movements on Spring Range

In this study calving areas were defined on the basis of the numbers of marked and unmarked females occurring in those areas between May 20 and June 10, and by the number of newborn calves recorded. Mirror wapiti were found in two main calving areas--Crystal-Amethyst creeks in the Lamar Valley and the Hellroaring Slopes Area. Eleven of 31 Mirror females were found in the same general calving area for 2-3 years suggesting a return of some individuals to a general calving area (Table 9). The influence of mortality on traditional use of calving areas was discussed earlier (p. 57).

TABLE 9

THE NUMBER OF MIRROR COWS USING THREE GENERAL
CALVING AREAS FOR 1, 2, OR 3 YEARS, 1966-68

<u>Number of Years</u>	<u>Number of Mirror cows using the calving area for 1, 2, or 3 years</u>			
	<u>Crystal-Amethyst Creeks</u>	<u>Little Buffalo- Hellroaring Slopes</u>	<u>Specimen Ridge</u>	<u>Total</u>
Area used by individual cows				
1	15	5	0	20
2	5	3	1	9
3	<u>2</u>	<u>0</u>	<u>0</u>	<u>2</u>
Total	22	8	1	31

Mirror cow 80 was marked as a calf by National Park Service personnel on June 5, 1956, near the Lamar Ranger Station. She was observed in the same vicinity as a 13-year old with a newborn calf on May 30, 1968. This was the only evidence of females returning to their own birthplace to calve.

There appeared to be at least four patterns of movement to and from calving areas. An unknown number of Mirror females left the winter range by late May and arrived in Pelican Valley to calve. They moved north in late June-early July to southern Mirror Plateau. Some Mirror wapiti remained on Hellroaring Slopes during most of May and calved there. These cows were considered late migrators to Mirror Plateau since many of them were observed on Hellroaring through late June. Other wapiti moved from Hellroaring Slopes to the Lamar Valley between May 20 and 31. They stopped in the Crystal-Amethyst creeks area to calve and then moved on to Mirror Plateau in late June. Still others calved in the Lamar Valley and then also migrated to Mirror in late June.

Thus, some Mirror cows began their spring migration early and some late. Some calved on the winter range and some calved enroute to the summer range. For some the migration was protracted while for others it was brief. Regardless of the pattern of calving and movement, most females arrived on Mirror Plateau near the end of June. Wapiti may return to the same general calving area and the variability in movement patterns suggests the importance of the individual family unit in determining how a home range is occupied and utilized.

Seasonal and Aggregate Ranges

Aggregate ranges of nine adult cows of Mirror Plateau varied considerably (Table 10). No. 183-3, observed 98 times, had an aggregate range size of 135 km^2 . Four other Mirror cows (Nos. 88, 96-4, 156 and 219-5) had similar aggregate ranges areas. No. 84 appeared to migrate via

different spring routes in 1963 (Route No. 3) and 1968 (Route No. 2) which greatly increased the size of her aggregate range (249 km^2). No. 187 exhibited consistent movement patterns, but she moved to the northern Park boundary in winter. None of the other Mirror cows in Table 10 were observed in the boundary area. Thus, variance in size of aggregate ranges was not due to observational bias but reflected the individual movement patterns of each cow.

TABLE 10
AGGREGATE HOME RANGE OF NINE MIRROR FEMALES

<u>Pendant No.</u>	<u>Number of Observations</u>	<u>Estimated Range (km^2)</u>
73	21	86
78-4	21	104
84	23	249
88	34	142
96-4	20	124
156	24	150
183-3	98	135
187	20	324
219-5	20	137

Seasonal ranges of seven Mirror wapiti were also variable (Table 11). No. 183-3's winter range (Fig. 13) was based largely on observations in 1968. No. 56-4 had a larger winter range based on fewer observations. This was due to her occurrence in the Lamar-Soda

Butte Area in winter 1967 and on Hellroaring Slopes in 1964 and 1966. The spring range varied mainly in the number of observations obtained on each wapiti during the actual migratory movement. Thus, 183-3's spring range is an area used during spring minus that area traversed to summer range. For Nos. 218 and 238 the area includes the spring

TABLE 11

SEASONAL RANGE OF SEVEN MIRROR WAPITI

Pendant No.	Seasonal Range (km ²)			
	Winter	Spring	Summer	Fall
183-3	62(47) ^a	21(31)	36(18)	--- ^b
21	---	36(9)	---	---
56-4	132(38)	---	---	---
88	---	---	41(15)	---
218	---	57(5)	---	---
238	---	83(9)	---	---
Raven ^c	---	---	44(21)	218(8)

^aNumber of observations in parentheses.

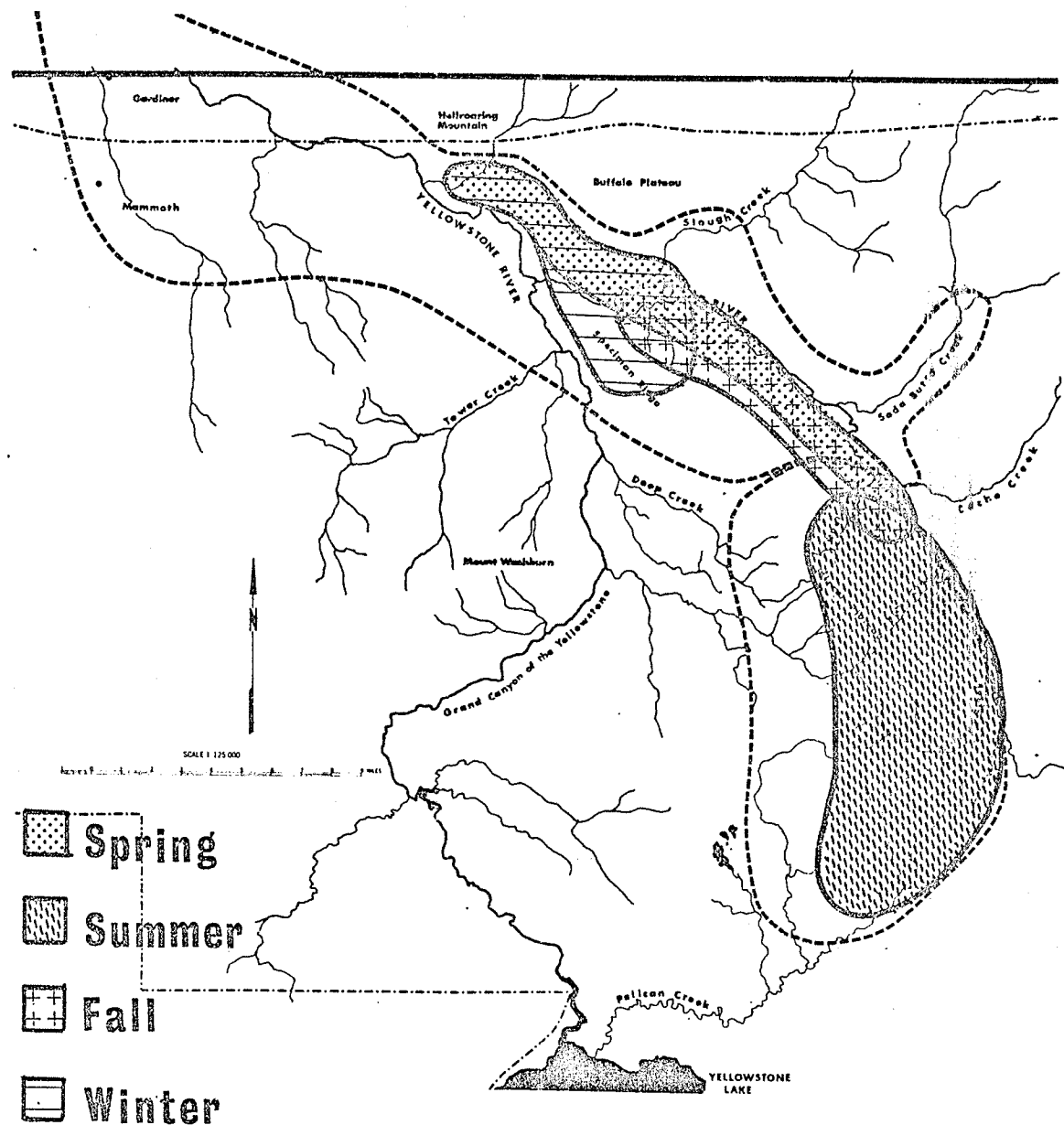
^bDate inadequate to show range.

^cYearling male

range and migratory route. Sizes of summer ranges of Nos. 183-3, 88 and Raven were similar although they occupied different areas of Mirror Plateau in summer and were never observed together. Data on fall ranges were limited to those for Raven in 1968, with the 20 km² being derived without observations of his movements in early December.

As might be expected, aggregate and seasonal ranges of

Figure 13. Seasonal areas occupied by Mirror cow 183-3 in 1967-68.



migratory wapiti in the Northern Yellowstone Herd was much greater than that of the non-migratory wapiti found in western Yellowstone Park (Craighead et al. 1973). Winter and spring ranges of migratory wapiti appear to be highly variable in size. However, summer range of many individuals may be similar in total area even if they are not found in the ~~same group or drainage~~. It appears that summer range of migratory wapiti and winter range of non-migratory wapiti in Yellowstone are the smallest of seasonal ranges.

INTRASPECIFIC ASSOCIATION

Joint Occurrence

Joint occurrence is the occurrence of two marked wapiti in a group which is spatially isolated from other groups by 0.4 km or more. The number of times that wapiti were observed jointly is thus a measure of intraspecific association. For example, females 218 and 219-5 were observed together only once in 39 observations of either animal, whereas cow 88 and 183-3 were observed together 10 times in a total of 81 observations of either animal. No difficulty was encountered in adhering to this definition while making field observations except on winter range. In winter, wapiti often occurred in large groups of 100 or more. Such large bodies were often distributed over an area which was greater than 0.4 km in diameter. When this occurred, some marked wapiti were more than 0.4 km apart. Nevertheless, these were recorded as jointly occurring as they belonged to single units.

During winter trapping operations, naturally occurring groups were forced to form large artificial groups when driven by helicopters. Thus, many wapiti were undoubtedly "forced" into the same group and

recorded in traps as "jointly occurring" more frequently than usual. This bias does not negate the validity of the data but emphasizes the relative rarity of naturally occurring associations.

Joint occurrence for 35 Mirror cows each of which were observed 15 or more times from 1963-68 is summarized in Table 12. Of 595 potential pairs or combinations of any two of the 35 marked females, 301 never occurred. For example Nos. 88 and 156 were never observed together in a total of 58 joint observations. Adult cows Nos. 183-3 and 118 bred in the same Opal-North creek area during three consecutive years. Yet they never occurred jointly in 64 observations.

TABLE 12

NUMBER AND FREQUENCY OF JOINT OCCURRENCES OF 35
MIRROR FEMALES; 1963-68

<u>Number of Joint Occurrences</u>	<u>Pairs of Females</u>	
	<u>Number</u>	<u>Frequency (%)</u>
0	301	51
1	180	30
2	79	13
3	20	3
4-10	<u>15</u>	<u>3</u>
Total	595	100

Only 35 pairs (6 percent) of these marked females were observed 3 to 10 times in the same combinations. The greatest number of joint observations were of females 88 and 183-3. They were observed together 10 times during the fall and winter of 1966. However, they were observed seven times in one harem within a 5-day period. The

remaining three observations were recorded at traps. Both wapiti were alive through 1968, but they were never observed together in 39 observations during 1967 and 1968.

Adult cows 218 and 219-5 were observed together once in the spring, summer, fall and winter seasons, respectively (Table 13). This suggests the existence of a loose band. However, the co-occurrence of cows 218 and 219-5 in the same group averaged one in 10 observations during all seasons, much less than expected if they frequently remained together. On a yearly breakdown, females 218 and 219-5 were observed together in 1964, 1967 and 1968. They were not seen together in 10 observations during 1965 and 1966.

TABLE 13

YEARLY, SEASONAL, AND JOINT OCCURRENCE OF MARKED PAIRS OF MIRROR COWS (Nos. 88 AND 183-3; Nos. 218 AND 219-5)

<u>Period</u>	<u>No. of Observations</u>		<u>Joint</u>	<u>No. of Observations</u>		<u>Joint</u>
	<u>88</u>	<u>183-3</u>	<u>Occurrence</u>	<u>218</u>	<u>219-5</u>	<u>Occurrence</u>
A. Seasonal						
Winter	7	13	3	3	7	1
Spring	6	10	0	5	4	1
Summer	4	8	0	3	5	1
Fall	17	16	7	8	4	1
Total	34	47	10	19	20	4
B. Year						
1964	3	0	0	2	4	1
1965	1	1	0	0	2	0
1966	20	17	10	8	0	0
1967	9	6	0	4	7	2
1968	1	21	0	5	7	1
1969	0	2	0	0	0	0
Total	34	47	10	19	20	4

A similar situation existed between No. 183-3 and other females with which she was most frequently seen. She was jointly observed with No. 63 (2-winter, 3-fall), No. 218 (1-winter, 4-fall), and No. 234 (3-winter, 2-fall). Females 183-3, 63, 218 and 88 were in the same harem in 1966, and 183-3 and 234 were in the same harem in 1968. Thus, as one might expect, these females associated for short periods of time (1-5 days) during the rut.

If close social relations exist between individual females, this relationship should be most apparent on specific portions of the summer range. Among marked females summering on the south end of Mirror Plateau during 1966-68, only five of a potential 136 pairs were observed in joint association two to three times; 24 pairs jointly occurred only once (Table 14). Mirror females did not appear to occur frequently in the same groups even on summer range.

TABLE 14

NUMBER AND FREQUENCY OF JOINT OCCURRENCES OF MARKED
FEMALES SUMMERING ON THE SOUTHERN END OF MIRROR
PLATEAU, JUNE 22 - SEPTEMBER 21, 1966-68

<u>Number of Joint Occurrences</u>	<u>Pairs of Mirror Females</u>	
	<u>Number</u>	<u>Frequency (%)</u>
0	107	79
1	24	18
2	4	3
3	1	--
Total	136	100

Marked bulls seldom occurred jointly (Table 15), but the number of observations per male was small. Marked bulls were not frequently observed during breeding. Most of the joint occurrences were on spring and winter ranges involving trapped bulls. Only two pairs of bulls (76M-3 and 223M; 69M and 8M) were jointly observed on summer range.

TABLE 15

NUMBER AND FREQUENCY OF JOINT OCCURRENCES OF 20
MIRROR BULLS FROM 1963-68

<u>Number of Joint Occurrences</u>	<u>Pairs of Mirror Bulls</u>	
	<u>Number</u>	<u>Frequency (%)</u>
0	150	79
1	30	16
2	9	5
3	<u>1</u>	<u>--</u>
Total	190	100

Coefficient of Association

Potentially Related Wapiti

No specific cow-calf combinations were marked during this study. Once wapiti were driven into a trap, the constant milling of the group made it impossible to distinguish specific family units. Many family units were split up when some wapiti were marked and released from the trap whereas others from the same trapped group were transplanted out of Yellowstone Park. However, all wapiti caught in Little Buffalo Trap were marked and released. It is assumed that many

family units were present in the trapped group thus making many of the wapiti potentially related. The associations of these wapiti trapped and released together (which included many family units) should, when re-observed as adults in following years during all seasons, reveal the degree of family cohesion.

The results of seven tests run on marked wapiti released from Little Buffalo Trap (Table 16) indicated that potentially related wapiti associated very little. Of 924 pairs tested, 37 (4 percent) were significant ($P < .05$) and 35 others (4 percent) were highly significant ($P < .01$). Of the significant pairs, 67 were positive associations. The five negative associations were in pairs with the radio-transmitted cow No. 183-3.

TABLE 16

ASSOCIATION OF POTENTIALLY RELATED WAPITI MARKED AND
RELEASED AT LITTLE BUFFALO TRAP

Trap Date	No. Marked Wapiti Tested	No. of groups (n)	No. pairs tested	Significant Associations $P < .05$	$P < .01$
1-9-64	16	103	120	2	1
1-22-64	19	104	171	5	2
2-14-64	19	104	171	7	6
1-11-65	10	103	45	0	1
1-13-65	19	94	171	10	5
2-4-65	9	104	36	4 ^a	1 ^a
1-13-66	19	98	171	10	5
Total	113	710	924	37	35

^a Negative association

In Fig. 14 association values of potentially related wapiti are clustered around zero. If wapiti retained family bonds as adults, one would expect a catenary-type curve on a histogram or all of the association values skewed to the positive side of zero. Association values largely clustered about zero (Fig. 14) suggest little pair cohesion in potentially related species.

The total number of calves caught at Little Buffalo indicated the minimum number of family units trapped (Table 17).

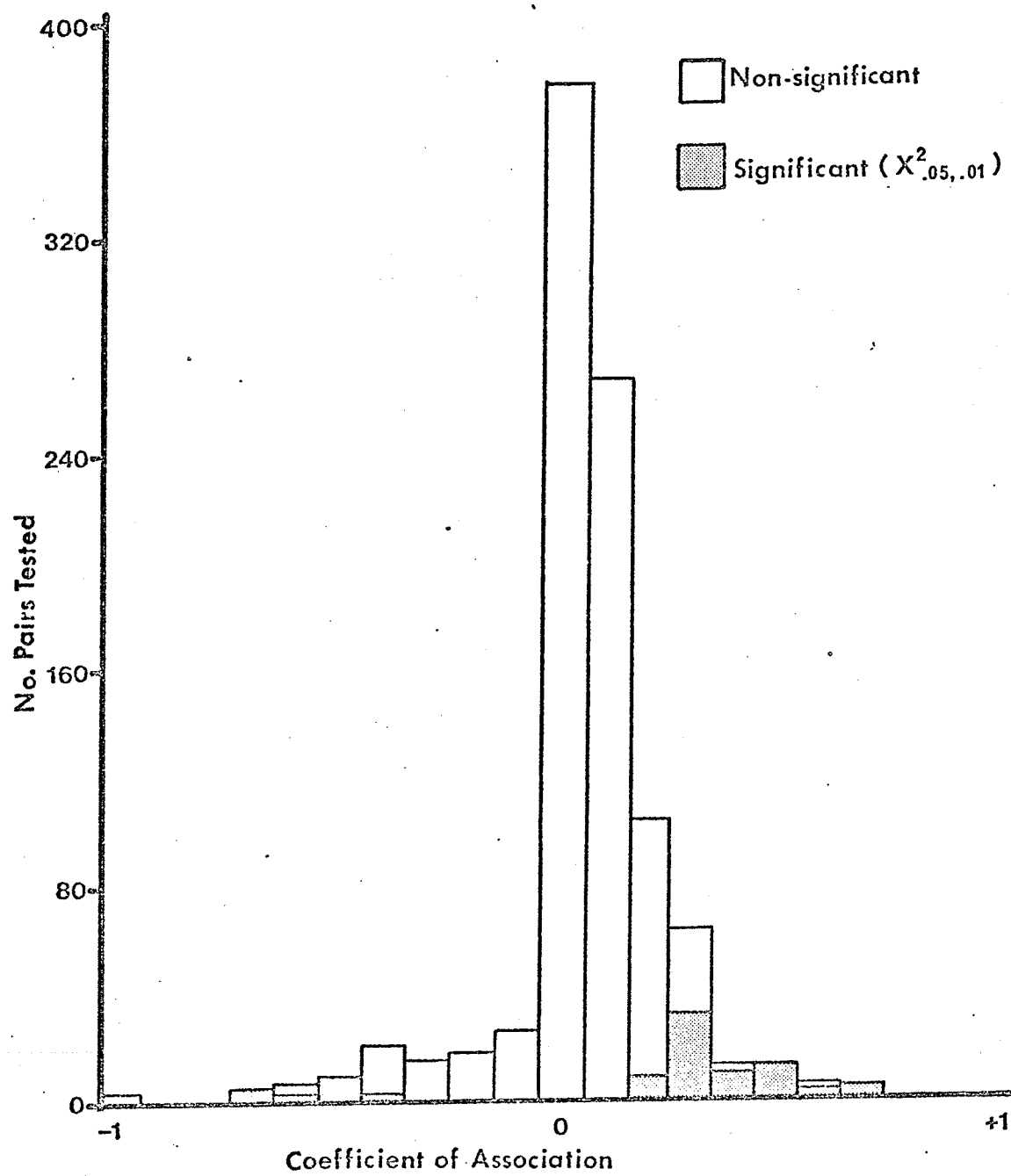
TABLE 17

THE ASSOCIATION OF FAMILY UNITS TRAPPED AND RELEASED
AT LITTLE BUFFALO

<u>Trap Date</u>	<u>No. of Family Units Trapped</u>	<u>Significant Associations P < .05, .01</u>
1-9-64	23	1
1-22-64	39	2
2-14-64	15	4
1-11-65	0	0
1-13-65	10	1
2-4-65	5	0
1-13-66	10	6
Total	102	14

If social bonding is prevalent and clans exist in wapiti, these family units should remain intact when the offspring reach maturity. However, less than 14 percent of the family units trapped were significantly

Figure 14. The association of potentially related wapiti trapped at Little Buffalo Trap.



associated after the calf became an adult. These data suggest that when calves become adults they establish individual movement patterns similar to those of their mothers.

