## ECOLOGY OF A PARTIALLY MIGRATORY ELK POPULATION

by

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#### ABSTRACT

In this thesis I investigate the ecology of a partially migratory (<100% of the animals migrate) population of elk (<u>Cervus elaphus</u>) in the Canadian Rockies. I radio-tagged elk in a 330 km<sup>2</sup> area of the Bow River valley (BRV) in Banff National Park, Alberta and followed them for 36 months. Elk movements to adjacent watersheds expanded the study area to 2900 km<sup>2</sup>. My goals were to describe the seasonal movements made by BRV elk and to reach some understanding of the causes of these movements.

The M/R (migrant/resident) ratios for adult bulls and adult cows were 4.3 and 0.5 respectively. Classified ground counts revealed that adult bulls made up only 11% of the population and that the overall M/R ratio for the population was 0.6. Migrations did not take elk beyond the foraging range of timber wolves (<u>Canis lupus</u>), their principal predator. Three cows changed migration status between years and some migrants were sympatric with residents during the rutting (breeding) season. These observations are consistent with the hypothesis that migration in elk is a conditional ESS (evolutionarily stable strategy).

Although 1 adult radio-tagged bull dispersed, individual annual home-ranges of the remaining elk overlapped from year-to-year. Elk were strongly philopatric to winter, summer, and rutting ranges. There were no differences detected in the relative philopatry of bulls and cows, or of migrants and residents.

Bulls had average 1-way migrations of 30 km horizontally and 840 m vertically. Cows had average 1-way migrations of 36 km horizontally and 1079 m vertically. The net energy and time investments for these movements were calculated and judged to be trivial.

Elk on both high and low elevation ranges ate primarily grasses and sedges during the autumn, winter, and spring, and the leaves of deciduous shrubs during the summer. Similarities outweighed differences between high and low elevation ranges.

Elk population characteristics (numbers, composition, survival, recruitment, predation, parasites, animal morphology) were measured during 1985-91 and compared with similar data gathered during 1944-69. In most respects, the population has not changed over these years and little is known of density-dependent processes.

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### CHAPTER 1. GENERAL INTRODUCTION

Migration in birds and mammals is generally defined as the annual return movement of individuals between 2 geographically separate areas. It implicitly follows that migratory animals establish a degree of philopatry to seasonal ranges and make relatively little use of areas between these ranges. In contrast, dispersers make one-way movements and nomads are not philopatric to seasonal ranges.

Although many species of animals have been classified as either migrants or non-migrants, intraspecific variation in seasonal movement patterns is common (Baker 1978). Partial migration occurs when a population contains both migrant and sedentary individuals, and differential migration when individuals within a population migrate varying distances (Ketterson and Nolan 1985, Lundberg 1988).

Partial migration has received considerable attention in bird migration studies in the context of evolutionarily stable strategies (ESS's). Maynard Smith and Price (1973) defined an ESS as: "a strategy such that, if most of the members of a population adopt it, there is no 'mutant' strategy that would give higher reproductive fitness." However, if seasonal movement behavior is an ESS, how is that both migrants and residents can coexist within a single population? Three solutions have been advanced: 1) a mixed ESS at the

population level (with equal fitness of migrant and resident morphs and inflexible individual behavior); 2) a conditional ESS in which morphs need not have equal fitness and can change their behavior (Lundberg 1988, Adriaensen and Dhondt 1990); and, 3) an unstable movement strategy (i.e. in transition) (Swingland 1983).

The observation that migratory restlessness is a heritable trait in some birds (Berthold and Querner 1981, Biebach 1983) suggests the existence of resident and migrant genetic morphs and is consistent with a mixed ESS explanation. However, a conditional ESS solution is supported by the fact that timing and distance of migration is facultative in some birds (Terrill and Ohmart 1984), and that individuals may switch between migration and residency (Baker 1978). Adriaensen and Dhondt (1990) explained this range of behaviors by suggesting that a within a population, individuals may have varying genetic biases. Those strongly predisposed to migrate, always do so; those with little migratory inclination, never migrate; and, those between these extremes, make a conditional assessment of the environment and decide to migrate or not.

A genetic basis for migration has not been demonstrated in mammals. In large mammals, explanations of partial migration emphasize the importance of learning in the development of seasonal movement

behavior (McCullough 1985). In this view, seasonal movement strategies of individuals would not be "closed program" ESS's in a genetic sense, but rather the product of cultural inheritance and individual experience. As Mayr (1974) argued, retention of phenotypic flexibility enabled by "open programs" would be of selective advantage for non-communicative behaviors such as habitat use in a varying environment.

Elk are often classified as migrants, despite the observation of coexisting non-migrant populations and populations with a mix of movement strategies. Morgantini (1988) suggested that variability in movement behavior by elk is an exhibition of the species's flexibility in coping with a varied environment and Boyce (1991) showed that seasonal fluctuations in the availability of food resources could determine the fitness of migratory and non-migratory elk populations. To-date, no studies have directly compared the ecology of migrant and sedentary individuals from a single population.

In this thesis, I examine a partially migrant elk population in the Canadian Rockies and address the general hypothesis that elk seasonal movements are conditional strategies (i.e. individually-based decisions). I first introduce the problem and study area (Chapter 1), I then examine the movement characteristics of the population (Chapter 2), the

related topic of philopatry (Chapter 3), the net cost of migration (Chapter 4), and the diet of migrants and residents (Chapter 5). I conclude by describing some population parameters (Chapter 6) that might be influenced by movement strategies.

### Study area

This study was centred in a portion of the Bow River valley (BRV) between Lake Louise and Canmore, Alberta in the Continental Ranges of the Canadian Rocky Mountains (Figure 1). The valley bottom elevation increases from 1341 m at Canmore to 1646 m at the Continental Divide. Approximately 330 km<sup>2</sup> of the BRV is below 1700 m elevation and is used by elk year-round. Migratory movements of elk from the BRV expanded the study area to 2900 km<sup>2</sup>. The BRV valley floor runs for approximately 80 km within Banff National Park and 4 km outside the park, and varies in width from 2-6 km. Mountains rise to elevations of 3000+ m on either side.

This area of the Rockies has a continental climate characterized by relatively long winters and short summers (Holland and Coen 1983). Below 1600 m, low snowfall coupled with sudden warming periods in winter, results in intermittent snow-free periods. Above 1600 m, snowpack is typically continuous from November through May or June except on very steep slopes or windswept ridges. During the study (1985-89), snowfall in the BRV was below average (58-83% of the long-term average of 248.9 cm).

The vegetation in and adjacent to the BRV has distinct altitudinal zonation (Holland and Coen 1983). The montane zone ( <1600 m) is characterized by mixed forests of evergreen trees (Pinus contorta, Pseudotsuga

<u>menziesii</u>, <u>Picea glauca</u>) and aspen (<u>Populus tremuloides</u>) interspersed with natural grasslands. Approximately 200 km<sup>2</sup> of the BRV is in the montane. The lower subalpine zone (1600-2000 m) has closed evergreen forests (<u>Pinus</u> <u>contorta</u>, <u>Pseudotsuga menziesii</u>, <u>Abies lasiocarpa</u>, <u>Picea</u> <u>Engelmannii</u>). Higher in this zone (2000-2300 m), the evergreen forest is interspersed with subalpine meadows. The alpine begins above 2300 m. In many places, avalanches descending from the alpine and upper subalpine have created openings through the lower forests.

The Trans-Canada Highway and Canadian Pacific Railway roughly parallel the Bow River through the study area. Both are major transcontinental transportation routes with large traffic volumes (Woods 1990). There are approximately 116 km of additional roads within the BRV. During 1983-87, 26 km of the easternmost section of the highway within the park were fenced on either side with 2.4 m high, ungulate-proof fencing. The remainder of the highway (58 km) was not fenced. Underpasses and bridges provided ungulates opportunities to cross beneath the fenced highway at 12 locations.

During the study, highway traffic peaked during July and August (26% of annual total) and was lowest during November (5% of annual total)(Woods 1990). A town (Banff) and a small service centre (Lake Louise) are located within the BRV and the town of Canmore is

located at the eastern edge. In addition to developments within the towns, there are numerous hiking trails, picnic areas, campgrounds, a grass-surfaced airfield, a golf course, and several lodges. Three downhill ski resorts (Mount Norquay, Sunshine Village, Lake Louise) are located directly above the BRV in the subalpine and alpine zones.

