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Seasonal range use, aerial survey observability and survivorship of male elk (*Cervus elaphus manitobensis*) in southwestern Manitoba

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© Kenneth Joseph Rebizant

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SEASONAL RANGE USE, AERIAL SURVEY OBSERVABILITY
AND SURVIVORSHIP OF MALE ELK (*Cervus elaphus manitobensis*)
IN SOUTHWESTERN MANITOBA

BY

KENNETH JOSEPH REBIZANT

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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ABSTRACT

The cause of the low male to antlerless elk ratios observed during winter aerial surveys of an elk population in southwestern Manitoba were investigated. Eleven radio-transmittered male elk provided insight into seasonal range use, movements and activity, dispersal and survival of males in the Spruce Woods population. An evaluation of observability bias between male and antlerless elk during the surveys were also analyzed, as well as sex bias in the harvests of Indians and poachers.

Though male elk generally were observed during the winter surveys in smaller groups than antlerless elk a significant number of males were not missed by observers. When surveys were undertaken during good survey conditions all radio-transmittered male elk were sighted.

Radio-transmittered male elk had large spring and fall ranges and smaller summer and winter ranges. Generally, immature males had larger seasonal ranges and were less likely to reuse established seasonal ranges than mature males. Immature male elk had greater distances between relocations and activity centers and undertook dispersal movements which increased their vulnerability to mortality factors.

The survivorship of radio-transmittered males was low. Elk which inhabited the east side of the Spruce Woods park had higher mortality than elk which inhabited the military reserve. The elk harvests in the study area by poachers and Indians were bias favoring males.

The low numbers of males was not an artifact of the survey method but attributed to differential natural mortality, dispersal of immature males and male bias Indian and poaching harvests.

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INTRODUCTION

Caughley (1977) pointed out that the causes of variation in adult sex ratios in animal populations are complex and may be influenced by several factors. In many species of polygynous ungulates adult females most often outnumber adult males (Dzieciolowski 1979, Berger 1983). This asymmetry has been attributed to greater male mortality associated with reproduction (Berger 1983) and the preponderance of males as dispersing individuals (Greenwood 1980, Dobson 1982). Generally, the defence and maintenance of a group of females by a male during the breeding season contributes to a reduced life expectancy of males in polygamous species (Clutton-Brock et al. 1982, Leslie and Jenkins 1985) and dispersing individuals tend to face greater risks than non-dispersers (Dobson 1982).

Typically in elk (*Cervus elaphus ssp.*) and red deer (*Cervus elaphus elaphus*) populations, both of which are polygamous cervids, there are more adult females than adult males in spite of an approximately equal sex ratio at birth (Darling 1937, Murie 1951, Picton 1961). The sex ratio at birth may vary slightly from equality depending on the quality of resources available to a particular population (Clutton-Brock et al. 1982). Several authors have documented a skewed adult sex ratio favouring females for both hunted and non-hunted elk populations (Schwartz and Mitchell 1945, Flook 1970, Craighead et al. 1973, Moody and Simpson 1978, Taber et al. 1982, Hernbrode 1984, Freddy 1987).

Mitchell et al. (1977) stated that the "natural" adult sex ratio of red deer have larger numbers of females, but rarely in excess of two females per male. Flook (1970) commented that in various hunted elk populations the deficiency of males was usually greater than could be accounted for by the many and various types of harvest systems. Houston (1982) found that the sex ratio of elk older than yearlings reflected continued differential high mortality (plus perhaps dispersal) of males throughout their adult lives.

Flook (1970) cautioned that the accuracy of elk population sex ratio estimates may be hampered by the solitary nature of males and their segregation from cow-calf herds for most of the year. This could under represent males in survey results and bias population estimates.

Several researchers have discussed the problems in elk populations with low male to female sex ratios in which yearling males have the opportunity to breed (Freddy 1987). These problems include higher winter calf mortality resulting from later conception and lower pregnancy rates (Prothero et al. 1979, Squibb 1985). The low number of male elk in some populations where the emphasis of the harvests had been on males has prompted wildlife managers to limit the number of males taken with hunting licence draw systems, much to the disappointment of many hunters (Kline 1981, Olterman 1983).

The Spruce Woods elk (Cervus elaphus manitobensis) population in southwestern Manitoba inhabits the Shilo Military Reserve, the Spruce Woods Provincial Park and surrounding private and Crown lands. This elk population is one of five major herds which inhabit the province.

A population increase of this elk herd was observed through the 1970's and documented by Hornbeck (1979) and Strong (1981). It attained a size by 1979 which allowed a managed harvest to be initiated (L. Bidlake, Manitoba Wildlife Branch, pers. commun.). Hornbeck (1979) suggested that the herd size had the capability of "exploding". Strong (1981) found that by 1981 the population had stabilized at between 600-700 after hunting seasons had been established.

Strong (1981) expressed concern over the herd's low bull to antlerless elk ratio observed during winter aerial surveys when compared to other elk populations in Manitoba. Hornbeck (1979) suggested that the ratio may have been low prior to the first hunting season. In response to these observations and associated concerns, the harvest by recreational hunters was changed from a bulls only season in 1979 to an any-elk season in 1981 and in later years to seasons which emphasized the harvest of cows and calves (L. Bidlake, Manitoba Wildlife Branch, pers. commun.).

Spatial segregation of wintering habitat between male and female elk has been documented for this population. Hornbeck (1979) found that a large portion of elk in the Spruce Woods Park were males. Strong (1981) showed a significant differential distribution of elk by sex between the west and east halves of the military reserve. A good biological understanding of both sexes is required to manage populations where segregation of sex occurs (Clutton-Brock et al. 1982). Because of this and the low male to antlerless ratio observed during winter surveys, Strong (1981) recommended that further study on the male segment was required to determine the resource requirements of this population. This suggestion and the slow recovery of the male segment of this population, despite hunting season changes, catalyzed the initiation of this study.

The objective was to determine the cause of the low male to antlerless ratio observed for the Spruce Woods elk population during the annual winter aerial surveys.

Hypotheses addressed are:

1. The annual winter surveys are biased favouring the observation of antlerless elk.
2. Male elk have large seasonal ranges which frequently extend into areas where they are susceptible to poaching and Indian hunting.
3. There is a dispersal of immature male elk from this population into satellite habitats.
4. Illegal hunters select male elk.
5. Indian hunters take more male elk than females.

LITERATURE REVIEW

A variety of survey methods and techniques have been used to assess different demographic parameters of mammal populations (Eberhardt 1978). Aerial surveys are generally considered the preferred method of inquiry when information is required on the population size and distribution of large mobile mammals (Norton-Griffith 1978). LeResche and Rausch (1974), Caughley et al. (1976) and Caughley (1977) cautioned that there are some concerns with aerial survey estimates. One of the most serious problems arising from aerial survey data is that some individual animals are likely always overlooked and an assessment of this bias generally is not considered (Caughley et al. 1976).

Populations of elk and red deer frequently are monitored using aerial survey techniques but the methods of the survey design vary widely (Flook 1970, Mitchell et al. 1977, Rounds 1981, Houston 1982, Samuel et al. 1987, Freddy 1987). Most wildlife managers agree that an intense aerial search by helicopter provides the most accurate information (Freddy 1987). Authors generally use the data collected from aerial surveys to produce a population estimate, sex and cow-calf ratios and population distribution. Some researchers have used an aerial count method with little structured survey design and/or no correction for the animals which may have been missed, to produce a minimum population estimate. The unreliability of data generated from this type of survey has been described (Lovaas et al. 1966, Peek and

Lovaas 1968). Other researchers have used rigorous survey designs which produce data used to calculate a statistically reliable population estimate bound by confidence limits and some account for missed individuals (Samuel et al. 1984).

Caughley and Goddard (1972) stated that, by missing individuals, aerial surveys usually underestimate the size of the ungulate population investigated. Peek and Lovaas (1968) pointed out that biases in sex ratio estimates are obtained when one sex is more conspicuous than the other. The general clustered distribution of elk during the winter may compound the visibility bias and sometimes preclude the application of standard survey designs (line transect, quadrat and strip transect) when the basic assumptions of these methods cannot be achieved (Samuel and Garton 1984).

Samuel et al. (1987) found that the most important factor contributing to visibility bias during helicopter surveys of elk in Idaho was the size of the group of elk which an individual was a member. The habitat type in which an elk was found was considered of secondary importance. They reported that individuals in smaller groups were less likely to be spotted by observers than elk in large groups and also warned that "visibility bias also may confound the estimates of age and sex ratios when males, females, or young have different visibility factors", where males tend to be more solitary than cows and calves. Jacobson and Cook (1978) described similar findings for white-tailed deer in which group size is a major component of aerial survey visibility bias.

As well, survey conditions are an important factor in affecting the observer's ability to detect animals (Knight 1970). Kimball and Wolfe

(1974) cited several studies which demonstrated a positive correlation between winter severity and the reliability of aerial surveys. Agreeing with Rounds (1981), Trottier et al. (1983) found that normally there was little observability difference among vegetation types in Riding Mountain National Park unless animals were actively seeking shelter during severe winter conditions and restricting themselves to dense conifer stands.

Adult sex ratios of ungulate populations are frequently used by managers to assess the relative health of a population. Bubinek (1982) stated that in a socially balanced elk population there should be 100 males per 120-150 females. Mitchell et al. (1977) pointed out that little is known about the "natural" sex ratio of red deer and elk populations but suggest that it is unlikely to approximate parity. He also adds that most studies reveal there are excesses of females but rarely more than two to one. Geist (1982) referring to sex ratios, stated that it is questionable whether natural populations of elk exist for a reference for herd managers.

In his pioneering work on elk in Jackson Hole, Wyoming, Murie (1951) recorded adult elk sex ratios of 25:100 (males:females). Craighead et al. (1973) reported a sex ratio of 20:100 for elk of the Madison Drainage in Yellowstone National Park. Moody and Simpson (1978) noted an adult sex ratio of 48:100 for an elk herd in Texas. The opinion that the adult sex ratio of healthy elk and red deer populations should approximate unity is primarily a European one (Dzieciolowski 1979, Freddy 1987).

Many North American elk herds are managed to sustain populations which approach the carrying capacity of their environment thereby enabling a large annual harvest (Freddy 1987). Hunting seasons usually emphasize the harvest of male elk in general and more specifically trophy male elk (Boyd and Lipscomb 1976, Squibb 1985). As a result, many elk populations have few males and excesses of females and sex ratios which are highly skewed favoring females. Taber et al. (1982) reported post-hunting season sex ratios of 9-16 males:100 females for the White River in Colorado between 1966 and 1972. Houston (1982) found sex ratios to vary between 26-46 males:100 females for the Northern Yellowstone elk herd. Freddy (1987) reported that the sex ratios for the White River elk herd between 1960 and 1985 varied between 4-24 males:100 females. Flook (1970) stated that elk herds in Banff and Jasper National Parks have adult male elk in the minority and that sex ratios averaged 36:100 and 37:100, respectively. Boyd and Lipscomb (1976) reported a pre-hunt classification ratio of 31:100 in 1971 for the White River elk herd and in response the state game commission implemented seasons to increase the numbers of trophy bulls in the population.

The possible harmful consequences of low sex ratios in ungulate populations have been well documented (Kimball and Wolfe 1974, Guinness et al. 1979, Prothero et al. 1979, Geist 1982, Bubinek 1982, Freddy 1987). Bubinek (1982) stated that deviations from the optimum sex ratio causes social friction in red deer. Normally, yearling males are not rivals for receptive cows, show little sexual interest and are easily driven off by mature males (Guinness et al. 1979). Studies have shown that in elk populations with a low ratio of males to females, the rut is prolonged, mature males may service more cows than normal and enter into the winter in poor condition; as a result, winter male mortality increases (Geist 1982). As well, yearling male elk have the opportunity to breed receptive cows in populations with a low ratio of males to females (Prothero et al. 1979, Taber et al. 1982).

Evidence from other ungulate species support concerns for breeding yearlings. Ozoga and Verme (1985) studying white-tailed deer observed that despite the lack of ritualized behaviour, yearling bucks successfully impregnated does as efficiently as mature bucks. Ozoga and Verme (1985) cautioned that the lack of a hierarchy in populations where yearling males are breeders might reduce the herd's genetic fitness in the long term.

Prothero et al. (1979) stated that although yearling elk are capable of breeding cows, in elk populations where yearling males significantly contributed to the breeding, one would expect to see calves born one month later in the spring and entering the winter smaller-than-normal. This could contribute to higher calf mortality in severe winters. Hines and Lemos (1979) reported that the impregnation rates of yearling males is significantly lower than mature males. Lower pregnancy rates and later birth dates when yearlings were sires, were again noted by Hines et al. (1985). Concerns over the long term genetic fitness of elk populations with breeding yearling males have also been expressed (Prothero et al. 1979). Squibb (1985) contradicted these findings and reported that yearling males are as equally capable of breeding cows as mature males. In some cases, females prefer yearling males over the more aggressive mature males as mates (Squibb 1985). Freddy (1987) theorized that, although younger males are capable of breeding females, the hyperactivity of older males which may stimulate females to ovulate and promote breeding synchrony is not achieved by younger males.

Home ranges have been used by wildlife researchers to delineate environmental and spacial requirements of many animal species. Seton (1909) stated that "no wild animal roams at random over the country; each has a home-region, even if it has not an actual home". Sanderson (1966) suggested that beginning with Seton (1909) the concept of home range for mammals has been accepted and used, but that the methods for determining home range parameters vary widely. Craighead et al. (1973) stated that the most accepted definition of home range is that of Burt (1943) who defined "that area traversed by the individual in its normal activities for food gathering, mating and caring for young".

Sanderson (1966) cautioned that comparing home range sizes obtained for different populations of one animal species may not be valid or biologically important even when using similar descriptive techniques and less valid when using different techniques. Applying Burt's (1943) definition to seasons, an animal's seasonal ranges can be described and defined by that area occupied and delineated within a season (Craighhead et al. 1973).

Red deer and elk home ranges can not be considered as territories, for resources within home ranges are not defended (Bowyer 1981). Several studies have provided area estimates of seasonal ranges for elk but few provide estimates for various male elk cohorts. Seasonal range estimates are difficult to ascertain and may have little importance and value with regard to migratory elk populations (Knight 1970). This could explain the lack of information on seasonal range size estimates for North American elk in the literature. Houston (1982) describing the movements of the Northern Yellowstone elk stated that herd migrates between summer and winter ranges and identification of other seasonal ranges was difficult.

Home ranges of red deer have been described as varying considerably (Clutton-Brock et al. 1984). Craighead et al. (1973) found that seasonal ranges were influenced by food availability, weather conditions, habitat requirements, breeding activities and parturition. Mitchell et al. (1977) stated that there is great differences in the size of home ranges occurs between populations of red deer. Clutton-Brock et al. (1984) found home ranges of red deer to be between 100 and 600 ha. Craighead et al. (1979) found that seasonal ranges for a non-migratory elk herd (cows and calves) in Yellowstone Park to be 0.1 to 1.5 mi^2 (26-388 ha) in winter, 0.7 to 2.4 mi^2 (181-621 ha) in spring, 1.2 to 6.5 mi^2 (310-1,683 ha) in summer and 2.0 to 6.4 mi^2 (517-1,657 ha) in fall. They did not provide specific estimates for males but add that male elk move more than the females. Irwin and Peek (1983) described seasonal ranges for cows and calves and bulls to average 1,259 ha in spring and fall, 820 ha in summer and 210 ha for winter. Irwin and Peek (1983) did not separate estimates by sex though added yearling males had slightly smaller summer ranges than other cohorts. Jenkins and Starkey (1982) found uncharacteristically large seasonal ranges for Olympic cow elk, seasonal ranges for summer and winter were similar and averaged 1,064 ha. Bowyer (1981) described home ranges for Roosevelt elk to be 400 ha. Franklin et al. (1975) found that bull elk not accompanied by cows, had larger home ranges than cows and during the winter and summer confined their activities to a 240 ha area. He also stated that males which associated with cow herds overlapped their home ranges extensively with the cows and often had ranges which extended beyond the cow herd's home range.

Seasonal ranges and seasonal movements for the different sexes and cohorts of cervid species have been compared in a few studies. The general consensus in the literature is that male cervids have larger ranges than females and that immature males have the largest ranges. Similar to findings on elk, several studies of white-tailed deer agree that males have larger home and seasonal ranges than females and the largest seasonal ranges are those of immature males (Kammermeyer and Marchinton 1976, Nelson and Mech 1984, Gavin et al. 1984, Tierson et al. 1985). Mitchell et al. (1977) comparing findings on red deer stated that males usually have larger home ranges and generally travel more than females and they frequently have seasonal ranges which may be several kilometers apart. Catt and Staines (1987) found that home ranges for two young male red deer were larger than those of females and ranges were the largest for a dispersing male. They stated that seasonal ranges of individual males may be separated from each other. Strong (1981) did not calculate seasonal range sizes for individual elk but indicated that males had larger ranges than females. Craighead et al. (1973) found that generally male elk move more than females.

Once established, seasonal range use is highly traditional in elk and red deer populations (Knight 1970, Craighead et al. 1973, Edge et al. 1985, Morgantini and Hudson 1988). Traditional range use is less pronounced in immature male cohorts. Irwin and Peek (1983) describe mature radio-transmittered elk as having high fidelity for seasonal ranges each year. They also report that only young bulls moved to distinctly new areas. Houston (1982) found that females apparently showed greater fidelity to summer ranges than males though both sexes demonstrated high traditional use of winter ranges. Morgantini and

Hudson (1988) found that female migratory elk in Banff had predictable movements between ranges and generally returned to the same ranges each year while the male elk which they had neck collared (2 immature individuals) did not. Gibson and Guinness (1980) report that male red deer traditionally return to a particular area to rut each year.

The social organization of male elk and red deer are similar in that the sexes live separately, males are usually solitary for most of the year and temporarily join cow herds during the breeding season (Franklin et al. 1975). The phenomena of sex segregation and separation of habitat utilization for elk and red deer have been documented extensively in the literature for both migratory and non-migratory populations (Murie 1951, Altmann 1952, Mitchell et al. 1977, Dzieciolowski 1979, Rounds 1980, Geist 1982, Skovlin 1982, Clutton-Brock et al. 1984, Clutton-Brock et al. 1985, McCorquodale et al. 1986, B. Bobek, University of Cracow, Poland, pers. commun.).

Franklin et al. (1975) reported that as males increase in age from yearlings to adults, they left the cow-calf herds and joined other males. Mitchell et al. (1977) stated that the extent to which the sexes stay apart is variable. Clutton-Brock et al. (1985) found that in red deer sex differences in habitat use and food selection are pronounced. Bobek (University of Cracow, Poland, pers. commun.) found that male red deer in Poland preferred thicker habitats than females in all season except during the rut. Flook (1970) observed that in mountainous areas, segregation occurs with males occupying higher elevations for most of the year and higher or lower areas than cows and calves during the winter. Prior to the rut, males in both cervid species occupy different areas in mountain habitats usually at higher elevations, juveniles show increased activity and separate from their normal ranges (Altmann 1960). Clutton-Brock et al. (1987) stated that for Scottish red deer sex segregation occurs for more than 80% of the year.

The selective forces favouring segregation of the sexes has been attributed to reducing intraspecific resource competition between males and cows and calves and may be kinship related when resource competition between a male and his offspring is reduced (Geist 1982). Geist (1982) theorized that spatial segregation of the sexes in elk is the result of bulls seeking out high quality abundant forage during most of the year and bulls compromising security in favour of foraging quality, while cows compromise on forage quality and abundance, in favour of security. Alternatively, segregation has been attributed to different food requirements, thermal regulatory behaviour and antipredation strategies between the sexes (Geist 1982, Clutton-Brock et al. 1987). Clutton-Brock et al. (1987) postulated that sex segregation results from larger grazers (males) requiring diets higher in fiber and lower in available protein than the smaller (females). This results in each sex occupying different habitats. Geist (1982) stated that, once segregated from cows after the rut, bulls hide in cover to recuperate from the effects of the rut and avoid predators.

In polygamous animal species, immature males are the predominant dispersers (Dobson 1982). It has been hypothesized that the causes of dispersal for immature males results from social pressure (Ozoga and Verme 1985), avoidance of inbreeding depression (Dobson 1982), competition for mates (Dobson 1982), to achieve optimum inbreeding thereby maintaining favorable genetic characteristics, and reducing possible mate competition between father and son (Nelson and Mech 1984).

Clutton-Brock et al. (1985) stated that dispersal in female red deer may be low because females which attempt to join unrelated groups of cows and calves may be persecuted.

Most North American cervid species follow the social strategy where immature males are the dispersing cohort (Ribonette 1966, Gasaway et al. 1980, Nelson and Mech 1984, Ozoga and Verme 1985). Clutton-Brock et al. (1982) stated that dispersal in red deer from the natal area is more frequent among stags than hinds. Staines (1978) reported that 2-3 year old males were the usual emigrants and may associate with separate red deer herds from that of their birth. Catt and Staines (1987) found that 4 of 5 marked male red deer dispersed (most at 2.5 years of age). These authors did not find any females to be dispersers. Houston (1982) stated that young elk, particularly young males, are more likely to disperse than other cohorts. Male elk are usually the first to recolonize new areas and are then later followed by cows and calves.

Most authors agree that dispersing individuals face greater risks and have a higher mortality rate than non-dispersers (Gavin et al. 1984). Increased mortality of males has been attributed to immature males which are likely disperse and the survival of dispersers is low (Kammermeyer and Marchinton 1976, Clutton-Brock et al. 1985). Flook (1970) stated that the dispersal of young males frequently took them to suboptimal habitats and contributed to their higher mortality. Flook (1970) also reported that the primary cause of the unbalanced sex ratio observed for mountainous park elk is the tendency for younger males to disperse. He added that the dispersal of young males to new areas may take some of them into unsuitable habitats and thus contribute to the mortality of males.