Mirror Wapiti

Seasonal associations of some Mirror wapiti, regardless of potential relationships, were determined to show how closely associated a segment of the Northern Yellowstone Herd was on and off summer range. Ten Mirror cows were selected for a control test by pulling from a hat 10 pendant numbers of the 35 marked wapiti examined for joint occurrence. The results suggested a low degree of association among these randomly selected Mirror cows. Nearly all of the association values were negative. Only one pair of Mirror females was significantly associated more frequently than by chance. It is possible that in a random selection most of the individuals chosen do not have overlapping home ranges. However, many of the individuals tested were observed in the same general area on summer range for nearly a month, but none were observed in the same group.

Only 36 of 1,305 potentially jointly occurring pairs of Mirror cows tested for seasonal association were significantly associated; four were negative (Table 18). Three of the four negatively associated pairs involved No. 183-3, the cow with the largest number of individual observations (47). Of the four negative associations during the rut, cow 118 was observed less frequently than by chance ($P < 0.05$) with either 88 or 183-3. The three cows bred in the same North-Opal creek area for three consecutive years but only females 88 and 183-3 were in the same harem ($P < 0.01$). In winter 183-3 was negatively associated ($P < 0.05$)

with cows 96-4 and 219-5.

TABLE 18
ASSOCIATION OF MIRROR PLATEAU WAPITI DURING SIX PERIODS

Period	No. Wapiti Tested	No. Groups Tested (n)	No. Pairs Tested	Significant Associations	
				P < .05	P < .01
Winter	20	73	190	2 ^a ,6	4
Spring	23	67	253	2	5
Calving	20	58	190	0	2
Summer	22	87	231	4	0
Early Fall	22	86	231	2 ^a ,2	3
Late Fall	21	49	210	3	1
Total	128	420	1,305	21	15

^aNegative association.

Significantly positive associations were found during all six time periods. The associated wapiti included 11 adult-calf, 19 adult-adult, six adult-yearling, three calf-calf and two yearling-calf pairs. (They were marked as calves, yearlings or adults in 1963; they were positively associated in later years when all were adults.) Superficially it appears easy to reconstruct a "family tree" or the kindred relations in a clan if all significant combinations were included. However, the significant associations of specific pairs were scattered throughout the six time periods. No pairs were associated in more than one time period. The identity of a clan would be most evident during the summer months; yet none of the marked wapiti were significantly associated at that time.

The values obtained in all seasonal tests were combined and summarized in Fig. 15. The association values are concentrated at -1 and on the positive side of zero suggesting little joint occurrence of Mirror wapiti. Nine hundred sixty-three pairs were negatively associated at -1.

The association of wapiti with transmitted cow 183-3 was analyzed in a test of not only one individual with the most observations but also of associations between Mirror and non-Mirror wapiti on winter and spring range. Eleven cows (seven Mirror, four non-Mirror) most frequently associated with 183-3 were selected. In Fig. 16 most of the coefficients were negative indicating that these wapiti jointly occurred less frequently than by chance.

Summary

Joint occurrence of marked wapiti, particularly among females from the same summer range, was seldom observed during any period of the year. Specific pairs of females occurred in the same harem for 1-5 days in any one breeding period. Although these marked females tended to summer, breed and calve in the same general area each year, they were never consistently observed with the same marked cohorts during the 3 years of this study.

Potentially related wapiti such as members of a family unit were not significantly associated when the calf or yearling became adults. Apparently there is no family cohesion beyond rearing of young. Schloeth (1966) found no family cohesion when he followed known calf-female family units of red deer for 3 years.

Figure 15. The association of adult cows from Mirror Plateau.

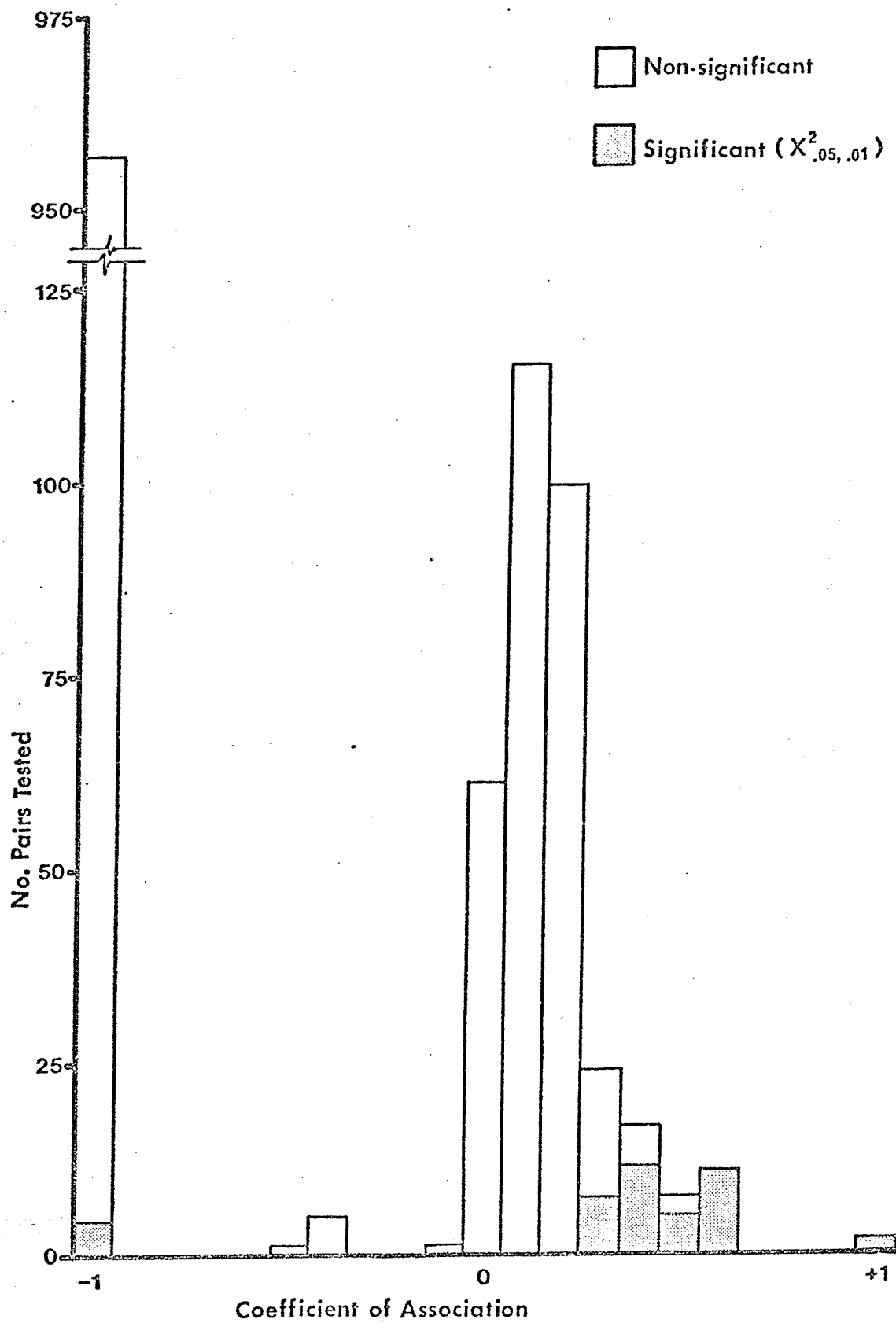
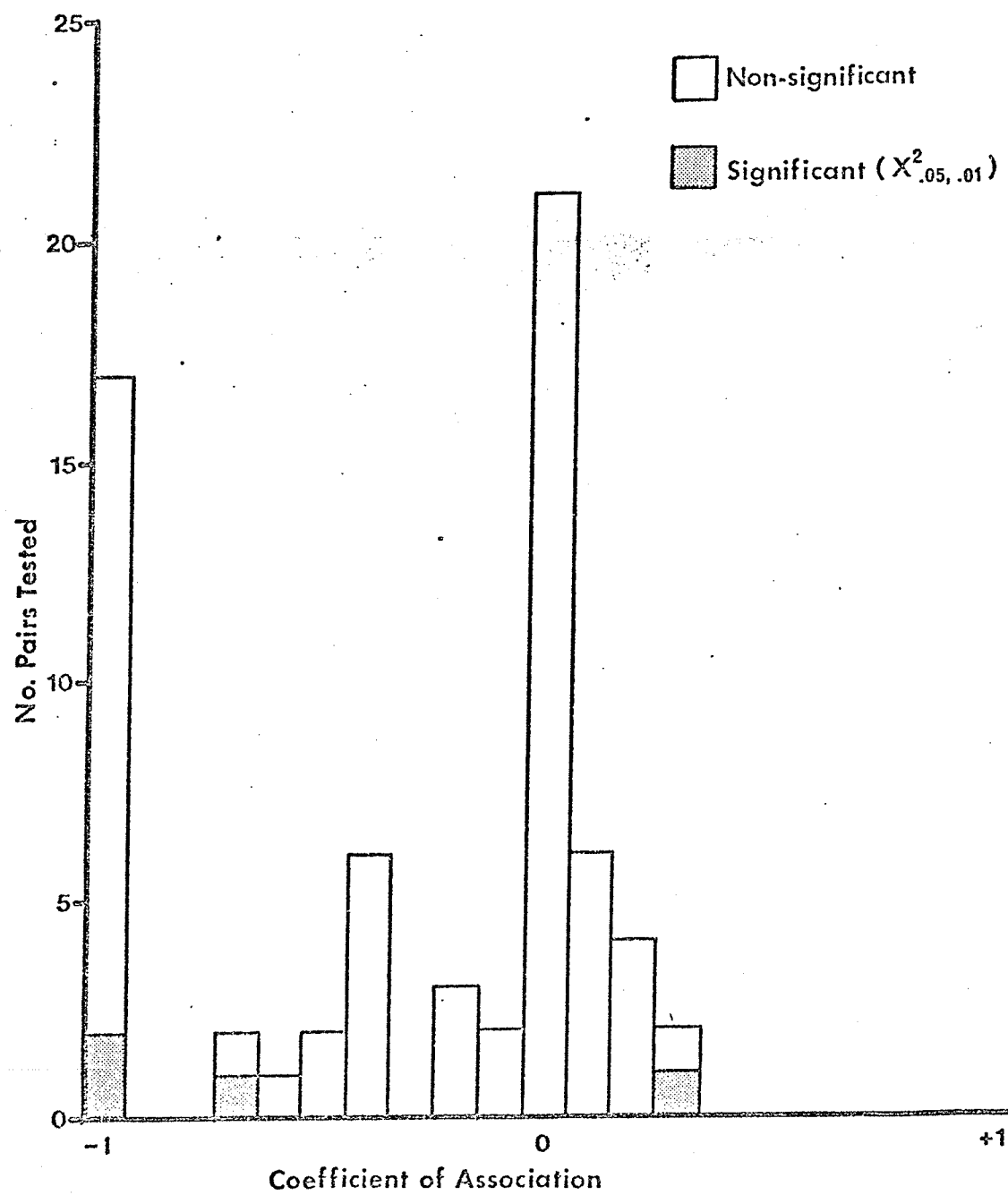


Figure 16. The association of marked wapiti with cow 183-3.



GROUP BEHAVIOUR

Exchange of Marked WapitiSummer Range

As shown in the previous section, the low degree of association among adult females suggests a high rate of individual exchange among groups. The midsummer observations of Mirror wapiti groups which contained marked females illustrate this exchange (Table 19). The sex-age composition of unmarked wapiti changed considerably between successive observations. Marked wapiti found in the same group with a specific marked cow were rarely observed with her the rest of the summer. This was best shown by cows 35, 41, 84, 107, 183-5 and 227-4.

Other marked wapiti were observed in different groups within the same general area and within a short period of time. For example, on July 29, 1968, cow 55 was one of 12 females feeding in the large meadow on Timothy Creek. Later that morning, she was bedded in the burned area with seven adult bulls, two yearling bulls, and three cows. None of the five marked wapiti in the two groups with cow 55 were common to both. At least 15 different wapiti had been associated with No. 55 between 6:10 and 7:15 A.M.

Marked wapiti which were observed in a group on summer range were not found together until the following breeding seasons (Nos. 88 and 218 in 1966) and usually not until the following winter (Nos. 183-3, 106-3, and 566 in 1967-68). In spite of over 600 observations of marked wapiti obtained during 7 summers, only Mirror cows 118 and 188 were observed together 2 or more summers (July 22, 1966, Timothy Creek; July 6, 1967, North Creek).

CHANGES IN GROUP COMPOSITION AND INTERCHANGE OF WAPITI IN GROUPS
CONTAINING A SPECIFIC MARKED COW ON MIRROR PLATEAU, 1966-68

Mirror Cow	Date	Location	Group Composition ^a				Marked Wapiti	
			AB	YB	Ca	Co	Total in Group	No. of Repeats
<u>1966</u>								
488	June 25	Flint Creek	0	0	1	13	4	-
	July 13	Flint Creek	0	0	0	2	1	0
	July 21	Timothy Creek	0	0	0	1	0	0
41	July 13	Flint Creek	2	0	5	27	8	-
	July 22	Timothy Creek	1	5	15	39	9	0
	July 23	Timothy Creek	0	1	5	9	2	1
118	July 13	South Creek	0	0	0	2	0	-
	July 22	Timothy Creek	1	5	15	39	9	0
	July 23	Timothy Creek	0	1	5	9	2	1
	July 27	Timothy Creek	0	0	0	1	0	0
227-4	July 16	Pelican-Raven Crks.	7	0	3	15	4	-
	July 21	Timothy Creek	0	0	0	2	0	0
	July 22	Timothy Creek	1	5	15	39	9	0
35	July 25	Opal Creek	4	0	0	3	0	-
	July 22	Timothy Creek	1	5	15	39	9	0
	July 23	Timothy Creek	2	4	2	12	0	0
84	July 13	Flint Creek	2	0	5	27	8	-
	July 28	Pelican-Raven Crks.	3	1	0	3	1	0
	July 28	Pelican-Raven Crks.	0	1	1	4	0	0
<u>1967</u>								
107	June 25	North Creek	0	0	0	3	0	-
	June 27	North Creek	0	0	0	2	0	0
	July 28	Timothy Creek	2	2	15	45	11	0
	July 29	Timothy Creek	3	0	1	12	3	1
183-5	July 1	Flint Creek	2	0	3	20	10	-
	July 2	Opal Creek	0	0	0	2	1	0
	July 5	Opal Creek	0	0	0	1	0	0
41	July 1	Flint Creek	2	0	3	20	10	-
	July 2	South Creek	0	0	0	3	0	0
	July 5	Flint Creek	2	0	0	9	0	0
84	June 30	North Creek	11	0	0	2	0	-
	July 1	South Creek	0	0	0	5	1	0
	July 29	Timothy Creek	3	0	1	12	3	0
<u>1968</u>								
566	July 18	Timothy Creek	0	0	6	12	2	-
	July 23	Timothy Creek	0	0	0	4	1	0
	July 30	Timothy Creek	1	0	0	5	1	0
188	July 11	Pelican-Raven Crks.	0	0	2	3	1	-
	July 18	Timothy Creek	0	0	6	12	2	0
	July 23	Pelican-Raven Crks.	1	0	0	2	0	0

^aAB = adult bull; YB = yearling bull; Ca = calf; Co = cow.

Limited evidence on marked bulls suggested exchange of males between groups. A 2-year-old male (230M) was alone on Opal Creek on June 25, 1966. The next day he was found with one yearling and two adult males on Flint Creek. On July 24, 1968, nine adult bulls including 59M and 100M were observed at the head of Raven Creek. The following day 59M was still in the area but only two unmarked bulls were with him. Thus, it was difficult to predict which individual males would be together during successive days.

Breeding Period

Frequent change in group composition characterized the breeding period although some marked cows remained in the same harem for 5 days. The dynamics of a harem, its formation and breakup involving four marked cows on northern Mirror Plateau in 1966, is outlined here. (Harem and harem bull were defined in the Appendix.)

Aug. 25. Cow 88 (at least 5 years old) was observed alone on Opal Creek.

Aug. 26. No. 88 joined a harem composed of a six-point bull, a yearling bull, two calves, and seven other cows on South Creek.

Aug. 30. Cow 183-3 (over 4 years old) was found at the head of North Creek in a harem of one bull and six other cows. A bachelor group of four young males was nearby.

Sept. 7 (A.M.). Cows 88 and 183-3 were on North Creek in a harem of two bulls (including 2-year-old 89M), one spike in velvet, three calves, and four other cows. Three-year-old bull 246M fed on opposite side of drainage.

Sept. 8 (P.M.). Cow 218 (3 year old) was observed with harem in early evening on North Creek. Group was minus one unmarked cow, the spike and a calf from the last observation.

Sept. 9 (A.M.). An unmarked cow and two calves joined the group; bull 89M was found nearly 1/2 mile across head of North Creek. A 3-year-old cow (63) and her calf, tended by a six-point bull, appeared in the area of the harem. Bull 246M was also in the vicinity near a bachelor group of 10 young bulls.