Overviews of the elk biology in the park have been presented by Flook (1967, 1970), Holroyd and Van Tighem (1983), Morgantini (1988), Woods (1990) and Chapter 6. Although native elk were found in BRV when the park was established in 1885, they had disappeared by 1906. In 1915, native elk reappeared in the park as summer migrants from British Columbia. During 1918-20, 235 elk from Yellowstone National Park were released at 2 locations within the BRV (Lloyd 1927). From 1941-69, nearly annual elk slaughters were conducted in and around the BRV. Since the 1970's, management interest in BRV elk has focused on elk-vehicle collisions on park roadways and on the railway (Woods 1990 and Chapter 6).

BRV elk were visually tagged as early as the 1960's. In the early 1980's, park wardens radio-tagged 7 adult cows and observed both resident and migrant elk (P. Jacobson, pers. comm.). Dispersal from the BRV and other remnant populations is believed to have established the Red Deer River population in the north-east of the park during the 1930's (Morgantini

1988). Radio-tracking and visual tagging programs in the adjacent Kootenay National Park documented dispersal into the BRV from the Kootenay River valley (Gibbons 1978). One of these dispersers subsequently moved to the Red Deer valley, a distance of approximately 150 km (Morgantini 1988).

Elk were the most abundant ungulate in the BRV during the study (1985-90) with an average population of approximately 900 animals (Woods 1990, Chapter 6). Based on classified count data and the observation that few, if any 1-year-olds breed (Chapter 6), the effective population size ( $N_e$ ) was approximately 450 (Chepko-Sade and Shields 1987, sex-ratio method). An additional population of 300 elk were estimated to winter in the area immediately east of the BRV (T. Nette, Alberta Wildlife, unpubl. data).

Since the majority of the BRV is within the national park, and since most migrant elk move to other areas of the park, this population is largely unhunted. Bow-hunting for elk is allowed during annual open seasons on provincial lands in the portion of the BRV between the park and Canmore. Those elk migrating out of the BRV via the Spray River watershed pass through an area of provincial land with an annual rifle-hunting season for elk.

Predation by timber wolves and collisions with trains and automobiles are the major mortality sources

for this population (Weaver 1979, Woods 1990, Chapter 6). Coincident with the start of this research, the wolf population apparently increased within the BRV (R. Kunelius, CPS, pers. comm.).

Since the 1940's, habituation to people has been a notable feature of BRV elk (Green 1949). Although both sexes are relatively indifferent to human presence, cows are noticeably more nervous. Some adult bulls regularly spend summer and winter within the urban boundaries of Banff townsite. Between the park and Canmore, elk are noticeably more wary of humans and adult elk are rarely found within the town of Canmore.

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Figure 1. The study area. (1=village of Lake Louise; 2=town of Banff; 3=town of Canmore)

#### CHAPTER 2. PARTIAL MIGRATION

#### Introduction

The study of animal movements has lacked continuous observations of individuals over significant fractions of their lifetimes (Wiens 1976, Baker 1978, Swingland 1983). Advances in technology, including radio-telemetry, aerial tracking, and satellite-based tracking, now make it possible to obtain detailed individual movement data for medium to large vertebrates. This allows us to re-examine animal movement, giving greater attention to individuality.

Individual animals are often either migratory or resident. Migrations in vertebrates can be defined as "the repetitive seasonal movements of individuals between distinct areas" (Sinclair 1983). Residents use the same area throughout the seasons. In "partial" migrant species, not all individuals migrate (Baker 1978). Partial migration is widespread amongst vertebrates (marine mammals, Wursig and Wursig 1980; cervids and bovids, Swingland 1983; wild horses, Berger 1983; bears, McLellan 1989; bats, Swingland 1983; passerine birds, Adriaensen and Dhondt 1990; fish and turtles, Sinclair 1983).

How can 2 or more strategies coexist within 1 species or population? Lack (1943) suggested that partial migration in the European robin (<u>Erithacus</u> <u>rubecula</u>) could be explained by the presence of 2

genetically distinct morphs whose average long-term pay-offs balance (i.e. a mixed ESS). Although migratory restlessness is a heritable trait in birds (Berthold and Querner 1981), the genetic polymorphism hypothesis is weakened by the fact that individuals may change their migratory status between years (Baker 1978), and by the observation of facultative migration in species such as the yellow-rumped warbler (<u>Dendroica coronata</u>) (Terrill and Ohmart 1984).

Recently, Adriaensen and Dhondt (1990) illustrated unequal pay-offs between residents and migrants (residents did better) in the European robin in Belgium. They presented a "conditional" explanation for the 2 behaviors. They suggest that individuals with strong genetic tendencies to migrate or to remain resident, will always do so. Between these extremes, individuals make a "conditional" assessment of their environment and choose to migrate/stay accordingly. This suggests that the choice might be density-dependent or that it might change with variation in the quality of the environment.

Unequal pay-offs are suggested by work on African ungulates (Fryxell and Sinclair 1988, Fryxell et al. 1988). Fryxell et al.(1988) observed that migrants were more abundant than residents and proposed a model that suggested that migrants might escape population regulation by sedentary predators by moving away from them for part of the year. At the individual level,

movements that reduce encounters with predators could increase fitness.

Boyce (1991) used a model to illustrate that seasonal fluctuations in food availability on summer (high elevation) elk ranges could determine the fitness of migratory and non-migratory elk. In areas with low seasonality, residents had the highest fitness because of the cost of migration. At moderate levels of seasonality, fitness of both morphs decreased, although fitness of residents decreased more steeply. The model did not address the problem of coexisting migrant and non-migrant elk within a single population.

Female-biased ratios of migrants to residents have been found in several species of birds (Adriaensen and Dhondt 1990). Although female-biased migration has been shown in 1-year-old elk (Boyce 1989), partial migration biases in mammals have received little attention. Greenwood (1980) reviewed sex-biased dispersal (non-return movement) and identified an apparent dichotomy: female-biased dispersal in the majority of birds and male-biased dispersal in the majority of strategy. In many birds, males defend resources (territories) and are monogamous. In many mammals, males defend females and are polygynous. Dispersal in mammals is thus most likely in the sex which defends mates rather than resources.

Elk have the widest natural distribution of any wild ungulate in the world (Clutton-Brock et al. 1982) and have a range of movement behaviors including migration, residency, and partial migration (Adams 1982). In mountainous areas, elk often make altitudinal migrations featuring considerable climatic and vegetation change over relatively short horizontal distances. They are seasonal breeders with a polygynous mating system.

In this study, I radio-tracked individual elk from a partially migrant population and described their seasonal movement patterns. I addressed the following questions: Is the observed pattern of migration consistent with a mixed ESS explanation?; Is partial migration in elk sex-biased? Are migrants more abundant than residents?; and, Do migrant elk escape the foraging range of their predators?.

Partial migration as a mixed ESS predicts that (1) resident and migratory individuals remain faithful to their movement strategies and that the pay-offs to migrants and residents must be equal. A conditional ESS predicts that (2) the movement strategy depends on status (e.g. sex, age) or an individual's assessment of environmental suitability. Fryxell's hypothesis of predator avoidance (i.e. migration takes elk out of the range of sedentary predators) predicts that (3) migrants should outnumber residents.

#### Methods

#### Radio-tagging

From January 1986 to April 1989, 53 adult elk were radio-tracked successfully within the BRV for more than 6 months. This sample consisted of 18 adult bulls (older than 2-year-olds) and 35 adult cows (older than calves) The cow sample included 1 radio-tagged mother-daughter pair. The daughter was radio-tagged as a calf and followed until she was a 3-year-old.

Radio-transmitters were distributed across the winter (October-May) distribution of elk as determined by previous aerial surveys conducted by park wardens (Woods 1990). Park wardens chemically immobilized elk by darting them from patrol trucks or after approach on foot. One animal was darted from a helicopter. The first elk offering a safe darting opportunity was selected. No more than 2 elk were captured from any group (animals within visual contact of each other) at a time. Two cows radio-tagged in previous studies within the BRV were re-tagged. Most animals were captured during the winter but 2 adult bulls and an adult cow were tagged in August.

Most transmitters placed on adult elk were attached to collars. These radios had a battery life of about 4 years and had mortality sensors that were triggered by 3 hours of inactivity. A numbered tag on the collar allowed individual visual recognition. All calf and most

1-year-old elk were fitted with solar powered ear-tag transmitters. Two of these ear-tag transmitters were later replaced with radio-collars.