There are many causes of elk and red deer mortality (Taber et al. 1982, Clutton-Brock and Albon 1982). Several investigators have documented a greater overall survival of female cervids over males (Craighead et al. 1973, Kimball and Wolfe 1974, Clutton-Brock et al. 1983, Gavin et al. 1984, McCorquodale et al. 1988). Both natural and human caused mortality may be sex biased and in most cases the mortality of male elk and red deer when compared to that of females is disproportional (Flook 1970, Kimball and Wolfe 1974, Mitchell et al. 1977, Houston 1982, Bobek and Kunelius 1983, Sauer and Boyce 1983, McCorquodale et al. 1988). Flook (1970) concluded that mortality of male elk older than yearlings contributed to sex ratios which favour females. Clutton-Brock et al. (1985) suggested that sex differences in mortality probably has several causes.

McCullough (1969) suggested that the greater mortality is attributed to male elk's greater aggressiveness and range of movement, and the injuries and energy depletion associated with the rut. Flook (1970) studying elk in Banff and Jasper National Parks, indicated that the losses of male elk did not appear to exceed females until 1.5 years of age and that between 1.5 and 2.5 years the change in loss between the sexes may be abrupt. Clutton-Brock et al. (1983) stated that the increased mortality of young, male red deer when compared to females is found in many species of dimorphic ungulates under conditions of food shortages and may be a consequence of males rapid growth rate and reduced fat reserves.

Male mortality may be directly associated with the rut as a result of combat between males for possession of cow-calf harems, a consequence of their polygamous mating system. Gavin et al. (1984) stated that higher male mortality following the rut in ungulates with polygamous mating systems is common. He added that Heptner et al. (1961) believed male red deer suffer a high mortality rate in winter which was proportional to their activity during the rut. Clutton-Brock and Albon (1979) and Geist (1982) described male red deer rutting challenges as highly ritualized. Antler contact only occurs when participants are evenly matched and the benefits of successful combat outweigh the risks.

Cervid antlers are highly developed lethal weapons (Suttie 1980, Clutton-Brock 1982) and several researchers have documented specific cases of combat-caused deaths in male elk and red deer (Craighead et al. 1973, Clutton-Brock et al. 1980, Leslie and Jenkins 1985, Gogan and Barrett 1987). Clutton-Brock et al. (1979) estimated that up to 6% of male elk are injured permanently each year and slightly more than 20% of male elk will be injured during their lifetime due to rutting combats. Geist (1982) stated that fighting mortality is by no means insignificant and reported that Muller-Using and Schloeth (1967) and Heptner et al. (1961) found 5% and 13% of males, respectively, die annually from rutting combat damage. Flook (1970) pointed out that male elk injured during the rut were usually mature.

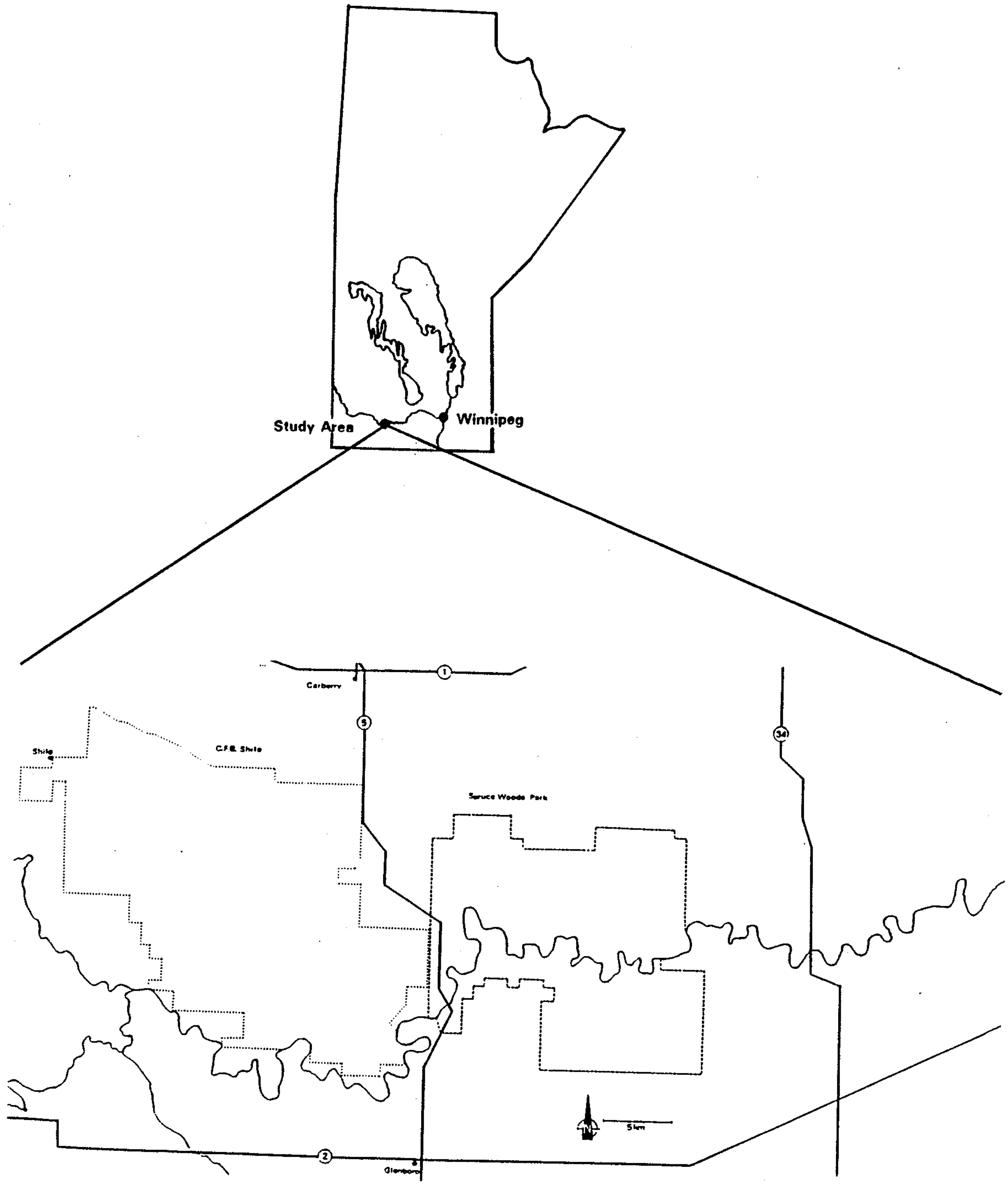
Indirectly, fighting between males and increased activity by males during the rut likely increase male mortality (Clutton-Brock et al. 1979). Clutton-Brock et al. (1979) suggested that fighting increases a stag's vulnerability to predation. Large male elk and red deer off set selection by predators by segregating from cows and calves and hide in cover to recuperate from the effects of the rut (Geist 1982). Craighead et al. (1973) observed that the first elk to die of starvation in the Northern Yellowstone herd were large bulls 6 to 8 years of age, some of which had been injured during the rut. Smith (1984) reported that male elk more so than cows were susceptible to a variety of diseases which caused their death and believed that the difference was due to stress from the rut. Feeding by males is reduced during the rut (Gibson and Guinnes 1980, Bowyer 1981), in addition energy expenditure is high which increases male mortality, particularly when populations are high and during severe winters (Clutton-Brock et al. 1985).

STUDY AREA

The intensive study area, approximately 150 km west of Winnipeg, consisted of the Shilo Military Reserve, Spruce Woods Provincial Park and the immediate surrounding private and Crown lands in southwestern Manitoba (Figure 1). The intensive study area generally is surrounded by farmland. The extensive study area includes those areas where elk that likely had originated from the Spruce Woods population were sighted and reported by a variety of sources. These areas generally followed and included wooded cover along river corridors of the Assiniboine and Souris Rivers and the many creek drainage systems radiating from the park and military reserve. In some cases areas inhabited by elk were satellite habitats, disjunct from travel corridors. Reports of elk from this population included sightings made at Melita, Oak Lake, Hallboro, Delta Marsh, Lowe Farm and Snowflake, Manitoba.

The climate is characterized as a mid-continental type with large seasonal temperature fluctuations, typical of this part of the Canadian prairies (Wier 1960). Mean monthly temperatures ranged from -25 C in January to 21 C in August (see Appendix 1 for details). The frost-free period usually exceeds 110 days and the growing season more than 170 days. Rainfall may occur in all months of the year when temperatures are higher than 0 C but generally occur between April and October. Mean annual rainfall is approximately 45 cm (Wier 1960). Continuous snow cover usually is present from November to March, with median snow

Figure 1. Location of intensive study area in southwestern Manitoba.


Study Area
Winnipeg
1
Carberry
5
34
Shilo
C.F.B. Shilo
Spruce Woods Park
5km
2
Glenboro

thickness ranging from 20 cm to 31 cm for January and February (Wrigley 1974).

The winters of 1982/83 and 1983/84 were mild with periodic mid-season melts and less than average snow fall. The winter of 1984/85 was normal with average snowfall and daily temperatures (Appendix 1).

Shilo Military Reserve

The Shilo Military Reserve encompasses approximately 60,000 ha of wild lands. The military reserve is bound by the Assiniboine River to the south, west by Provincial Road #340, Provincial Road #5 to the east and north by the Canadian National Railway (Strong 1981). The Epinette Creek bisects the north half of the reserve on a northwest-southeast diagonal. The military reserve has restricted public access and is patrolled regularly by military range patrol officers.

Military exercises are undertaken year-round on the reserve with the most intense training occurring from May to October by West German armoured tank crews (W. Gordon, Shilo Military Reserve, pers. commun.). Military exercises frequently use live ammunition which sometimes cause range fires on the military reserve. Strong (1981) described the extent of past range fires which frequently accompanied spring and summer exercises. Extensive range fires had occurred on central portions of the military reserve each year for five years prior to this study. Extensive burning of the military reserve was again repeated in 1981 and 1982. In the summer of 1983 and 1984, approximately 80% of the military reserve south of the Epinette Creek swamp burned. The area north of and including the Epinette Creek swamp has not sustained wild fire in the 20 years prior to this study. It contains a large portion of the wooded cover present on the military reserve.

The military reserve had been open for the deer and/or elk hunting seasons each fall to hunters who register for access with the military range patrol personnel prior to venturing onto the reserve to hunt.

Spruce Woods Provincial Park

The Spruce Woods Provincial Park was created in 1970. Its 23,800 ha area borders the east side of the military reserve. The park has a history of being protected from wild fires and therefore a large portion of its area consists of mature and near mature wooded cover.

The park is bisected near its centre by the Assiniboine River, forming north and south halves which are referred to in this text as park blocks. Both park blocks have several uncontrolled access roads and entrance into the park is unrestricted. The park is patrolled infrequently by park personnel throughout the year. Cattle grazing and haying is permitted in some parts of the park.

The park is utilized year-round for many types of recreational activities which include cross-country skiing, snowmobiling, hiking, camping and hunting. The park has been open to both deer and elk hunting.

Surrounding Private and Crown Lands

The park and military reserve are surrounded by Crown and private lands devoted to mixed farming. Much of the adjacent farmland is pasture for cattle and woodlots. Laut (1974) reported that between 1.5% and 8.0% of the farmland in the study area is woodland. The highest proportion of wooded farmland occurs east of the park. Cereal crops comprise a large percentage of agricultural production on private land adjacent to the park and military reserve. The percentage of land planted to cereal crops increases farther from the park and military reserve. Between 1980 and 1984, specialty crops such as corn, sunflowers and potatoes were grown in increasing amounts on these surrounding agricultural lands.

Vegetation

The study area is composed of a mosaic of diverse vegetation types which are generally referred to as the parkland or aspen parkland (Budd 1987). The aspen parkland is located geographically at the transition between the grassland, coniferous forest and temperate forest biomes (Wrigley 1974).

Scoggan (1957) pointed out that relic colonies of scattered white spruce (Picea glauca) associated with creeping juniper (Juniperus horizontalis) are found in the study area. Wrigley (1974) identified and described seventeen different plant communities within the study area. These include mixed-grass prairie, aspen-oak savanna, aspen-oak forest, elm-maple-ash riparian forest, marsh, and relic forests of white spruce, black spruce and tamarack swamp.

Several major plant communities as described by Wrigley (1974) and Wier (1960) are important in the context of this study. The dominant overstory species associated in those communities are as follows: a) the broadleaf deciduous forest occurs throughout much of the study area with the dominant species being aspen (Populus tremuloides) and in some dry areas bur oak (Quercus macrocarpa); b) the evergreen forest community, dominated by white spruce and scattered juniper; c) the floodplain deciduous forest, dominated by American elm (Ulmus americana), ash (Fraxinus pennsylvanica) and Manitoba maple (Acer negundo); d) the larch-spruce swamp community occurs on peaty soils associated with wet meadows, dominated by larch (Larix laricina) and black spruce (Picea mariana).

Understory and shrub vegetation species frequently associated with the described communities include: willow (Salix spp.), horsetail (Equisetum spp.), bearberry (Arctostaphylos uva-ursi), wolf willow (Eleagnus argentia), various cherry species (Prunus spp.), saskatoonberry (Amelanchier spicatum), alder (Alnus rugosa), dwarf birch (Betula glandulosa), beaked hazel (Cornus cornuta), high-bush cranberry (Viburnum opulus) and red-osier dogwood (Cornus stolonifera) and sedges (Carex spp.).

The mixed-grass prairie consists of several grass species dominated by spear grasses (Stipa spartea and S. comata), blue stem grasses (Andropogon scoparius and A. gerardii) and blue grama (Bouteloua gracilis).

Frequent wildfire on the Shilo Military Reserve have resulted in large areas of mixed grasslands and shrub savanna. Approximately 70% of the habitat on the military reserve is mixed grasslands interspersed with young aspen stands. Extensive wildfire on the central portion of the reserve have greatly reduced the mature white spruce and aspen stands.

Mature stands of deciduous forest and white spruce form the dominant vegetation type to the north of the Epinette Creek ridge. Marsh, elm-maple-ash riparian, and tamarack-black spruce communities also are found along the Epinette Creek and Assinibione River on the military reserve.

The Spruce Woods Park is characterized as having more mature plant communities and less mixed-grass prairie than the military reserve. Most of the park consists of a mosaic of mixed-aspen and spruce forest plant communities. Approximately 5% of the park is comprised of grasslands (Hornbeck 1985). Marsh, tamarack-black spruce and elm-maple-ash riparian communities are found along the Assinibione River and Epinette Creek in the park.

Lands surrounding the park and military reserve generally are privately owned or Crown-leased farmland. Some of the land is pasture interspersed with mixed deciduous and spruce forests, other is cropland. A few of these areas contain native grasslands though most are grazed by cattle.

METHODS

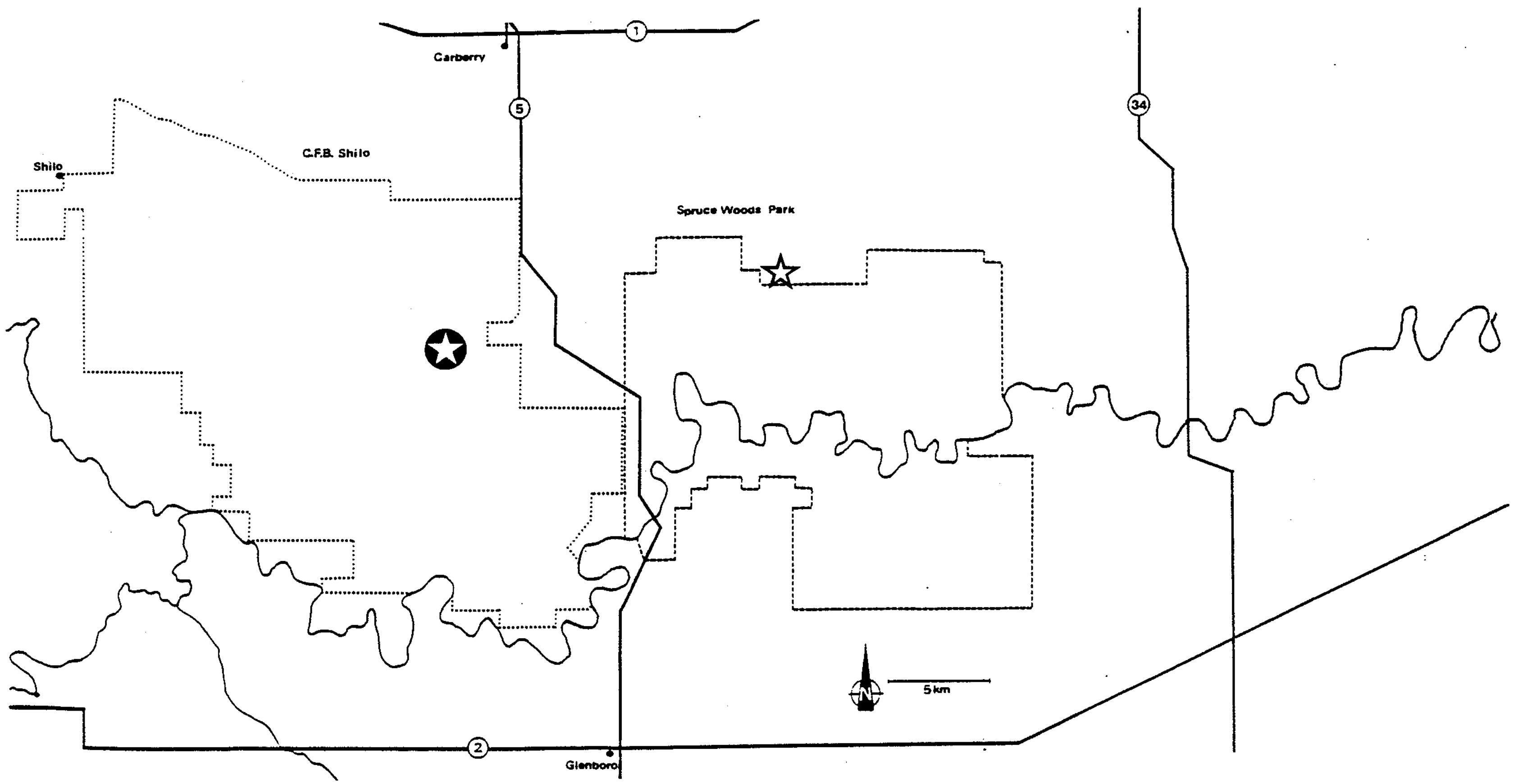
Capture, Instrumentation and Anomalies

Male elk were captured in a baited, self-tripping corral trap in the winters of 1982/83, 1983/84 and springs of 1983 and 1984. Corn, sunflower heads and alfalfa hay were effective trap lures which were used in the winter and early spring, while salt was used in late spring and summer since it was more effective at that time (Pedersen 1977).

One corral trap was located approximately 0.5 km south of the Epinette Creek in the eastern half of the military reserve (Figure 2). Male elk were known to winter in this area (Strong 1981). This trap was set to capture elk opportunistically usually following a prebaiting period of about one week. When set the trap was checked on a daily basis in the early morning. A second corral trap was erected on the north side of the park on private land. This trap was prebaited on many occasions in the winter and spring but was never set to capture elk because of the lack of elk sign in the area.

Trapped elk were immobilized with xylaxine hydrochloride (Rompum) (Herbert et al. 1982) using a dart syringe shot from a Chapture dart gun. The live weight of a trapped elk was estimated visually and xylazine hydrochloride (100 mg/ml) (Olsen and Renecker 1984) was administered intramuscularly at 1.5 mg/kg of body weight to achieve immobility (Coates, Glenboro Veterinary Services, pers. commun.). If

Figure 2. Corral trap locations in the study area.



☆ - Park Trap ✪ -Military Reserve Trap

the first injection did not produce complete immobilization of the elk, a second dosage was administered at 0.75 mg/kg. The preferred injection site was the large muscle mass of either hind quarter or the muscle mass over either shoulder.

The general physical condition of immobilized elk was assessed visually and anomalies noted. A cover was draped over the immobilized animal's eyes to prevent retinal damage and an antibiotic salve placed on the injection site wound. The body temperature of elk immobilized in hot weather was monitored with a rectal thermometer. Immobilized elk were wetted with cool water and/or ice and shaded from the sun to combat hyperthermia during hot weather.

Standard measurements including total length, heart girth, hind foot, tail and ear length from the ear notch to tip were recorded (Blood and Lovaas 1966). Age was determined or estimated from dental wear and replacement (Quimby and Gaab 1957). For some elk, a lower canine was removed and the age of the elk determined in the laboratory by the number of dental cementum annuli present in the root of the tooth (Sergeant and Pimlott 1959, Thomas 1977). Elk were classified as yearlings (>1 and <2 years), immature (>2 and <5 years) and mature (>5 years) as in Bubenik (1982).

Both ears of captured elk were marked for future identification with a coloured and numbered aluminum cattle eartag. Eartags had the Wildlife Branch, Department of Natural Resources address engraved in a visible area to facilitate tag return. All elk were fitted with a solar-powered radiotransmitter manufactured by Telemetry Systems, Incorporated (Meguon, Wis.) attached to a colour coded neck collar. Each neck collar also had the Wildlife Branch address and "$20.00 reward if returned" engraved on a visible metal plate to aid in neck collar returns.

Immobilized elk were administered 5-25 ml of penicillin (Pendure Neat) subcutaneously to combat natural and capture related infections. Elk were left in the trap until fully recovered from the immobilant effects before being released. For the last trapped elk (Sp8406), yohimbine was injected intramuscularly (at 0.33 mg/kg body weight) to antagonize the effect of the tranquilizer (Olsen and Renecker 1984). Recovery time for this elk was reduced to two minutes from a mean recovery of 390 minutes for elk which were immobilized and no antagonist was available.