Sept. 9 (P.M.). An unmarked cow and calf had left the harem by evening. Bull 246M (a small six-point) displaced the larger unmarked 6-point from No. 63 and her calf.

Sept. 10 (A.M.). One unmarked cow and No. 63 joined the main harem. Bull 89M was still in the vicinity but 246M was not observed. No. 63 had been tended by one small six-point and two large six-point bulls in less than 36 hours.

Sept. 10 (P.M.). A fourth calf was observed in the main harem but cow 218 was feeding by herself nearly 3/4 mile down the drainage.

Sept. 11 (A.M.). Two calves and three unmarked cows were absent from main harem. Cow 218 was not observed. Bull 246M was found with two other bulls.

Sept. 12 (A.M.). Cow 63 and 183-3 and their calves fed across the head of North Creek and were last seen moving south and west along a branch of Deep Creek. Harem bull, cow No. 88 and an unmarked cow were not present.

Sept. 13 (A.M.). None of the individuals of the above harem was found. Another harem composed of a six-point bull, a spike in velvet, a calf and five cows occupied the area.

Individual exchange of adult females, calves and yearling bulls among harems was common. On August 29, 1966, cows 73 and 235 were in a harem of one bull, three calves and three cows. Overnight, 78-4 replaced 73 in the group. Two of the calves were not observed; two young bulls other than the harem bull were nearby. No. 73 had rejoined this harem by evening as had an unmarked cow and two calves. The young bulls and cow 78-4 were gone. On September 7, No. 235 was found in the same area with cow 53-4, a harem bull, one calf and two unmarked cows; Nos. 73 and 78-4 were not found.

No two marked cows were observed in the same harem in two or more breeding seasons although marked cows frequented the same breeding areas each year from 1966-68. Cow 183-3 was observed in harems on northern Mirror with females 218, 63, and 88 in 1966, no other marked

wapiti in four harem observations in 1967, and with Nos. 113, 133-4 and 234 in 1968. All but cow 113 returned to that same breeding area in at least 2 or 3 years of study.

The marked Mirror bulls appeared for brief periods in the rutting area. Three-year-old bulls 220M and 115M-4 were observed only 1 day in 1966 and 1968 respectively. Another 3-year-old male (246M) was observed four times between September 7 and 11, 1966. No. 89M (2-year-old) remained in the same area for 3 days (September 7-10, 1966). None of these bulls possessed harems. Other Mirror bulls (208M, 59M, 223M, 211M, 100M, and others) 4-year-old and older were never found during the rut. They were presumed to participate in breeding on southern Mirror Plateau. Since harem bulls observed on northern Mirror were unmarked, it remained unknown whether harem bulls moved as much as some marked bulls without harems appeared to.

Winter and Spring Range

From January through May, large groups of wapiti were found on Hellroaring Slopes. Most of these winter and spring groups contained 10 or more marked Mirror wapiti. The original identity of a group in the Hellroaring Area was soon lost if each Mirror wapiti was traced through successive observations (Table 20). For example, on May 3, female No. 15 was with a group of 125 wapiti of which 11 were Mirror wapiti. The next day, she was in a group of 50-75 of which 17 were Mirror wapiti, on May 21 she was observed with 16 Mirror wapiti and later the same day with only three. There were few repeats among marked wapiti between successive observations.

Few marked wapiti remained in the same group with radio-transmitted cow 183-3 during successive observations on winter and spring

range. Mirror wapiti did not reoccur with No. 183-3 as often as non-Mirror wapiti. Cows 61-5 and 183-3 were together on February 19 and

TABLE 20

GROUP EXCHANGE OF MIRROR WAPITI IN THE HELLROARING SLOPES
AREA DURING WINTER AND SPRING, 1966

Pendant No.	Date	Estimated Group Size	Mirror Wapiti	
			Total Marked in Group	Repeats from Previous Observation
15	May 3	125	11	-
	May 4	50-75	17	1
	May 21	Unknown	16	2
	May 21	45	3	2
134-3	Feb. 20	19	2	-
	April 20	175	3	0
	May 20	175	10	0
236-1	Feb. 20	19	2	-
	May 4	125	13	0
	May 4	50-75	17	3
	May 19	16	1	0
	May 2	200	8	-
	May 3	125	11	1
	May 4	125	13	5
	May 18	50-75	3	0
	May 21	Unknown	16	0
	May 3	125	11	-
	May 20	175	10	2
	May 21	Unknown	16	3
180M	May 21	45	3	2

March 27. However, 61-5 was not with 183-3 the four times they were observed during the 35-day interval.

Spring Migration

Mirror cows did not move en masse as organized groups from

calving areas to summer range. Data on six cows (Table 21) indicated an individual and family unit movement from group to group during spring migration. Late migrators from Hellroaring Slopes, such as 48-5 and 187 in 1967, moved to Mirror Plateau about the same time, but they were never found in the same group. Other marked Mirror cows

TABLE 21

GROUP EXCHANGE OF MIRROR COWS DURING SPRING MIGRATION WITH
INDIVIDUAL COWS THAT CALVED (A) ON HELLROARING SLOPES AND
(B) IN THE CRYSTAL-AMETHYST CREEKS AREA

Pendant No.	Date	Location	Size	Group Composition	
				Total No. of Marked Mirror wapiti	No. Repeats
A. Hellroaring Slopes					
48-5	6-19-67	Hellroaring Slopes	95	4	--
	7-1-67	Opal Creek	9	2	0
	7-6-67	North Creek	12	6	0
129	6-15-68	Hellroaring Slopes	118	6	--
	7-17-68	South Creek	2	0	0
187	6-18-67	Hellroaring Slopes	66	2	--
	6-24-67	Opal Creek	3	1	0
	6-25-67	Opal Creek	8	5	0
B. Crystal-Amethyst Creeks Area					
70	7-9-68	S. of Junction Butte	63	3	--
	6-3-68	Jasper Creek	6	0	0
		Raven Creek	34	6	0
214	5-24-68	Crystal Creek	35	4	--
	6-19-68	Chalcedony Creek	13	1	0

observed with the three females movement from Hellroaring Slopes (Table 21A) were never observed with the three cows on summer range.

Not one pair of the 29 Mirror wapiti observed on eight occasions occurred together. The large groups observed on Hellroaring in mid-June dwindled to family units and small bands in the first observations on Mirror Plateau.

Cows which calved in the Crystal-Amethyst creeks area exhibited a similar pattern (Table 21B). No joint occurrences were found among 14 Mirror cows on five observation dates.

Table 22 shows the same independence of Mirror cows from a different aspect. Two groups of cows observed on Mirror in early summer were traced back to spring range to see if each group maintained its identity based on the occurrence of Mirror cows. There were five marked Mirror cows in a female group observed June 25, 1966, on Flint Creek (Table 22A). None of the five were observed together in eight previous observations on spring and summer range. No other Mirror cows observed with them on spring range were present in the Flint Creek group.

This independence was true of marked cows observed in a large group on Raven Creek, July 9, 1968 (Table 22B). None of the 12 previous spring dates and locations listed for the seven Mirror cows found together on summer range were repeats. None of the other 23 Mirror wapiti observed with them on spring range occurred more than once in successive spring observations or in the July 9 observation.

Group Size

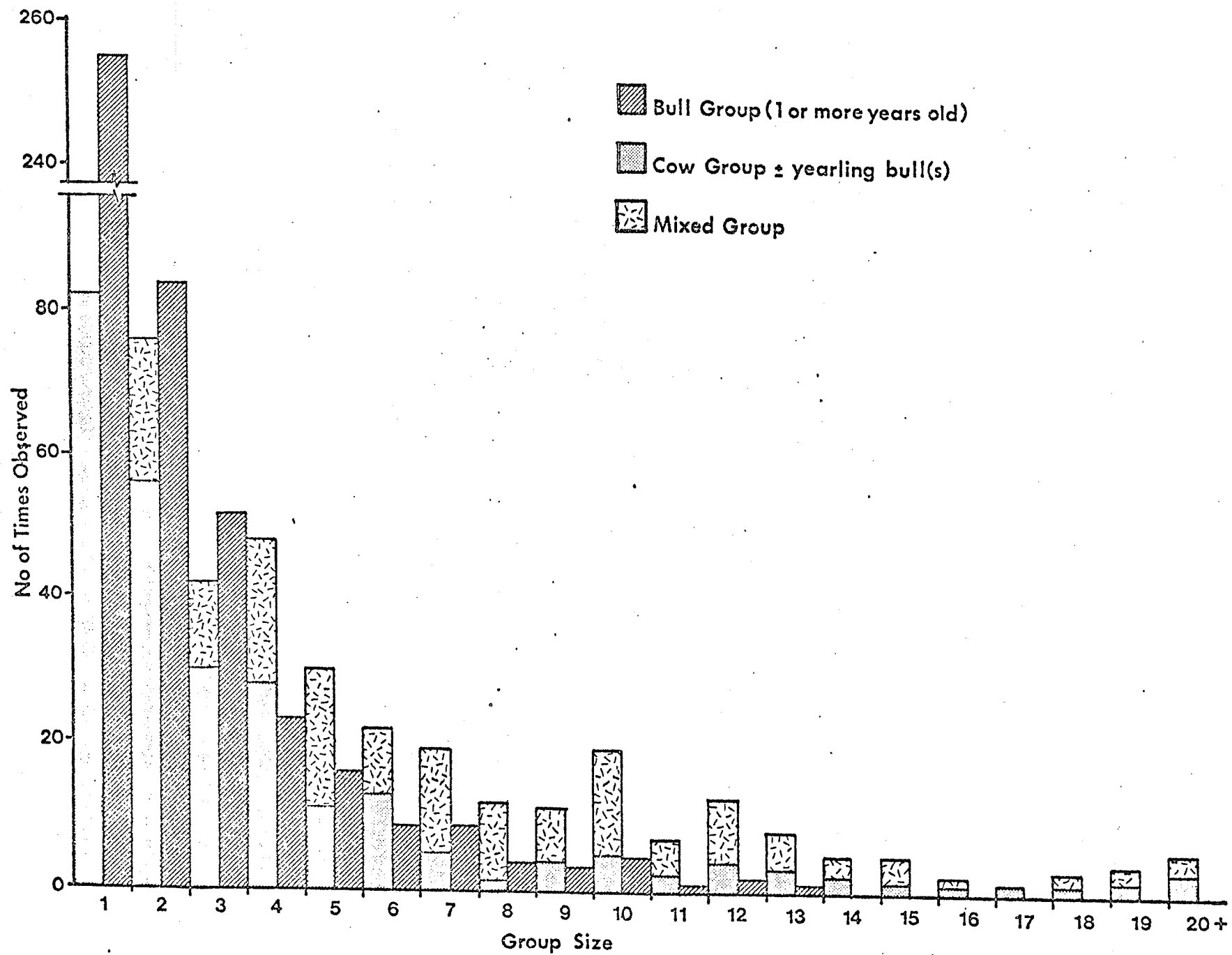
Group size of wapiti on Mirror Plateau ranged from one to an estimated 150, but over 95 percent of the groups observed numbered 20 individuals or fewer (Fig. 17). Cows were usually solitary or found

TABLE 22

THE SPRING ASSOCIATION OF MIRROR COWS WHICH APPEARED
IN THE SAME GROUP IN EARLY SUMMER ON (A) FLINT CREEK
AND (B) RAVEN CREEK

Pendant No.	Date	Location	Size	Group Composition	
				Mirror	Other Marked Wapiti
A. Flint Creek (June 25, 1966)					
78-4	4-22-66	Junction Butte	15		0
	5-20-66	Hellroaring Slopes	150		10
	5-22-66	Crystal Creek Trap	15		2
	5-25-66	Crystal Creek	20		
129	5-2-66	Coyote Creek	10		0
477	No Spring Observations				
488	5-5-66	Little Cottonwood Creek	75		6
	5-19-66	Little Cottonwood Creek	45		1
133	6-12-66	North Creek	5		2
B. Raven Creek (July 9, 1968)					
31-3	5-29-68	1 1/2 mi. SE Little Buffalo Trap	23		1
	6-1-68	1 mi. SE Little Buffalo Trap	6		1
18-3	4-9-68	1 mi. East of Garnet Hill	125		10
	5-18-68	1 1/2 mi. North of Junction Butte	40		2
	5-21-68	1 1/2 mi. North of Junction Butte	35		1
45	3-21-68	Quartz Creek	7		0
46	5-26-68	Amethyst Creek	25		1
47-3	3-16-68	Little Buffalo Creek	46		1
70	4-9-68	Hellroaring Slopes	48		1
	5-15-68	North End of Specimen Ridge	65		3
	6-3-68	Jasper Creek	6		0
187	4-8-68	Hellroaring Slopes	75		2

Figure 17. Frequency of group size of Mirror wapiti on summer range.



in cow-calf combinations. Bulls most frequently occurred in groups of 1-3, the largest being 13. Knight (1970) and Ahlen (1965) reported similar findings in wapiti and red deer, respectively.

Mean group size during the summer breeding periods changed markedly for mixed groups and cow groups (Fig. 18). Bull groups gradually decreased in size through mid-October.

Mixed (cow-bull) groups were consistently the largest, particularly during July and early August. In early August a mean group size of 34 was greatly increased by several large groups of at least 100 wapiti. Mixed groups increased toward the end of the breeding period. Young bulls were allowed to join harems and several small harems coalesced at that time.

Mean size of cow groups was greatest in late June and again in late October. A mean group size of 3-4 for July and August suggested that 1-2 cow-calf-yearling units were characteristic groups on the summer range.

The frequency of occurrence of 15 different social groups observed during the summer-breeding periods from 1966-68 is summarized in Table 23. Data for 1963-65 were not included because yearling males were not recorded separately from older bulls in the field classifications.

Single adult bulls and adult bull-adult bull groups were the most common types observed. Single cows, cow-cow, cow-adult bull, and cow-calf groups followed in order of frequency of observation. Solitary bulls were observed three times as frequently as single cows. Adult bull-adult bull groups (154) were more numerous than the total number of cow-cow, cow-calf, cow-yearling bull, and cow-yearling bull-calf

Figure 18. Trends in mean group sizes of Mirror wapiti on summer and fall ranges.

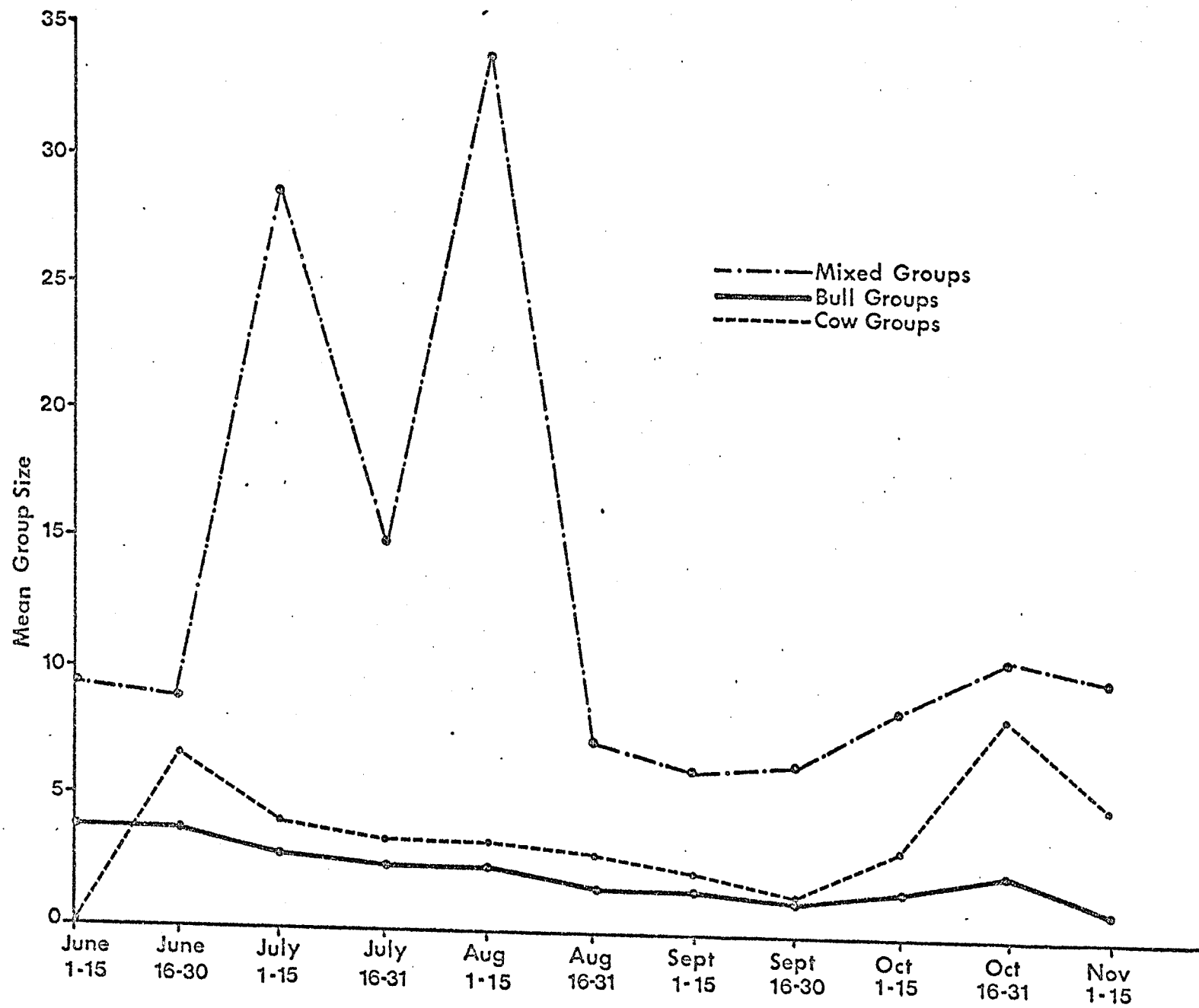


TABLE 23

CHANGES IN SOCIAL GROUPING OF WAPITI ON MIRROR PLATEAU
FROM SUMMER TO BREEDING PERIODS, 1966-68

Social ^a Group	Number of Groups Observed				Significant ^b Change
	Summer Period	Breeding Period	Total	Rank	
AB	91	111	202	1	0
AB-AB	116	38	154	2	-
Co	45	24	69	3	-
Co-Co	57	11	68	4	-
Co-AB	36	27	63	5	0
Co-Co	42	15	57	6	-
Ca-AB-Co	12	34	46	7	+
Ca-YB-Co-AB	7	8	15	8	0
YB	3	11	14	9	+
YB-AB	7	4	11	10	0
Ca-YB-Co	10	1	11	10	-
YB-Co	8	2	10	12	-
YB-Co-AB	5	4	9	13	0
YB-YB	1	1	2	14	0
Ca	1	1	2	14	0

^aCo = cow; Ab = adult bull; YB = Yearling bull; Ca = calf (Each symbol represents one individual).