From January 1986 until February 1989, the presence of radio-tagged elk within the BRV was determined by ground searches during daylight hours at intervals of 7 days or less. Observers drove the entire length of the highway and made frequent stops (usually <3 km) to scan radio frequencies using a portable radio receiver and hand-held antenna. During a typical week, 100% of the radio-transmitters within the BRV were located during 2-3 days of ground searches.

When a radio-transmitter was heard, the observer drove as close as possible to the animal's location and took 3 or more bearings from points approximately 0.5 km apart. These bearings were then plotted on study area maps (1:50,000) in the field. If the resulting polygon was greater than 0.2 km in any dimension, additional bearings were made to reduce the size of the polygon. The centre of the final polygon was converted to a grid reference with a resolution of 0.1 x 0.1 km. The elevation of this point was estimated to the nearest 30 m contour interval from maps of the study area. If a radio-tagged elk was seen during a survey, its identity was determined from the number on the collar and confirmed by checking its radio frequency.

In addition to ground triangulation, major

tributaries of the Bow River and passes connecting the BRV to neighboring valleys were searched from the air during daylight hours at monthly intervals in 1986, and biweekly thereafter, to locate animals absent from the BRV. A mobile receiver in a helicopter with 2 externally mounted antennae allowed all functioning radios to be located throughout the study. Repeated low-elevation passes with the helicopter allowed point estimates of the elk's position. Elevations were estimated from study area maps and cross-checked with the helicopter's altimeter. The animal's position was converted to a grid reference.

Radio signal "bounce" was encountered frequently but these spurious signals became obvious when multiple bearings were plotted in the field. Additional bearings were taken until the bounce problem was eliminated. Field trials suggested grid reference positions were typically within 0.2 km of the animal's true position. The actual error of each mapped ground observation was not measured but believed to be a complex function of position in the valley and observer experience.

Concurrent radio-tracking of 2 timber wolf packs by the park warden service and by D. Huggard (pers. comm.), allowed general comparisons of wolf and elk movements.

#### Data analysis

Individual locations were transcribed into a computer file and plotted sequentially by date and elevation, and by date and horizontal position. On an annual basis, all radio-tagged animals within the BRV were classified as either migrants or residents. Sequential location plots were examined and animals classified as migrants if they made at least 1 return movement lasting more than 2 weeks between 2 separate areas. This definition of migration implies philopatry to seasonal ranges and relatively little use of areas between these ranges. The remaining elk were classed as residents.

Horizontal movements were estimated for each individual by calculating the difference between extreme observation points for the entire period an individual was tracked. These were then adjusted to represent the shortest possible movement route for an elk when topographical features (e.g. cliffs) barred straight-line travel. Vertical movements were estimated as the maximum elevation minus the minimum elevation point. Departure and return dates of migrating animals were estimated as the last day of radio contact within the BRV and the first day of contact when that animal returned.

Seasonal ranges were identified by partitioning the data into 3 periods: winter, October 1 to May 30;

<u>summer</u>, June 1 to August 31; and, <u>rut</u> (breeding), September 1 to September 30. In winter, most elk were within the BRV, and in summer most migratory animals were out of the valley (Woods 1990). The rut season embraces the height of breeding activity for this population (Struhsaker 1967). Average elevations were calculated from all available observation points for an individual for each season.

The migrant/resident (M/R) ratio for each sex was based on the number of radio-tagged elk that were later defined as either migrants or residents. Individuals that switched movement status between years, or that were captured in the summer, were excluded from these calculations. An estimate of the overall composition of the population was calculated by summing the number of elk observed during 6 autumn and 6 spring classified counts (Chapter 6) into 2 categories: adult bulls and adult cows (calves and 1-year-olds are believed to migrate with adult cows). The M/R ratio for each sex was then used to estimate the number of migrants and residents in the overall population.

The fate of all radio-tagged adult elk was known. Therefore, dispersal could be separated from mortality. Survival rates and 95% confidence intervals were calculated for radio-tagged elk using the Kaplan-Meier procedure as modified for staggered entry and censored (Pollock et al. 1989).

#### Results

#### Seasonal movement patterns

Elk were located on 7640 occasions for periods of 6-36 months. Sequential plots of locations demonstrated that both sexes had resident and migrant individuals (Table 1, Figure 2). One adult bull made a return migration in 1986 and then dispersed about 150 km west. Migrants moved over a significantly greater horizontal and vertical range than residents (Table 2). Three elk had narrow home-ranges along the valley floor with dimensions comparable to the travel distances of vertical migrants. Two of these (cows) did not make discernible return movements between segments of the valley and were classified as residents. They produced the extreme ranges reported for residents in Table 2. The third, a bull, made repetitive movements between distinct areas in the valley and was classed as a migrant.

Twenty-five elk did not migrate (Figure 2a,c) and 25 did (Figure 2b,d,h). Fifteen migrants made 1 migration cycle per year and 10 made 2-3 cycles within a year (Figure 2h). These additional cycles included returns to low elevation during the summer, returns to high elevation during the winter, and repetitive oscillations between low and high elevations throughout the year. Two bulls spent most of the summer at high elevations, returned to low elevations in advance of the

rut, moved back to high elevations after the rut, and then descended again in the early winter (Figure 2h).

The elevational distribution of migrant and resident elk differed markedly between seasons (Figure 3). In winter, both migrants and residents were in the montane zone of the BRV. In summer, most migrants moved to the subalpine and their mean elevation was significantly higher than that of residents (Wilcoxon pairs test, P<0.05). In the rut, many migrant bulls returned to the BRV and were sympatric with residents. However, the mean elevation of migrant cows during the rut was significantly higher than that of resident cows.

Most migratory individuals initiated their migrations in early June and returned in September (Table 3). Although median departure dates were similar for both sexes, bulls returned to the BRV slightly earlier than cows. Fewer than 25% of the radio-tracked elk migrated during any weekly period. During any year, most individuals migrated within 17 days of their migration date the previous year.

The presence of timber wolves was suspected of delaying the migration of 1 adult cow elk. In June 1988 this elk was radio-tracked 12 km from the BRV part way along the migration route she had used during 1986 and 1987. At this point she encountered a wolf pack containing a radio-tagged individual (D. Huggard, pers. comm.). The next day the elk returned to the BRV.

Fifty-four days later she retraced the route and continued 70 km to her summer range.

Seven mature bulls (2 residents, 5 migrants) moved to specific areas of their annual home-ranges only used during the rut. Both of the resident bulls moved from within the Banff townsite to peripheral areas. For 1 of the 5 migrant bulls, a rutting season excursion to low elevation was the only return movement observed. Most migrant cows moved to low elevations before or during the rut. They did not have specific areas used only during the rutting season.

Adult cow elk are secretive at calving time, and it was thus difficult to determine whether or not a cow had a young calf. There was only 1 case of an apparent movement to a specific calving area. This resident returned to small fenced bison (<u>Bison bison</u>) enclosure to bear her young during 3 consecutive years. The remaining residents apparently calved in a variety of locations within their annual home-ranges.

The median departure dates for migrant elk coincided with the calving season (late May-early June, Table 3). Incidental observations of radio-tracked migratory cows indicated that calving could take place on either winter or summer ranges, or in the case of 1 radio-tagged cow, between ranges. After 3 weeks in this location, she completed her migration.

The majority (94%) of elk showed the same movement

strategies from year-to-year. A cow radio-tracked in the BRV in 1981 and determined to be resident (P. Jacobson, pers. comm.), was a still a resident during this study (1986-89). However, another previously studied adult cow made a brief duration vertical movement in 1981 (P. Jacobson, pers. comm.), but was resident throughout 1987-89.

During the study, 3 cows switched strategies between years. One alternated between migration, residency, and migration. (Figure 2e). A 1-year-old elk, resident in 1986, migrated up an adjacent slope as a 2-year-old (Figure 2f). An adult radio-tagged in August 1986, remained in the BRV throughout 1986, but made migrations during 1987 and 1988 (Figure 2g). None of these elk had to cross the fenced highway corridor to migrate.