In March, 1984, a Bell 206 helicopter was chartered from Mid-West Helicopter (Winnipeg, Manitoba) to immobilize and transmitter free-ranging male elk in the north block of the Spruce Woods Provincial Park. A combination of the immobilants [carfentinal (at 0.0125 mg/kg body wt) and xylazine hydrochloride (at 0.3 mg/kg body wt)] was administered by rifle-dart injection from the pursuing helicopter (Meuleman et al. 1984, Bailey et al. 1985).

Immobilized elk were handled and radiotransmitters affixed in a similar manner as those which were captured in the corral trap. Diprenorphine (M50-50) was injected intravenously as an antagonist for the immobilants. Recovery times for all tranquilized elk administered the antagonist were less than two minutes.

A total of 9 elk, all of which were males, were caught in the corral trap on the military reserve between January, 1983 and July, 1984. The absence of cows and calves in the sample of elk which were trapped was expected because the trap was located in an area where male elk had frequently wintered in previous years.

Two male elk trapped together were released by military range patrol personnel prior to being immobilized. Another mature male elk broke down the corral gate and escaped after being shot with a drug-dart but before the tranquilizer took effect. An intensive search of an area in which it may have escaped was unsuccessful in finding this elk.

In total, 6 male elk were captured successfully in the corral trap, immobilized and fitted with neck collars. Of the trapped elk 2 were mature males, 3 were immature males and one was a yearling male.

Most of the elk captured were in good physical condition though there were some exceptions. One immature male (B8303) had a partly healed puncture wound on the posterior side of its right front leg. On close inspection, the wound was abscessed, approximately 15 mm in diameter and more than 10 mm deep. The wound was between the radius and metacarpus. The wound was cleaned superficially and antibiotic cream applied topically. Ten ml of penicillin (Pendura Neat) was injected in the adductor muscles dorsal to the wound. Upon release, this elk noticeably favoured the wounded leg. No impairment of mobility was observed when this elk was sighted in the field approximately one month after being captured.

One immature male elk (SP8304) in the park was immobilized and transmittered after it was approached on foot. This elk was lethargic, appeared sick and could be approached to within 20 m before becoming aware of an approaching human and eliciting a flight response. SP8304 was monitored for approximately 4 weeks in the spring of 1983. During that time it remained within 300 m of where it had been originally immobilized. At the end of the 4 weeks it became emaciated, could no longer stand and was sacrificed. A necropsy was performed at the

Provincial Veterinary Laboratory, Winnipeg and morphological diagnosis revealed non-suppurative meningitis and encephalopathy with glial activation, neuronal necrosis and mineralization of brain tissue. The specific cause of the lesions within the neural tissue was not determined (Neufeld, Provincial Veterinary Laboratory, pers. commun.).

No other elk observed during this study displayed similar behavioral symptoms. Relocation data obtained from this elk were not used for analysis.

Four immature male elk (3 spike-antlered and 1 branch-antlered) were tranquilized and radio-transmittered in the north block of the park from a helicopter. During pursuit one spike-antlered male (SP8404) tore adductor muscles over the right radius area and favoured this limb upon release. The injury was such that no treatment could be administered by the attending veterinarian (G. Glover, Assiniboine Zoo, pers. commun.). No mobility impairment was noticed when this elk was observed 1 week after being tranquilized.

Eight of the 9 elk captured in the corral trap were branch-antlered male elk (> 2.5 years). The preponderance of branch-antlered male elk in the trapped sample may be because the trap was set to capture the first elk which entered. Feeding site dominance by larger males would cause large male elk to be captured first.

The helicopter enabled the selection of elk which were to be immobilized. Four immature male elk (3 spike-antlered, 1.5 years of age and one branch-antlered male elk, 3.5 years of age) were tranquilized selectively from the helicopter. Immature male elk were selected to provide a large enough sample of this cohort for comparison purposes.

Telemetry

Eleven male elk were fitted with radiotransmitters and monitored during the study. Six male elk (B8301, B8302, B8303, Sp8305, B8405, Sp8406) were trapped in the corral, four (Sp8401, B8402, Sp8403, Sp8404) were captured from the helicopter and one (Sp8304, which appeared abnormally ataxic) was immobilized from the ground (see Appendix 2 for capture summary). One male (1633) captured and radio-transmittered by Strong (1981), was also monitored during this study.

The neck collar package (including radio-transmitter and counter weight attached to the nylon web collar) weighed approximately 800 g, representing less than 1% of an elk's body weight and therefore not likely large enough to impair normal movement of an elk. Each radiotransmitter broadcast a radio signal on a different frequency between 150-152 MHZ to facilitate individual identification of transmittered elk.

Transmittered elk were relocated using standard radio-telemetry techniques (Brander and Cochran 1969). Four different types of reception antenna systems were used. Two 14-element (Model Ra-26, Yagi design Telonics Telemetry-Electronics Consultants) beam antenna mounted on rotatable 4.5 m stationary masts were located 5 km apart along the Epinette Creek ridge on the military reserve. These antenna were used most often to obtain triangulation fixes on radio-transmittered elk in the eastern half of the military reserve. A portable 7-element antenna was constructed from the drive half (rear half) of a 14-element antenna (Model Ra-26, Yagi design) and mounted on a collapsible 4 m aluminum mast. This antenna was used for much of the ground telemetry relocation work. A portable, hand-held 2-element antenna (Model Ra024K, Telonics) was used to approach transmittered elk through various habitat types when visual inspection was required.

Triangulation of direction estimates from 2 or more different reception hills were used to estimate a radio-transmittered elk's location from the ground (Strong 1981, Klenner 1982). The direction of a transmittered elk from a reception hill was estimated using the "loudest-signal" method (Sprinter 1979). The intersection of two or more compass bearing estimates from different high points of ground (reception hills) determined the estimated location of a transmittered elk. Reception hills were chosen, where possible, to obtain directional bearings which intersected at 90 angles and provided the most precise location estimate (White 1985).

The accuracy of the antenna systems were assessed. The mean angle of error was calculated for the antenna systems from repeated readings on a test collar that contained a radiotransmitter (see Appendix 3). The mean errors were found to be 7.1 ($\underline{n}$ = 7, SD = 5.66) and 6.4 ($\underline{n}$ = 28, SD = 4.84) for the stationary 14-element and portable 7-element (Model Ra-26) antennas, respectively. As discussed by Lee et al. (1985) some accuracy in the portable telemetry systems was sacrificed over using only stationary antenna.

A 4-element antenna (Hy-Gain Model 23, Yagi design) mounted parallel to the wing, on each wing strut of a Cessna aircraft was used to relocate elk from the air. Differential receiver signal strength between antenna was used to guide the aircraft in a circular pattern until the transmittered elk was spotted or the signal strength was extreme and a difference could not be detected between the loudness of the signal received between the antennas. This implied that the elk was directly under the aircraft.

The telemetry receiver used for all telemetry work was a model LA12 manufactured by A.V.M. Instrument Company, Champaign, Illinois. Earphones aided in signal detection and were particularly helpful on windy days during ground telemetry work and when in the aircraft.

Radio-transmittered elk were relocated on an opportunistic basis, usually during daylight hours. Consecutive relocations of individual elk were usually one or more days apart to ensure independence of relocation data (Swihart and Slade 1985). Aerial relocation techniques were used to relocate transmittered elk that were difficult to locate from the ground. This technique was generally used to search for a elk that had not been relocated from the ground for more than one week. Monitoring effort was hampered by several factors including access to the military reserve, financial constraints, seasonal variation in radiotransmitter interference and the large area over which transmittered elk inhabited.

Winter Aerial Survey

The winter aerial surveys were a systematic strip transect design (Caughley 1977, Eberhardt 1978). Norton-Griffith's (1978) technique was used as the logistical guide for conducting the surveys. The basic survey design had been employed since 1979 (Strong 1981).

Transect lines were flown north-south, 1 km apart, in Canadian Forces Military Bell 206 helicopters. Flight altitude was approximately 150 m and ground speed was 145 km/hr. The pilot was accompanied by a left side observer-recorder in the left front seat and a right side observer in the right rear seat. Each observer had experience in flying large ungulate surveys. The survey was usually 2 days in duration. Two complete survey teams flew simultaneously on each consecutive day. The study area was divided to be flown so that possible movement of elk between areas surveyed was unlikely between survey days. This reduced the possibility of double counting or missing elk which had moved overnight.

Each observer was responsible to survey a strip of ground 0.5 km in width on their side of the aircraft. Frequently, the observer's ability to judge the distance of the 0.5 km strip was checked by the navigator who pointed out landmarks at the correct distance to the observer. The survey method assumed complete coverage of the area surveyed and produced a minimum population estimate of the elk population (Strong 1981).

In the February 1985 survey, the observers also were required to divide their viewing field of 0.5 km into two, 0.25 km survey strips. The observers then recorded the differential distribution of elk in groups with five or fewer individuals sighted in the 0.25 km strip farthest from the aircraft (outer strip) from those observed in the 0.25 km strip closest to the aircraft (inner strip). This was done to determine if elk in smaller groups (likely males) were missed in the outer strip.

All groups of elk observed during the surveys were counted and their composition of individual elk classified into the number of antlerless elk (including cows and calves), spike-antlered male elk (males more than one year and less than two years of age) and branch-antlered male elk (males 2 or more years of age) (Schwartz and Mitchell 1945). This information and the location of each elk group sighted was recorded on a 1:50,000 topographic map. All male elk observed were scrutinized visually to determine if an individual possessed a neck collar. Each neck collared male elk observed was individually identified by the colour code of the neck collar.

Flight transect lines were less than 35 km in length. Survey flights were less than 1 hour each in duration between refueling stops. A rest period of 1.5 hrs between flights was usually provided for observer rest.

In addition to the regularly surveyed area, an area of approximately 7,000 ha surrounding and including the Souris River Bend Wildlife Management Area and an area of approximately 32,000 ha along the Arden Ridge were surveyed on two separate days in 1985 using a strip transect survey design and a Cessna 180 fixed-wing aircraft. Transect strips were 0.4 km wide and flown in a similar manner as those during the helicopter surveys, though in both areas, transect strips were flown in an west-east direction.

Ground Observations

The location, herd composition, date and time of all groups of elk encountered while traversing the study area were recorded. Observations were aided with the use of 7X Elan military binoculars. The study area was travelled with the use a four-wheel drive truck, a three-wheel all-terrain vehicle and a snowmobile.

Observations of groups of elk which were sighted by local people and hunters and parks, wildlife and military personnel were recorded when reports were obtained. When possible the location, herd composition, date and time of these sightings were recorded.

In 1983, an elk observation record form was included with the hunter questionnaire sent by L. Bidlake, Manitoba Wildlife Branch (unpublished data) to bow, landowner and special draw hunters who hunted elk in Game Hunting Area 30 (approximates the intensive study area). The questionnaire asked the hunter to categorize each elk by location and age/sex observed while hunting.

Poaching Information

Information on the number, sex and location of elk that had been poached in the study area was recorded when possible. A poached elk was defined in this study as any elk which had been taken illegally. This definition included elk which were killed by Indian hunters on lands where access had not been permitted.

Reports of illegally shot elk were obtained from local Natural Resource Officers and military, parks, and wildlife personnel and local people. When acquiring voluntary information from local people on illegally shot elk, care was taken not to demand more details of the poaching incident than those which were offered readily. This precaution was undertaken to avoid being mistrusted or frightening the informant. Therefore, it was not always possible to confirm that a single poaching incident had not been reported previously.

Landowners who purchased 1983 landowner elk hunting licenses for Game Hunting Area 30 were interviewed by telephone to assess the extent of poaching in the study area. They were asked if poaching occurred in their area and if they perceived it as a problem. Additional information on specific poaching incidencts were recorded when provided by the landowners.

In 1984, a traffic counter (obtained from the Manitoba Highways

Department) was situated in the north block of the park on a major access road. The counter indicated hourly vehicle traffic levels from September 18th to November 19th, 1984.

Indian Harvest

The number, sex, time, date and location of elk which were harvested by Indian hunters in the study area were recorded when possible. Information was provided by reports from Natural Resource, parks, wildlife and military personnel, local people and Indian hunters.

In 1983, a telephone interview was conducted with leaders of 3 Indian bands in close proximity to the study area. Natural Resource Officers reported that members of the 3 bands hunted elk in the study area. Band leaders were asked to provide an estimate of the number of elk harvested from the Spruce Woods population by band members during 1983 and to categorize harvested elk by sex and age.

In 1984, at the request of band leaders a harvest questionnaire was sent to 5 Indian bands replacing the telephone interview. The questionnaire requested information on the sex and age composition of elk harvested each year from the Spruce Woods population between 1982 and 1985.

Data Analysis

All statistical comparisons were made using SPSS/PC+ (1988) computer software package run on a Mind personal computer. Analysis of relocation data to obtain seasonal range size, activity, movement and fidelity estimates was done using an APL computer program package purchased from W. Klenner (Klenner 1982) and run on the University of

Manitoba Computer Services main frame facility in preparation for statistical comparisons. Seasons were bound by the same dates for all years, winter (December 1 to March 15), spring (March 16 to June 30), summer (July 1 to August 30) and fall (September 1 to November 30), approximating those of Craighead et al. (1973). Only seasonal range location data sets in which 9 or more relocations were obtained per season for an individual transmittered elk were used for statistical comparisons.

Seasonal range area estimates were determined using the minimum convex polygon (Mohr 1947) and Jennrich-Turner Index (Jennrich and Turner 1969, Koeppl et al. 1975; with 95% utilization ellipses). The Jennrich-Turner index estimates of seasonal ranges were used to test for statistical differences between cohort and yearly differences using a two-tailed Mann-Whitney U test comparison (SPSS/PC+ 1988). Seasonal range areas were outlined with 95% utilization ellipses (Jennrich-Turner) on a Hewlett Packard computer and plotter using a program written by B. Johnson and B. Knudsen (Manitoba Department Natural Resources, Wildlife Branch).

Seasonal activity was assessed by the distances between consecutive relocations of elk within a season. Distances calculated were the straight line distance between consecutive telemetry relocations. Comparisons between cohorts and seasons were made using a two-tailed t-test (SPSS/PC+ 1988).

Seasonal range shifts were determined by distances between activity centers for consecutive seasonal ranges and distances between years for the same type of seasonal range. Significant seasonal and cohort differences were tested using a Mann-Whitney U test of two-sample comparisons. Fidelity of seasonal range use was also determined if there was an overlap between seasonal ranges compared.

Ratio comparisons were tested using Yates (corrected for continuity) contingency table comparison of homogeneity (SPSS/PC+ 1988). Differences were tested between paired ratio data.

$P < 0.05$ was required for significance in all statistical tests.

RESULTS

Aerial Survey

Winter aerial surveys, to determine an elk population estimate and winter distribution were undertaken each winter in the intensive study area when conditions permitted. Survey results are illustrated in Table 1.

The inadequate snow cover conditions during the 1982/83 survey prevented complete intensive study area coverage. Only the area between Provincial Road #340 and Provincial Highway #5, including most of the military reserve, was covered by helicopter crews before the survey was discontinued. Results from this survey were not used to determine a population estimate.

In total, 191 elk were tallied during the 1982/83 survey of which 165 were cows and calves. Seven spike-antlered male elk and 19 branch-antlered male elk were counted. Most of the elk observed, 89 cows and calves and 14 branch-antlered male elk were located on the military reserve. Elk sign observed during the survey, including snow packed trails and feeding craters suggested that some groups of elk which were sighted on the military reserve occasionally were travelling to agricultural fields adjacent to the military reserve and feeding on available forage.

Four radio-transmittered male elk were present in the areas which were

Table 1. Numbers of elk observed in different areas during the winter aerial surveys of the study area, 1982-1985.

Year	Shilo Reserve			Location Sprucewoods Park			Surrounding Lands		
	Cows Calves	Spike Bulls	Branch Bulls	Cows Calves	Spike Bulls	Branch Bulls	Cows Calves	Spike Bulls	Branch Bulls
1984/85	79	8	17	24	4	8	129	6	14
1983/84*		N.A.			N.A.			N.A.	
1982/83**	89	0	14		N.A.		76	7	5

* Survey not conducted because of inadequate snow cover.
** Incomplete area coverage because of poor survey conditions.

covered by helicopter crews during the 1982/83 survey. Only 2 of the radio-tramsmittered male elk were spotted by survey crews. Both elk were observed in wooded cover along the Epinette Creek and were members of elk groups with 5 or fewer individuals. The 2 transmittered elk not spotted were relocated with telemetry equipment in wooded cover north of the Epinette Creek ridge on the military reserve immediately after the survey. The group size of which these elk were members during the survey was not determined.

During the winter of 1983/84, there was not sufficient snow to initiate an aerial survey.

The entire intensive study area was covered during the 1984/85 survey under good survey conditions. Two hundred and eighty-nine elk were observed during the survey of which 36 were branch-antlered male elk, 22 were spike-antlered males and 231 were cows and calves (see Table 1 for details).

In 1985, the survey method was tested to determine if a significant number of male elk were being missed because of the solitary nature of males. In previous winter surveys male elk were sighted in smaller groups than cows and calves. The probability of sighting an elk is influenced by the size of the group of which it is a member. Larger groups are more easily spotted by observers as discussed by Samuel et al. (1984). This suggests that previous surveys may have favoured the observation of elk in large groups and therefore underestimated the number of males in the population.

To obtain a "corrected" population estimate, elk were categorized by the size of the group observed. All elk in groups with more than 5 individuals were assumed to have been observed during the survey. The census of this portion of the population consisted of 204 individuals and represented 71% of the elk observed. One hundred and ninety-five cows and calves and 9 spike-antlered male elk made up this count. No branch-antlered males were observed in groups with more than 5 individuals.

Twenty-nine percent of the elk (85 individuals) observed during the survey were in groups with 5 or fewer individuals. The frequency distribution these groups occurring in the inner or outer halves of each survey transect strip was recorded. These data were used to determine if a significant number of elk were missed in the outer portion of the survey strips (Table 2). A significant difference in the probability of observing elk between inner and outer halves of the survey strip would effect the population size estimate and possibly the population sex ratio.

Male elk and antlerless elk (cows and calves) made up 57% (49 individuals) and 43% (37 individuals) of the elk which were observed in groups of 5 or fewer individual elk, respectively. More elk in these small groups were observed in the inner half (n = 50) than in the outer half (n = 32) of the transect strips, though the difference was not significant (X^2 = 0.994, df = 1, P > 0.30). If this difference was significant, a weighted adjustment using inner half strip results to estimate the number of elk in small groups expected in both strip halves, would only increase the population estimate by 18 elk. The resulting change in the male:antlerless elk ratio would have been 28:100 (n = 307) and is not significantly different from the ratio which was observed during the survey of 25:100 (n = 289) (X^2 = 0.28, df = 1, P = 0.596).

Table 2. Distribution of elk, in groups with 5 or few members, observed in the inner and outer halves of the transect strips during the 1984/85 winter survey.

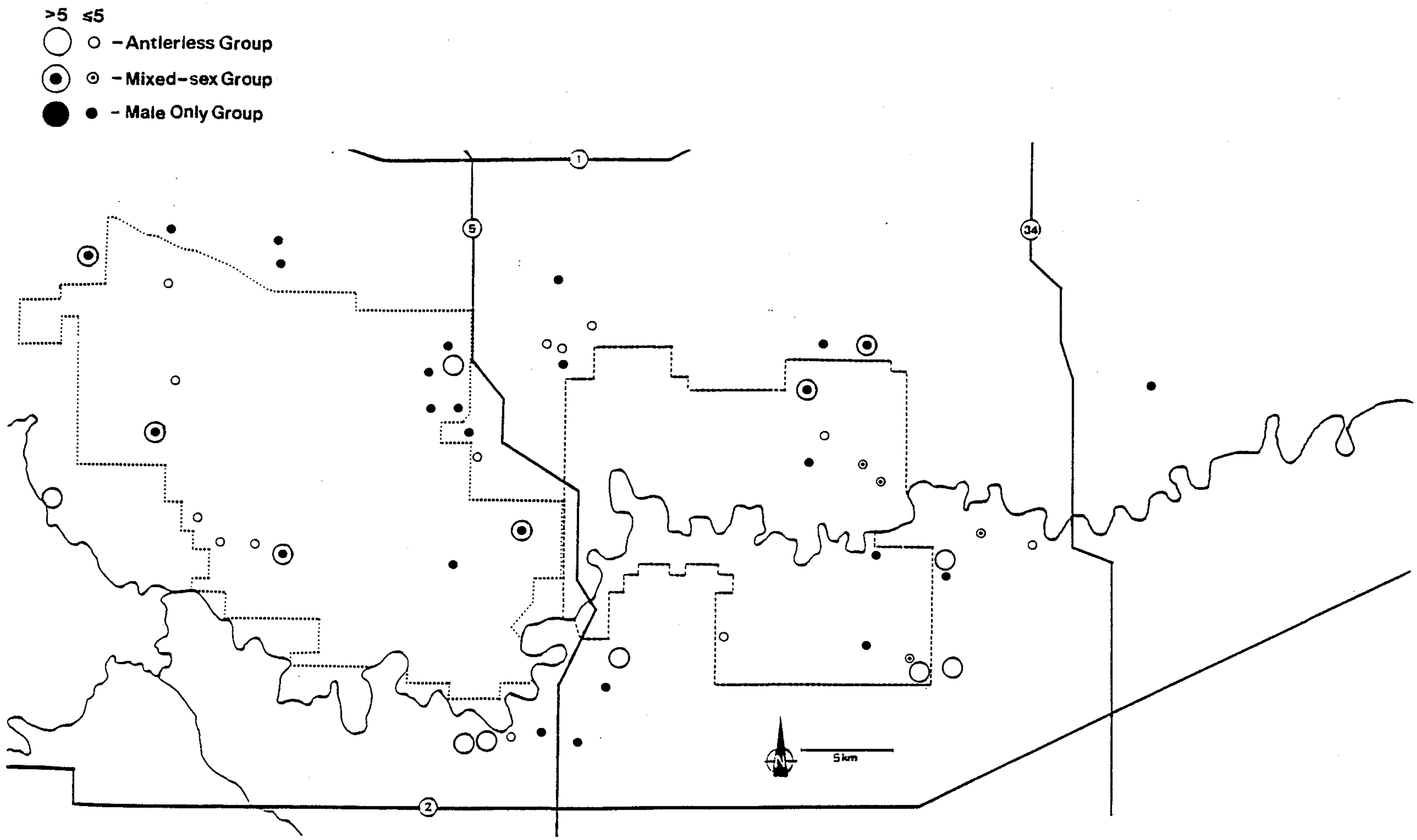
Elk Group Size	Survey Halves							
	Elk Number Inner Half				Elk Number Outer Half			
	Branch Bulls	Spike Bulls	Cows Calves	Total	Branch Bulls	Spike Bulls	Cows Calves	Total
1	5	0	6	11	4	0	0	4
2	2	2	4	8	5	2	1	8
3	6	1	5	12	0	0	3	3
4	0	0	4	4	2	4	6	12
5	10	2	3	15	0	0	5	5
Total	23	5	22	50	11	6	15	32

All 5 radio-transmittered male elk present in the study area during the 1984/85 survey were observed by survey crews. A "Peterson estimate" applied to this data as a mark-recapture index suggests that all elk in the survey area were observed (Seber 1973). A population estimate using the Peterson estimate method was calculated to be 289 (SE = 128.12) elk, as discussed in Gauthier and Theberge (1985). All transmittered elk were observed in small groups with five or fewer individuals and were found in wooded cover during the survey.