^b0 = no change; + = increase; - = decrease

groups (146). Solitary calves and yearling male-yearling male groups were least frequently seen of all the social groups.

Several trends in occurrence of different social groups were apparent. There was an increase in solitary yearling males and adult bull-cow-calf groups from summer to breeding periods. However, there was no change in number of yearling bull-yearling bull groups nor in groups containing yearling and adult bulls. Groups in which yearling bulls were associated with adult cows or adult bulls decreased, the former significantly.

During the breeding periods, 1966-68, 57 percent of the elk groups observed were bull groups (Table 24). Sixteen percent were cow groups and 27 percent were harems. Cow groups were only 11 percent in 1968.

TABLE 24

NUMBER OF BULL, COW AND HAREM GROUPS OBSERVED ON MIRROR PLATEAU DURING THE BREEDING PERIODS, 1966-68

Group	1966		1967		1968		1966-68	
	No.	Percent	No.	Percent	No.	Percent	No.	Percent
Bull	61	53	44	56	79	61	184	57
Cow	21	18	18	22	14	11	53	16
Harem	<u>33</u>	<u>29</u>	<u>17</u>	<u>21</u>	<u>36</u>	<u>28</u>	<u>86</u>	<u>27</u>
Total	115	100	79	100	129	100	323	100

Bull groups were composed almost entirely of adults 2 years old and older (Table 25). Cow groups fluctuated in size from 2.3 (1966) to 2.0 (1967) and 3.9 (1968). Yearling bulls were present in cow groups only in 1966. Most cow groups were 1-2 family units in size as had been found during the summer.

TABLE 25

COMPOSITION AND MEAN GROUP SIZE OF BULL, COW AND HAREM
GROUPS DURING THE BREEDING PERIODS, 1966-68

<u>Group Characteristic</u>	<u>1966</u>	<u>1967</u>	<u>1968</u>	<u>1966-68</u>
A. Bull Group				
Mean size	1.5	1.2	1.8	1.3
No. adult bulls	1.3	1.2	1.6	1.2
No. yearling bulls	0.2	0.0	0.2	0.1
B. Cow Groups				
Mean size	2.3	2.0	3.9	2.5
No. yearling bulls	0.2	0.0	0.0	0.1
No. calves	0.6	0.3	0.9	0.5
No. cows	1.5	1.7	3.0	1.9
C. Harems				
Mean size	6.9	5.2	7.0	6.6
No. adult bulls	1.3	1.2	1.4	1.3
No. yearling bulls	0.2	0.3	0.4	0.2
No. calves	1.5	0.6	1.4	1.1
No. cows - Mean	3.9	3.1	3.8	3.7
Range	1-8	1-8	1-17	1-17

VI. MOVEMENTS AND BEHAVIOUR OF WOODLAND CARIBOU

MOVEMENTS

Periodic Distribution

The periodic distribution of woodland caribou at Reed Lake is depicted in Table 26 and Fig. 19 similarly to that for wapiti. The aggregate range of all 11 caribou with radio transmitters is outlined on a seasonal basis.

Summer

The aggregate summer range was restricted to a central eight percent of the total area and overlapped all other seasonal ranges. The size of the aggregate summer range (142 km^2) generally reflected the sedentary habit of caribou during the fly season and calf-rearing. Daily movements increased in early September and several shifts, associated with rutting, by two bulls were apparent.

Fall

The aggregate fall range was much larger than the summer range since it included rutting movements of males and seasonal shifts to winter range by females. Red (an adult female) shifted 38 km. to her winter area in mid-October, possibly before she was bred. Other females remained in breeding areas until well into December and early January before moving into wintering areas.

Winter

The winter aggregate range was the largest and encompassed all other seasonal ranges. The total area ($1,780 \text{ km}^2$) superficially represented the aggregate home range of caribou on Reed Lake. However, as the study proceeded and knowledge concerning the use of Reed Lake by

TABLE 26

THE PERIODIC DISTRIBUTION AND SEASONAL RANGE SIZE OF ALL
WOODLAND CARIBOU WITH RADIO TRANSMITTERS AT REED LAKE

Period	Duration of Period	Range Area (km ²)	Percent of Total Area	Areas of Frequent Observations
Summer	June 21-Sept.21	142	8	North and West Reed Lake
Fall		1,162	65	
Breeding	Sept.22-Nov.30			North and West Reed Lake
Movement	Dec.1-Dec.20			Mitchell Lakes Iskwasum Lake North Reed Lake
Winter	Dec.21-Apr.9	1,780	--	Mitchell Lakes Iskwasum Lake North Reed Lake McClarty Lake
Spring		517	29	
Pre-movement	March 21-Apr.9			
Movement	April 10-30			Mitchell Lakes Iskwasum Lake McClarty Lake North Reed Lake
Calving				North and West Reed Lake

individuals accumulated, it became apparent that two herd subunits or populations as suggested by Miller (1968) were under study.

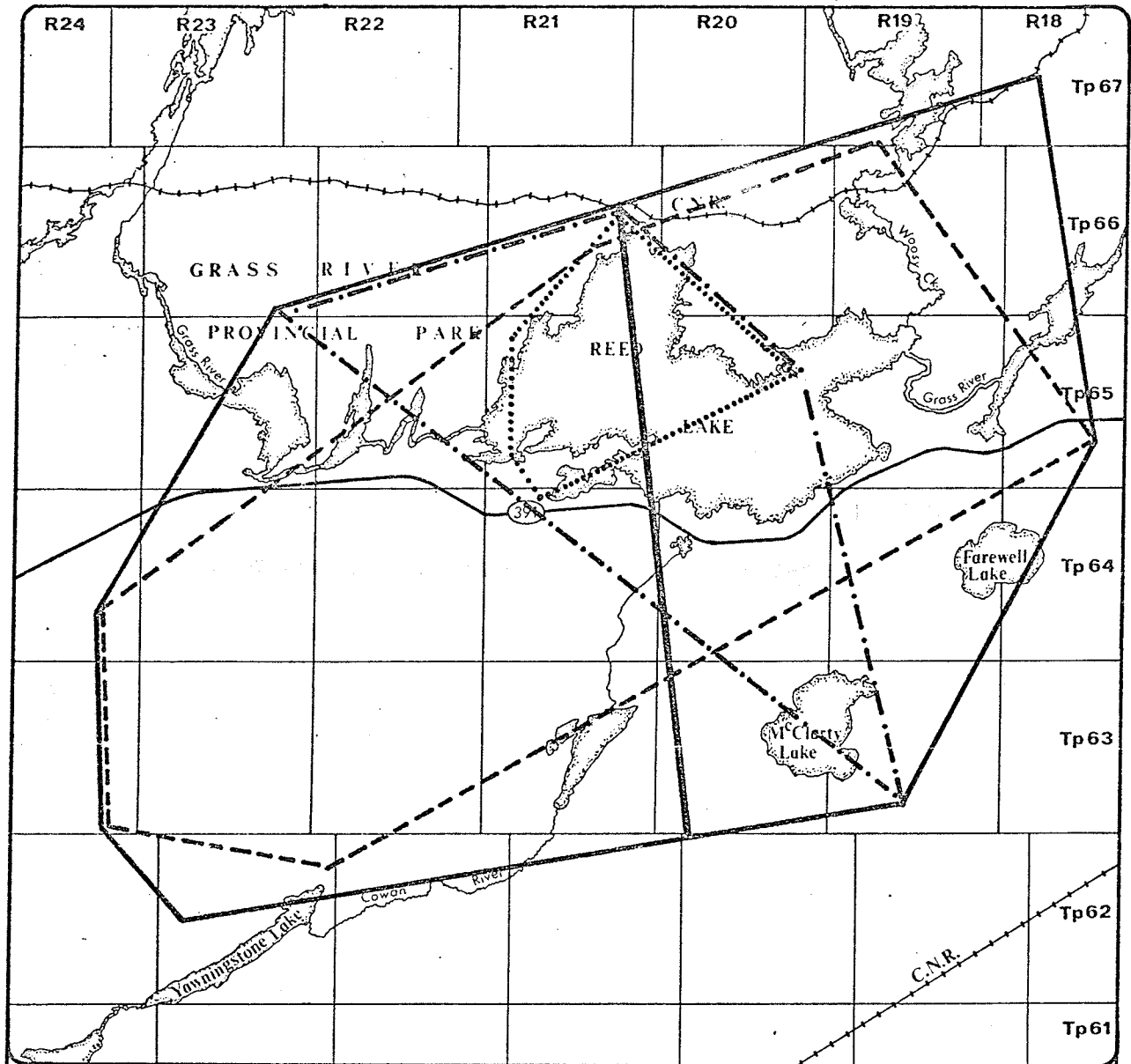
Miller op. cit. described one caribou herd ranging from north of Pothier Lake to Elbow Lake and from Goose Lake to Louck's Lake west of Reed Lake. A major crossing on the Simonhouse Road (No. 391) between Simonhouse Lake and Reed Lake and Iskwasum Lake was mentioned. A second herd was believed to use the Reed, Morton, File, Woosey, Herblet and Wekusko lakes area.

"The main wintering groups have been found in the Cowan River drainage to the south shore of Reed Lake, in the Tramping, Farewell and Hargrave lakes region and north of the Miteshto River to Ferguson Creek." (Miller 1968:3).

During this study, a natural barrier of open water seemed to divide Reed Lake on a north-south basis (Fig. 19) according to caribou use and distribution. Adult females Candy, Red and Rainbow, their offspring and Devil remained west of the line and probably were a part of Miller's Pothier-Elbow-Goose-Louck's lakes population. Adult females Old Yella, Blue and Flame, their offspring, as well as Sundog and Bull remained east of the line apparently in the Reed-Morton-File-Wekusko lakes population.

Individuals of the "east" and "west" Reed Lake groups occasionally occupied the same area along the line but at different times of the season or year. These were forced movements of Candy and Old Yella by tagging crews; they returned to their usual areas within 2-3 days. Even the adult male (Devil) that travelled extensively during the rut spent several days near the "barrier" at the east end of Fourmile Island, but he did not cross to the east or north sides

Figure 19. The seasonal ranges and distribution of woodland caribou at Reed Lake.



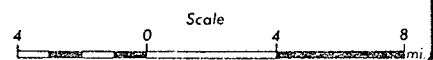
SEASONAL RANGES

Spring

Summer

Fall

Winter



and mix with the east Reed Lake group.

Caribou were distributed throughout the aggregate winter range. While the radio-transmitted females and their calves left the Reed Lake Area in winter, other caribou were observed within the aggregate summer range. Whether these caribou had remained there from summer to winter or had moved into the area for the winter is unknown. Nonetheless, some individual caribou did leave summer areas for separate wintering areas whereas others may not have moved at all.

Spring

The spring aggregate range was only about 1/3 the size of the winter range and included all of the summer range. Three sub-periods --pre-movement, movement, calving--were recognized based on the activity of females. Movements to traditional calving areas or islands occurred in late April. Once the females had returned to these areas, the spring and summer ranges became essentially the same area.

As far as could be determined, the adult male (Devil) remained in the Louck's Lake area and moved very little during this period.

Seasonal Movements

Spring Movement to Calving Area

Spring movements of females to calving areas occurred during April. Calving was observed as early as May 17 and as late as May 29 (recent observations indicate that Flame calved on May 31). The peak calving period reported for other populations (Bergerud 1974) is June 1. Most of the adult females at Reed Lake had apparently calved by then. Miller (1968) thought the peak of parturition at Reed Lake was no later

than June 1 and was likely to be earlier.

Two adult females (Red and Old Yella) exhibited similar spring movements to calving areas from different portions of the spring range (Fig. 20). The independent movements occurred sometime during a 2-week period (April 10-23) when snow cover had melted from the small openings and clearings but still remained in the mature spruce and jack pine areas. The interval of actual movement may have been much shorter than 2 weeks, but observations were not intensive enough to determine this.

Both females remained in the pre-movement area (2.6 km^2) 6-10 days. They were solitary before, during and after the movement (both had lost their previous year's calves) based on track observations. Travelling probably required little effort since the lakes and bog areas were still frozen, and snow cover was minimal.

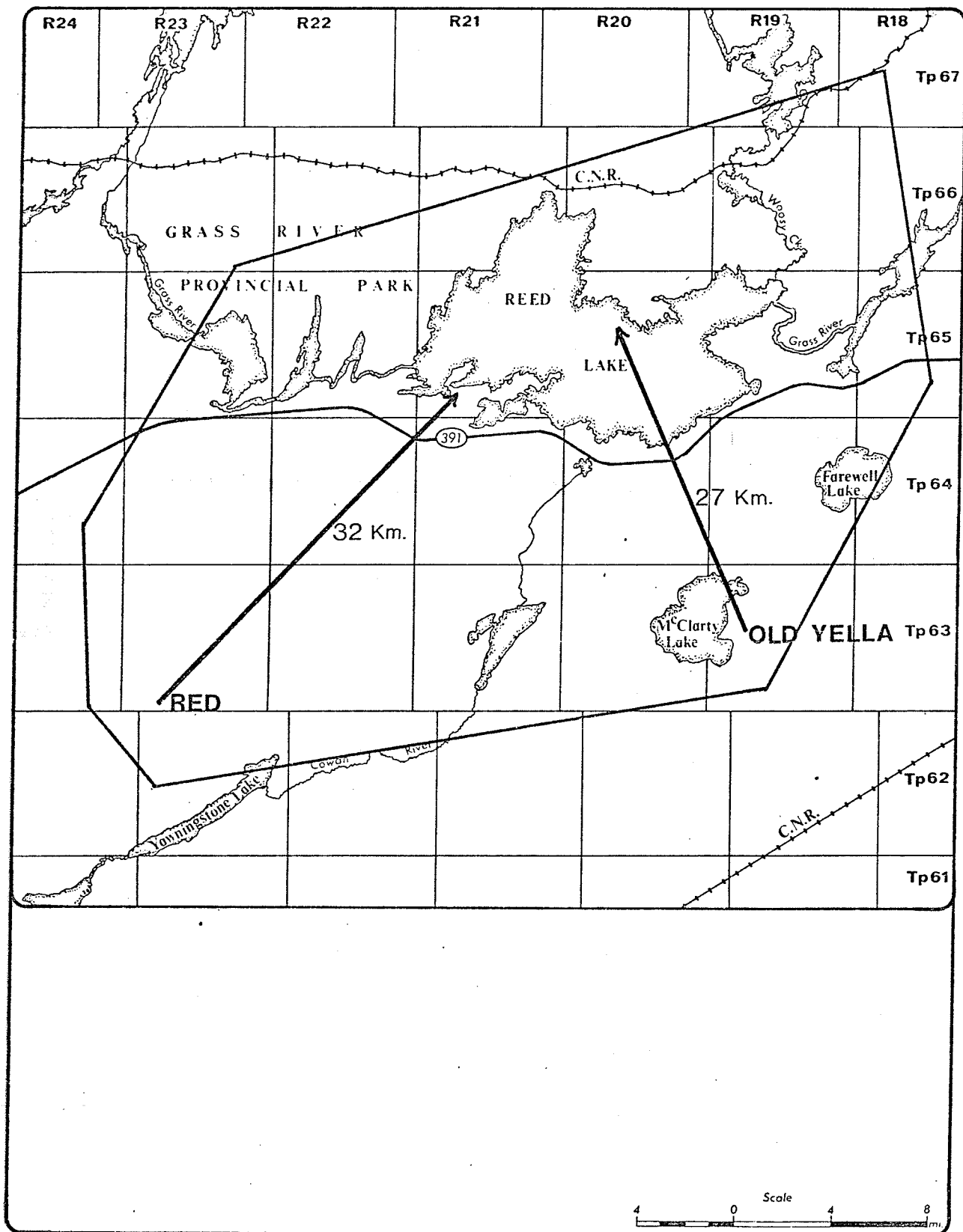
Candy had returned to her calving area in 1974 and 1975 by early May, but since her wintering area remained unknown, it was difficult to ascertain the extent of her movements and earliest date of arrival at the calving area.

Calving Areas

The calving areas included that portion of the spring range that fell entirely within the summer range. Indications that calving had occurred or was about to were the sedentary habit of adult females remaining in a specific location (an island) for 2-3 weeks.

In 1975, Old Yella remained on a small island from May 22 through June 4 at which time she was observed with a new calf. Candy remained on a small island from May 22-30, 1975. Calving may have been earlier in 1976 than in 1974 or 1975, possibly due to the mild winter (1975-76)

Figure 20. The movements of Old Yella and Red from winter range to spring calving areas in 1975.



and early snow melt.

The same general calving areas were used by Candy and Old Yella from 1973-76 (Figs. 21 & 22). Candy calved on the same island for 3 consecutive years. Old Yella calved in the same area in 1974 and 1975 but was found on islands 4-7 km west of this location in 1973 and 1976.

All females with newborn calves were relatively sedentary and infrequently moved short distances between islands. Whether they were found on the mainland or islands, it was usually near the shoreline.

Summer Movements

The adult females moved in a generally circular pattern during the summer. Old Yella remained in a specific area for 5-7 days, then moved 3-5 km. This movement usually was associated with a low pressure system and occurred overnight. She would be back at her "starting" point in a month's time.

Females with calves remained on islands in the lake during most of the summer. It was not until mid-August that the mainland was used significantly and, even then, nearly all activities were associated with the shoreline.

Unmarked caribou were seldom seen swimming in the lake or standing along shore of an island or the mainland during tracking operations. Other caribou were obviously present but not more than 10 could be accounted for in any 1 year on Reed Lake; most of these unmarked caribou were seen in the Fourmile Island area. This apparent scarcity of caribou on summer range may be due to 1) relatively low

Figure 21. Candy's summer ranges in 1974 and 1975.