In 3 cases, calves of radio-tagged cows were captured and followed for up to 29 months. The female calf of 1 migrant accompanied her mother for 2 years. In her 3rd year, she separated from her mother but migrated to the same areas she had travelled to as a calf and as a 1-year-old. One female and 1 male calf of resident elk stayed with their mothers for at least 9 months after birth. Although both where observed the following winter within their mother's annual home-ranges, both of their transmitters had failed.

### Migrant-resident ratio and sex-biases

The corrected migrant/resident ratio for the entire BRV population was 0.6 (Table 1). When these data were sub-divided into the areas west and east of Banff townsite (West-BRV, East-BRV), they demonstrated a migrant/resident ratio <1 in the East-BRV and >1 in the West-BRV.

In the BRV as a whole and in both sub-divisions, more bulls migrated than cows. This difference was consistent, and statistically significant in the entire area and in East-BRV (Table 1). In West-BRV, the sample size (15) was too small to reject the null hypothesis of equal numbers of migrants and residents, but 12 of 15 animals migrated.

## Survival

Thirteen radio-tagged adult elk of known migratory-status elk died during the study. All mortalities occurred at low elevations within or adjacent to the BRV. These deaths included equal numbers of residents and migrants. Human-related elk mortalities outnumbered natural mortalities 7:6. Human-caused mortalities included road-kills (4), railway-kills (1), hunting (1), and miscellaneous (1). Natural deaths included parasites (2), unknown (2), and wolf predation (2).

Although survival rates of radio-tagged adult elk were highest for migrants (0.97 cow, 0.86 bull),

confidence intervals on these estimates were too broad to reject the null hypothesis (Table 4).

Concurrent radio-tracking studies of timber wolves showed that wolves rarely used East-BRV (D. Huggard, pers. comm.). One pack used a den in the subalpine zone within the West-BRV and the other used a den approximately 20 km south of the BRV beside the Spray River and along an elk migration route.

Movements by individual wolves equaled or exceeded elk migration distances. Migration could take individual elk into the range of other wolf packs. The farthest elk migration (74 km) was across the Continental Divide and into an area where wolves were seen or heard throughout this study. Although there were small areas of high elevation range where wolves were not seen, in general, elk and wolves were sympatric at all seasons. Other potential predators preying on elk, and observed during the study included: grizzly bears (<u>Ursus arctos</u>), black bears (<u>Ursus americanus</u>), and cougar (<u>Felis concolor</u>). Of these, grizzlies were the most commonly seen and were sympatric with resident and migrant elk during the spring, summer, and autumn.

Table 1. Migrant/resident ratio<sup>a</sup> for radio-tracked adult elk in Banff National Park, 1986-88.

Sex	Area			
	BRV	BRV-West <sup>b</sup>	BRV-East <sup>c</sup>	
Bulls	4.3	7.0	3.0	
	(13/3) <sup>d</sup>	(7/1)	(6/2)	
Cows	0.5°	2.5	0.3 <sup>f</sup>	
	(10/21)	(5/2)	(5/19)	
Population <sup>g</sup>	0.6	2.7	0.4	

a excludes 3 cow elk that switched movement strategy between years and 3 elk captured in the summer

<sup>b</sup> radio-tagged west of Banff townsite in area frequented by timber wolves

<sup>c</sup> radio-tagged east of Banff townsite in area rarely used by timber wolves d numbers in brackets indicate observed number of

- individuals
- significantly smaller than the corresponding bull migrant/resident proportion, 2x2 Contingency table with Yates' correction, P=0.003; all statistical tests were made on the STATGRAPHICS software (Statistical Graphics Corporation) run on a microcomputer.
- f significantly smaller than the corresponding bull migrant/resident proportion, 2x2 Contingency table with Yates' correction, P=0.018
- <sup>g</sup> weighted by the estimated population composition (11% adult bulls, 89% adult cows, calves, and spike bulls)

Table 2. Horizontal and vertical movements<sup>a</sup> of migrant and resident radio-tracked adult elk<sup>b</sup> in Banff National Park, 1986-89.

Migrants		Residents	
Average (N) <sup>c</sup>	Range	Average (N)	Range
)			
30 <sup>d</sup> (14)	18-70	11 (4)	5-20
36 <sup>d</sup> (10)	18-74	14 (22)	7-36
$840^{d}(14)$	396-1147	419 ( 4)	122-945
1079 <sup>a</sup> (10)	701-1432	296 (22)	122-884
	Average (N) <sup>c</sup> 30 <sup>d</sup> (14) 36 <sup>d</sup> (10) 840 <sup>d</sup> (14) 1079 <sup>d</sup> (10)	Average Range (N) <sup>c</sup> 30 <sup>d</sup> (14) 18-70 36 <sup>d</sup> (10) 18-74 840 <sup>d</sup> (14) 396-1147 1079 <sup>d</sup> (10) 701-1432	Average Average $(N)^{c}$ Range Average $(N)$ 30d(14) 36d(10)18-70 18-7411 14 (22)840d(14) 1079d(10)396-1147 701-1432419 296 (22)

a calculated as the difference of the extreme observed locations during entire study period

<sup>b</sup> excludes three cows that switched movement classes between years

<sup>c</sup> numbers in brackets indicate observed number of individuals

<sup>d</sup> value for migrants significantly different from corresponding values for residents (Wilcoxon pairs test, P<0.05).</p>
Table 3. Median migration dates for radio-tracked adult elk in Banff National Park, 1986-88.

Depart/Return				Yea	r					
Sex	1986		(N) <sup>a</sup>	1987		(N)	1988		(N)	
Depart										
Bulls	June	2	(8)	June	7	(7)	June	8	(8)	
Cows	June	6	(9)	May 2	6	(12)	June	17	(13)	
Return Bulls	Sept	5	(6)	Sept	9	(7)	Sept	13	(8)	
Cows	Oct	3	(9)	Oct	2	(12)	Sept	19	(13)	

a numbers in brackets indicate observed number of individuals

Class	N	S	CIP	
Year				
Migrant cows			_	
1986-87	9	1.00	1.00-1.00	
1987-88	10	1.00	1.00-1.00	
1988-89	10	0.90	0.72-1.08	
Average	10	0.97	0.91-1.03	
Migrant bull				
1986-87	9	0.69	0.44-0.94	
1987-88	11	0.89	0.71-1.07	
1988-89	11	1.00	1.00-1.00	
Average	10	0.86	0.72-1.00	
Resident cow				
1986-87	20	0.89	0.75-1.02	
1987-88	20	0.94	0.84-1.05	
1988-89	20	0.90	0.76-1.03	
Average	20	0.91	0.78-1.03	
Resident bull				
1986-87	3	1.00	1.00-1.00	
1987-88	4	0.75	0.38-1.12	
1988-89	3	0.67	0.13-1.20	
Average	3.	0.81	0.50-1.08	

Table 4. Annual survival rates (S) and 95% confidence intervals (CI) for migrant<sup>a</sup> and resident radio-tagged adult elk in the BRV, 1986-89.

a excludes 3 cows that switched strategies between years <sup>b</sup> calculated following Pollock et al. (1989)

Table 5. Migrant/resident ratios (M/R), hunting status<sup>a</sup>, and timber wolf<sup>b</sup> status for various elk populations in the Rocky Mountains

Area	M/R	Huntir	ng Wolves	Reference
BRV, AB <sup>c</sup>	<1	N	Y	this study
Red Deer, AB	>1	Y	Y	Morgantini (1988)
East Kootenays,				-
BCc	>1	Y	Y	Woods and Hlady (1988)
Sun River, Mont	: >1	Y	N	Knight (1970)
Jackson Hole,WY	: >1	Y	N	Boyce (1989)

<sup>a</sup> classified as hunted if most of the population in a sport hunting zone during the hunting season <sup>b</sup> timber wolf status at time of study, all populations

had mountain lions present <sup>c</sup> AB=Alberta; BC=British Columbia

;

















Figure 2. Examples of elevational movements of 8 radio-tagged elk, BRV, 1986-88.



Figure 3. Mean elevation of resident and migrant radio-tagged elk during winter, summer, and rut, BRV, 1986-88. Letter above bars indicate sex (F/M), number indicates sample size, and asterisk indicates significant difference between migrants and residents.