The systematic design of the surveys allowed for comparisons of the elk population distribution (Table 1). During the 1984/85 survey 35% (104 individuals), 12% (36 individuals) and 53% (149 individuals) of the observed elk were located on the military reserve, the park and on private and Crown lands, respectively. Figure 3 illustrates the distribution of groups of elk observed during the 1984/85 survey. Few elk were sighted on the central part of the military reserve or park. The groups of elk that constituted the large number observed outside the military reserve and park frequently were found in wooded cover near agricultural fields. Several trails lead to feeding craters in the fields suggested that these elk were utilizing the available forage remaining. For example, one large group of elk (48 cows and calves) was sighted west of the military reserve along the Assinibione River adjacent to several corn fields. Feeding craters in the fields suggested that this group was extensively feeding on the available corn.

The overall ratio of male elk to antlerless elk (including cows and calves) observed during the 1984/85 survey was 25:100 ($\underline{n}$ = 289). An adult elk sex ratio of 29:100 (males:females, $\underline{n}$ = 197) was calculated

Figure 3. Distribution of groups of elk observed in the study area during the 1984/85 winter aerial survey.


>5 ≤5
- Antlerless Group
- Mixed-sex Group
- Male Only Group
1
5
34
2
5 km
N

using the observed male to antlerless ratio obtained from the survey and the cow:calf ratio (100:66, n = 166) obtained from a cow-calf survey of this population conducted in November 1984 by L. Bidlake (Manitoba Wildlife Branch, unpubl. data). The adult sex ratio is significantly smaller than the approximately equal (50:50) sex ratio of elk calves at birth (X^2 = 31.4, df = 1, $P < 0.001$) as reported by several authors (Houston 1982, Taber et al. 1982) and used in the model presented in Freddy (1987).

The sex ratio of elk calves harvested during the hunting seasons was used as an estimate of the sex ratio of calves for this population. The sex ratio of calves 95:100 (males:females, n = 76), calculated from pooled data of calves harvested during the hunting seasons between 1980 and 1984 as reported by Bidlake and McPhail (1984) and McPhail (1985), was significantly larger than the calculated adult sex ratio from the 1984/85 survey data (X^2 = 28.7, df = 1, $P < 0.001$) suggesting a differential mortality or dispersal of male elk older than 0.5 years.

The observed male to antlerless elk ratios and corresponding calculated sex ratios for various areas covered in the 1984/85 winter survey are presented in Table 3. In general, segregation of elk by sex was observed by area during the survey. Elk also were observed in sex segregated groups even when in the same general area. Most notably branch-antlered males were absent from antlerless elk groups; only on a few occasions were spike-antlered males observed as members of mixed-sex groups.

In total, 50 groups of elk were observed during the 1984/85 survey of which 40% (n = 20), 38% (n = 19) and 22% (n = 11) of the groups were cow and calf only, male only and mixed-sex, respectively. All branch-

Table 3. Male:antlerless and sex ratios for areas surveyed during the 1984/85 winter aerial survey.

Surveyed Area	Elk Observed				
	Branch Bulls	Spike Bulls	Cows Calves	Male:Antlerless Ratio	Calculated Male:Cow Ratio
Shilo Reserve	17	8	79	32:100 (n=104)	48:100 (n=77)
North of Epinette Ridge*	13	1	6	233:100 (n=20)	350:100 (n=18)
South of Epinette Ridge*	4	7	73	11:100 (n=84)	25:100 (n=55)
Spruce Woods Park	8	4	24	50:100 (n=36)	75:100 (n=28)
Surrounding Areas	14	6	129	16:100 (n=149)	24:100 (n=105)
Total	39	18	232	25:100 (n=289)	29:100 (n=197)

* Area within the Shilo Military Reserve.

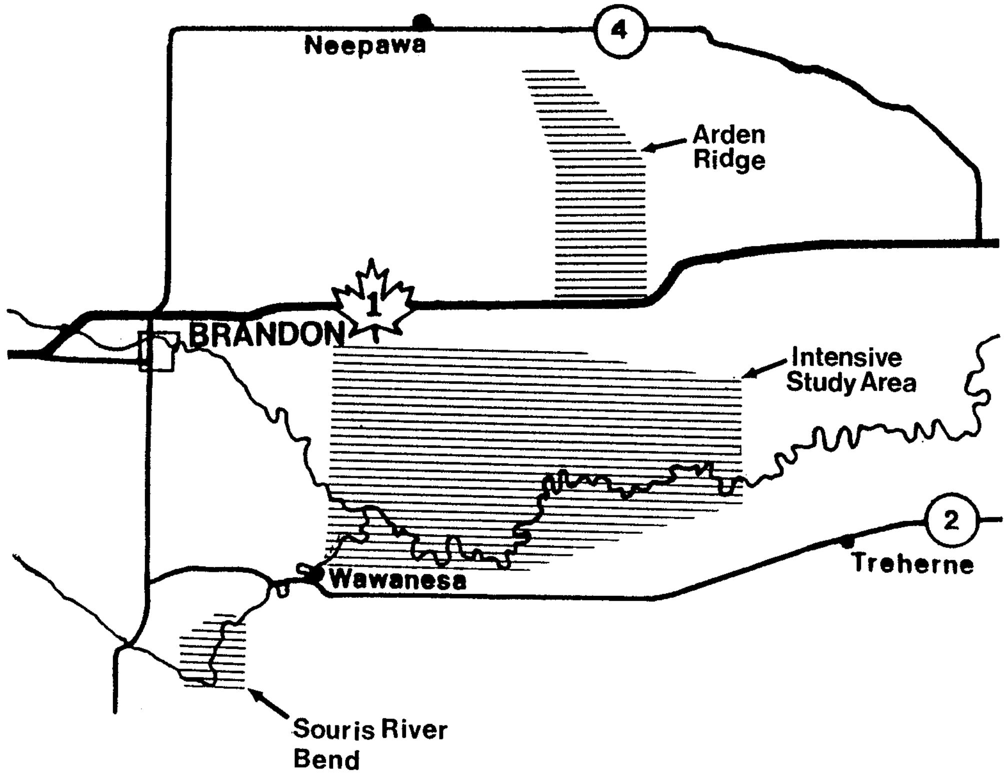
antlered males observed were members of male only groups. All of the mixed-sex groups were composed of several cows and calves with spike-antlered males. Usually only 1 or 2 spike-antlered males were present in each mixed-sex group.

Segregation of elk by sex also occurred within areas surveyed. On the military reserve, sex segregation of different areas was most evident. Fifty-six percent ($\underline{n}$ = 14) of all male elk and 76% ($\underline{n}$ = 13) of branch-antlered males observed on the military reserve were sighted north of and along the Epinette Creek. The male to antlerless elk ratio observed north of the Epinette Creek ridge of 233:100 ($\underline{n}$ = 20) was significantly larger than that observed for the rest of the military reserve, 11:100 ($\underline{n}$ = 84) ($\underline{X}^2$ = 25.61, df = 1, $\underline{P}$ < 0.001) and was the largest ratio in the survey.

Differences in the male to antlerless elk ratio between other areas surveyed were less striking. The male to antlerless ratio observed in the park 50:100 ($\underline{n}$ = 36) was larger than on surrounding private and Crown lands 16:100 ($\underline{n}$ = 149), ($\underline{X}^2$ = 6.70, df = 1, $\underline{P}$ = 0.010). Significant differences of observed male:antlerless elk ratios also occurred between the military reserve (32:100, $\underline{n}$ = 104) and surrounding private and Crown lands (16:100, $\underline{n}$ = 149). A larger male to antlerless ratio was observed in the park (50:100, $\underline{n}$ = 36) than on the military reserve (32:100, $\underline{n}$ = 104) though this difference was not significant ($\underline{X}^2$ = 0.79, df = 1, $\underline{P}$ = 0.76).

In 1984/85 two supplementary areas were surveyed as described in the methods (Figure 4). Landowners in both areas had reported sighting elk on several occasions. One branch-antlered male elk and little elk sign (trails and feeding craters) were observed during the survey of the

Figure 4. Additional areas surveyed during the 1984/85 winter aerial survey.


Neepawa
4
Arden
Ridge
1
BRANDON
Intensive
Study Area
2
Treherne
Wawanesa
Souris River
Bend

Souris River Bend Area. A cow elk, observed by D. Chranowski (Manitoba Wildlife Branch, pers. commun.) during a deer survey of this area one week earlier, was not sighted. No elk were observed during the survey of the Arden Ridge area. In one location along the ridge some trail systems and feeding craters were sighted which could have been made by elk.

The two areas surveyed outside the intensive study area did not contain a large number of elk. Both areas were inhabited by deer which may have made most of the feeding craters and trail systems observed.

Ground Observations

During ground observations elk were sighted in all months of the year. The majority of the recorded sightings were of elk in the intensive study area, though elk also were reported in adjacent areas. Elk which likely had originated from the Spruce Woods population were sighted as far away as Melita, Dominion City, southeast of Neepawa, Delta Marsh and Snow Flake, Manitoba and approximately 117, 118, 36, 60 and 71 km from the boundaries of the park or military reserve, respectively. Areas where elk were observed outside the intensive study area usually were connected to the intensive study area by wooded habitat corridors which were frequently along river and creek drainage systems.

Most of the elk observed outside the intensive study area were males. The composite male to antlerless ratio of pooled data for elk observed in areas greater than 30 km from the boundaries of the military reserve or the park (outside the intensive study area) between 1979 and 1985 was 113:100 (n = 49). This ratio is significantly larger (X^2 = 48.53, df = 1, P < 0.001) than the male to antlerless elk ratio of 18:100 (n = 2699) from pooled annual winter aerial surveys data between 1979 and 1985 (L. Bidlake, Manitoba Wildlife Branch, unpubl. data).

Elk observed outside the intensive study area were usually in small male only or mixed-sex groups. Only one group of antlerless elk was reported outside the intensive study area. Twenty-two groups of elk comprised the 49 elk reported observed outside the intensive study area between 1979 and 1985. Of those 22 groups, 82% (n = 18), 14% (n = 3) and 4% (n = 1) were male only, mixed-sex and antlerless groups, respectively.

The male to antlerless ratios of elk observed on the military reserve, in the park and on surrounding private and Crown lands between 1982 and 1984 are presented by year in Table 4. In general, a larger ratio of male elk to antlerless elk was sighted in the park, and surrounding private and Crown lands than on the military reserve as demonstrated by pooled data ratios.

The observed ratios obtained for the park were significantly larger than on the military reserve for 1983 (X^2 = 9.63, df = 1, P = 0.002) and 1984 (X^2 = 12.49, df = 1, P < 0.001). The small sample of elk observed in the park during 1982 likely prevented a significant difference for this year (X^2 = 3.65, df = 1, P = 0.056). This ratio was significantly larger for areas on private and Crown lands surrounding the military reserve and park than on the military reserve for 1982 (X^2 = 37.22, df = 1, P < 0.001) and 1984 (X^2 = 45.12, df = 1, P < 0.001) but not for 1983 (X^2 = 2.97, df = 1, P = 0.085).

The male to antlerless elk ratios observed in the park and on surrounding private and Crown lands were similar overall. The composite ratio from pooled data in the park 145:100 (n = 98) was not different

Table 4. Male:antlerless elk ratios for elk observed from the ground 1982-1985.

Year	Male:Antlerless Ratio by Area		
	Shilo Military Reserve	Sprucewoods Park	Surrounding Areas
1982	21:100 (n=335)	100:100 (n=8)	106:100 (n=74)
1983	67:100 (n=112)	245:100 (n=38)	114:100 (n=90)
1984	23:100 (n=58)	112:100 (n=53)	296:100 (n=107)
Pooled Data 1982-85	29:100 (n=505)	145:100 (n=98)	158:100 (n=271)

from that observed on surrounding private and Crown lands 158:100 (n = 171) (X^2 = 0.03, df = 1, P = 0.866). Yearly ratios were similar for 1982 (X^2 = 0.00, df = 1, P = 1.000) and 1983 (X^2 = 2.77, df = 1, P = 0.096). The observed ratios were significantly different for 1984 (X^2 = 6.81, df = 1, P = 0.009).

The male to antlerless elk ratios obtained from ground observations in 1984 in the intensive study area, as reported in Table 4, were generally different than those obtained during the 1985 winter aerial survey, as reported in Table 3. The male to antlerless elk ratio of 112:100 (n = 53) calculated from ground observations of elk within the park was not significantly different than the ratio of 50:100 (n = 36) obtained during the 1985 winter aerial survey of the park (X^2 = 2.55, df = 1, P = 0.110). The male to antlerless elk ratio of 296:100 (n = 107) for elk on surrounding private and Crown lands obtained from ground observations was significantly larger than the ratio of 16:100 (n = 149) obtained during the 1985 winter aerial survey of those areas (X^2 = 95.89, df = 1, P < 0.001). The ratio of elk on the military reserve obtained from ground observations of 23:100 (n = 58) was similar to the ratio of 28:100 (n = 101) obtained during the 1985 winter aerial survey (X^2 = 0.30, df = 1, P = 0.584).

One hundred and seventy-five archery and 122 special draw rifle hunters responded to the 1983 questionnaire. Fifty-nine landowner-hunters were interviewed by telephone. The male to antlerless elk ratios observed by the different hunter types are presented in Table 5.

As demonstrated by pooled data, archery and special draw hunters in the park and on surrounding private and Crown lands reported sighting significantly larger male to antlerless elk ratios (159:100, n = 101 (X^2

Table 5. Male:antlerless elk ratios for elk observed by hunters during the various hunting seasons in 1983.

Hunter Type	Male:Antlerless Ratio by Area		
	Shilo Military Reserve	Sprucewoods Park	Surrounding Areas
Landowner	N/A	N/A	63:100 (n=288)
Archery	6:100 (n=325)	49:100 (n=793)	32:100 (n=2149)
Special Draw	22:100 (n=1294)	159:100 (n=101)	44:100 (n=171)
Pooled Data	19:100 (n=1619)	57:100 (n=894)	36:100 (n=2608)

= 135.32, df = 1, $P < 0.001$) and 44:100, $n = 171$ ($X^2 = 64.93$, df = 1, $P < 0.001$); respectively) than hunters on the military reserve (19:100, $n = 1294$). Hunters hunting in the park saw larger ratios of male to antlerless elk than hunters on surrounding private and Crown lands ($X^2 = 30.77$, df = 1, $P < 0.001$).

The composite male to antlerless elk ratios reported from by all hunters on the military reserve ($X^2 = 41.94$, df = 1, $P < 0.001$), in the park ($X^2 = 17.36$, df = 1, $P < 0.001$) and on surrounding private and Crown lands ($X^2 = 30.40$, df = 1, $P < 0.001$) were significantly larger than those collected for respective areas from ground observations for 1983 as presented on Table 4.

The differences between the male to antlerless elk ratios obtained from the winter aerial survey, ground and hunter observation results are difficult to interpret and less powerful than comparing differences between the male to antlerless elk ratios for different areas obtained by the same observation method. Inherent biases between methods may cause the observed variability.

In general, larger ratios of male to antlerless elk were observed in the park and on surrounding private and Crown lands than on the military reserve. This was reported by hunters in 1983 and from ground observations in general but not obtained from the 1985 aerial survey results. These differences may be explained by the various dates at which the different types of data were collected. Male elk during the fall are more active than cows and calves. Their mobility and frequent excursions during the rut may result in their being over represented in elk observed while travelling on the ground in the study area than what they represent in the population demographics. Sex bias movements of elk between the military reserve and surrounding private and Crown lands, and the military reserve during the late fall before the winter surveys could also account for these differences. As well, the winter surveys only provide information on the winter distribution of elk in the study area. Ground observations were collected year-around.

Telemetry

A total of 894 telemetry relocations were obtained on the radio-transmittered elk between January, 1982 and February 1985. The monthly tally of telemetry relocations for individual elk are presented on Appendix 4. All radiotransmitters did not function nor did all radio-transmittered elk survive through to the completion of the study.

A mature male elk (1633) was trapped and transmittered in March 1981 on the military reserve by Strong (1981) and was found dead in early October 1983 in the south-central part of the military reserve. This elk was last relocated in the same area on September 24, 1983. The cause of 1633's death was determined to have been a bullet wound which fractured the thoracic vertebrae midway along the spine.

A mature male elk (B8301) which had been trapped and transmittered on the military reserve in January 1983 was last relocated on September 18, 1983 in the vicinity of where 1633 had been found dead. B8301 was not relocated again for the duration of the study even though extensive aerial telemetry searches were undertaken to regain radio contact with this elk.

B8301 and 1633 were likely shot by an Indian hunting party which illegally ventured on to the military reserve on September 23, 1983. This hunting party was observed crossing the Stockton ferry when leaving the military reserve on September 24, 1983, and were in possession of 4 branch-antlered male elk and one spike-antlered male elk. The hunting party had eluded pursuing Natural Resource and military officers before escaping across the ferry. All elk in the hunting party's possession were believed to have been shot on the military reserve.

Male elk, SP8305 was transmittered on the military reserve in April 1983, and was shot by a landowner hunter approximately 1 km north of the park in November 1984. Male elk, SP8403 was transmittered in the park on February 28, 1984, and was shot by a landowner hunter in September 1984, approximately 22 km northeast of the park.

The radiotransmitter attached to the neck collar from male elk, SP8401 was found by Indian hunters and returned in September 1984. This elk had been captured and radio-transmittered on February 28, 1984 in the north block of the park. The neck collar from SP8401 had been cut off and discarded; therefore, SP8401 likely had been poached in the north block of the park in early September 1984 in the vicinity of where it had been last relocated.

An immature male (SP8404) was transmittered on February 28, 1984, in the park and last relocated on November 15, 1984, in the north block of the park. Extensive aerial searches failed to relocate this elk. Radio-transmission ceased at the same time that Natural Resource Officers received reports of extensive Indian and illegal hunting activity occurring in the north block of the park. This elk was suspected to either have been poached or harvested by Indian hunters and the neck collar not returned.

The 2 transmittered elk which were suspected to have been illegally shot could alternatively have emigrated from the study area or had radiotransmitter failure. Both alternate explanations are unlikely for extensive aerial searches undertaken to relocate both elk failed to find either. As well, observers did not sight either male elk during the 1984/85 winter aerial survey.

The radiotransmitter of male elk B8402 malfunctioned in June 1984. The transmitter thereafter could only be detected using aerial telemetry techniques when the aircraft was flying directly over the elk. A break in the transmitting antenna likely caused the failure. This elk was only occasionally relocated after June 1984 until the end of the study. B8402 was visually sighted during the 1984/85 winter survey.

Four radio-transmittered male elk, B8302, B8303, B8405 and SP8406 survived without transmitter failure, from the time of their capture until the termination of the study in February 1985.

Telemetry relocations provided data to calculate seasonal range size estimates, seasonal range fidelity and overlap, seasonal activity and dispersal for different radio-transmittered male elk.

Seasonal Range Use

Radio-transmittered male elk utilized lands in the military reserve and park and surrounding agricultural areas. Meaningful cohort range use comparisons are produced when transmittered elk are separated into those which were trapped on the military reserve from those which were captured in the park.