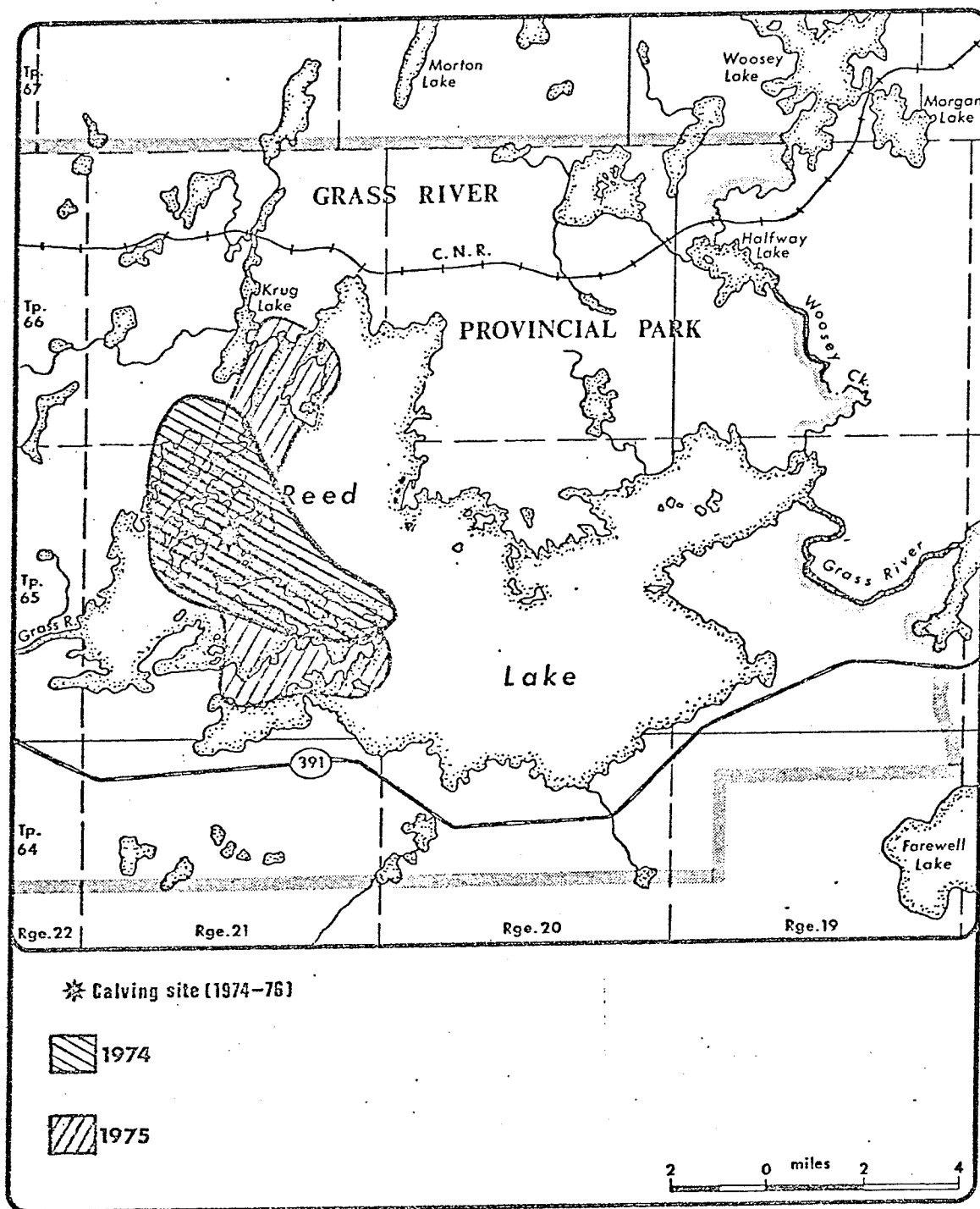
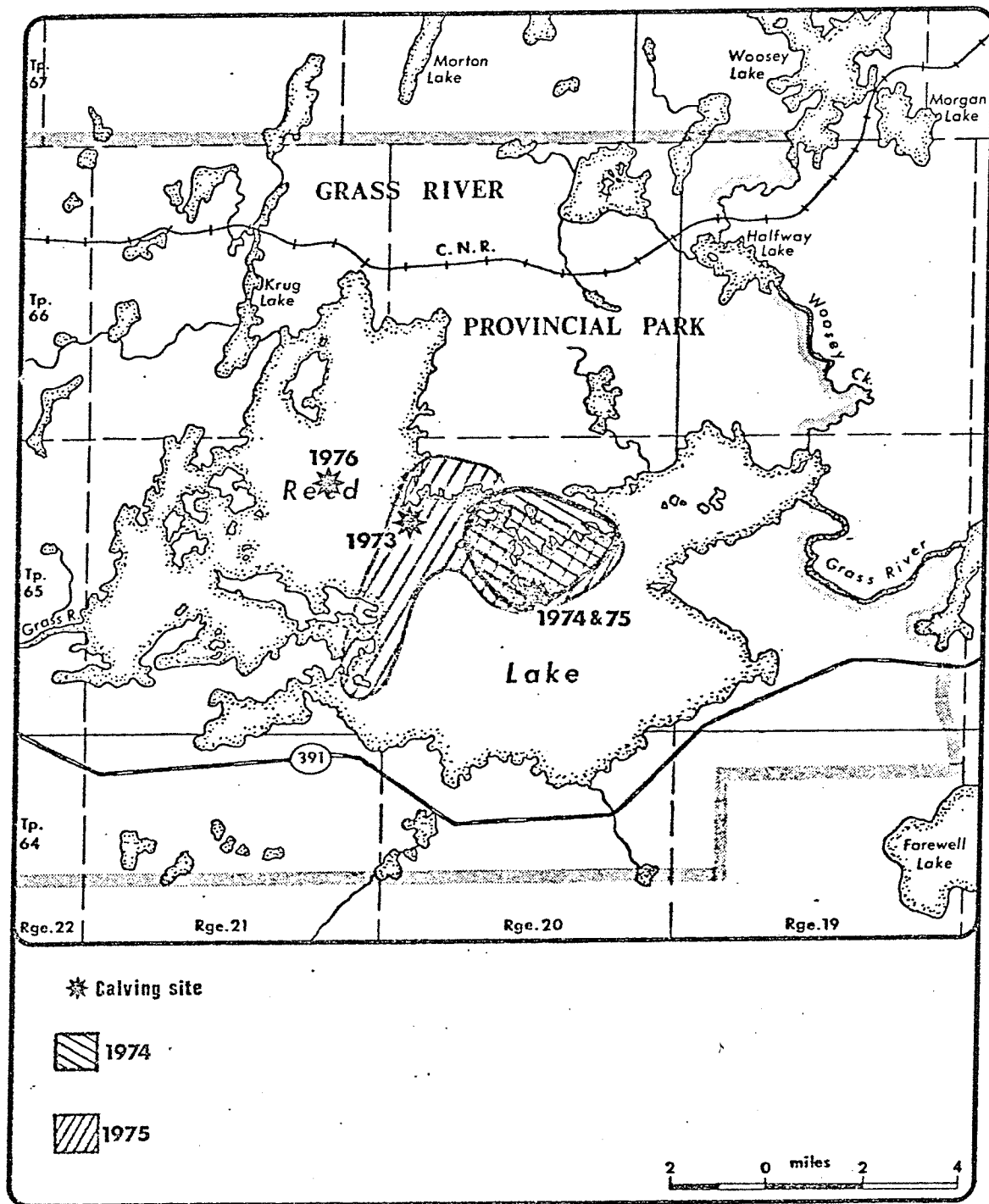


Figure 22. Old Yella's summer ranges in 1974 and 1975.



densities in an area 2) sedentary and secretive habits during calf rearing 3) the existence of "island" and "mainland" caribou depending on individual habits. Evidence from radio-instrumented caribou suggested that the combination of factors best described the caribou at Reed Lake.

The fly season may have contributed to the caribou's extensive use of islands. Mosquitoes were prevalent by mid-June and usually lasted until September 1. Biting flies (horseflies, deer flies, black flies, face flies, nostril and warble flies) were not found until early July and were usually gone by early August. There were few low swampy areas on the islands and caribou were often seen on semi-open rocky outcrops near shore where they were in even a slight breeze from the lake.

The islands also offered isolation from major predators in the area during the time the calf was developing. Blue and her calf were apparently killed by wolves in early July during the only time that she was found on the mainland since calving. Candy had spent some time on the mainland in mid-August 1975, and her calf, Tiny, was not observed beyond this time. When seen again in late August, Candy was alone and walked with a noticeable limp. Wolves may have taken Tiny when the caribou first left the islands for the mainland.

Fall Movements

The fall range was greatly expanded from the summer range due to the extensive movements of the males during breeding and the shift of all transmitted caribou to winter range (December 1-20).

The seasonal ranges of the calves strongly overlapped that

of their mothers. They remained with their mothers throughout the breeding period.

Bull left the north end of Reed Lake about September 21 and moved to the east side, south across Highway No. 391 to a small unnamed lake north of Farewell Lake. Here he remained until his transmitter was apparently lost in November. When his transmitter was found in early May, I found considerable sign of rutting bulls (several small spruce trees rubbed in a semi-open jack pine area).

Devil remained in the general area of his initial capture south of Fourmile Island from August 6 to 20, 1975. The mean daily movement for this 11-day period was 1.2 km. He subsequently was not relocated until September 26 some 15 km west of Reed Lake and near Leak Lake. Two other bulls and one cow with him indicated that the rut had begun.

Devil was not relocated until October 10th nearly 25 km northeast of the previous location and 1 km south of the east end of Fourmile Island. He moved very little for 8 days, then shifted northwest to the Krug Lake Area. Here he remained through mid-November and was found with other bulls, cows and calves including Candy.

The activities of Devil indicated considerable movement of adult bulls during the rut, apparently in search of females. Once a female was found, he remained with her until she was bred. Other bulls may have been present and competing for the same female.

Red moved to her winter range location between October 11 and 24, 1974. The movement was from the southern end of Reed Lake to Yawningstone Lake, a distance of 38 km. Here she remained relatively

sedentary until mid-December.

Home Range

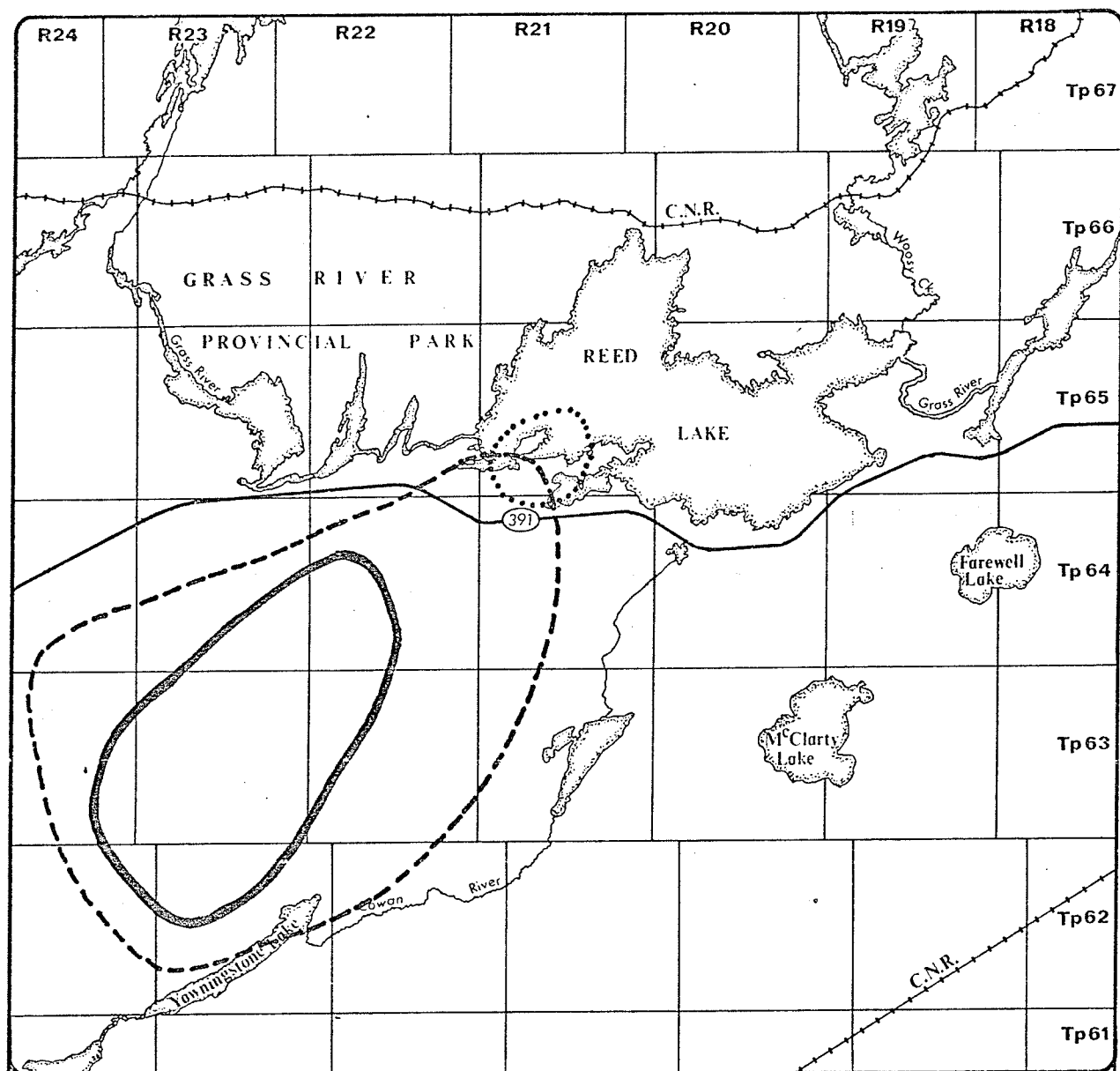
The home ranges for three adult females (Red, Candy and Old Yella) indicated how individuals from the two population units used the Reed Lake area.

Red's seasonal ranges from summer through winter 1974-75 are shown in Fig. 23. The spring range was not shown since only five locations were obtained before the radio transmitter quit. However, the spring range as it was known was encompassed by the fall and summer ranges. The winter and summer ranges were entirely separate; the fall range was by far the largest.

Candy's winter ranges in 1974 and 1975 were unknown. In 1974 she appeared to have moved into Red's winter range but was not relocated until May 1975. She was not re-observed until the following May, again near her calving island. Candy's spring, summer and fall ranges are illustrated in Fig. 24. Unlike Red, Candy's summer range generally included the spring and fall ranges. The summer and winter ranges were undoubtedly separate.

In the eastern population unit, Old Yella's winter range was the largest seasonal range (Fig. 25). Summer and fall ranges were comparatively small and included the northern portion of the winter range. Her shift to winter range did not occur until early January whereas Candy and Red moved during the fall period.

Figure 23. The 1974-75 seasonal ranges of Red.



SEASONAL RANGES

Summer 1974

Fall 1974 - - - - -

Winter 1974-75 —————

Scale
4 0 4 8
mi.

Figure 24. The 1975 seasonal ranges of Candy.

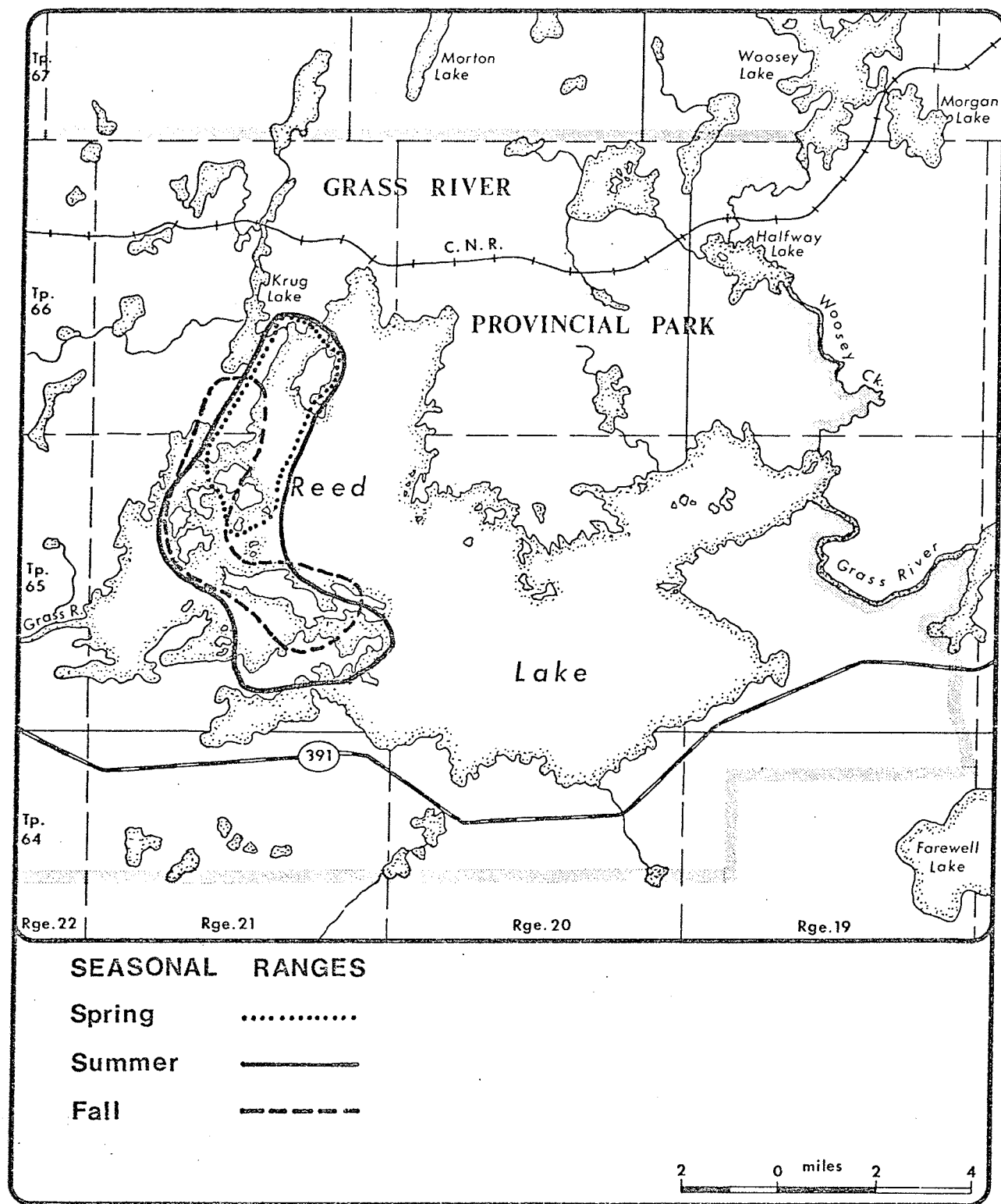
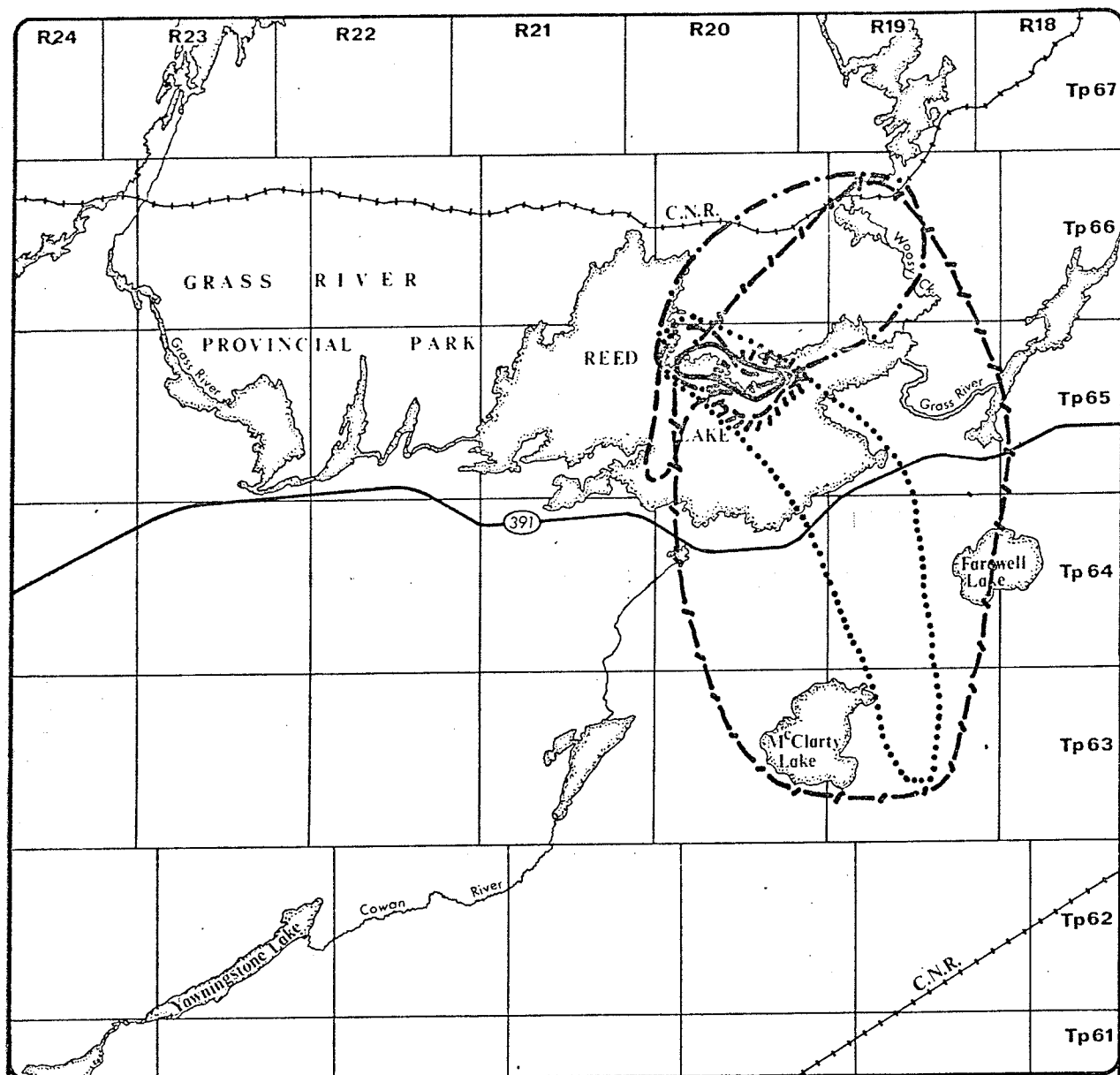
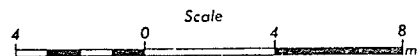


Figure 25. The 1974-75 seasonal ranges of Old Yella.