#### Discussion

#### Seasonal movement patterns

Although elk at Jackson Hole, Wyoming moved in large groups (Boyce 1991), elk in a Montana population migrated singly or in matriarchical groups (Knight 1970). The staggered dates of migrating BRV elk suggest that elk in this population migrated singly or in small groups. Further, although most BRV migrants wintered at low elevation and summered at high elevations, individual behaviors such as multiple migration cycles per year, and specific migrations to rutting areas, illustrated that migration patterns varied widely between individuals. Because of the generally forested nature of the BRV and surrounding area, this behavioral variation could not have been identified without radio-tracking.

The failure to detect "calving grounds" (places where cow elk return to bear their young) agrees with research by Knight (1970) in the American Rockies and by Morgantini (1988) in an adjacent area of the Canadian Rockies. However, calving areas were identified by Boyce (1989) for the Jackson elk herd. A clear definition of what constitutes a calving area is lacking in these studies and it is possible that the discrepancy is semantic.

"Rutting grounds" (places where elk return to breed each autumn), have been reported for resident bull elk

in California (Franklin et al. 1975). In the BRV, cows were concentrated in the valleys during the rut (resident cows plus some of the returning migrants) but rarely entered the townsite. Movement by bulls to rutting grounds within the valley, but outside the townsite, probably gave these bulls access to more cows than would have been available on their summer ranges. Migrant bulls generally returned to the valley at the onset of rut (early September), before the peak in mating opportunities (mid to late September). This movement placed them in the sites with the most mating opportunities at the onset of the sexual receptivity of cows. Since migrant cows generally returned at the end of the rut, I presume that most of them mated with migrant bulls that remained on summer ranges or that they mated late in the rut.

## Mixed ESS

Although partial migration has been observed in many elk populations (Scotland, Darling 1937; Scandinavia, Langvatn and Albon 1986; coastal and mountainous areas of the United States, Adams 1982, McCullough 1985; Canadian Rockies, Morgantini 1988), there is little information on fidelity to movement strategy. The existence of "switchers", such as demonstrated in this study, requires relatively long-term, continuous tracking and therefore may be more common than is reported in the literature.

On the basis of high ratios of 1-year-old bulls spending the summer on the "winter" range of the Jackson Hole elk, Martinka (1969) and Boyce (1989) suggested that 1-year-old bull elk are less likely to migrate than are other sex/age classes. The Jackson Hole herd has a migrant/resident ratio >1. Therefore, most of these young bulls presumably migrated during their first summer with their mothers but failed to do so during the following summer (=switching). There are no data to suggest a disproportionate number of 1-year-old bulls at low elevation in the BRV during the summer.

Since young elk accompany their mothers at least through their first summer and autumn, the female-bias in resident BRV elk should result in more calves being exposed to the residents than to migratory individuals. However, by the time they are adults, there are fewer bulls in the population (Flook 1970, Chapter 6), and most of these are migrants. Either more bulls "switch" to migration as a strategy, or unbalanced mortality (or dispersal) results in the change of ratio. Between the ages of 1 and 2, the proportion of bulls to adult cows decreases sharply in this population (Flook 1970, Chapter 6). Flook (1970) speculated that this might be due to greater dispersal by 1- or 2-year-old males. If this is the case, then bulls in these age classes with resident mothers should be the most frequent dispersers. This could be tested by radio-tracking bull calves of

resident mothers from birth through to their 3rd birthday.

Since most bulls and many cows return to the valley during September, many migrants are sympatric with residents during the rut. This makes the existence of 2 genetically distinct sub-populations unlikely.

# Learning

An alternative explanation for choice of movement strategies based on learning, has been presented by Murie (1951), McCullough (1985), and Baker (1978), who suggest that young animals develop patterns of home-range use through association with others (especially their mothers) and by individual experience. Strategies proven to work (the calf survived to breeding age) should be preferred over unknown strategies in the absence of intervening variables (climatic extremes, the appearance of predators, shortage of mates).

In the single instance where a mother-young pair was continuously tracked in the present study, the daughter adopted the movement strategy of her mother. Although Clutton-Brock et al. (1982) demonstrated a close association between mother and daughter red deer (also <u>Cervus elaphus</u>) during the first years of the daughter's life, this trait has not been extensively documented in elk or other ungulates. More empirical data are needed of tracked mother/young pairs from partial migration populations to investigate if most

young adopt the movement pattern of their mothers.

Morgantini (1988) stressed that flexibility in movement patterns allows elk to adjust to a variable environment and Boyce (1991) noted that such phenotypic plasticity can be shaped by natural selection. Bergerud (1974) developed much the same argument to explain variation in caribou (<u>Rangifer tarandus</u>) movements, and suggested that adaptability was a major adaptation in that species. The patterns and variations observed in this study support these views. Flexibility would allow elk to make a conditional assessment of density and environmental variables, and to either migrate or stay accordingly.

## Migrant/resident ratio

The excess of migrants over residents in African ungulates (Fryxell et al. 1988) contrasts to my results for the BRV as a whole (M/R= 0.6). However, as Fryxell et al. (1988) noted, the short distances involved in altitudinal migration may not take migrants beyond the foraging range of their principal predators.

Although migrants outnumbered residents (M/R= 2.7) within the West-BRV, this difference was not statistically significant. In addition to being the primary area used by wolves in the BRV, West-BRV differs from East-BRV in elevation, snowfall, vegetation zones, and human densities. A larger sample of radio-tagged elk studied over a range wolf densities is required to

establish a relationship between migrant/resident ratios and predation in this population.

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Predators can migrate too. This appears to be the case in the mountain lion-elk population studied by Seidensticker et al. (1973). These lions made altitudinal movements in concert with migrating elk and deer (<u>Odocoileus</u>). Harestad (1979) suggested that risk of predation might be less for migrating black-tailed deer (<u>Odocoileus hemionus columbianus</u>) during the period when wolves are feeding young at den sites. However, the deer he studied migrated on average less than 5 km from their wintering areas. In my study area, wolves moved over much larger distances and wolf mobility equalled or exceeded the elk migratory range during all seasons. The hypothesis that wolves are less likely to capture elk on summer ranges remains to be tested.

The BRV elk population is unusual today in that wolves are principal predators, few BRV elk are subject to sport hunting, and migrant/resident ratio is <1 (Table 5). These differences are likely to confound comparisons with other populations.

As Lima and Dill (1990) observed in their review of behavioral decisions made under the risk of predation, the failure to avoid predators has both immediate and permanent consequences on individual fitness. Hornocker (1970) noted that elk and deer reacted to kills by mountain lions by moving away from the kill sites,

sometime to adjacent drainages. Numerous authors have demonstrated that sport hunting can disturb elk movement patterns (Altmann 1956, Morgantini and Hudson 1985, Edge et al. 1985, Merrill et al. 1988, Boyce 1989).

It seems likely that, where elk are hunted, they avoid human contact as much as possible. This could result in a different ratio of residents to migrants and discourage return to low elevations. The potential for human influence on the migrant/resident ratio is illustrated by the seasonal movements of elk in the Red Deer River drainage immediately north of the BRV (Morgantini 1988). "Most" animals in this population were migratory and had a two-stage migration from winter range outside the park, to an intermediate range inside the park, and then to summer range farther within the park. They reversed this pattern in the autumn. Although timber wolves were principal predators of elk in both the BRV and the Red Deer River valley, Red Deer elk were hunted and were not habituated to humans. Although they left the winter range at about the same time as BRV elk, they remained within the protection of the park for about a month longer in the autumn.

During the 1940's, disturbance by humans and timber wolves in the BRV may have influenced the timing of the autumn elk migration and the migrant/resident ratio. In 1943-44, an intensive effort to reduce the elk population began and prescribed numbers were shot during

the late autumn or early winter (Chapter 6). Coincidentally, wolves reappeared in Banff and were relatively common by 1947 (Flook 1970). At the start of this period, migration was believed to be restricted to adult bulls and migrants were thought to return in September (K. Mitchell, CPS, 1944, unpubl. data). By autumn 1948, the park was unable to provide an accurate estimate of elk numbers because most of them had not returned to the valley (K. Mitchell, CPS, 1948, unpubl. data). Green (1949) speculated that this was due to either shooting disturbance or the presence of timber wolves.

Like movements of mountain lion (Seidensticker et al. 1973), use of space by elk is flexible. Simple categorization of populations as either migrant or resident may mask the relationships driving the system. As Morgantini (1988) and Boyce (1991) suggested, phenotypic plasticity (flexibility) in elk appears to be an adaptation to cope with a variable environment.