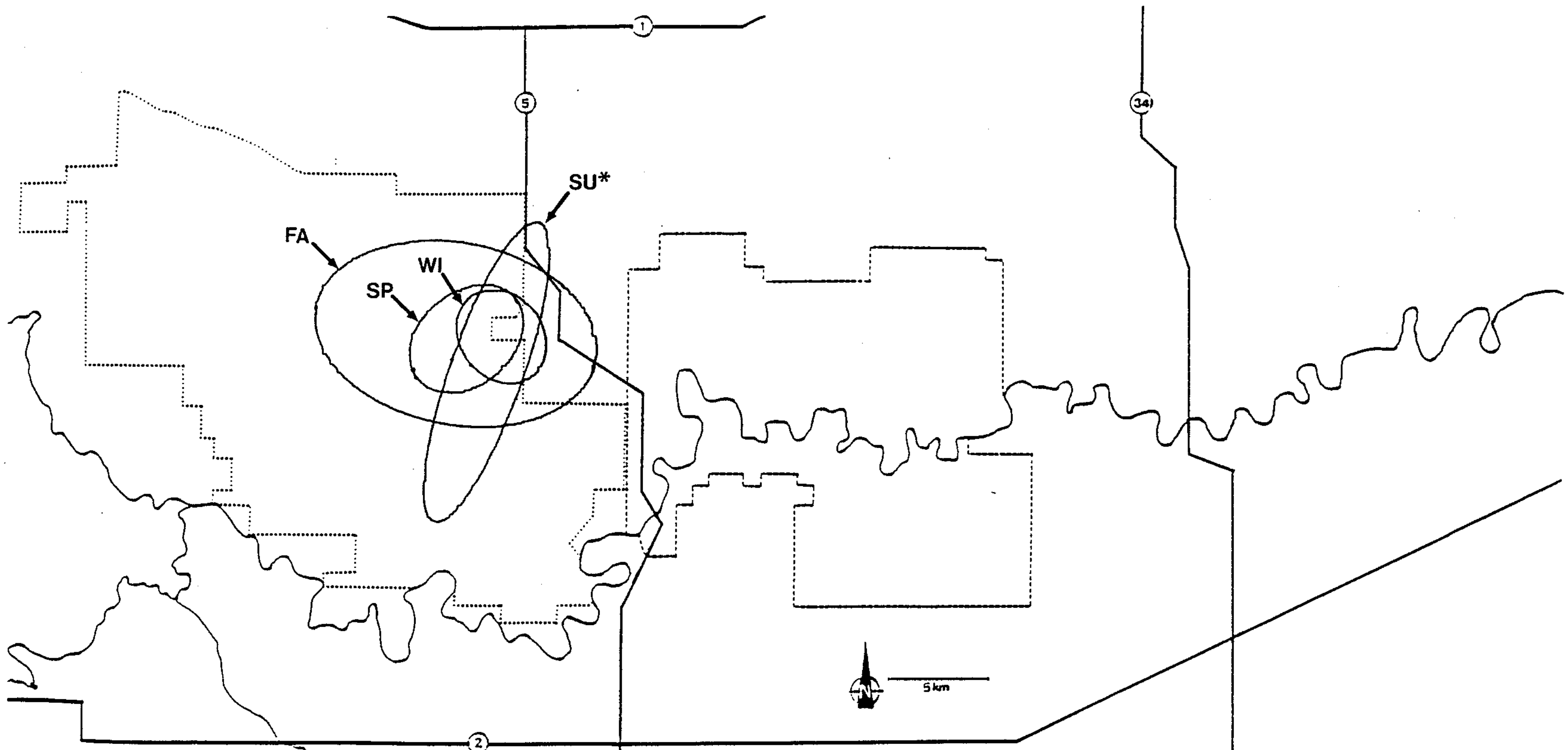
Mature male elk trapped on the military reserve extensively utilized the military reserve for most seasons. The 3 mature male elk (1633, B8301, B8302) which inhabited the military reserve were located infrequently outside the military reserve. Excursions made outside the military reserve were believed to be foraging trips to agricultural crops near the north and east boundaries of the military reserve. These males rarely were located outside the reserve during the fall. Mature male elk, on average had 88% of their seasonal relocations within the military reserve. Two mature male elk (1633 and B8302) were relocated for more than one year. Seasonal use of the military reserve by 1633 and B8302 were similar for both years.

All mature male elk extensively used the area north of and along the Epinette Creek in the northeast corner of the military reserve. This area was used in the spring, summer, winter and to a lesser extent in the fall. Three mature males (1633, B8301, B8302) had fall ranges which extended south of the Epinette Creek approximately 7 km to a large grassland plain where a large number of cows and calves inhabited during the fall. On several occasions 1633 and B8302 were both sighted holding harems in this area. Similar fall range use were repeated by 1633 and B8302 for both years monitored. Representative seasonal ranges of mature male elk trapped in the military reserve are illustrated by those obtained for B8302 in Figures 5 and 6.

Immature male elk captured on the military reserve undertook more frequent and extensive excursions outside the reserve than mature males. As well, seasonal range use had greater variation than mature males. Immature males were located outside the military reserve in spring, summer, fall and winter, though most winter relocations were within or near the northeast corner of the reserve.

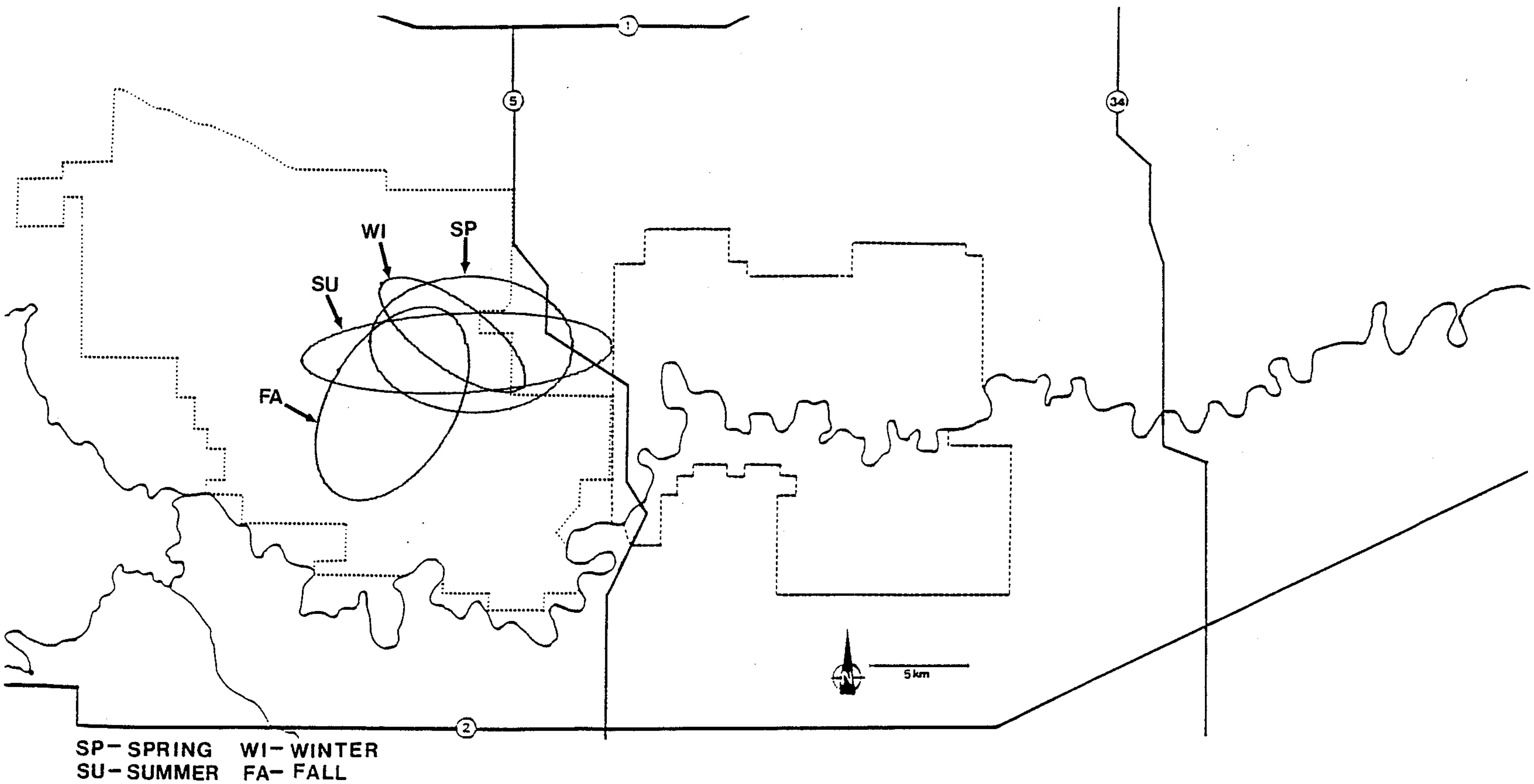
Immature male elk on average had only 50% of their seasonal relocations within the military reserve. When not located on the military reserve, immature males were found to the east on agricultural lands or in the

Figure 5. Seasonal range use of mature male elk B8302 in 1983.



SP– SPRING WI– WINTER
SU– SUMMER FA– FALL
* – Fewer than 9 relocations

Figure 6. Seasonal range use of mature male elk B8302 in 1984.


1
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SP- SPRING WI- WINTER
SU- SUMMER FA- FALL

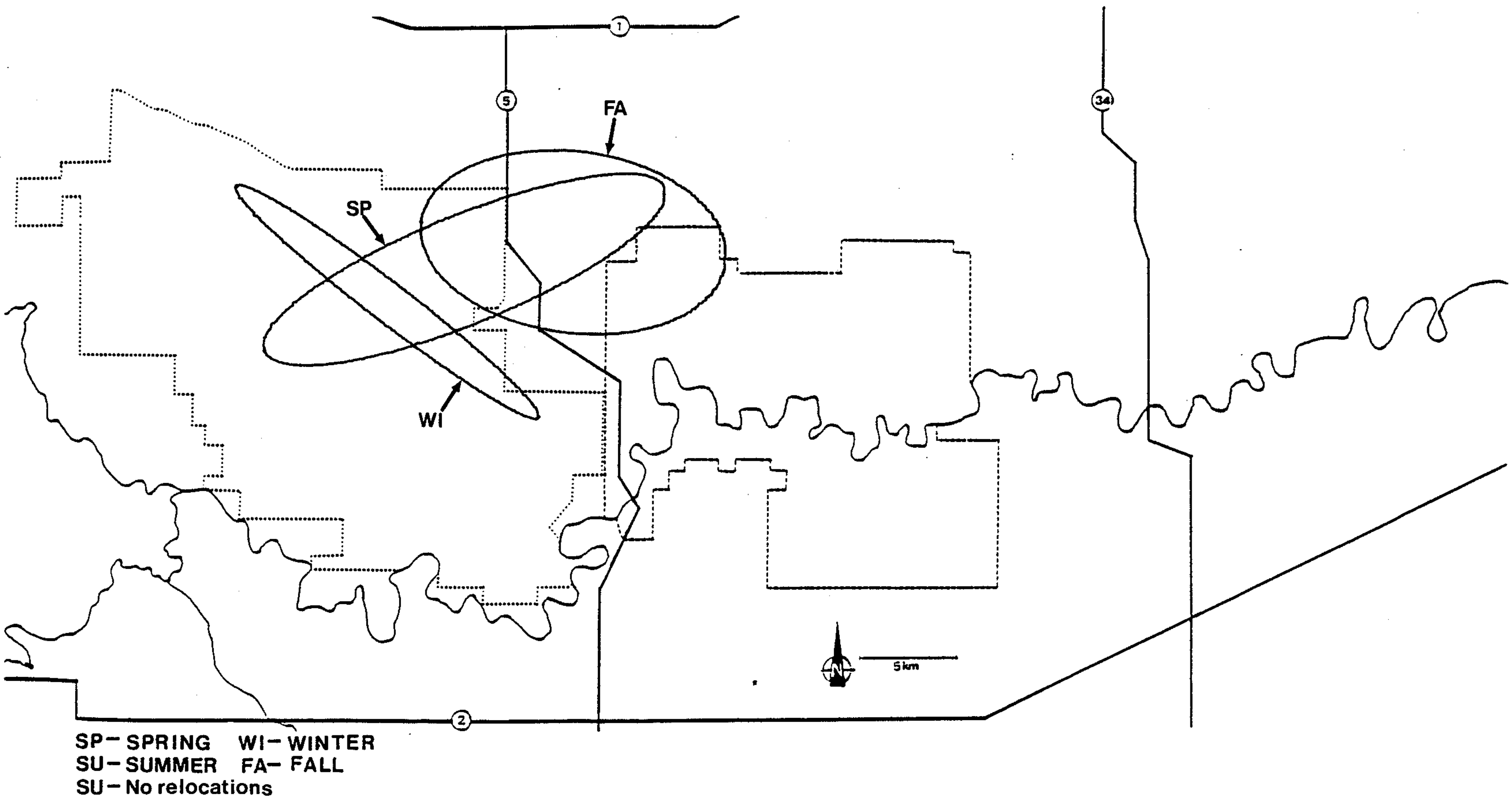
park. Two immature males (B8303 and SP8305) were observed feeding on corn, alfalfa and sunflowers east of the military reserve on several occasions. Only the seasonal ranges of B8303 and SP8305 will be discussed in detail. Seasonal ranges of these two elk illustrate the variation typified by the immature males.

Immature male B8303, had seasonal ranges in 1983 which incorporated the military reserve, surrounding agricultural lands and the park (see Figure 7). Seasonal range use by B8303 (5 years of age in 1984 and therefore graduated to mature status) in 1984, as illustrated in Figure 8, was similar to 1983. This elk followed the general pattern of wintering in the northeast corner of the military reserve and having a spring range which included agricultural lands east of the reserve. B8303 was located in the summer east of the reserve in agricultural lands and the park and had a fall range which included the summer and later its traditional winter range in the military reserve. In the fall of 1984, B8303 was observed tending a harem east of the military reserve.

Immature male elk SP8305, had a different pattern of seasonal range use than B8303. SP8305 had a large spring range in 1983 which included part of the military reserve, adjacent agricultural land and the park. This elk then had summer and fall ranges in the east side of the park. In 1983, SP8305 wintered in the park, approximately 25 km east of where it likely wintered in 1982 (see Figure 9). SP8305 was not transmittered during 1982 but was captured in the military reserve during the early spring of 1983 and therefore likely inhabited an area in the northeast corner of the military reserve in the winter of 1982/83.

In 1984, P8305 used summer and fall ranges (illustrated in Figure 10)

Figure 7. Seasonal range use of immature male elk B8303 in 1983.



1
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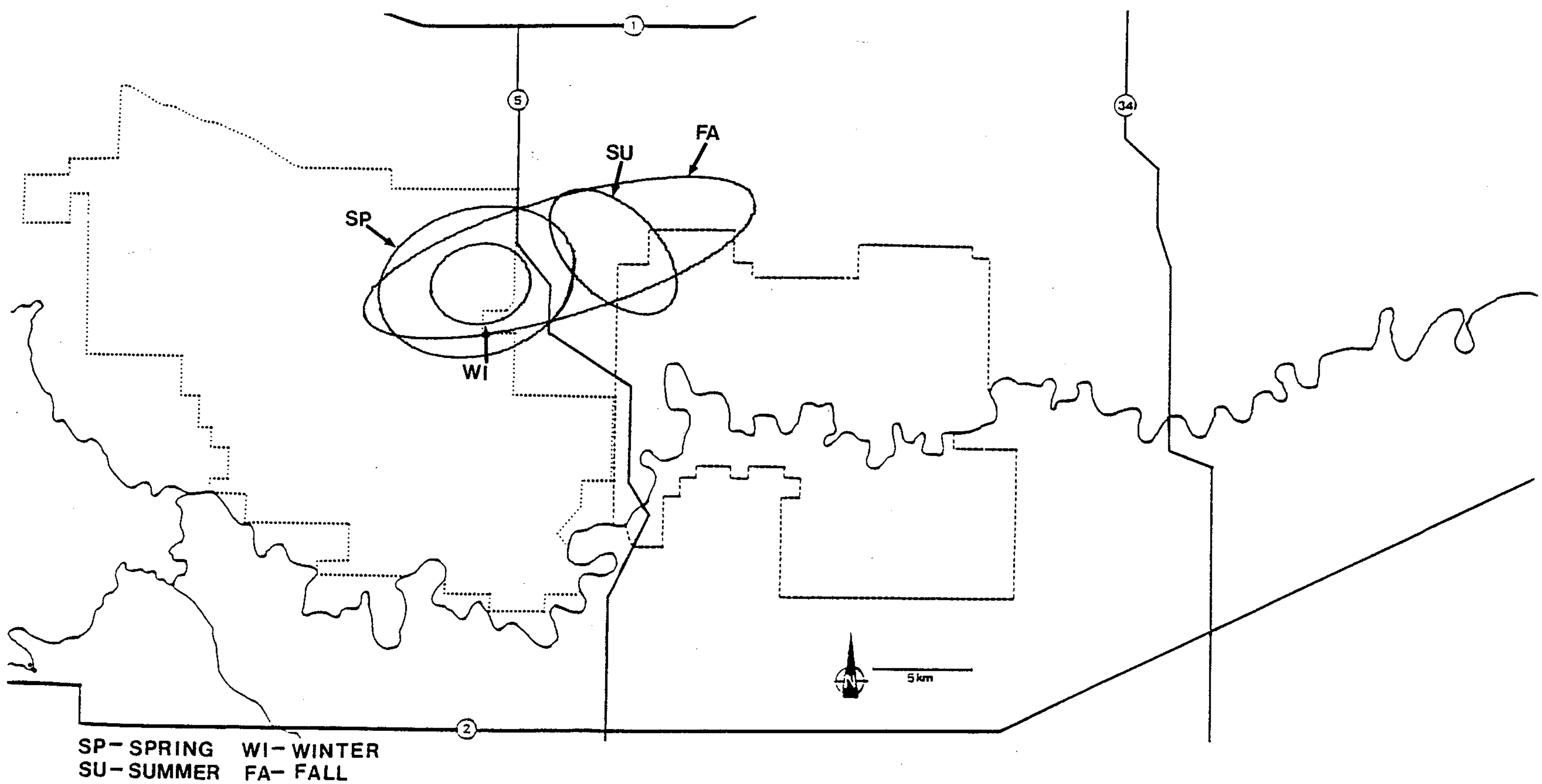
5km
N
SP– SPRING WI– WINTER
SU– SUMMER FA– FALL
SU– No relocations

Figure 8. Seasonal range use of mature male elk B8303 in 1984.



1
5
34
SU
FA
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WI
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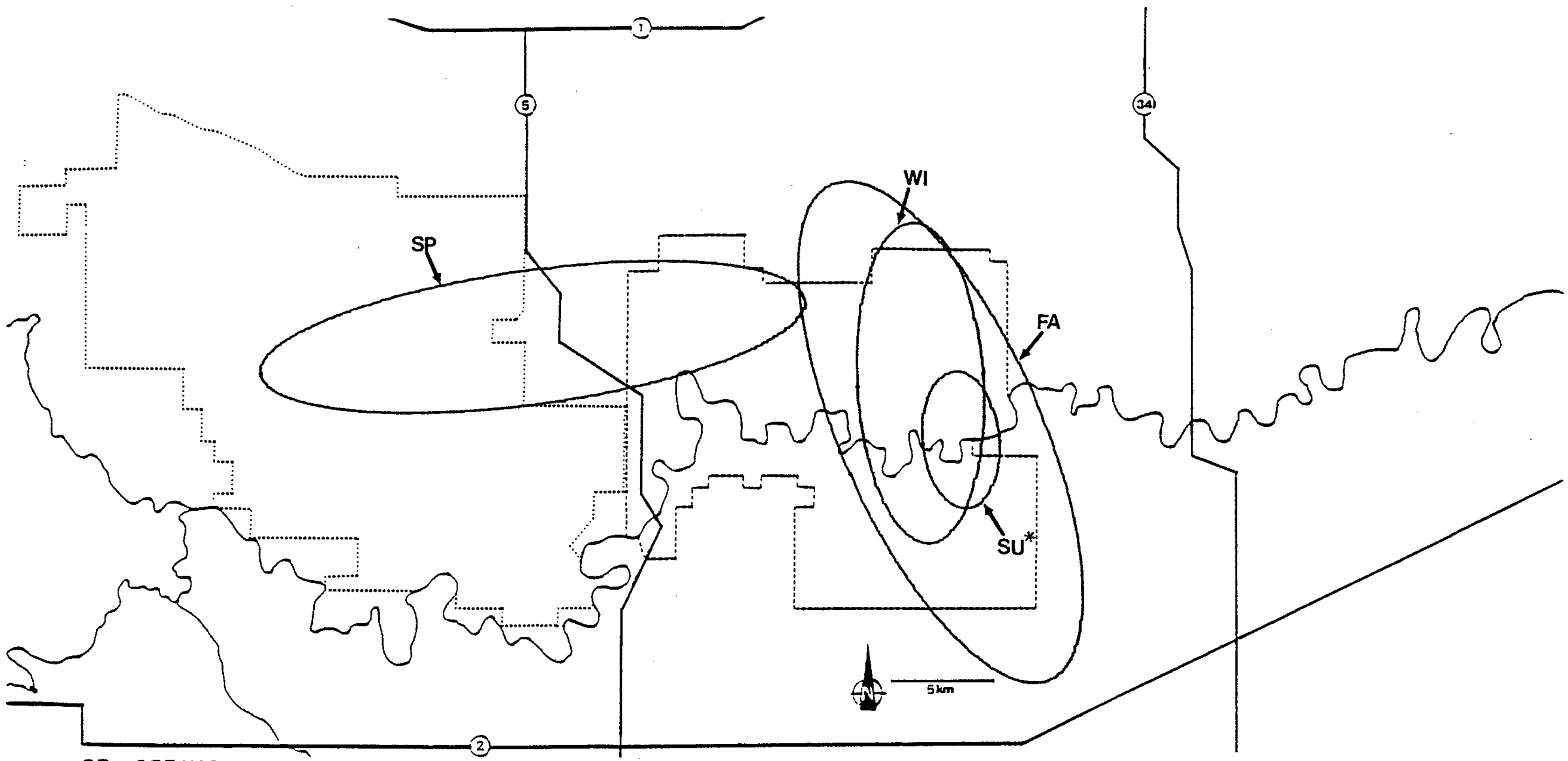
5 km
SP– SPRING WI– WINTER
SU– SUMMER FA– FALL