SEASONAL RANGES

Summer 1974	-----
Fall 1974	- . - . - .
Winter 1974-75	— / — / —
Spring 1975
Summer 1975	— — — — —
Fall 1975	—————



Seasonal Ranges

Individual Range Size

Only Old Yella's spring range size could be estimated. It was 107.7 km, including her movement to the calving area.

The summer range of all transmitted-caribou was the smallest of all seasonal ranges (5.5-22.1 km²) (Table 27). In 1975 Candy and Old Yella had larger summer ranges than expected due to disturbance and forced movements during replacement of transmitters. Their expected summer range was about half the observed range. Taking this into account, the mean summer range size for all sex and age classes was 13.0 km². Those for males and the yearling female were less than for adult females. Devil's summer range was probably much larger than the 2.2km² determined for him for August 3-20. He was not observed again until September 26, nearly 13 km. southwest (south of Iskwasum Lake) of his previous location.

The mean fall range size of all transmitted caribou was 69.3 km² (Table 27). The size varied considerably between years for adult females and among individual caribou for a given year. Range size was greater in 1974 than in 1975 for adult females.

Since intensive observations were not made during the winter, it was difficult to estimate the winter range size for any individual caribou except Old Yella and Red. During 1974-75, their winter ranges included 124.3 and 382.5 km², respectively. Old Yella's winter range was larger since her shift to the wintering area south of Provincial Road No. 391 did not occur until late January whereas Red had already moved in late October.

TABLE 27

THE 1975 SUMMER AND FALL RANGE SIZE OF WOODLAND
CARIBOU AT REED LAKE (km²)

Name	Summer Range	Fall Range
<u>Adult Females</u>		
Old Yella	14.8	4.9
Candy	22.1	24.8
<u>Young Female</u>		
Flame	5.5	6.9
<u>Calves</u>		
Sundog	13.0	0.5
Hornet	13.3	4.6
<u>Yearling Male</u>		
Bull	12.2	18.7
<u>Adult Male</u>		
Devil	--	114.7
$\bar{X} \quad \div$		
13.0		69.3

Seasonal Range Overlap

Summer

In 1974 and 1975 Candy's summer ranges overlapped considerably; however, exclusive portions enlarged her aggregate summer range by several square kilometers (Fig. 21). In September 1975 she was found in breeding groups at both extremes of her seasonal range. The calving site was near the geographical and general activity centers of the summer ranges during both years.

Old Yella's summer range was significantly smaller than Candy's. However, her calving areas (Fig. 22) were scattered beyond her known summer range and were not consistently near the geographical center as was Candy's. Old Yella's 1974 and 1975 summer ranges overlapped but the 1975 summer range extended considerably west-southwest to include the eastern end of Fourmile Island. Her use of this area resulted from disturbance and forced movements by tagging crews in late June. If the "disturbed" portion of the 1975 summer range is removed, the 1974 and 1975 summer ranges would be essentially the same.

Summer-Fall

Old Yella's summer and fall ranges in 1974 were largely separate; however, the 1975 fall range was entirely within her summer range area (Fig. 25). The 1975 fall ranges of Candy and Sundog were also largely within their summer range area (Figs. 24 and 26). Flame utilized two seasonal areas which overlapped (Fig. 27), but the shapes were determined by a shift in association between social units which is discussed later. Bull had essentially separate summer and fall ranges in 1975 (Fig. 28). He left the summer range area about the time his velvet was shed and he became sexually active.

Figure 26. Sundog's summer and fall ranges in 1975.

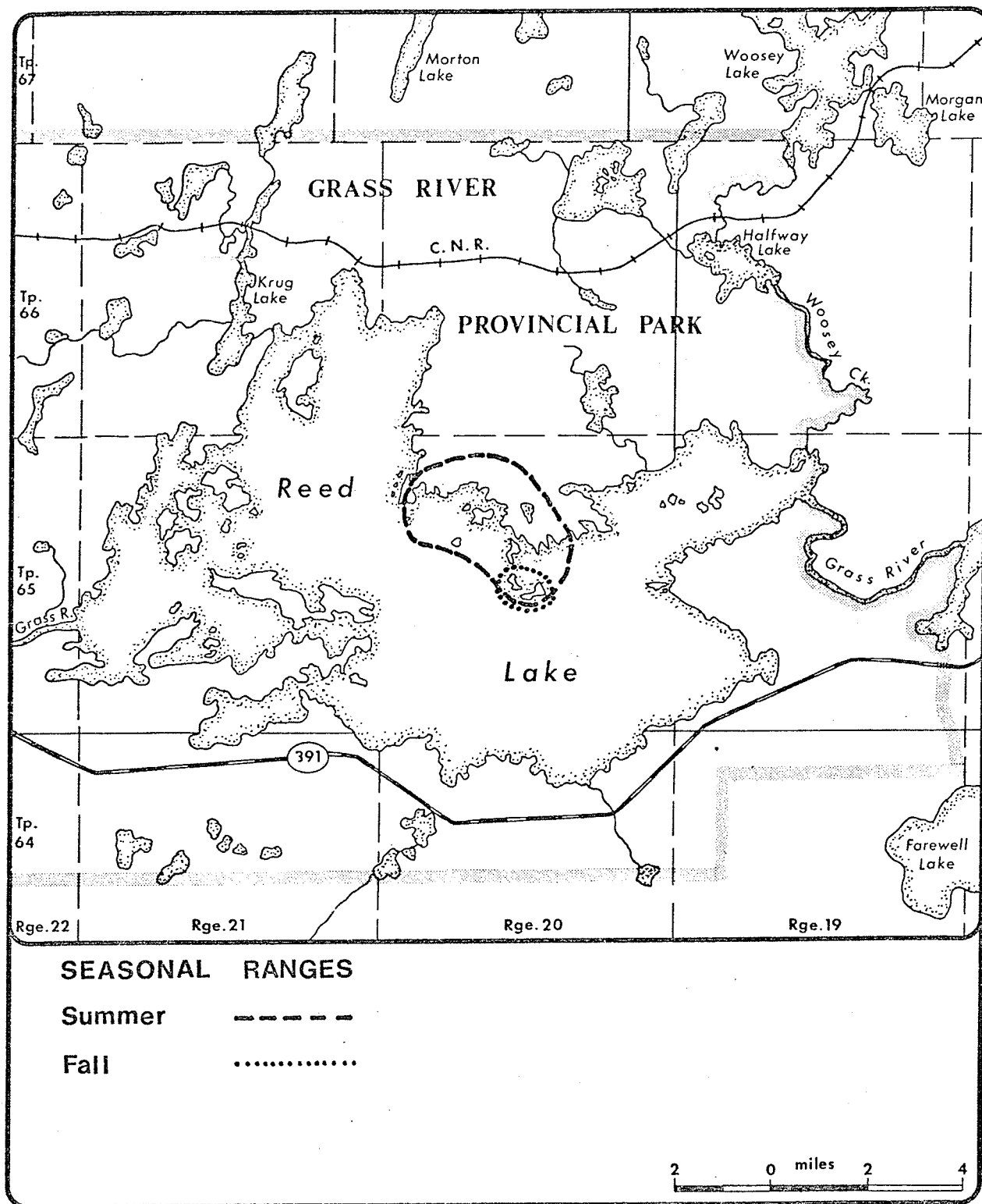


Figure 27. Flame's summer and fall ranges in 1975.

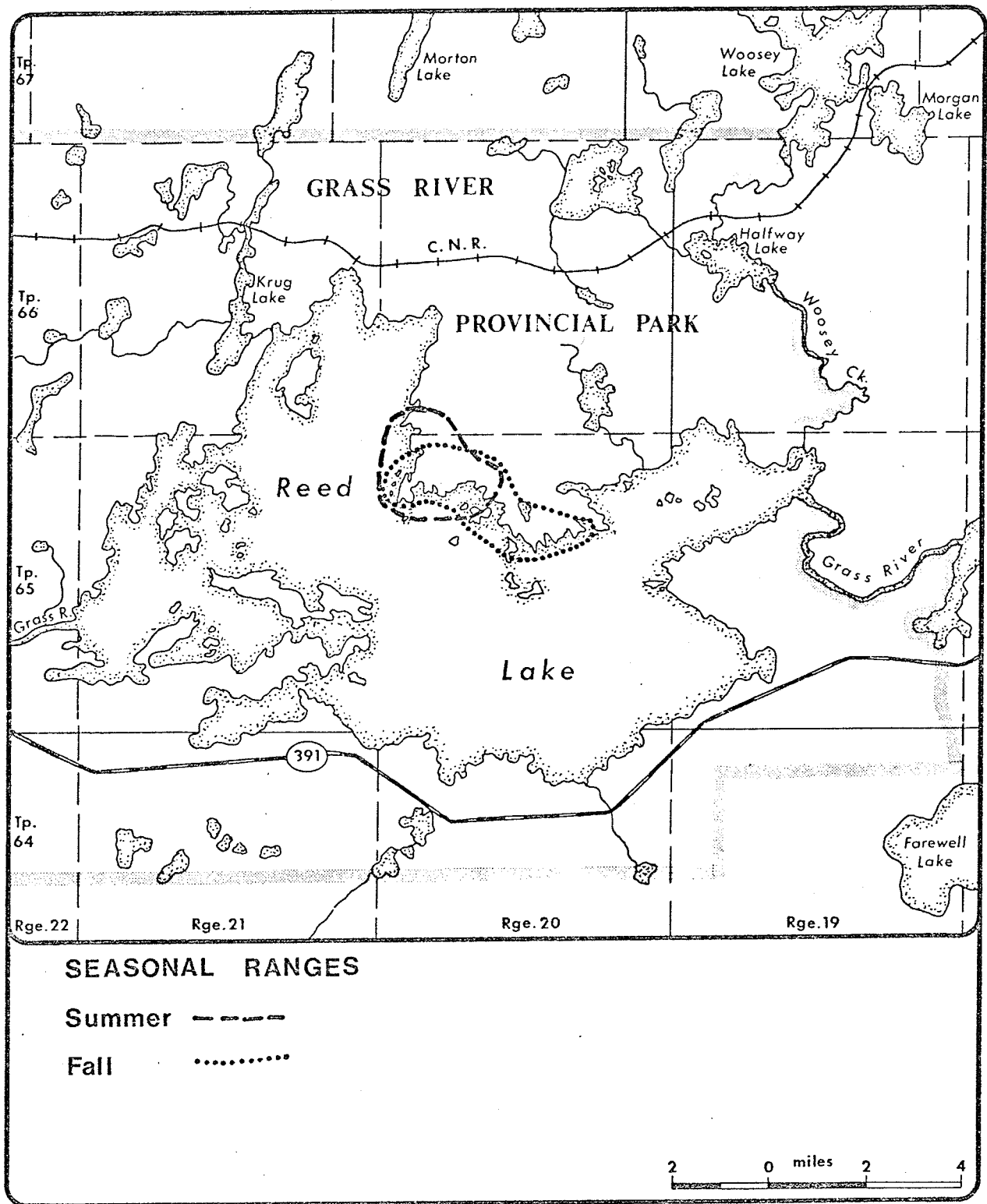
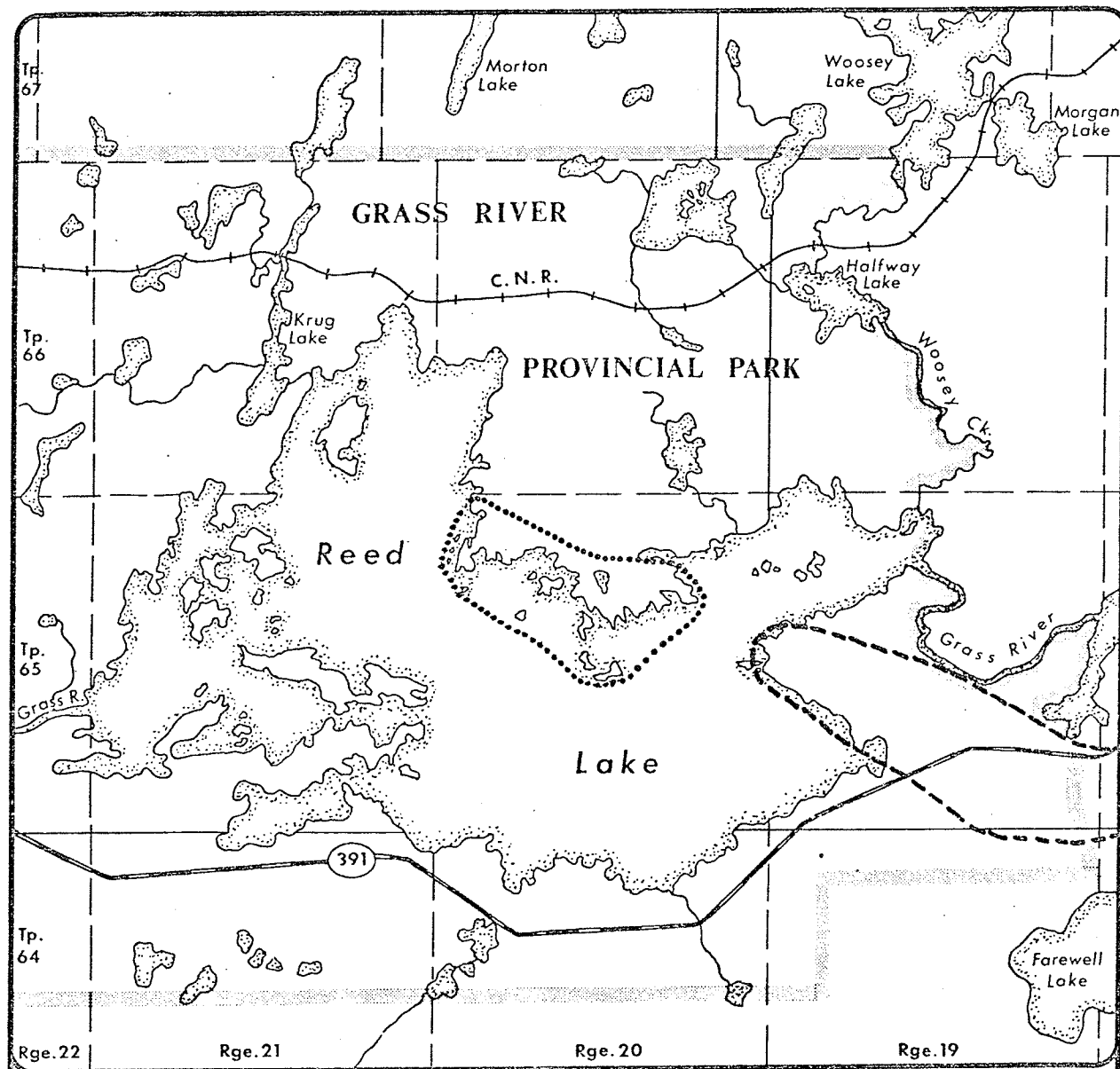


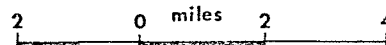
Figure 28. Bull's summer and fall ranges in 1975.



SEASONAL RANGES

Summer

Fall - - - - -



GROUP BEHAVIOUR

Social Groupings

Since only nine woodland caribou were observed with any degree of frequency, no attempt was made to quantitatively analyze intraspecific association by the method used for wapiti. Nevertheless, radio-equipped caribou were followed for long periods. The details of caribou group behaviour were summarized by individuals as follows.

Old Yella-Bull-Hornet

Old Yella remained solitary with her female calf throughout the summer of 1974. No other caribou including Bull (then a yearling) were seen with her or in the immediate vicinity. Between August 31 and September 19, Old Yella and her calf shifted to the western portion of the summer range and were found in a group with one bull and two other cows for the remainder of the breeding period. The calf apparently died in mid-winter 1974-75.

During 1975 Old Yella was alone with her new calf (Hornet) from late May until June 9 when she was seen with Cow A and Sundog. By June 11 a third cow and her calf had joined them. The three family units remained together until they were split up on June 17 by tagging crews. Old Yella, Cow A and their calves were re-observed together on July 8th. They remained in the same area for the next 3 weeks but were not in the same group.

On July 31, Bull, Old Yella's calf from 1973, joined her and Hornet. During the next few weeks Bull stayed in the same area as Old Yella and Hornet, and on several days they were together.