### CHAPTER 3. PHILOPATRY

# Introduction

Movements of individuals within and among populations are of central importance to genetics, ecology, and conservation. However, analysis of these movements is complicated by problems of consistency in definitions and inequalities of scale (Chepko-Sade and Halpin 1987). For example, migration in the context of genetics refers to the dispersal of genes between populations (Chepko-Sade and Shields 1987). In vertebrate ecology, migration describes the seasonal return movements of individuals between alternate ranges (Sinclair 1983). Therefore, even though migrant individuals might undertake extensive movements, if they return to the same area to breed, they remain part of a restricted population in a genetic sense.

The tenacity with which an organism returns to specific areas or groups, is generally referred to as philopatry (Greenwood 1980). In contrast, dispersers either move away from their place of birth (natal dispersers) or move between breeding sites (breeding dispersers) (Shields 1987). In practice, the distinction between philopatry and dispersal is less clear. A bird which might be philopatric on a regional scale, might not be philopatric at some other scale (e.g. patch).

In response to this problem, definitions of "dispersers" have become numerous in field studies.

Dispersers have been defined as those animals which left the study area and never returned (Mech 1987, Boonstra et al. 1987), or as those that moved some fixed distance away from where they were born or where they previously bred. These distances have been established on the basis of the maximum movements of migrant individuals (Bunnell and Harestad 1983), numbers of territories or home-ranges traversed (Shields 1987, Arcese 1989) or simply whether or not consecutive home-ranges overlapped (Edge et al. 1985).

Detailed studies of several large terrestrial mammals have suggested high degrees of adult philopatry (Knight 1970, Adams 1982, Nelson and Mech 1987, Morgantini 1988) and have related inbreeding to conservation (Weishampel 1990). However, theoretical criteria for defining philopatry (or dispersal) are lacking.

Many studies have noted that elk habitually return to seasonal ranges (Knight 1970, Adams 1982, Edge et al. 1985, Morgantini 1988, Boyce 1989). Elk are polygynous, seasonal breeders, with female-biased adult sex ratios (Flook 1970). Populations may be resident, migratory, or partially migratory. According to Greenwood's hypothesis, polygynous species such as elk should have male-biased dispersal (Greenwood 1980), and females should show the greatest site attachment. While there is evidence that 1-year-old bulls (spikes) are the

most frequent dispersers in elk (Boyce 1989), good evidence of male-biased dispersal is lacking. There also are few comparative data on philopatry of resident versus migrant animals within a population. Since residents move over a smaller total range than migrants, they might be more philopatric.

In this study, I measured the consistency with which adult elk in a partially migratory population returned to seasonal ranges in the BRV. Strong philopatry predicts that individual elk use the same areas repetitively, such that the distances separating seasonal ranges during consecutive years are less than predicted by a random model. I also compared the degree of philopatry to test whether cows and residents were less philopatric than bulls and migrants.

### Methods

I examined philopatry using the radio-tagged sample of 53 elk, field methods, and definitions described in Chapter 2.

Consistency in use of annual home-ranges was measured by comparing successive annual home-ranges of individual elk. Annual home-ranges were estimated using McPAAL software (Stuwe and Blohowiak 1985) to generate minimum convex polygons. These polygons are formed by connecting the outermost locations without creating any interior angle greater than 180 degrees. Annual polygons were generated from February to February, for 3 years (1986-89). Successive annual home-ranges for an individual were superimposed on a digital plotter and the area of overlap was calculated as a percent of the total area.

Consistency in use of seasonal ranges was measured by partitioning the data into 7 periods starting with winter 1986 and ending with winter 1989. Seasons were defined as <u>winter</u>, <u>summer</u>, and <u>rut</u> as described in Chapter 2 (p.18).

If only 1 point was available per season (as was the case for some migrants in the rutting season), that point became the centre of activity. Otherwise, for each radio-tagged elk, I determined the harmonic centre of its observed locations on a 1000 m grid for each season (Dixon and Chapman 1980). I then calculated the

straight-line distances between these centres in that season in consecutive years (e.g. the distance between individual's rutting season activity centres in 1986 and 1987).

The frequency distributions of observed seasonal centres of activity were then compared to a frequency distribution derived from a model simulating random location of successive activity centres. The random model was generated by calculating the point-to-point distances for 1000 random pairs in a hypothetical square of 196 km<sup>2</sup>. This area approximates the montane zone of the BRV which is available to elk on a year-round basis. The model generated a unimodal distribution of distances between seasonal ranges in different years with a mean of 10.62 km and a range of distance classes from 0-1 to 19-20 km. The actual dimensions of the available area are approximately 40 x 5 km in winter and 90 x 40 km in summer and would have generated frequency distributions with higher means and ranges. The Kolomogrov-Smirnoff 2-sample test on was used to compare distributions.

### Results

### Overlap of consecutive annual home-ranges

One bull left the BRV and did not return subsequently (emigration rate 0.008). The remaining animals either stayed in the BRV throughout the year, or made seasonal migrations from the BRV with travel distances of up to 74 km (Tables 2,6).

All radio-tracked resident and migrant elk had overlapping annual home-ranges in consecutive years (Table 7). Annual home ranges of 26 elk tracked for 3 years, also had overlapping ranges. The 2 radio-tagged elk with known home-ranges in 1981 had ranges that overlapped with the 1981 ranges in 1986-89.

Two cows originally marked in Kootenay National Park were recovered within the BRV during the study. One was radio-tagged 13 years previously, when she wintered 73 km to the west along the Kootenay River. The other was ear-tagged 9 years earlier just west of the Continental Divide approximately 5 km from where she was recovered. Both cows were 2-year-olds when originally marked.

# Distances between inter-annual seasonal ranges

Average inter-annual distances between consecutive activity centres for winter, summer, and rutting ranges were from 3.0-4.2 km. The frequency distributions were skewed to the right (Table 8, Figures 4,5,6). There were no significant differences in the frequency

distributions of cows and bulls, or of migrants and residents.

The mean inter-annual distances between seasonal centres of activity were significantly less than predicted by the random model in all cases (Table 8, Figures 4,5,6).

The majority (75%) of migrant elk returned to the BRV before or during the rut (Table 9). Therefore, residents and migrants were sympatric at this time and most (87%) radio-tracked elk were in the BRV.

Of the 6 cows which remained out of the BRV during 1 or more rutting seasons, 3 returned to the BRV for at least 1 rutting season. The 3 which never returned during the rut had the longest migration distances recorded.

Of the 3 bulls not in the BRV during 1 or more ruts, 1 died after 1 year. Another migrated during the last year of the study to an adjacent elk population 13 km west of the Continental Divide during the rut and later returned to the BRV. The last animal was out of the BRV during the rut during the first 2 years of the study, and then returned to the BRV during the last rutting season.

Status	19	1986		1987	1988		
	MIG	RES	MIG	RES	MIG	RES	
Bull	9	3	8	4	9	3	
Cow	9	17	13	18	13	18	
Both	18	20	21	22	22	21	

Table 6. Numbers of migrant (MIG) and resident (RES) radio-tracked elk<sup>a</sup> in Banff National Park, 1986-88.

a includes three cows which switched between migrant and resident status between years

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Table 7. Overlap (%)<sup>a</sup> of annual home-ranges during consecutive years for radio-tracked elk in Banff National Park, 1986-88.

Elk group	NÞ	Ove	Overlap			
Years		Mean	Min.	Max.		
Cows				·····		
1986-87	21	54	16	80		
1987-88	28	55	24	78		
1986-88	20	40	15	63.		
Bulls						
1986-87	8	55	43	71		
1987-88	10	69	42	90		
1986-88	6	44	25	70		
Both sexes						
1986-87	29	54	16	80		
1987-88	38	59	24	90		
1986-88	26	40	15	. 70		

a percentage of aggregate area overlapped by consecutive ranges <sup>b</sup> sample size

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Table 8. Distances (km) between inter-annual home-range centres<sup>a</sup> during consecutive years for radio-tagged elk in Banff National Park, 1986-88<sup>b</sup>.