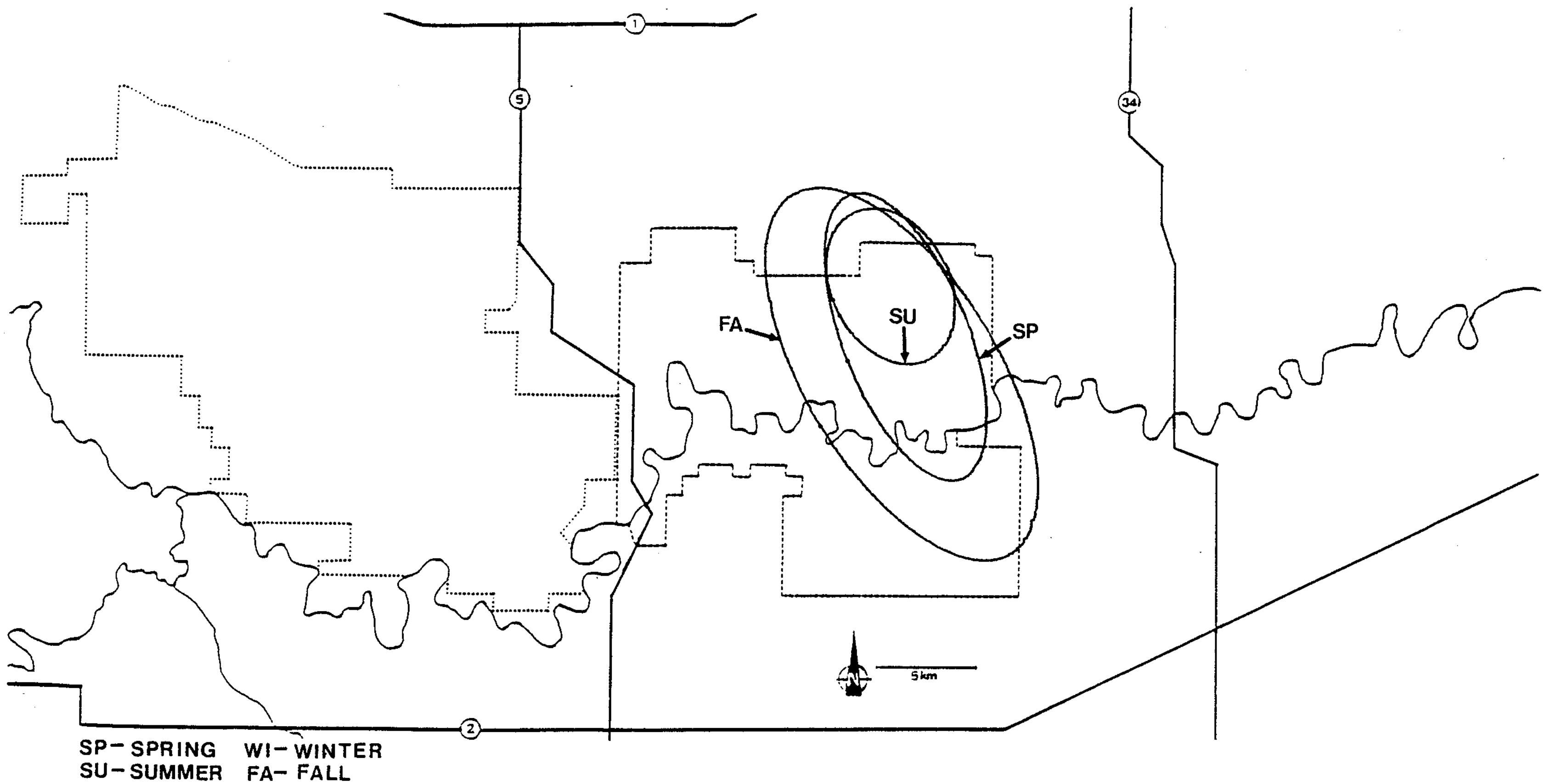
Figure 9. Seasonal range use of immature male elk SP8305 in 1983.



SP– SPRING   WI– WINTER
SU– SUMMER   FA– FALL

* – Fewer than 9 relocations

Figure 10. Seasonal range use of immature male elk SP8305 in 1984.



1
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SP- SPRING WI- WINTER
SU- SUMMER FA- FALL

similar to those of 1983. After leaving the military reserve in the spring of 1983, SP8305 did not return. In the fall of 1983 and 1984, SP8305 was observed tending small elk groups of cows and calves in the east side of the park during the breeding season.

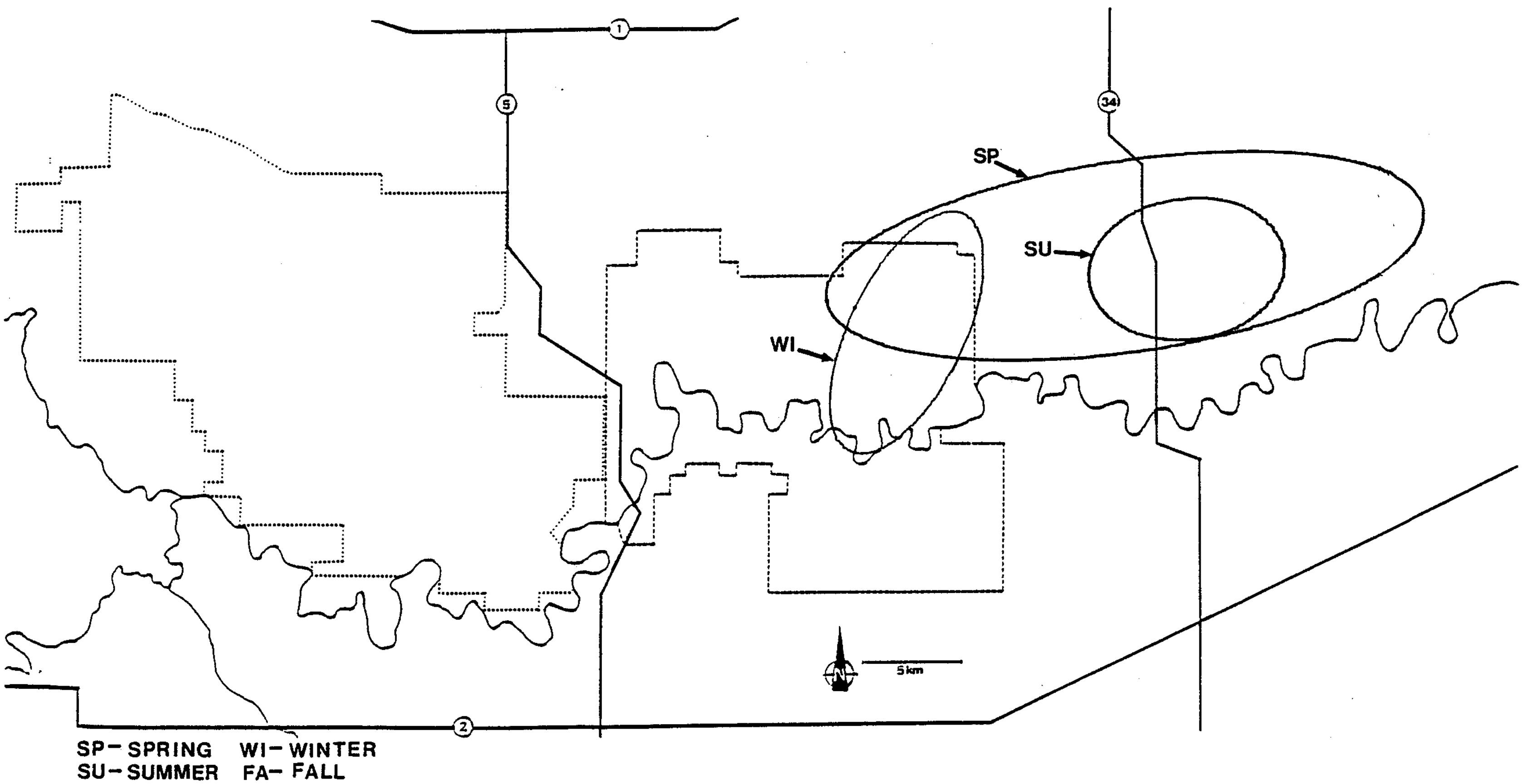
Male elk captured in the north block of the park used lands in the park and on surrounding agricultural lands. The 4 immature male elk (SP8401, SP8403, SP8404, B8402, 3 spike-antlered males and 1 branch-antlered male, respectively) had similar seasonal range use. All 4 male elk had winter ranges within the northeast corner of the park in 1983. During the spring of 1984, all 4 males moved approximately 11 km east of the park and established summer ranges north and east in areas close to agricultural crops including corn, alfalfa, fall rye and sunflowers. Three males (SP8401, B8402 and SP8403) had summer ranges in 1984 approximately 13 km east of the park in an area of leased Crown and private lands. In the fall of 1984, only SP8401 returned to the east side of the park (Figure 11).

Radio-transmitter failure occurred with B8402 in the late summer of 1984. B8402 was observed during the 1984/85 winter where it had summered in 1984, approximately 13 km east of the park. SP8403 had spring and summer ranges east of the park (as illustrated in Figure 12) and was later shot in early September east of the park before a fall range could be determined.

SP8404 had a large summer range north and east of the park. This elk returned to the park in the fall of 1984.

Seasonal range use patterns of transmittered elk which inhabited areas east of the park were supported by comments made by landowners living east and north of the park. Several landowners complained that elk had

Figure 11. Seasonal range use of immature male elk SP8401 in 1983 and 1984.


1
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34
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SP
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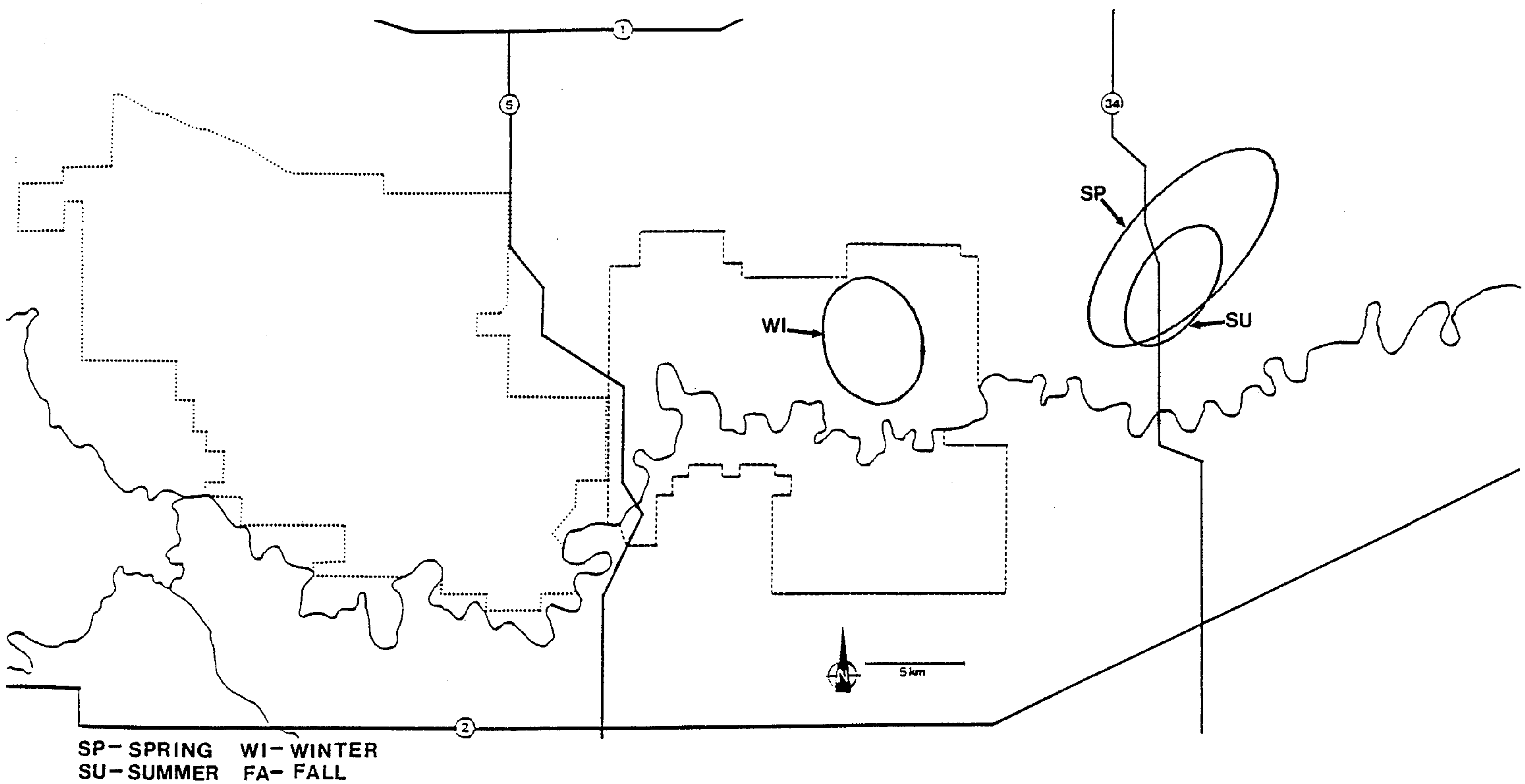
SP- SPRING WI- WINTER
SU- SUMMER FA- FALL

Figure 12. Seasonal range use of immature male elk SP8403 in 1983 and 1984.


1
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34
SP
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5 km
2
SP- SPRING WI- WINTER
SU- SUMMER FA- FALL

fed on their crops during the summer and early fall then moved out before the they had the opportunity to hunt them during the landowner season. As well, most of the elk reported by landowners feeding in agricultural fields east of the park were males.

Seasonal Range Comparisons

Seasonal range areas of radio-transmittered male elk cohorts were compared. A list of mean seasonal range size estimates calculated by the Jennrich-Turner Index and the Mohr's Minimum Area Polygon estimate for various male elk cohorts are presented in Table 6. Individual seasonal range size estimates for radio-transmittered elk are presented in Appendix 5.

Male elk cohorts had large spring and fall ranges and smaller summer and winter ranges (Table 6). Fall and spring ranges for immature male elk were significantly larger than winter ranges (131.7 km^2 vs 34.3 km^2, $\underline{U} = 0$, $\underline{P} = 0.016$; 114.8 km^2 vs 34.3 km^2, $\underline{U} = 5$, $\underline{P} = 0.003$, respectively). All other seasonal ranges for immature male elk were not statistically different (spring vs fall, $\underline{U} = 16$, $\underline{P} = 0.622$; spring vs summer, $\underline{U} = 12$, $\underline{P} = 0.284$; summer vs fall, $\underline{U} = 6$, $\underline{P} = 0.222$; summer vs winter, $\underline{U} = 12$, $\underline{P} = 0.284$).

Seasonal range size differences for mature males were similar to those for immature males. Fall ranges were significantly larger than winter (80.2 km^2 vs 21.4 km^2, $\underline{U} = 0$, $\underline{P} = 0.016$). All other seasonal ranges comparisons were not significantly different (spring vs summer, $\underline{U} = 4$, $\underline{P} = 0.393$; summer vs winter, $\underline{U} = 6$, $\underline{P} = 0.786$) though spring vs fall, spring vs winter and fall vs summer range comparisons approached statistical significance and may have been so with larger samples (42.4

Table 6. Seasonal range area estimates of male elk cohorts by the Jennrich-Turner Index and Mohr's Minimum Area Polygon methods.

Male Cohort	Season	N	J.T. Index (km^2) Mean	SDV	Range	Mohr (km^2) Mean	SDV	Range
Immature								
	Spring	8	114.8	68.59	36.5-232.5	50.9	32.69	18.5-104.9
	Summer	5	84.4	102.19	20.0-265.7	29.3	29.34	8.8- 80.9
	Fall	5	131.7	56.74	48.7-198.7	48.0	19.14	27.4- 74.2
	Winter	8	34.3	22.68	16.0- 78.9	13.4	10.06	5.8- 35.0
Mature								
	Spring	5	42.4	15.21	22.3- 58.6	23.5	12.21	9.0- 37.9
	Summer	3	28.8	18.72	11.1- 48.4	8.6	4.16	3.9- 11.8
	Fall	4	80.2	21.18	52.7- 98.7	29.3	13.17	17.8- 41.3
	Winter	5	21.4	8.21	15.9- 35.2	9.5	5.34	5.3- 18.6
Yearling								
	Spring	0	----	---	---------	---	----	---------
	Summer	0	----	---	---------	---	----	---------
	Fall	1	26.8	---	---------	9.5	----	---------
	Winter	1	89.0	---	---------	31.5	----	---------

vs 80.2, $\underline{U} = 2$, $\underline{P} = 0.064$; 42.4 vs 21.4, $\underline{U} = 3$, $\underline{P} = 0.056$; 80.2 vs 21.4, $\underline{U} = 0.0$, $\underline{P} = 0.057$).

A similar pattern in seasonal range areas was not demonstrated by the single yearling male which was radio-transmittered. The yearling male had a larger winter (89.0 km^2) than fall (26.8 km^2) range. This male was monitored for less than one year and therefore seasonal range size estimates for all seasons were not obtained.

Generally, immature males had larger ranges in all seasons than mature males. Mature male elk range size estimates for all seasons were less than 65% the size of corresponding immature male elk seasonal ranges. The difference between paired seasonal range comparisons for corresponding seasons of both cohorts was significant for spring (103.6 km^2, immature vs 67.7 km^2, mature, $\underline{U} = 4$, $\underline{P} = 0.019$) but not significantly different for summer (84.4 km^2 vs 28.8 km^2, $\underline{U} = 4$, $\underline{P} = 0.393$), fall (131.7 km^2 vs 80.0 km^2, $\underline{U} = 4$, $\underline{P} = 0.191$) or winter (34.3 km^2 vs 21.7 km^2, $\underline{U} = 11$, $\underline{P} = 0.222$). The yearling male's fall range (26.8 km^2) was smaller than respective immature (131.7 km^2) and mature (80.2 km^2) fall ranges. The yearling male elk's winter range was larger than immature (34.3 km^2) and mature (21.7 km^2) male winter ranges.

Differences between seasonal range size estimates between 1983 and 1984 could not be tested statistically because of the small sample sizes for both cohorts between seasons for each year. Trends were evident between years for mature males (Table 7). Mature male elk had similar spring ranges in both years (56.7 km^2 vs. 40.5 km^2, 1983 and 1984 respectively). Summer and fall ranges between years were approximately equal (summer, 29.8 km^2 vs. 26.9 km^2, fall 83.1 km^2 vs. 96.8 km^2, 1983 and 1984, respectively). Winter ranges for 1983 were larger than 1984

Table 7. Seasonal range area estimates of mature male elk by the Jennrich-Turner Index and Mohr's Minimum Area Polygon methods for 1983 and 1984.

			J.T. Index (km^2)			Mohr (km^2)		
Year	Season	N	Mean	SDV	Range	Mean	SDV	Range
1983								
	Spring	4	56.7	27.36	31.9-95.3	26.4	10.28	12.9-37.9
	Summer	2	29.8	26.45	11.1-48.5	7.9	5.57	3.9-11.8
	Fall	2	83.1	42.99	52.7-113.5	24.9	9.97	17.8-31.9
	Winter	2	26.6	5.52	22.7- 30.5	11.0	1.63	9.8-12.1
1984								
	Spring	2	40.5	25.67	22.3- 58.6	20.0	15.49	9.0-30.9
	Summer	1	26.9	-----	----------	10.1	-----	--------
	Fall	2	96.8	2.76	94.8-98.7	40.7	0.85	40.1-41.3
	Winter	2	15.9	0.00	15.9-15.9	7.5	0.00	7.5- 7.5

(26.6 km^2 vs. 15.9 km^2). The larger winter range in 1983 may reflect the unseasonably mild conditions and little snow cover during this year.

Distance Between Successive Relocations

Differences in distances travelled between successive relocations for various male elk cohorts closely paralleled differences between cohort seasonal range sizes (compare Table 6 and Table 8).

Generally, male elk travelled greater distances in spring and fall than in summer and winter. Mean seasonal distances between locations for mature male elk were 1.9 km in spring, 2.3 km in fall, 1.9 km in summer and 1.8 km in winter. For immature male elk, mean seasonal distances between locations were 4.9 km in spring, 2.9 km in fall, 2.3 km in summer and 1.9 km in winter.

Immature males likely underwent searches in the spring to establish summer ranges with adequate water and forage. In the fall, searches for mating opportunities likely were reflected in the large distances travelled between relocations. The smallest distances between relocations for both immature and mature cohorts were in the winter when energy expenditure during travel is greatest. Distances travelled by the yearling male between locations in the fall and winter were similar in length.

Immature male elk travelled greater distances between relocations in all seasons when compared to mature male elk. Table 8 shows the comparison of movements between immature and mature male elk respectively for spring (2.9 km vs. 2.3 km), summer (2.3 km vs. 1.9 km), fall (2.9 km vs. 2.3 km) and winter (1.9 km vs. 1.7 km). Only the difference between spring ranges was significantly different ($\underline{t}$ = 2.77,

Table 8. Seasonal variation in distances between successive relocations for male elk cohorts.

Male Cohort	Season	N	Mean	SDV	Range
	Distances between sucessive relocations (km)				
Immature					
	Spring	171	4.8	12.96	0.00-17.90
	Summer	84	2.3	2.05	0.30-15.98
	Fall	84	2.9	2.43	0.10- 9.60
	Winter	102	1.9	1.48	0.00- 8.98
Mature					
	Spring	148	1.9	1.42	0.10- 8.49
	Summer	39	1.9	1.49	0.20- 8.68
	Fall	59	2.3	1.81	0.24-10.02
	Winter	97	1.8	1.16	0.14- 6.41
Yearling					
	Spring	0	---	----	----------
	Summer	0	---	----	----------
	Fall	15	1.6	----	----------
	Winter	13	1.5	----	----------

$\underline{P} < 0.001$). Differences between means of seasonal distances travelled by immature male elk and mature male elk are similar to those differences between means of seasonal range sizes between the two cohorts. Immature males compared to mature males, may be unfamiliar with their seasonal ranges and therefore undertake more frequent and extensive exploratory excursions particularly during the spring.

The yearling male elk had the shortest distances between locations for fall (1.6 km) and winter (1.5 km) of any cohort. The small sample of this cohort prevented statistical comparisons with other cohorts.