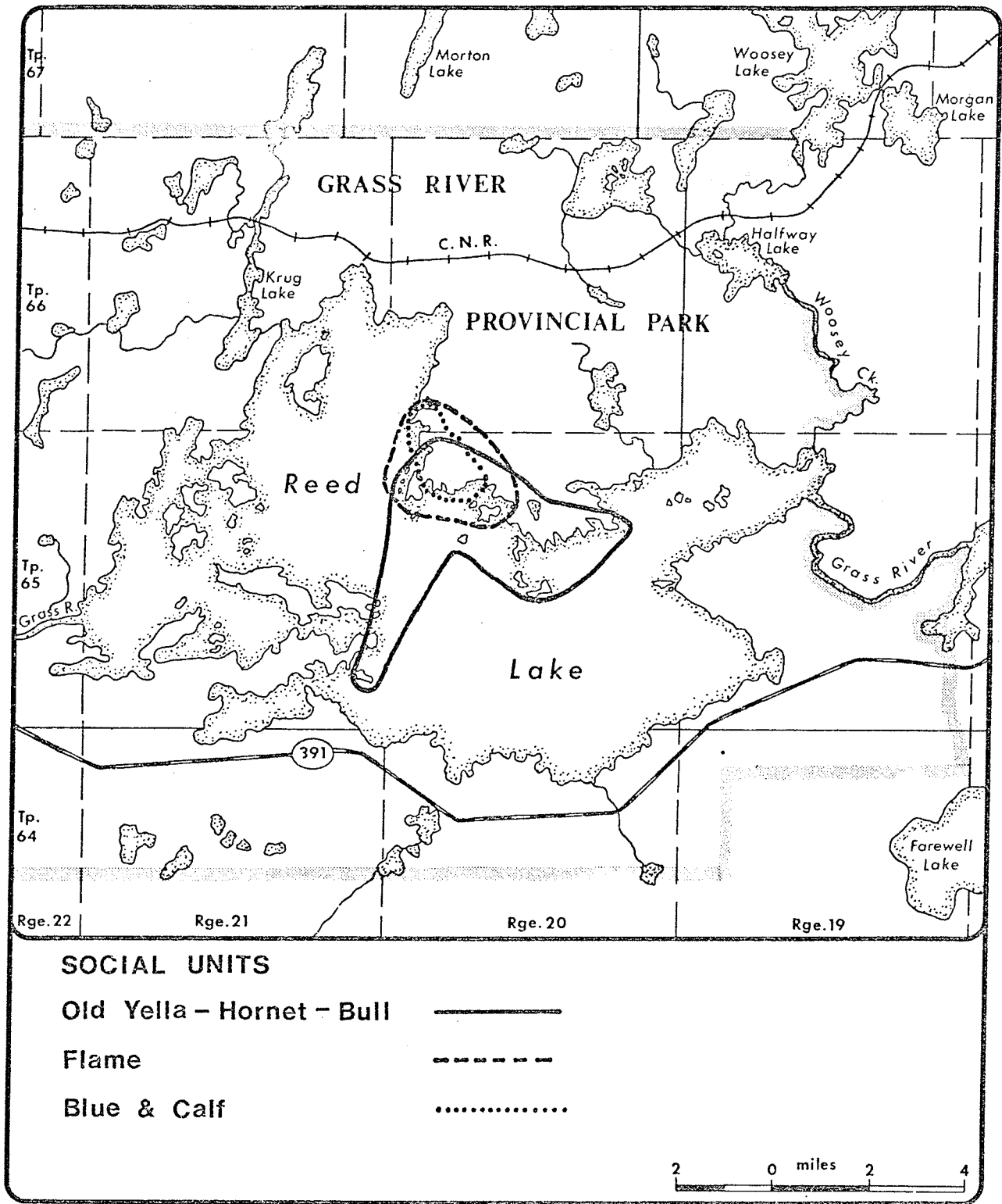
Following the death of Blue in mid-July, Flame moved into Old Yella's area, and by August 21, she had joined Old Yella. From then on this group of four animals were together most of the time. When they were seen together, Old Yella led, followed by Hornet, Flame and Bull. These four caribou occasionally were found in two groups of two, a group of three and one solitary or all solitary.

Old Yella's group stayed in the same area until September 14 when Bull left and moved to the east side of Reed Lake. When Old Yella was observed later on September 22, she was accompanied by a much larger bull. Old Yella, Hornet, Flame and the large bull remained together generally as a group for the duration of rutting season. They were last seen together on October 23, and by November 12, the bull had left Old Yella's group.

Flame-Blue

Flame was believed to be 2 or 3 years old when initially captured and equipped with a transmitter in June 1975. She was antlerless and had milk in her udder at the time of her initial capture (June 17) although a calf was never found with her. Blue and her young calf were also captured near Flame on June 17. During the next month, Flame remained in the same area as Blue and her calf. They occasionally were observed together. Blue and her calf were apparently killed by wolves on July 13th at which time Flame shifted 2.6 km. southeast to a small island just off the mainland. She remained there for the rest of July. By August 6, Old Yella, Hornet and Bull moved into this area. Flame remained with Old Yella and Hornet for the remainder of the summer and fall. Her summer range was the same as that known for Blue

Figure 29. The 1975 summer ranges of three caribou social units.



(Fig. 29). The fall range overlapped that for Old Yella and Hornet.

Sundog-Cow A

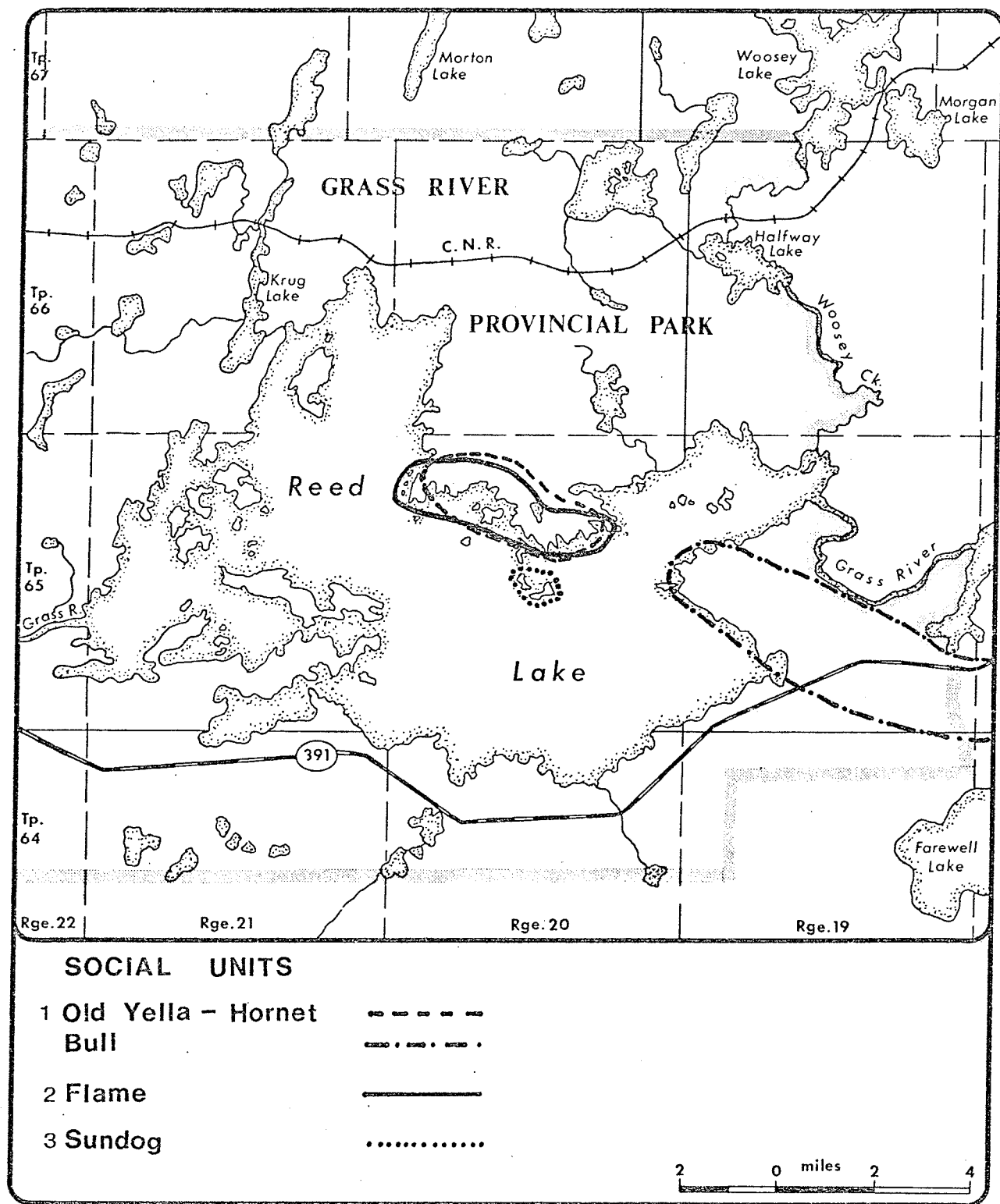
Sundog and Cow A were captured on June 18, 1975. The cow was eartagged and neckbanded; the calf received a radio collar. Sundog remained with her mother in the western half of their summer range until early September. They were in the same general area as Old Yella's family unit, but were only observed in the same group on one occasion.

Between September 6 and 20, Sundog moved to her fall range area; Cow A was not observed after September 6. Once Sundog was without her mother, she remained on two small islands until well after freezeup.

Recent evidence suggests that Cow A died on the mainland about the last time she was seen with Sundog and only 2 km from Sundog's fall range. Bull had left Old Yella's family unit and was in the area of Cow A's remains on September 11-16. Cow A may have stayed with Bull until she died of unknown causes.

The fall movements and behaviour of the family units just described are summarized in Fig. 30. Flame gradually shifted from her summer range to the fall range of another family unit. Possibly, if her calf had survived in 1975, she would have maintained a more independent existence, as she subsequently did in 1976. On the other hand, Sundog maintained a separate fall range without her mother and with Old Yella's family unit in the general vicinity. Bull left the summer range for an entirely separate fall area; however, the family units essentially remained on summer ranges past mid-November.

Figure 30. The 1975 fall ranges of three caribou social units.



Candy

In 1974 Candy remained alone with her new calf from late May through August. She was not observed again until well into the breeding period. On October 23 Candy and her calf were with an adult bull and two other cows. She remained in this group until November 12. By November 28 Candy had left the area for winter range.

In 1975 Candy spent the majority of her time alone. She was accompanied by her calf from May until at least August 6. When she was observed again on August 10 she was alone and had apparently lost her calf. She was then seen with a smaller caribou, believed to be a cow identified with her later. On October 19 Candy was accompanied by a smaller, antlerless cow, a calf and a young bull. She stayed with them at least until November 10 when they were joined by Devil. Devil and Candy were still together on November 16 when she was last seen.

Devil

Devil was alone when captured on August 6, 1975, and he remained solitary until the rut. On September 26 he was found with two larger bulls and one cow. When again observed on October 12 he was alone; however, Rainbow was seen in the same location on October 11 as Devil had been located on October 10.

Devil was observed alone on October 18 but by the next day had joined with a smaller bull, a cow and a calf. The following day he had left the area. By November 6 he had joined with Candy as described earlier.

Mean Group Size

Group size of woodland caribou at Reed Lake ranged from 2-14

with an overall mean of 2.5 for marked females (Table 28). Larger groups of 15 and 17 caribou were reported by Miller (1968) in late winter, but apparently this is near maximum group size for caribou in the general area.

The trend in mean group size is greatest in November and December just following the breeding period (Fig. 31). Group size gradually declined over the winter to a low in April just prior to adult females returning to calving areas and remained low (below the annual mean) well into the breeding period.

The mean group size of marked females was greatest in fall during the breeding period (Table 28). However, the summer group sizes confirm that basic social units of adult cows with young calves were the main grouping.

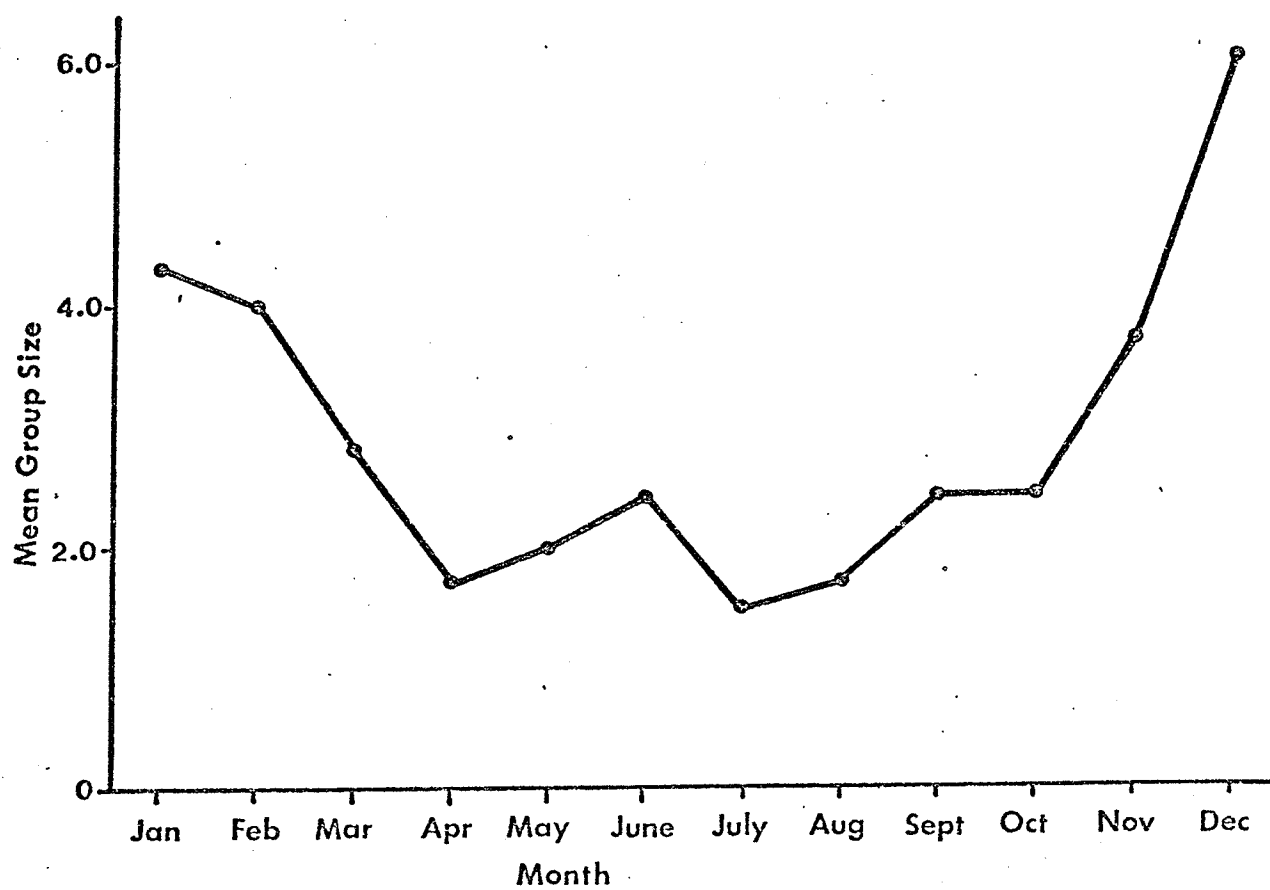
TABLE 28

MEAN GROUP SIZES OF WOODLAND CARIBOU AT REED LAKE

Type	Spring	Summer	Fall	Winter	Annual
A. Marked Caribou					
Females	2.8(18 [*])	1.8(89)	4.5(21)	3.3(16)	2.5(144)
Males	-	2.1(11)	3.0(5)	-	-
Calves	1.7(3)	1.6(42)	1.0(11)	-	-
B. Unmarked Caribou					
	-	-	-	5.2(20)	-
\bar{x}	2.6(21)	1.7(144)	3.2(38)	4.6(36)	-

* Number of groups observed in parenthesis.

Figure 31. Monthly trend in mean group size of woodland caribou at Reed Lake.



VII. DISCUSSION AND CONCLUSIONS

The only enduring social units of wapiti consisted of individual adults and female family units (an adult female, her calf and possibly yearling offspring). Individually marked wapiti were usually found in groups of constantly changing composition. Occurrence of two adult females in the same group in the same season during successive years was rare. Adult females, even those with overlapping ranges, were individualistic during migratory movements. Wapiti tended to group but did so independently of specific individuals other than their immediate progeny (calves and yearlings).

A sample 2 x 2 contingency table was provided on page 32 to illustrate the coefficient of association analysis. Included here are two contingency tables with hypothetical data. Part A represents the data as might have been used by Darling (1937). Two wapiti/red deer were present together in 85 of 100 observations, but were infrequently seen in the absence of one or the other. There were few observations when neither were present in groups in the same area. The C_7 value of +.309 in this case is statistically significant ($P < 0.05$).

Part B illustrates the revised concept as a result of this study. The pair of marked wapiti/red deer were rarely found together and usually present in a group in the absence of the other. The C_7 value (-.906) indicated association less frequently than by chance alone and was statistically significant ($P < 0.05$).

The major difference between the two concepts lies in the means in which the data were obtained. Darling made numerous assumptions based on a few individually recognizable red deer [Altmann (1952) as well for

wapiti] and observed behaviour of many unmarked individuals. My study was the first of its kind in having nearly 1500 individually marked wapiti in the Northern Yellowstone Herd and 236 on the Mirror Plateau summer range during the study period. The intent is not to provide an opposing concept to Darling's but to alter his to a more satisfactory explanation of wapiti/red deer behaviour based on solid data. It is basically the same concept suggested by Schloeth (1966) and Lowe (1966) for red deer and by Harper (1964), Craighead et al. (1972) and Knight (1970) for wapiti although they did not have long-range quantitative data to substantiate it.