Elk group	NÞ	Distances	between	seasonal	centres <sup>c</sup>
Season		Mean	Min.	Max.	
All elk					
Winter	117	3.	.0 0.	0 24.6	
Summer	73	4.	.2 0.	1 33.7	
Rut	69	3	.0 0.	0 12.1	
All residents					
Winter	60	2 .	.7 0.	0 18.8	
Summer	37	2.	.3 0.	1 6.6	
Rut	33	2	.6 0.	0 8.7	
All migrants					
Winter	50	3.	.5 0.	3 24.6	
Summer	31	6	.8 0.	2 33.8	
Rut	31	3	.3 0.	6 12.1	
All cows					
Winter	88	2	.7 0.	0 18.8	
Summer	55	4	.7 0.	1 33.7	
Rut	51	3	.2 0.	5 12.1	
All bulls					
Winter	29	3	.9 0.	1 24.6	
Summer	18	2	.9 0.	2 12.1	
Rut	18	2	.1 0.	0 9.8	
Model <sup>d</sup>	1000	10	.8 0.	2 19.3	

winter-winter, summer-summer, rut-rut
data for all years pooled
harmonic centres

<sup>d</sup> random pairs in a 196 km<sup>2</sup> square

.

Table 9. Number of radio-tagged elk within and outside the BRV during the rutting seasons, 1986-88.

	·····		
Location	······································	Year	
Class	1986	1987	1988
Within BRV	· · · · · · · · · · · · · · · · · · ·		<u> </u>
Resident cow	17	18	18
Migrant <sup>a</sup> cow	- / /	õ	10
Regident bull	3	2	±0 2
	3	4	3
Migrant <sup>a</sup> bull	1	1	8
Total in BRV	31	38	39
Outside BRV			
Migrant cow	5	4	3
Migrant bull	2	1	1
migrane buil	2	-	-
Total out of BRV	7	5	4
Total Tracked	38	43	43
Percent in BRV	82	88	91

\* returned to the BRV before or during the rut



Figure 4. Distances between centres of consecutive winter ranges.



Figure 5. Distances between centres of consecutive summer ranges.



Figure 6. Distances between centres of consecutive rutting ranges.

#### Discussion

## Seasonal ranges

During 4 consecutive years in the Upper Red Deer River valley, Morgantini (1988) observed that 11 of 18 radio-tagged elk returned to the same summer ranges and 16 of the 18 returned to the same winter ranges. However his criteria for defining "return" were not presented. Similarly, Knight (1970) found that most (but not all) adult elk in his Montana study area, returned to the same winter and summer ranges. The results obtained in my study confirm that most adult elk persistently centre their seasonal activities on the same ranges from year-to-year.

Greenwood's (1980) hypothesis suggests that elk have male-biased dispersal, and female- and resident-biased relative philopatry. Although the only radio-tagged elk to permanently leave the BRV during the study was an adult bull, adult cow dispersal was demonstrated for 2 animals immigrating to the BRV from Kootenay National Park. These data are too meagre to support or refute the hypothesis of sex-biased adult dispersal. There were neither female- or resident-biases in relative philopatry of adult elk, as predicted by Greenwood's hypothesis.

Based on their work on white-tailed deer in Michigan, Nelson and Mech (1987) suggested that the restricted movements made by many large mammals could

lead to the development of demes with little reproductive contact. Amongst the radio-tagged elk followed in this study, most animals centred their rutting season activities within a few km of their previous rutting season range and most of the population was sympatric during the rut. However, a few radio-tagged elk did not return to the BRV during the rut and could have bred either with other BRV migrants, or with elk from other populations sharing a common summer/rut range. This is illustrated by radio-tracked elk sharing a summer/rut range in the Kananaskis Lakes area of Alberta and returning to winter ranges 200 km apart near Sparwood, British Columbia and Canmore Alberta (Woods and Hlady 1988; T. Nette, Alberta Fish and Wildlife, unpubl. data). Since some elk alternated between rutting in the BRV and other areas, and some alternated between resident and migrant status (Chapter 2), return migrations may promote gene flow.

Although breeding dispersal was rare amongst these elk, natal dispersal rates in elk have not yet been studied. Amongst most mammals, young bulls are thought to be the predominant dispersal group. In the case of elk, young of both sexes typically stay with their mothers for the first year and become sexually mature after 2 years. Therefore, future research on philopatry should focus on 1-, 2-, and 3-year-olds, especially males.

### Definitions of philopatry

In most studies mentioning persistent use of annual or seasonal home-ranges by elk, home-range overlap is the implicit definition of philopatry. Edge et al. (1985) explicitly defined site fidelity (=philopatry) as any overlap. However, since all of their study animals (31 cows) had overlapping ranges, the issue of adjacent, non-overlapping ranges and dispersers was not addressed. In the present study, of 68 cases where year-to-year overlap of annual home-ranges could be determined, 67 overlapped.

The problem with the overlap definition is that it disregards the distance moved. Clearly, animals moving to adjacent home-ranges have different consequences for both population ecology and gene flow than do long-distance dispersers.

Both the modified Cole's association index (values 0 to 1) used by Edge et al.(1985) and the percent overlap (values 0 to 100) used in the present study, are difficult to use in assessing the degree of philopatry. Indices of overlap of successive home-ranges are highly dependent on the shape of the home-range and the method used to calculate the range. Although the 100 % minimum convex polygon is commonly employed to map home-ranges, it is also very susceptible to distortion due to outlying points (Dixon and Chapman 1980). A single outlying point can greatly alter the calculated

area of overlap. It is also possible that the identified area of overlap falls in an area not used during either year and is an artifact of the mapping technique. Another problem is that of scale. In a small study area, home-range could overlap by chance, whereas in a large area this is unlikely.

Bunnell and Harestad's (1985) definition of dispersal as a distance greater than any observed return migration (5 km) for black-tailed deer on Vancouver Island, is arbitrary and limiting. In the present study, migrants travelled up to 74 km; and in other areas of the western mountains, migrations of up to 100 km are quite common (Boyce 1989). In Europe, migratory red deer travel up to 150 km (Langvatn and Albon 1986). Of the 3 elk that changed their winter ranges during this study (1 emigrated from the BRV and 2 immigrated to the BRV), all were within the known maximum migratory range for the species.

Application of distance rules based on home-range diameters (Shields 1987) are subject to problems of mapping technique and determination of the number of diameters home-range diameters which create the significant distance. As Arcese (1989) pointed out, home-range sizes may vary with population size, and therefore do not provide a universal scale for inter-specific comparisons. In addition, empirical data on song sparrow (Melospiza melodia) dispersal did not

demonstrate that relatedness decreased with numbers of territories traversed in a study of short-range dispersal (Arcese 1989).

Approaching the problem of philopatry from a probabilistic point of view accepts that philopatry and dispersal are relative rather than absolute terms. Therefore, an observed distribution can be tested against another observed or hypothetical distribution. In the present study, this allows the comparison of residents with migrants, bulls with cows, and the population as a whole with a random model. I conclude that relative to a random distribution, this population of adult elk is philopatric.

## CHAPTER 4. NET COST OF MIGRATION

## Introduction

Migration should be favored when the benefits of moving outweigh the benefits of not moving (Baker 1978). Potential benefits of seasonal migration include: 1) access to better quality and quantity of food; 2) reduced competition for food; 3) escape from predation and other forms of harassment; 4) access to increased mating opportunities; and, 5) avoidance of severe seasonal weather (Sinclair 1983, Festa-Bianchet 1988, Sinclair and Fryxell 1988, Chapter 3). Potential costs of migration include: 1) energy requirements for travel between ranges; 2) time lost from other activities; and, 3) increased mortality due to travel hazards and predation. Within a species, all individuals may not face the same costs and benefits. For example, the cost/benefit ratio evaluation may vary with the size of the individual (Tucker 1975) and individuals may vary in their genetic tendencies to move (Berthold and Querner 1981).

Migrations by terrestrial mammals are generally less extensive (<100 km) than migrations by birds, and are assumed to be less costly energetically (Baker 1978), although these migration costs have rarely been quantified. However, there is a growing body of information on the cost of locomotion, particularly for large ungulates (Parker et al. 1984, Gates and Hudson

1978) so it is now possible to combine empirical data on migration with physiological information to estimate the energetic costs of migration.

Partial migrants (species that include both residents and migrants) offer the opportunity to compare net costs and benefits of migration. In this study, I used data on movements of residents and migrants to calculate energy and travel time costs and asked the following questions: 1) Are energy and time costs for migration significant relative to other life-history costs?, 2) How do energetic costs of migration vary between age/sex classes? and, 3) Do the relative costs of migration allow predictions on the relative mobility of age/sex classes?