No physical obstacle in the study area appeared to restrict elk movement. Radio-transmittered elk crossed highways, railway tracks, open fields, swamps and rivers during the study.

Seasonal Range Stability and Fidelity

Seasonal range shifts (distances between consecutive seasonal range activity centers) were calculated for individual radio-transmittered male elk, (see Appendix 6).

Immature males generally had seasonal ranges which were farther apart than mature males. This was evident when distances between seasonal activity centers were compared (see Table 9). Immature males had larger shifts between activity centers than mature male elk between winter to spring, spring to summer, and fall to winter seasons, though only the distance between spring to summer activity centers (5.78 km vs. 3.04 km immature and mature cohorts, respectively) were significantly different ($\underline{P} < 0.05$). Small sample sizes for summer to fall and fall to winter distances likely prevented statistical cohort differences of these shifts. Distances between summer to fall ranges were similar for both

Table 9. Distances between successive seasonal range activity centers for male elk cohorts.

Male Cohort	Distances between successive seasonal activity centers (km)				
	Season	N	Mean	SDV	Range
Immature					
	Winter/Spring	5	9.41	6.279	2.15-16.63
	Spring/Summer	6	5.78	7.938	0.95-21.83
	Summer/Fall	4	3.50	2.069	1.07- 5.91
	Fall/Winter	3	4.37	4.918	0.74- 9.97
Mature					
	Winter/Spring	5	1.87	1.441	0.35- 4.110
	Spring/Summer	3	3.04	3.466	0.86- 7.04
	Summer/Fall	2	3.44	0.948	2.77- 4.11
	Fall/Winter	3	3.66	1.232	2.26- 4.57

cohorts (3.50 km vs 3.44, immature and mature cohorts, respectively).

Activity center shifts for consecutive seasonal ranges of immature males varied between seasons. Differences in seasonal range shifts were not demonstrated by mature male elk. Immature males appeared to have greater shifts from winter to spring (9.41 km) than spring to summer (5.78 km), fall to winter (4.37 km) or summer to fall (3.50 km), though no comparison (with adequate sample sizes) was significantly different. Seasonal variation in distances between seasonal ranges were not significantly different for mature males though the distance between winter and spring ranges were smaller than other shifts (see Table 9).

Only 2 mature male elk (B8302 and B8303) and one immature male elk (SP8305) had seasonal ranges which were determined for more than one year and could be used for comparisons of traditional range use.

The mature males demonstrated greater seasonal range fidelity than the immature male. Mean distances separating consecutive yearly spring, fall and winter range activity centers for mature male cohorts were 0.68 km (SD = 0.26), 3.15 km (SD = 2.23) and 2.54 km (SD = 1.54), respectively (see Table 10). The distances between consecutive ranges for spring and winter were less than those for fall and summer. The distance between consecutive yearly seasonal range activity centers for the immature male elk were 19.10 km, 7.79 km and 2.75 km for spring, summer and fall ranges, respectively.

Seasonal range overlap between years was also used to determine range use fidelity. Mature male elk reused parts of seasonal ranges in consecutive years more often than immature male elk. Eighty-six percent ($\underline{n}$ = 6) of the seven successive seasonal range pairs compared for mature males had some overlapping range use between years. Only 33% ($\underline{n}$ = 1) of

Table 10. Distances between seasonal range activity centers of successive years for male elk cohorts.

Male Cohort	Distances between seasonal activity centers (km) Season	N	Mean	SDV	Range
Immature					
	Spring/Spring	1	19.10	-----	---------
	Summer/Summer	1	7.79	-----	---------
	Fall/Fall	1	2.75	-----	---------
	Winter/Winter	0	----	-----	---------
Mature					
	Spring/Spring	2	0.68	0.255	0.50-0.86
	Summer/Summer	0	----	-----	---------
	Fall/Fall	2	3.15	2.227	1.57-4.72
	Winter/Winter	3	2.54	1.537	1.30-4.26

the three seasonal range pairs compared for the immature males had overlapping ranges between years. No data was available for distances between activity centers of successive summer ranges for mature males or winter ranges for immature males.

A subjective evaluation of all relocation data for mature male elk supports traditional range use. No mature male demonstrated major shifts of seasonal ranges between years. All were frequently located seasonally in the same area in consecutive years. To illustrate, B1633 was monitored from the fall of 1980 to the fall of 1983. B1633 was located in the same areas for all seasons each year it was monitored. Fidelity of seasonal range use was most pronounced by extensive range overlap for the winters this male elk was monitored. The area north of the Epinette Creek ridge in the military reserve was repeatedly used as a wintering area for B1633. B1633 returned to this wintering area in each year which it was monitored from areas occupied to the south during the rut.

Dispersal of Radio-Transmittered Elk

Strong evidence for dispersal movements was demonstrated by radio-transmittered immature male elk. No transmittered mature male undertook what could be considered a dispersal movement. All dispersal movements undertaken by males, whether they originally inhabited the military reserve or the park, were towards the east and northeast.

One immature elk (SP8305) trapped on the military reserve, travelled (approximately 25 km east) to the park in the spring of 1983. All subsequent relocations of this elk were in the east side of the park. The initial dispersal movement by SP8305 was undertaken in the spring.

Immature branch-antlered male B8402 likely underwent a dispersal movement. In the spring of 1984, this elk travelled to an area approximately 15 km east of where it had wintered in the park in 1983. All following relocations, including two winter observations in 1984, were east of the park. Radio-transmitter failure allowed only 5 relocations of B8402 after June 1984 and prevented definitive seasonal range determination.

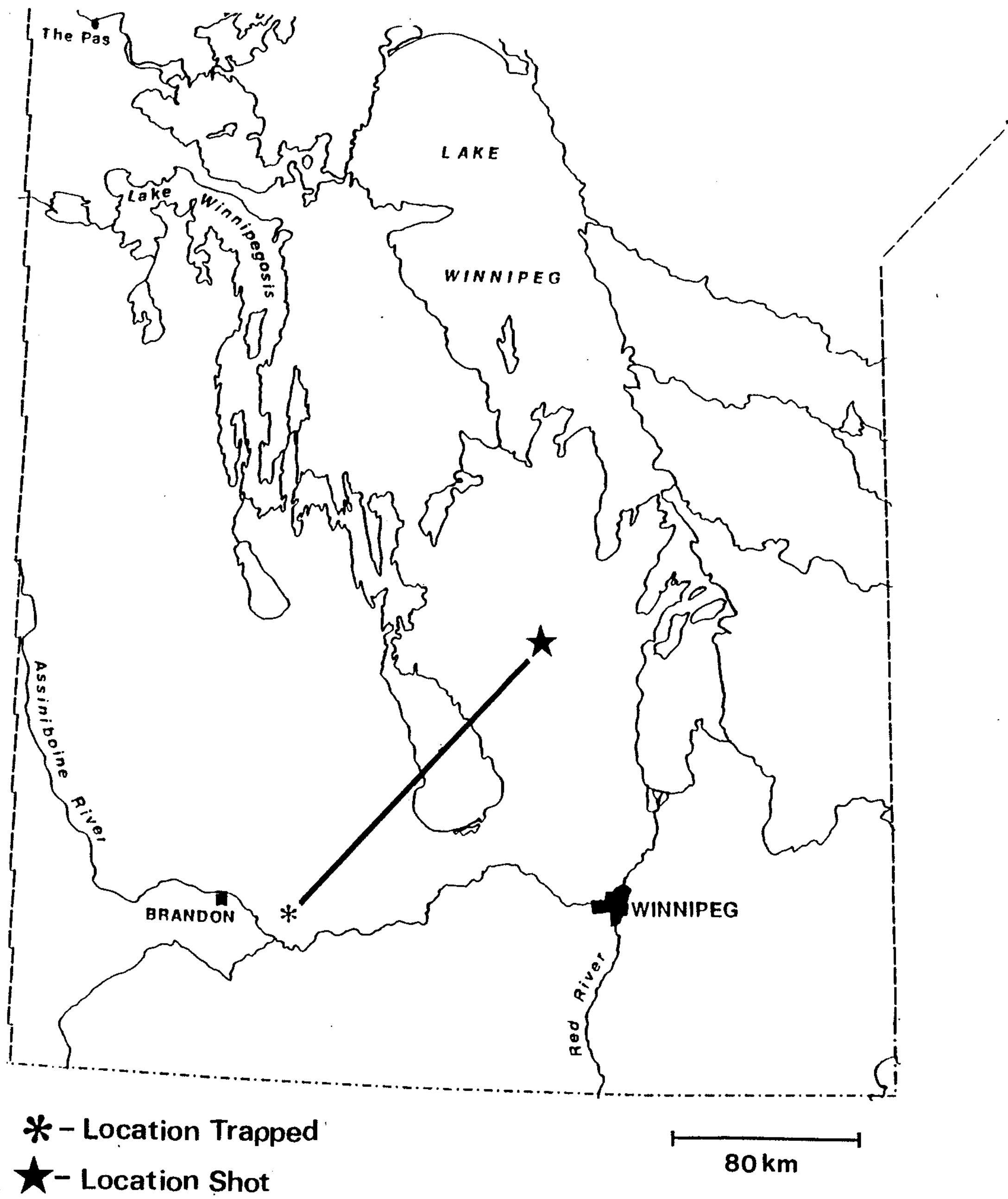
One male elk which had been radio-transmittered by Strong (1981) as a calf (0.5 years of age) on the military reserve in 1979, was harvested by a hunter at Fisher Branch, Manitoba in 1981. This elk was shot approximately 200 km northeast of where it had been captured, an extensive dispersal movement undertaken while the male was immature (see Figure 13). Radiotransmitter contact was lost soon after its capture and therefore the time, route and duration of this movement was not determined.

Survival of Radio-Transmittered Elk

Mortality of radio-transmittered male elk was high. Only 5 of the 11 males monitored survived to the end of the study. Four male elk which survived, were monitored for less than one year after being captured.

Of the 6 transmittered males which succumbed, 33% (*n* = 2) were harvested by landowner hunters and 66% (*n* = 4) were suspected to have been shot illegally or harvested by Indian hunters. All 4 radio-transmittered elk which were suspected to have been shot illegally or harvested by Indian hunters were last relocated in the fall between September and November. This period coincided with the time at which the majority of the poaching activity and Indian hunting occurred in the

Figure 13. Dispersal movement of a radio-transmittered immature male elk.


The Pas
LAKE
WINNIPEG
Lake Winnipegosis
Assiniboine River
BRANDON
WINNIPEG
Red River
* - Location Trapped
★- Location Shot
80 km

study area and also the elk breeding season.

Unfortunately, the cause for the disappearance of transmittered elk that were illegally shot is only speculative. Poachers were known to conceal their activities. The neck collar with radiotransmitter of a male elk monitored by Strong (1981), was buried by the poacher who shot the elk. The poacher feared that the radio transmitter would lead Natural Resource Officers to convict him for illegally shooting the elk. This incident would have been unknown without the right informant contacts. Radiotransmitters from elk which were suspected to have been poached in this study may also have been hidden.

Survival of transmittered male elk which had seasonal ranges in the military reserve was greater than those elk which inhabited the park and surrounding private and Crown lands. Sixty-seven percent (n = 4) of the 6 male elk which had seasonal ranges which included parts of the military reserve survived to the end of the study. Two of these elk had been monitored for 24 months. One elk (B1633) which inhabited the military reserve was found dead from a suspected poaching incident after being radio-transmittered for 43 months.

In contrast, only 1 of the 5 male elk which had seasonal ranges outside the military reserve survived to the end of the study. Generally, these elk inhabited the eastern half of the study area and had seasonal ranges within the park and on private and Crown lands. Two of these elk were harvested by landowner licensees and two were suspected of being poached. Of these 5 elk, only one (SP8305) had been monitored for more than 12 months.

The differential survivorship between radio-transmittered elk was likely a result of restricted public access on the military reserve.

Poaching

Poaching of elk took place in the study area. Poaching complaints were reported throughout the year though most poaching incidence occurred between July and December.

The prevalence of poaching in the study area was assessed in a telephone interview of local landowners. Fifty-nine percent ($\underline{n}$ = 37) of the 62 landowners who purchased a landowner elk licence in 1983 replied that poaching was a problem in their area. This information was based on a sample of 71% ($\underline{n}$ = 62) of landowner elk licensees.

The high incidence of poaching, as suggested from the interviews of landowners, was not reflected in the Natural Resources Officer's convictions. Local Natural Resource Officers concentrated their patrol effort during the night when the chances of apprehending a violator were aided by aircraft spotters. The spotters were guided by the lights of poachers to the location of the infraction. The likelihood of intercepting a poacher during the daylight hours was hampered by the ease at which poachers could conceal their activities during the day.

Comments made by local people to Natural Resource Officers suggested that most poaching occurred at dawn and dusk. Traffic occurrence data collected by a traffic counter concealed along an access road in the north block of the park in the fall of 1984 supported this. Most the traffic activity recorded, which could not be attributed to the travels of parks personnel, occurred just before and after sunset, (see Appendix 7). Few vehicles crossed the counter during the night or early morning.

Information on 81 elk poached in the study area between 1979 and 1985 was collected. The proportion of poaching incidents that were reported to Natural Resource Officers was not determined; therefore, an estimate of the total number of elk poached during the study could not be determined.

Poaching took place on the military reserve, the park and on surrounding private and Crown lands. Elk sightings reported in the extensive study area by local people frequently were accompanied by a comment of concern about the safety of the elk.

Poaching occurred mostly on private land. The location of 47 poaching incidents were determined of which 55% ($\underline{n}$ = 26) and 45% ($\underline{n}$ = 21) occurred on private land verses on the military reserve and park, respectively. Poaching on the military reserve was deterred by military personnel who regularly patrolled the reserve. The park was only periodically patrolled by Natural Resource Officers.

The illegal kill was bias favouring the harvest of male elk. The sex of 77 elk poached between 1979 and 1985 was 61% ($\underline{n}$ = 47) males and 39% ($\underline{n}$ = 30) antlerless elk, respectively. The male to antlerless elk ratio of poached elk was 157:100 ($\underline{n}$ = 77) and significantly larger than the pooled male to antlerless elk ratio of 18:100 ($\underline{n}$ = 2699) calculated from the annual winter aerial surveys between 1979 and 1985 ($\underline{X}^2$ = 110.37, df = 1, $\underline{P}$ < 0.001).

Candid conversations with local people who had poached elk or had the opportunity to poach elk supported this finding. One local farmer commented that while hunting deer he had the good fortune to observe a group of cows and calves at close range and did not indicate he would have liked to shoot one. The same man criticized his son two days later for not illegally shooting a large branch-antlered male elk he had surprised while deer hunting. Another local farmer indicated that he did not have a preference for any sex of elk but wanted to poach as close to his farm as possible. Elk which inhabited areas close to this farmer's yard were usually males.

The bias in poaching favouring male elk may stem from the belief of many local people that by taking a bull, poachers have a minimal effect on the reproductive potential of the elk herd and are therefore not "really harming" the population. Some poachers defend their activities with this argument.

Approximately 40% of the 27 poaching incidents which the date of the occurrence was known occurred between September 1 and October 30, approximating the breeding season. A male to antlerless elk ratio of 300:100 ($\underline{n}$ = 12) was recorded for elk poached during the rut. This ratio was larger than the ratio determined for elk poached during the rest of the year (88:100, $\underline{n}$ = 15) though the difference was not significant ($\underline{X}^2$ = 1.20, df = 1, $\underline{P}$ = 0.276). Male elk may be more susceptible to being poached during the breeding season than cows and calves because of their level of activity, large range size and responses to commercial elk calls.

Indian Harvest

Treaty Indians from several reserves hunted elk in the Spruce Woods area. Most Indian hunters were from 5 local reserves but Indians from reserves as far away as Anama Bay, Manitoba and White Dog, Ontario were observed hunting elk in the study area.

Indians had the right to pursue elk on unoccupied Crown land in the study area which included undeveloped park land and surrounding leased Crown land. Access by Indians on the military reserve for hunting had been restricted to the elk and deer hunting seasons. Indians could not hunt on private land where access was denied. Indians hunted throughout the study area but concentrated their efforts in the park, with the north block of the park receiving the most use.

Phone interviews revealed that 16 elk were reported taken in 1983 by members of 3 bands. The sex ratio for harvested elk was estimated by band leaders as approximately 50:50. Reports of elk harvested by Indians from local people and Natural Resource Officers suggested this estimate was low.

A repeat telephone interview in 1984 of 5 local Indian bands was met by requests from band leaders to provide a letter to each council outlining the questions to be addressed. Responses were not received from the 5 bands contacted even after follow-up phone contacts were made.

Information on sex-age composition of elk which were harvested by Indians in the study area between 1979 and 1985 were collected from Natural Resource Officer reports and local people. A male to antlerless elk ratio of 133:100 ($\underline{n}$ = 31) was calculated from the pooled data collected on the elk harvested by Indian hunters. This ratio was significantly larger than the composite male to antlerless elk ratio of 18:100 ($\underline{n}$ = 2699) calculated from the annual winter aerial surveys between 1979 and 1985 ($\underline{X}^2 = 27.95$, df = 1, $\underline{P} < 0.001$) and suggests a male bias Indian harvest.

The bias Indian harvest was supported also by observations made by bow hunters in the park who saw Indian hunters using the bugling of male elk to key in on areas to hunt. Three hunters remarked that while they were in tree stands using a commercial male elk call to attract elk, Indian hunters approached their stands in anticipation of stalking a bull. Conversations with Indian hunters suggest that they were opportunistic and did not specifically select one sex of elk over another. The activity of male elk, their bugling during the rut, and the areas in which Indians hunted may have made male elk more susceptible to being harvested than cows and calves. This would account for the large portion male elk represented in the Indian harvest.

DISCUSSION

Aerial Surveys

Previous studies by Hornbeck (1979) and Strong (1981) had conducted winter aerial surveys of the Spruce Woods elk herd and estimated a population of between 500-900 individuals. Hornbeck (1979) calculated a population high of 919 elk in 1979 from a quadrate-type survey. Strong (1981) stated that from minimum population estimate counts the Spruce Woods elk population was 600-700 individuals between 1978 and 1980. Following the completion of those studies, continued annual winter survey were conducted and the results had suggested a population decrease (L. Bidlake, Manitoba Wildlife Branch, pers. commun.). Winter aerial surveys undertaken during this study found that by 1985 this population had decreased to 289 elk. Two areas of satellite habitat adjacent to the intensive study area were flown in 1985 as a precaution to enumerate individuals which may have undertaken a major movement out of the study area and not been observed in previous surveys. Only one additional elk was observed during these surveys.

Several authors report that male elk and red deer are frequently observed in smaller groups than cows and calves during most of the year and that this difference becomes most pronounced in the winter (Knight 1970, Flook 1970, Mitchell et al. 1977, Rounds 1980, Houston 1982). Hornbeck (1985) and Strong (1981) found that this social grouping behaviour also occurred in the Spruce Woods population. Strong (1981) stated that cow elk were commonly in groups of more than 20 individuals while bulls were solitary or in small groups except during the rut. Since group size effects the visibility bias as indicated by Samuels et al. (1987), previous aerial surveys which did not account for this bias could, therefore, have theoretically underestimated the male segment of the population.

Winter aerial survey results from this study have shown that male elk were found in smaller groups of elk during the winter than antlerless elk. However the survey method did not miss a significant number of elk in small groups (5 or fewer individuals) and underestimate the number of males in the population. The survey technique therefore did not contribute to the skewed sex ratio when surveys were undertaken during good survey conditions.

Survey crews missed a significant number of radio-transmittered male elk when little snow was present which hampered observability as in 1984. During the winter survey of 1985, which was conducted with adequate snow conditions, all radio-transmittered elk in the study area were sighted by survey crews. A significant number of elk, specifically males, were not overlooked during the 1985 survey. The observed male to antlerless elk ratio did not differ from the calculated "corrected" ratio. The observed sex-ratio obtained from the winter surveys therefore is not likely effected by a significant visibility bias between male and antlerless elk. The reliability of the survey results can be attributed to the survey method. Intense survey area coverage and the use of a helicopter as the survey aircraft aided in producing relatively unbias counts. Supporting these findings, Leon et al. (1987)

found that there was no sex or age bias in the composition of white-tailed deer encountered during helicopter surveys.

Sex ratios obtained from winter surveys have been used in Manitoba to assess elk populations and the effects various hunting seasons have on those populations. Strong (1981) cites several ratios for different elk populations in Manitoba. Davies (1979) found an average male to antlerless elk ratio over a seven year period for Duck Mountain elk to be 31:100. In 1983 and 1985 this ratio was reported as 33:100 and 18:100, respectively, for the Duck Mountain population (Ball 1987). An elk population in Manitoba's Interlake was reported to have a male to antlerless ratio of 29:100 for 1983 (Crichton 1985). The various methods used to survey these elk populations may have contributed to the sex ratio differences. It is likely that the true sex ratios of other elk populations in the province are even closer to 50:50 than those reported. Surveys conducted on these populations did not account for elk which were overlooked and these were likely males.

Prior to the initiation of an elk hunting season, Hornbeck (1979) noted that the male:antlerless elk ratio for the Spruce Woods population was low and averaged 17:100 between 1976 to 1979. Strong (1981) found that the male:antlerless ratio for elk on the military reserve averaged 15:100 between 1978 and 1980, with ranges from 13:100 to 17:100 during January winter surveys. When elk which were observed during the survey in other parts of the study area were included, the ratio averaged 20:100 (Strong 1981). Strong (1981) stated that the male to antlerless elk ratios he found for the Spruce Woods population were lower than in other Manitoba elk populations even though other populations in the province had been subjected to many years hunting of both sexes and all cohorts. These ratios were low even in comparison to those elk populations in Manitoba where hunting seasons occurred which emphasized the harvest of male elk.