A. Darling's Concept

Red Deer/Wapiti B

		Present	Absent	Totals	+.309
Red Deer/ Wapiti A	Present	a 85	b 7	a+b 92	
	Absent	c 4	d 4	c+d 8	
	Totals	a+c 89	b+d 11	n 100	

B. Revised Concept

Red Deer/Wapiti B

		Present	Absent	Totals	-.906
Red Deer/ Wapiti A	Present	a 2	b 59	a+b 61	
	Absent	c 33	d 6	c+d 39	
	Totals	a+c 35	b+d 65	n 100	

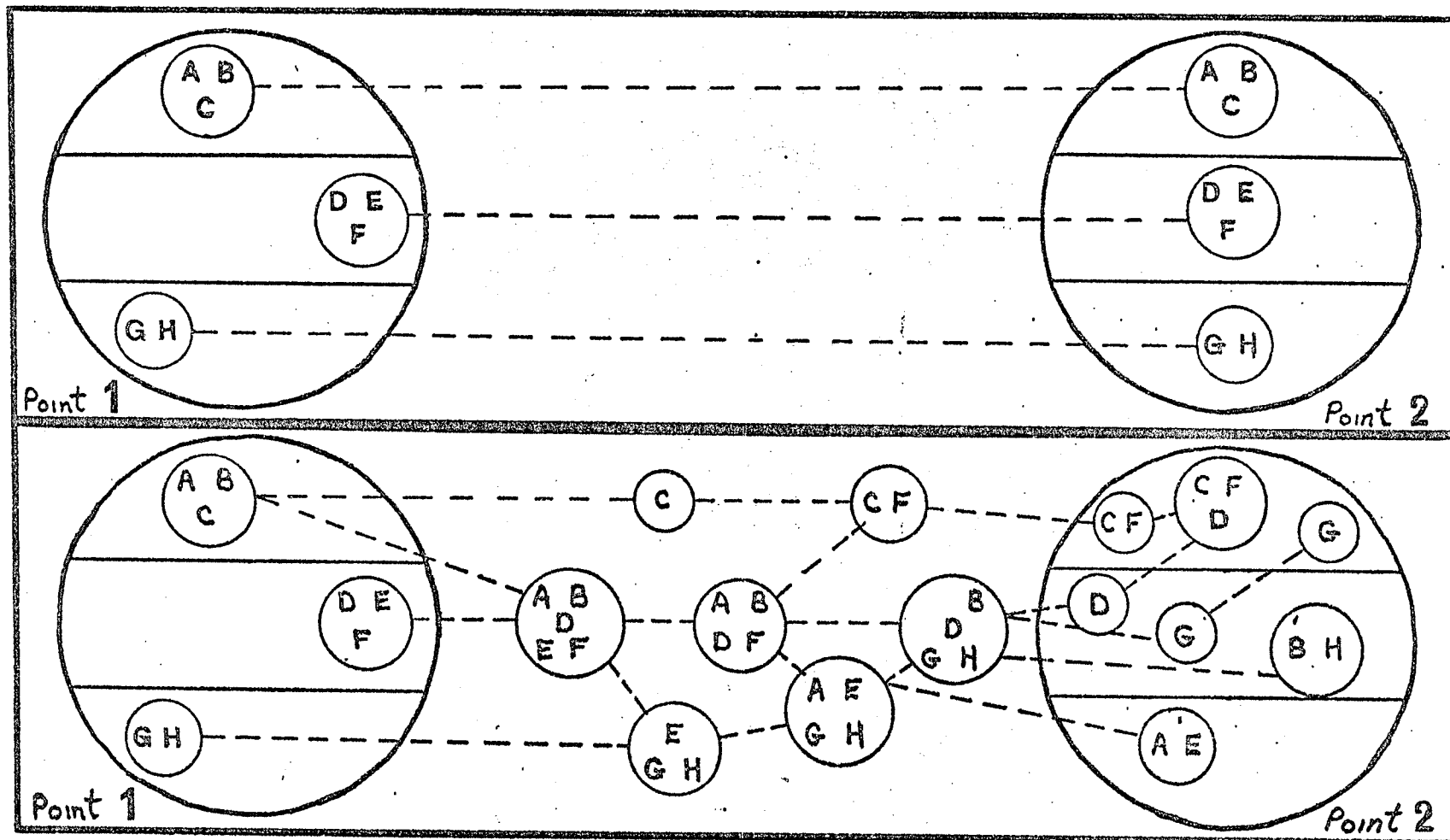
The modified concept of wapiti sociality is illustrated in Fig. 32. Assume that there are two geographical areas (large circles at Points 1 and 2) each of which is divided into three sections. Each section is occupied by a group of wapiti (small circle). Within each group are individuals A to H. The pattern of movement from Point 1 to Point 2 for these individuals or the entire group is shown by the dashed line.

The upper portion of the figure conveys the impression of relatively static groups of wapiti or red deer moving from one area to another. While the illustration is an over-simplification, it summarizes the general conclusions of Darling (1937) and Altmann (1952).

The movement patterns and corresponding changes in group behaviour illustrated in the lower portion of Fig. 32 illustrate the results of this study. The movement patterns between Points 1 and 2 may be migratory, mid-winter shifts, movements across summer range, or movements of harems. Changes in group composition may occur hourly, daily, or seasonally with little association between specific individual adult wapiti.

The figure could represent the early fall movements of marked wapiti to northern Mirror and the associated changes in group composition of harems. It could also describe the spring migratory movements of family units from Hellroaring Slopes to summer range and their independent occurrence in groups. Letters D and G could represent the movements and group behaviour of a yearling bull such as Raven which moved in a family unit during spring migration until he was rejected by his mother (F or H) during

Figure 32. A comparison of the concepts of group behaviour and related movement patterns as found in earlier studies (upper portion) and during this study (lower portion). Small circles represent groups of wapiti or caribou. Large circles represent general areas such as winter range, calving area, etc. Letters refer to individual or family units of wapiti or caribou.



parturition. Many other examples reported earlier could be summarized in this manner.

The social system of wapiti is correctly described as matriarchal. However, due to the dynamic grouping and individual movement patterns observed during this study, I conclude that the basic social unit is limited to the family unit. It is not a band of 10-30 closely related individual wapiti which form a closed social group or clan as indicated by Altmann (1956a). Wapiti can derive the benefits of social living such as increased protection from predators and optimum utility of available resources (Allee 1951; Murie 1951) and still maintain individual ranges. They do this by independent movements of individuals or family units from group to group.

The concept of group constancy above the family unit level was rejected with several reservations. Findings were based on marked individuals, each being observed three to 47 times from 1963-69, but accurate estimates of mortality of marked individuals could not be obtained. Some adults may have been associated throughout the year, but this was not detected because marked animals were not frequently observed. Continuous observation during a 3-5 year period by radio telemetry of specific adult females and their progeny would be required to determine such associations.

The Mirror population was reduced by 50 percent through selective culling of females and young. The impact of the reduction program on the social structure was not anticipated at the beginning of this study. Possibly the large female groups observed on Mirror in late

July did have an intact "family tree" as Darling (1937) implied for red deer. However, intensive trapping had removed key "branches" of the tree. By 1968, the removal of unmarked wapiti and calves for 6 years resulted in "skeleton" family units of adult cows and calves of the year. Older progeny of the second or third generation, which Darling (1937) and Eygenraam (1963) claimed remained with their mother in red deer, had been transplanted from Yellowstone. For example, if an adult cow and her female calf were both marked in 1965, any significant association after 1967 would suggest the retention of familial bonds between adult and matured progeny. Retention of such bonds was not observed in this study, but if the progeny had frequently been transplanted, the bonds could not have existed. However, I believe the test of potentially related wapiti (of several summer populations) indicated that mother and progeny do not associate significantly when both are adults, a point made in earlier work by Schloeth (1966). An analysis of association would best be conducted in an undisturbed population in which mortality resembled that which would be expected under pristine conditions.

Since the end of my field investigations in Yellowstone, Franklin et al. (1975) have reported on the social organization of Roosevelt wapiti. They observed a small herd of 2-27 that was described as matriarchal and "a semistable association in which elk entered and left the group freely. The adult females and their calves formed the most constant part of the herd."

Recent evidence from three other studies supports these conclusions. Craighead et al. (1973) observed frequent group exchange of radio-tracked adult female wapiti in the non-migratory herd which resides

in the western part of Yellowstone Park. In that herd, females and young were not being selectively removed. Knight (1970) found no group cohesion in the Sun River Herd. A telemetric study of wapiti movements conducted by R. Ream and P. Wegge (personal communication) in the Sapphire Range, Montana, revealed that adult females which were trapped together at a bait trap and instrumented with radio collars were rarely found together on spring range. Cows and calves were harvested by hunters from the populations mentioned in the last two studies. The evidence supports the views of Schloeth (1961) and Harper (1964) who were the first to present the idea of adult independence in red deer and wapiti.

Harper (1964) observed individual exchange between small groups of Roosevelt wapiti. This subspecies in the northwestern U.S.A. occurs in groups from family unit to herd size. However, Troyer (1960) and Batchelor (1965) found that Roosevelt elk transplanted to Afognak Island (Alaska) remained in herd-sized groups throughout the year. This suggests closed groups of elk with little individual exchange. McCullough (1966) reported distinct herds of tule elk in California. Possibly wapiti which are subjected to severe environmental restrictions or which have range limitations tend to remain in static groups throughout the year. Marking and observing individuals in these herds would reject or substantiate this.

De Vos et al. (1967) described the basic unit of social organization of Rangifer as the herd. However, Miller et al. (1974) suggested that the basic social unit of barren ground caribou was the mother-calf pair. In this study, woodland caribou were basically solitary. The basic

social unit was the adult female, her calf and occasionally her yearling from the previous year. Seasonal movements were essentially non-migratory in terms of the extensive movements of barren ground caribou; however, seasonal shifts in the use of the Reed Lake area did occur. The only groupings of any significant size occurred during breeding. When grouping did occur, there was a constant turnover in group composition, particularly during breeding. This supports similar findings by Bergerud (1973) and Lent (1965) for other subspecies of Rangifer. The lower portion of Fig. 32 reflects the movements and group behaviour of woodland caribou found in this study.

The following passage accurately describes the social behaviour of female caribou at Reed Lake.

"...each doe has her own calving territory of one square kilometer. When her calf is about three weeks old a doe may join with one of two other females, but most does spend the whole summer alone with their calves. Both males and females are mainly solitary animals in summer..." (Montonen 1972:269).

Although it was written to describe the social behaviour of non-domesticated reindeer (Rangifer tarandus fennicus) in Finland, this passage illustrates how two distinct races of Rangifer which occupy closed habitat have very similar social behaviour. If barren ground caribou were introduced at Reed Lake, I predict they would become solitary just as woodland caribou introduced on the barren lands would become gregarious. I have already discussed this principle relative to wapiti and it seems to hold for other Cervinae (Schaller 1967; Grzimek 1972).

Gregariousness is an adaptation for life in the open and a change from antisocial to social habits was prerequisite to abandoning

the concealment strategy (Estes 1974). The urge to band together in the open could have a psychological basis; the herd takes the place of cover for the individual. Thus, large groupings of deer in open habitats afford the same protection to the individual as does a closed forest for solitary species. Many deer species can adapt (at least temporarily) to open and closed habitats merely by aggregating into groups or remaining solitary depending upon the specific environmental context.

Wynne-Edwards (1962) argued that social behaviour of animals ultimately regulates their population size and that regulatory mechanisms could only have arisen through a process of group selection. The results of this study indicate that social organization of deer did not evolve through group selection. Primitive deer were solitary and natural selection of behavioural traits undoubtedly occurred at the individual level. Darling (1937) and Altmann (1956a) implied group selection in their description of the basic social unit of an advanced species, Cervus elaphus, as the familial herd or band. More recent evidence and the results of this study confirm that the basic social unit of wapiti is at the individual level (mother-calf) in which, despite a tendency for mother-offspring bonds to linger beyond the first year, independent movements and associated behaviour of individuals are characteristic, not atypical.

Wapiti have a tendency to over-exploit their food resources. They have a relatively high biotic potential (Greer 1966) and, afforded special protection (no hunting, predator removal), will temporarily

exceed their food supply. This is particularly apparent in areas such as Yellowstone National Park where natural predators have been removed and social behaviour mechanisms (i.e. group feeding, social dominance) have not sufficiently regulated their numbers. Wapiti in Riding Mountain National Park also have a tendency to over-exploit their food resource with significant predation by wolves and hunting by man along the Park boundaries. I prefer not to think in terms of social behaviour or food resources as being single over-riding factors in population regulation, but as both being significant forces among others which ultimately determine population size.

De Vos et al. (1967) stated that the basic social unit of Rangifer was the herd. However, I conclude that woodland caribou, similarly to wapiti, are socially organized at the mother-calf level. Miller et al. (1974) suggested this for tundra caribou, the most gregarious of all deer.

Woodland caribou as in most forms of Rangifer have a high biotic potential (Shoemith 1976) but also encounter high environmental resistance and a low rate of population increase. Again, social behaviour has become adaptive in influencing population size but there are extrinsic factors operating as well.

VIII. SUMMARY

1. A population of wapiti summering on Mirror Plateau, Yellowstone National Park, was investigated in aspects of movement and social behaviour. The summer range of Mirror wapiti extended from Amethyst Mountain to Pelican Valley. From 1963-69, a minimum of 45 percent of the Mirror cows and 25 percent of the Mirror bulls returned two or more summers to specific drainages on Mirror Plateau. Twenty-four marked wapiti were observed on Mirror 4-5 summers indicating extended traditional use of a summer range by at least some wapiti.
2. During August, Mirror wapiti shifted east and north on the Plateau from mid-summer locations to breeding areas. Those wapiti which summered on northern Mirror were not observed during the breeding period. Twelve marked wapiti were found on northern Mirror during 2-3 breeding periods suggesting traditional use of a breeding area by some animals.
3. Four spring and fall migratory routes were recognized. The Northern Herd segment that summers on the east side of Yellowstone Lake uses one of the routes as do some Mirror wapiti, but the two summer populations do not appear to mix on summer range. Mirror wapiti are individualistic in their use of the routes. Some may use the same route each fall, spring, or both fall and spring.
4. The early spring and precalving distributions of Mirror wapiti were similar to that in winter. Most of the females were found in three general calving areas--Hellroaring Slopes, Crystal-Amethyst Creeks, and Specimen Ridge. Eleven Mirror cows calved in the same general

calving area in 2-3 years suggesting habitual use of calving areas.

Some Mirror cows spent the entire spring and calving periods on Hellroaring Slopes or the Lamar Valley and migrated with their calves to Mirror in late June. Other cows moved in May from Hellroaring to Crystal-Amethyst creeks to calve, then migrated to Mirror in late June.

5. Aggregate ranges of nine Mirror females varied from 135 to 323 km² according to the extent of winter range movements and shifts in seasonal ranges from year to year. Three Mirror wapiti had summer ranges of 36-44 km² which did not overlap. The 1968 winter range (62 km²) of a radio-tracked cow was only half the size of that of another wapiti that had different winter ranges in 1964 and 1967 (132 km²).
6. Although the same cows returned to the same specific area of summer range, they seldom remained together in the same group for more than 1-5 days. Usually a pair of cows observed together once on Mirror were not seen together again until the following breeding period or winter. Social bonds between specific pairs of adult wapiti were not apparent. Cows and calves of family units trapped, marked and released at Little Buffalo Trap were rarely observed together when both were adults. Statistically, some Mirror wapiti associated less frequently than by chance alone. Few significant associations of Mirror wapiti were found on seasonal or aggregate ranges.
7. Groups containing Mirror wapiti were dynamic; individuals and family units entered and left groups daily. Mirror wapiti did not

frequent the same harem or associate with the same marked individuals during the same period in successive years although they were observed in the same general area each year. Individuals and family units apparently migrated by moving from group to group along the particular routes traversed. Those groups which did appear to move to the Plateau from the calving area as a static band contained marked cows which were never observed together on spring range.

8. Over 95 percent of the groups of Mirror wapiti on summer range contained 20 individuals or less. A mean group size of 3-4 suggested that individual family units were common in July and August. Single adult bulls and adult bull-adult bull groups were more common on summer range than single cows, cow-cow, cow-adult bull and cow-calf groups. Solitary bulls were three times more common than solitary cows.
9. The number of solitary cows, cow-calf, cow-cow and adult bull-adult bull groups which were observed declined sharply at the beginning of the rut. Single yearling bulls were more common during the rut than in summer. Mean harem size ranged from 5.2 to 7.0. Means in composition of harems were 1.3 adult bulls, 0.3 yearling bulls, 1.2 calves and 3.7 cows. Harems were comprised of 1-4 family units.
10. Aspects of movements and social behaviour were examined in woodland caribou at Reed Lake, Manitoba. The 11 radio-equipped caribou under study were divided between two herd subunits which remained on the east and west halves of Reed Lake in summer.
11. The fall/winter aggregate ranges were larger than their spring and

summer counterparts. Seasonal range size of individual caribou was much smaller and averaged 253.4 km^2 in winter, 107.7 km^2 in spring, 13.0 km^2 in summer and 69.3 km^2 in fall. Seasonal ranges tended to overlap, particularly spring, summer and fall. Seasonal shifts from wintering areas occurred in late April whereas fall shifts to wintering areas occurred at any time from late October to early January.

12. Nearly all late spring, summer and early fall activities of caribou occurred within 100 meters of the shore of an island or the mainland. Caribou shifted from predominant use of islands to the mainland as the fall rut began.
13. Repeated use of seasonal ranges from year to year was obvious in four adult females. One female calved on the same island in 3 successive years whereas another calved near the north end of Reed Lake 4 years in a row.
14. Mean group size was 2.5 and generally reflected the relatively solitary behaviour of this closed habitat form. The largest group sizes were observed in November and December just following breeding. Group size was lowest in April when caribou were returning to spring and summer ranges.
15. The basic social unit of woodland caribou is the family unit. Adult males and adult females with calves were relatively solitary except during breeding. Subadult males and females tended to occupy their mothers' summer ranges. Calves orphaned during the summer months returned or remained near their birth sites until freezeup.

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X. APPENDIX

GLOSSARY OF TERMS

ADVANCED--a character which has changed significantly from the homologous character in the stem stock.

AGGREGATE RANGE--a. "the total area with which an animal has become familiar, including seasonal ranges, excursions for mating, and routes of movement." Jewell (1966). b. lifetime range, particularly the area occupied by migratory animals.

BAND--a concrete social group of mobile animals of any kind, composed of two or more individuals...(Dice 1952). a. Female--two or more individual females and/or family units occurring together. b. Male--two or more males occurring together. c. Mixed--two or more adult wapiti or caribou of both sexes occurring together.

CLAN--"a clan is a society including several families, all members being related more or less closely through descent from a common progenitor." Dice (1952).

FAMILY UNIT--a. MATRIARCHAL--an adult female and any of her offspring of several generations which are observed with her. A family unit normally consists of an adult female, her fawn or calf, often her yearling female or occasionally her yearling male. b. PATRIARCHAL--similar to above but in which the adult male exhibits pair bonding and parental care.

FEMALE--a general term which refers to a cow, hind, or doe in deer.

GROUP--a unit of observation which describes any aggregation of two or more elk occurring as a family unit, a band, or a herd. a. Cow--two or more females occurring together. This may include calves and yearling males. b. Bull--two or more males occurring together. c. Mixed--two or more elk or caribou occurring together in which at least one is an adult female and one is an adult male.

HAREM--a group of female deer which is found with one or more sexually mature males during the breeding period. A harem bull is a sexually mature male which attempts to maintain a group of females for breeding.

HERD--all wapiti or caribou tending to remain in a given geographical area; synonymous with topodeme (a local population) or population when used in general terms.

HOME RANGE--"that area about its established home which is traversed by the animal in its normal activities for food gathering, mating and caring for young." Burt (1940).

MALE--a general term which refers to a bull, stag or buck in deer.

MIRROR WAPITI--a neck-banded individual observed at least once on the Mirror Plateau summer range. This term includes unmarked wapiti in certain designated cases. A non-Mirror wapiti is a neck-banded individual which was never observed on Mirror Plateau.

PLEISOMETACARPI--those cervid genera possessing rudiments of metacarpal II and V retained at the proximal end of the cannon bone.

PRIMITIVE--a character which has not changed significantly from the homologous character in the stem stock.

SEASONAL RANGE--that area occupied by an animal within its home range on a seasonal basis.

TELEMETACARPI--those cervid genera possessing rudiments of metacarpals II and V retained at the distal ends of the cannon bone.

WAPITI--the common name of Cervus elaphus nelsoni Bailey used in this study.