Sex ratios obtained during this study were within the range reported for most North American elk herds though generally lower than that suggested necessary for a socially stable population (Freddy 1987). The male to antlerless elk ratio obtained during this study in 1985 was 25:100 and the calculated adult sex ratio was 29:100. The increase in the male to antlerless ratio over that reported by Hornbeck (1979) and Strong (1981) was likely due to a slight recovery of males from changes in the regulated elk harvest. The elk harvest by recreational hunters had changed in response to hunting season changes implemented by the Department of Natural Resources. This ratio increase was small considering the dramatic changes in the recreational harvest of male elk since Hornbeck (1979) and Strong (1981) and suggests that male elk continued to have been lost from the population by other means. Hunting seasons in 1982 and 1983 were changed to antlerless-only seasons in response to the low sex ratios observed in previous surveys and in other years to reduce the male harvest (L. Bidlake, Manitoba Wildlife Branch, pers. commun.).

In this study radio-transmittered, immature male elk were observed holding small harems of cows and calves during the rut. The short term detrimental effects of yearling male elk contributing significantly as breeding sires, which have been described, were not evident. Small, late-born calves were not observed and conception rates of harvested cow elk were high (L. Bidlake, Manitoba Wildlife Branch, unpubl. data). This is in support of Strong (1981) who stated that by 1980 it was unlikely that the Spruce Woods elk population was affected negatively by the scarcity of males. Strong (1981) did note that a delay in the breeding season may have occurred in 1978. He suggested this delay possibly resulted from a disturbance of breeding activity caused by military exercises or from hunters or possibly from breeding by yearling bulls. The latter is unlikely for Freddy (1987) suggests that a decline in the pregnancy rate of cows does not occur until the bull:cow ratio falls below 10:100.

Seasonal Range Utilization and Movements

Seasonal range estimates obtained for this study were generally larger than those described in the literature for male elk. Strong (1981) and Hornbeck (1979) outlined similar seasonal range areas for radio-transmittered male elk which they monitored but did not provide size estimates. Differences between results may be explained in part by the different methods used for collecting range data and differing methods of analysis (Klenner 1982). The Jennrich-Turner estimate of seasonal range sizes used in this study usually provides larger estimates than the Mohr's method which is used by most authors. Habitat differences and population densities also effect range sizes (Clutton-Brock et al. 1982).

The differences obtained in seasonal range sizes and activity between male elk cohorts and seasons are supported by the findings of several authors. Strong (1981) describes movements of bulls as far more extensive than cows and found that younger elk moved more than older ones. Immature male cervids generally have larger ranges than older male cohorts. Gavin et al. (1984) disagree with this generalization and found that as male white-tailed deer got older their seasonal ranges increased in size. Geist (1982) describes elk wandering as occurring at a maximum in one to two year old bulls.

Similar to the findings reported in this study, other authors reporting on both sexes and all cohorts generally have found that elk and red deer have large spring and fall seasonal ranges and are more active during these seasons than in the summer and winter (Franklin et al. 1975). Craighead et al. (1973) described spring ranges for cow elk as larger than winter but that summer and fall ranges are the largest. Elk respond to increases in energy expenditure while travelling during the winter by reducing movements (Craighead et al. 1973). Snow thickness greater than 40 cm hampers elk travel and areas with more than 70 cm of snow cover are avoided by elk (Sweeny and Sweeny 1984).

Hornbeck (1979) stated that winter movements and ranges of elk in the Spruce Woods area were restricted. Strong (1981) found that winter ranges of some elk were extensive and attributed the disparity with the findings of Hornbeck (1979) with differences in habitat types between the military reserve and park and snow depths in the different years of the two studies.

Elk increase their activity and ranges in the spring in response to receding snow and increased availability of succulent forage (Picton 1960, Craighead et al. 1973, Marcum and Scott 1985). Strong (1981) describes seasonal movements as highly individual and found spring movements of elk to be more extensive than in summer. Summer ranges are likely within areas explored during the spring which will provide adequate resources to enable elk to acquire fat reserves. Fall ranges of males may be large and include areas occupied during the summer and include those areas where the rut occurs. Bowyer (1981) found that male elk increased their activity during the rut. Franklin et al. (1975) reported increased wandering by Roosevelt elk during the fall.

Radio-transmittered mature males in this study that were monitored for more than one year demonstrated seasonal range use fidelity. The area north of the Epinette Creek was used repeatedly in 1983 and 1984 by mature male elk which inhabited the military reserve during the summer, spring and winter. To a lesser extent, mature male elk occupied the same areas during the rut in different years. Immature male elk showed less traditional use of seasonal ranges though few immature males were monitored for more than one year. Edge et al. (1985) stated that home range fidelity is advantageous to elk because it imparts knowledge of seasonal availability of forage and cover.

This study supports earlier findings which have documented sex segregation occurring in the Spruce Woods population during winter surveys and range use of radio-transmittered elk by Hornbeck (1979) and Strong (1981). Strong (1981) found that elk observed on the east half of the military reserve frequently were males. As well, radio-transmittered male elk monitored by Strong (1981) frequently were relocated and had seasonal ranges within the wooded cover north of and along the Epinette Creek. Habitat in this area generally offered more thermal and escape cover than available in other areas of the military reserve and may provide large quantities of fibrous forage. Hornbeck (1979) found that a greater proportion of elk in the park were males. These findings were supported by the results of this study. Radio-transmittered male elk frequently used areas east of the park and north of the Epinette Creek on the military reserve where cows and calves rarely were observed. As well, the sex ratios of elk observed while traversing the study area support the view of sex segregation due to differing habitat requirements and use.

The segregation of elk by sex in the Spruce Woods area may result in males occupying areas in which they are exposed to greater mortality risks. The park and the area east of the park are the primary areas where Indian hunters and poachers concentrate their activities. Indian hunting and poaching also is known to occur along the boundary of the military reserve which is frequented by male elk.

In this study the frequency to which immature males dispersed could only be speculated to have been relatively high. One dispersing immature male travelled extensively and eventually associated with a different elk population in Manitoba. Other immature male elk showed more restrictive dispersal movements and established seasonal ranges away from their suspected natal areas. Both types of dispersal movements likely increased the dispersing individuals vulnerability to a variety of mortality types. Hornbeck (1979) and Strong (1981) studying the Spruce Woods elk populations also found that males were the dispersing cohort.

Mortality

During this study and other studies (Hornbeck 1979, Strong 1981) of the Spruce Woods population, male elk mortality caused directly from rutting activity (ie mortal wounds from antler combat) was not observed. Although differential male mortality from rutting activity cannot be disregarded as contributing to the low observed sex ratio, this type of mortality is unlikely to be significant.

Generally, male cervids travel greater distances than females, are more active and more vocal and thus may be more vulnerable to human caused mortality than cows. Human-caused mortality was believed to have the greatest impact on the Spruce Woods population and account for most elk deaths. Altmann (1952) reports that male elk take more chances when faced with danger than cows and calves and often were hesitant to flee from danger. Immature male elk during the rut may act irrationally and be unconcerned about danger when normally they would be cautious (Altmann 1960). Reports of accidental deaths of elk are frequently males. During the course of this study three elk which died accidentally due to vehicle collisions all were males.

The findings from other researchers on hunting cervid species agree with those of researchers studying elk and red deer, that males are more vulnerable than females (Roseberry and Klimstra 1974, Burgoyne 1978, Paloheimo and Fraser 1981, Ozoga and Verme 1985). Houston (1982) feels that male elk and especially yearling males are vulnerable to hunting removals. Picton (1961) supports these statements with findings from harvest data on the Sun River and Judith River elk herds in Montana but found that two year old males cohort were the most susceptible to being harvested by hunters. Clutton-Brock et al. (1984) found that male red deer were more likely than females to wander out of their protected study area and get shot. Between 1974 and 1979, only two resident females were shot in other parts of the Island of Rhum while 35 males were shot during the same period (Clutton-Brock et al. 1984).

In the Spruce Woods, the recreational hunter elk harvest was generally governed by the type of hunting season. Hunters in 1981 and 1982 could only harvest females and calves and there was no hunter vulnerability harvest bias. Sex bias cohort hunting vulnerability have implications for both the poaching and Indian harvests and the landowner season. The bias in these types of harvests are affected by the location of hunting activities and timing of the hunting. The high mortality rate of radio-transmittered male elk support the view that there is sex bias vulnerability of harvests by landowners, poachers and Indians.

The Indian harvest of elk during this study was not dictated by regulations under the Wildlife Act. Harvest data suggest that Indians hunters harvested a larger portion of male elk from the Spruce Woods population than represented in the population. Since Indian hunters did not prefer male elk and did not purposefully select male cohorts, Indian harvest ratios reflect the relative vulnerability of males to hunting over females and in part, where the Indian harvest takes place.

Definitive information on poaching of elk was difficult to ascertain during this study and this aspect of elk mortality is not well documented in the literature. Gogan and Barrett (1987) report that of the seven Tule elk (3 females and 4 males) reintroduced onto Grizzly Island, California, one male was poached. Kimball and Wolfe (1974) state that the Cache elk herd show an approximately equal sex distribution of illegally shot elk. A skewed adult sex ratio favouring females for this elk herd suggests that poaching take was bias for males (Kimball and Wolfe 1974). Mitchell et al. (1977) found that male red deer were more likely to be shot as "marauders" than females. Freddy (1987) reports that in one year 5% of 20 radio-transmittered cows are harvested illegally in the White River elk herd, the rate at which radio-transmittered male elk were poached was not reported. Harper et al. (1967) concluded that one of the major causes of death of Roosevelt elk in California was poaching and that the mature male cohort segment of the population was affected severely by this type of mortality.

Regarding the Spruce Woods elk populations, Hornbeck (1979) reported that of the 13 elk he knew were poached, 10 were males. He theorized that since males tend to be more wide-ranging, they were likely to undertake frequent "out-of-range" movements and as a result are heavily poached. Strong (1981) reports one radio-transmittered male was poached during his study. He felt that illegal elk hunting in the Spruce Woods area was probably sporadic and not large enough to deplete the population seriously. The telephone interview of local landowners showed that poaching in the study area was a problem and occurred to a greater extent than suggested by Strong (1981). This study agrees with other studies in that males are poached disproportionately to their representation in the population. Male elk may be more vulnerable to being poached because of their increased activity during the rut when most of the poaching occurred and they generally inhabited areas where poaching activity frequently occurred in the study area. As well, poachers may select males over females for "pseudo" ethical reasons.

SUMMARY AND CONCLUSIONS

Factors causing the low male to antlerless ratio observed in the Spruce Woods elk population during the winter aerial surveys were investigated. Biases in the aerial survey techniques, seasonal range utilization and movements of radio-transmittered male elk cohorts, mortality and dispersal of radio-transmittered male elk, poaching and Indian harvest biases were examined as possibly contributing to the skewed male to antlerless elk ratio.

The aerial survey conducted in the winter of 1984/85 documented a decrease in the population from that reported by previous studies. The observed male to antlerless elk ratio and calculated sex ratio from the 1984/85 survey was lower than reported in other populations in Manitoba but within the range reported for other North American populations.

Analysis of the survey techniques indicated that the survey method, when conducted under good survey conditions, did not miss a significant number of elk. The survey visibility bias, specifically referring to males which tend to be more solitary than cows and calves and therefore more likely to be overlooked during the survey, did not contribute to the low numbers of males observed in this population.

Seasonal range utilization of immature male elk and mature male elk were determined by monitoring radio-transmittered elk. Comparisons of the two cohorts revealed that generally immature male elk had larger seasonal ranges and undertook more extensive seasonal movements than mature males. Immature male elk also had greater distances between seasonal ranges and were less likely to reuse traditional seasonal ranges than mature male elk. As well, all radio-transmittered elk that undertook dispersal movements were immature males. Dispersing immature males used seasonal ranges that were in unfamiliar areas. Dispersal movements were usually towards the east and northeast. Elk which were observed in areas outside the military reserve and park were often males.

Aerial surveys, the study of range use by radio-transmittered male elk and ground observations indicated that male and female elk utilized different areas for much of the year. Sex segregated habitat use occurred on the military reserve. In addition, male elk frequently used areas east and north of the park.

Mortality of radio-transmittered elk was high. Male elk which inhabited the military reserve had greater survival than elk which had seasonal ranges in the park or incorporated parts of the surrounding private and Crown lands in their ranges. Radio-transmittered elk were harvested by landowner hunters and also were suspected to have been shot by poachers and Indian hunters. Natural mortality of male elk was not observed during the study but likely occurred disproportionately between the sexes, thus, contributing to the low numbers of male elk in this population.

Poaching of elk frequently occurred in the study area. The extent which this activity occurred may have been underestimated by previous studies. The poaching take of elk was biased favouring the harvest of male elk. Areas inhabited by male elk, their increased activity and their lack of wariness during the rut and a preference for male elk by poachers contribute to the high proportion of males which were poached.

Indian hunters from several areas hunted elk in the study area. Indian hunters did not hunt male elk selectively although the sex ratio of their harvest was significantly larger than the population and indicates a sex bias harvest. The activity of male elk during the rut (when most Indian hunting was undertaken) and the areas where Indians hunted may make male elk more vulnerable to being harvested by Indian hunters.

The low male to antlerless elk ratio was real and not an artifact of the survey method. The low numbers of male elk in the Spruce Woods population was attributed to differential natural mortality, dispersal of immature males from the population and male bias poaching and Indian harvests.

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Appendix 1. Mean monthly temperature, precipitation and snow thickness at Brandon, Manitoba, 30 km northwest of study area.

Year	Month	Mean Temperature (C) *	Total Precipitation (mm) *	Mean Snow Cover (cm) **
1982	Jan	-25.5	24.5	25.3
	Feb	-15.4	4.9	31.4
	March	-7.0	24.2	23.6
	April	2.0	39.9	7.1
	May	11.3	55.0	-
	June	13.7	43.7	-
	July	18.7	144.1	-
	Aug	16.0	48.2	-
	Sept	11.2	62.1	-
	Oct	5.7	61.7	-
	Nov	-6.4	3.8	Trace
	Dec	-10.3	23.7	4.4
1983	Jan	-12.2	13.1	18.5
	Feb	-11.0	13.2	18.1
	March	-7.8	42.6	28.9
	April	1.8	2.2	5.7
	May	7.7	49.4	Nil
	June	15.9	68.0	-
	July	20.2	70.4	-
	Aug	21.2	65.3	-
	Sept	11.5	43.6	-
	Oct	5.1	15.2	-
	Nov	-2.4	22.4	6.1
	Dec	-21.1	7.8	15.2
1984	Jan	-13.8	5.5	15.6
	Feb	-4.8	7.0	14.9
	March	-6.5	19.7	15.4
	April	6.3	95.0	4.7
	May	9.7	16.6	Nil
	June	16.4	52.1	-
	July	19.1	30.9	-
	Aug	20.1	26.0	-
	Sept	9.0	80.3	-
	Oct	4.1	71.5	-
	Nov	-6.4	28.7	15.2
	Dec	-19.4	17.7	35.2
1985	Jan	-18.0	9.4	43.8
	Feb	-17.1	14.5	51.0

* Data obtained from Brandon Airport (Environment Canada).
** Data obtained from Dan Chranowski (Manitoba Wildlife Branch, Brandon).

Appendix 2. Background information on male elk captured and radio-transmittered during the study.

Capture Date	Animal #	Age at Capture (Years)	Capture Method + Location	Comments
Jan. 28/83	B8301	5.5*	T, Area 8 Trap	B.A., large
Feb. 3/83	B8302	8.5*	T, Area 8 Trap	B.A., large
Feb. 23/83	B8303	3.5**	T, Area 8 Trap	B.A., Left antler broken, injury to left front leg
April 5/83	Sp8304	1.7**	H, North Park Block	S.A., Appeared sick
April 28/83	Sp8305	1.9**	T, Area 8 Trap	Replacing antlers
Feb. 28/84	Sp8401	1.5**	H, North Park Block	S.A.
Feb. 28/84	B8402	3.5**	H, North Park Block	B.A., large
Feb. 28/84	Sp8403	1.5**	H, North Park Block	S.A.
Feb. 28/84	Sp8404	1.5**	H, North Park Block	S.A., Torn leg muscles
May 9/84	B8405	3.0*	T, Area 8 Trap	Replacing antlers
July 25/84	Sp8406	1.1**	T, Area 8 Trap	S.A.

* Age estimated from body size and dental wear.

** Age determined from cementium annuli and/or dental irruption.

T - Captured by trap.

H - Captured by helicopter.

Appendix 3. Telemetry error measurements for two antenna systems used during the study.

Antenna Type	Distance to Test Collar (km)	Error Degrees	Orientation From Test Collar
Modified 7 Element Portable	2.6	0	0
	2.6	5.6	left
	2.6	0	0
	2.6	5.6	left
	2.6	2.3	left
	2.6	0	0
	2.6	5.6	left
	2.6	2.3	left
	3.7	7.9	right
	3.7	7.9	right
	3.7	11.3	right
	3.7	11.3	right
	3.7	14.1	right
	3.7	14.1	right
	3.7	2.3	right
	3.0	0	0
	3.1	11.3	right
	3.1	0	0
	3.3	7.9	left
	4.7	7.9	right
	4.8	7.9	right
	2.5	5.6	right
	5.1	2.3	right
	1.9	7.9	left
	1.8	11.3	right
	1.8	2.3	left
	5.1	16.9	right
	3.1	7.9	right
	Mean Error = 6.411 ($\underline{n}$ = 28, SD = 4.838)		
14 Element Stationary	3.8	11.3	left
	3.8	5.6	left
	3.8	16.9	left
	3.8	2.3	left
	3.8	5.6	right
	3.8	7.9	left
	3.8	0	0
	Mean Error = 7.086 ($\underline{n}$ = 7, SD= 5.661)		

Appendix 4. Monthly tally of relocations obtained for radio-transmittered elk during the study, 1982-1985.

Transmittered Male Elk	Months of Year 1982												1983												1984												1985	
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
B1633	0	0	0	2	0	0	0	2	4	3	3	6	5	13	2	7	14	21	3	9	3 *																	
B8301													1	9	3	6	14	0	0	2 *																		
B8302														11	1	6	14	21	4	5	3	10	2	6	4	5	6	4	12	3	2	1	1	7	6	1	13	1
B8303														5	2	4	7	6	0	0	3	5	1	5	3	5	6	3	17	10	7	14	7	11	5	2	13	1
SP8305																1	14	6	0	8	3	8	3	4	1	2	11	1	14	8	7	12	3	7	9 **			
SP8401																										3	11	0	11	11	7	12	2 a					
B8402																										2	12	0	15	11	1b	0	0	2	0	0	1	1
SP8403																										2	11	0	11	10	7	13	1 **					
SP8404																										2	11	1	15	10	8	7	6	10	6 a			
SP8405																													16	8	7	9	7	13	6	2	13	1
SP8406																															1	5	7	9	0	1	12	1

* Radio-transmittered elk which was likely poached.

** Radio-transmittered elk shot by landowner hunter.

a Radio-transmittered elk suspected to have been poached.

b Radio-transmittered failure.

Appendix 5. Individual radio-transmittered elk seasonal range size estimates (km^2) in southwestern Manitoba during the study.

Male Elk	Age	Year	Jennrich-Turner Index (km2)				Mohr's Estimate (km2)			
			Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
B1633	7a	1982	*	*	74.4	35.2	*	*	18.0	18.6
	8	1983	45.1	11.1	*		26.9	3.9	*	
B8301	4b	1982				16.0				5.8
	5	1983	31.9	*	*		12.9	*	*	
B8302	5b	1982				17.3				6.4
	6	1983	54.3	48.4	52.7	22.7	37.9	11.8	17.8	9.8
	7	1984	22.3	*	98.7	15.9	9.0	*	41.3	5.3
B8303	3a	1982				*				
	4	1983	95.3	*	113.5	30.5	28.0	*	31.9	12.1
	5	1984	58.6	26.9	94.8	15.9	30.9	10.1	40.1	7.5
SP8305	3a	1983	139.7	*	198.7	78.9	64.2	*	57.7	35.0
	4	1984	74.8	37.9	165.9		34.4	19.0	74.2	
SP8401	2a	1983				59.1				21.0
	3	1984	232.5	56.5			104.9	22.9	*	
B8402	3b	1983				29.2				12.4
	4	1984	193.8	*	*	*	91.6	*	*	*
SP8403	2a	1983				24.1				7.2
	3	1984	55.5	20.0	*		22.1	8.8	*	
SP8404	2a	1983				20.8				8.1
	3	1984	90.6	265.7	131.9	*	43.6	80.9	48.8	*
B8405	3b	1984	36.5	41.8	48.7	16.0	18.5	14.7	27.4	5.8
SP8406	1a	1984		*	26.8	89.0		*	26.8	89.0

* - Season in which fewer than 9 relocations were obtained.
a - Age determined from tooth replacement and/or dental cementum annuli.
b - Age estimated from tooth wear and body size.

Appendix 6. Distances between successive seasonal range activity centers for individuals radio-transmittered elk.

Male Elk	Year	Distance between Seasonal Activity Centers (km)			
		WI-SP	SP-SU	SU-FA	FA-WI
B1633	1982	-	-	-	2.60
	1983	1.13	1.23	-	-
B8301	1983	1.14	-		
B8302	1983	2.35	0.86	4.11	4.57
	1984	0.32	-	-	2.26
B8303	1983	-	-	-	9.97
	1984	4.11	7.04	2.77	4.16
SP8305	1983		21.83	1.07	2.41
	1984	2.15	2.60	4.44	
SP8401	1984	12.66	3.16	-	
B8402	1984	12.13	-	-	-
SP8403	1984	16.63	1.98	-	-
SP8404	1984	3.50	4.13	5.91	-
B8405	1984	-	0.95	2.97	0.74
SP8406	1984		-	-	5.65

WI - Winter seasonal range.
SP - Spring seasonal range.
SU - Summer seasonal range.
WI - Winter seasonal range.

Appendix 7. Cumulative hourly vehicle traffic activity on an access road in the north block of the park during the fall of 1984.