#### Methods

### Energy calculations

The net energy cost of migration was calculated as the estimated locomotion cost for migration less the estimated locomotion cost expended by non-migrating elk during the same time interval. Energy expenditures (kcal·kg<sup>-1</sup>·km<sup>-1</sup>) for locomotion on level and up-sloping ground were computed using the equations for elk presented by Parker et al. (1984):

 $E_{level} = 2.97 \times M^{(-.34)}(kg)$  (1);

 $E_{up} = 3.57 \times M^{(-.13)}(kg)$  (2).

Resident cow elk made only insignificant vertical movements during the spring migration period (results to follow), and (1) was used to estimate their movement energy expenditures. For migrant elk, I considered migrations to consist of a 4 km upslope component resulting in a 1 km vertical rise (Chapter 2), and a level component for the remainder of the migration distance:

$$E_{mig} = (E_{up} \times 4) +$$

 $((E_{level} \times (Dist-4)) (3),$ 

where Dist is the estimated 1-way travel distance in km.

I scaled the net energy expenditures for migration by daily energy expenditures estimated for resting elk using the equation presented by Bobek et al. (1983) to estimate kcal·kg<sup>-1</sup>·day<sup>-1</sup> :

$$E_{rest} = 90 \times M^{(0.75)}(kg) (4).$$

## Time and distance estimates

On an annual basis, average horizontal distances traveled by migrant and resident elk (Chapter 2, Table 2) were used to calculate average time requirements for movements. Average hourly speeds were not determined but assumed to be  $3.0 \text{ km} \cdot \text{h}^{-1}$ , a rate observed by Gates and Hudson (1978) in an experimental situation. This is slightly faster than the  $2.5 \text{ km} \cdot \text{h}^{-1}$ . rate observed by Craighead et al. (1973) for free-ranging elk.

During May and June 1988, elk with previous histories of migratory behavior were monitored on a daily basis within the valley. When their radio signals disappeared, an attempt was made to track them each day until they reached their summer range. Incidental observations of radio-tracked elk allowed additional calculations of travel times. During May 1988, I followed 10 resident cows (1 switched to migrant status later in the summer) on a daily basis and estimated their net daily movements. For both migrants and residents, the daily movement distance was assumed to be a straight line between relocation points. Since observations were made at comparable times during consecutive days, observed travel times are expressed in km day<sup>-1</sup>.

The net time cost of migration was calculated as the estimated time for migration less the estimated time spent moving by non-migrating elk during the same time
interval.

# Body weights and sex/age classes

Body weights were obtained from freshly-killed, intact elk which had died in collisions with automobiles and trains within the BRV. In most cases, the seasonal movement status of the dead elk was unknown. These data were partitioned into seven categories based on age and sex: newborn calves (June), July calves, September calves, 1-year-olds, 2-year-olds, >2-year-old cows, and >2-year-old bulls. The newborn weight was that of the largest fetus measured during the study. July calf weight estimated the mass of a young elk shortly after making its first upslope migration (in June) and data from September weights estimated the masses of calves during their first return journey.

#### Results

## Migration time and speed

Most migrations between winter and summer ranges took 3 days or less. An exception was a cow elk that calved between ranges. She did not move for 3 weeks after calving and then moved to her summer range.

In May and June 1988, migration speed of bulls averaged 7.1 km·day<sup>-1</sup> and cows averaged 9.2 km·day<sup>-1</sup> (Table 10). The farthest movement in a single day recorded during the study was 24.2 km (an adult cow). Travel speed in km·h<sup>-1</sup> could be determined in a single case where an adult cow moved 21.43 km in 4 h (5.1 km·h<sup>-1</sup>).

# Body weights

The largest elk fetus examined in the study weighed 21 kg. July and September weights for calves averaged 51 kg (N=7) and 104 kg (N=8) respectively, while 1- and 2-year-old elk averaged 165 kg (N=21) and 202 kg (N=11). Cows and bulls >2 years old weighed an average of 238 kg (N=29) and 339 kg (N=22) respectively, and were significantly heavier than other age classes (t-test, P<0.05).

#### Net costs

Net energy costs for migration based on annual movements averaged 12.84 kcal·kg<sup>-1</sup> for bulls and 15.33 kcal·kg<sup>-1</sup> for adult cows (Table 11). The relative net energy requirement for migration decreased with

increasing body size (Figure 7).

The net energy cost for migration based on observed cow elk movements during the spring of 1988 was 8.86  $kcal\cdot kg^{-1}\cdot day^{-1}$  (Table 10). Making the assumption that resident bulls moved similar distances as resident cows, the net energy cost for migration by bull elk was 7.47  $kcal\cdot kg^{-1}\cdot day^{-1}$ .

The calculated daily resting energy requirements for adult cow and bull elk were 22.91 and 20.98  $kcal\cdot kg^{-1}\cdot day^{-1}$  respectively.

Net time requirements for migration based on annual movements averaged 6.3 h for bulls and 7.3 h for cows (Table 11).

Table 10. Daily travel distances of resident<sup>a</sup> elk compared to daily travel distances of migrant<sup>b</sup> elk during migration, May and June, 1988.

Sex	Status	Sample	km/day	(S.E.)
Cow	Resident	10	1.2	(0.15)
	Migrant	8	9.2°	(1.28)
Bull	Migrant	7	7.1°	(1.31)

average straight line distance between locations measured daily May 16-22, 1988

<sup>b</sup> average straight line distance between locations measured while the elk was migrating, May 18-June 18, 1988

c significantly different from resident average
(Wilcoxon pairs test, P<0.05)</pre>

Table 11. Net 1-way travel times (h) and energy requirements (kcal·kg<sup>-1</sup>) for migrant elk based on annual movements of migrant and resident radio-tracked elk.

Net requirement	Bull	Cow
Timeª		
Average Minimum Maximum	6.3 5.1 16.6	7.3 2.4 12.7
Energy <sup>b</sup>		
Average Minimum Maximum	12.84 10.38 25.54	15.33 10.25 22.72

 $^{\rm a}$  computed from data presented in Table 2 Chapter 2 and an estimated walking speed of 3  $\rm km \cdot h^{-1}$ 

<sup>b</sup> computed from data presented in Table 2 Chapter 2 and formulae presented in the text



Figure 7. Net cost (Kcal.kg) of an upslope migration (36 km) for various weight classes of BRV elk. (A=new-born calf, B=July calf, C=September calf, D=1-year-old, E=2-year-old, F=>2-year-old cow, G=>2-year-old bull)

# Discussion

Bobek et al.(1983) modeled the energy budget of BRV elk and calculated the annual energy requirements to be 3.09 x 10<sup>6</sup> kcal for adult bulls and 3.57 x 10<sup>6</sup> kcal for pregnant cows. Based on annual movements, the average 1-way net cost of upslope migration estimated in this study represents 0.14% and 0.10% respectively of these requirements. Based on the direct comparison of migrant and resident elk movements in the spring of 1988, the net migration cost for cow elk was 0.06% of the estimated annual energy requirement.

In comparison, Bobek et al.(1983) estimated costs of reproduction for adult cows as 0.67 x 10<sup>6</sup> kcal or 18.8% of the annual energy budget of pregnant cows. Nelson and Leege (1982) presented data suggesting that the annual energy expenditure for a pregnant cow elk would be approximately 2.77 x 10<sup>6</sup> kcal, of which 14.5% (0.40 x 10<sup>6</sup> kcal) would be required for pregnancy and lactation. Relative to the costs of reproduction, I conclude that net energy costs for migration in BRV elk are trivial.

The horizontal and vertical distances traveled by migrating BRV elk are within the observed ranges for other elk populations and other North Temperate Zone cervids (Table 12). North Temperate Zone cervids have reported average migration distances in the range of 2-67 km horizontally and 200-1000 m vertically. With the

exception of tundra caribou which travel up to 2500 km, reported maximum migration travel distances for other cervids ranged 3-150 km. For the maximum reported migration distance in <u>Cervus elaphus</u> (150 km, Norway, Table 12), the energy investment would be less than 1% of the species' annual energy budget. Most migrations would require much less then 1%.

## Speed of travel

Descriptive accounts of the speed of migration in elk present conflicting views. Brazda (1953) described migration as "movements to higher elevations as the elk season progressed", while Peek and Lovaas (1968) reported migration started in August and ended in November and December. Other authors report migration as a rapid event, sometimes accomplished overnight (Knight 1970, Hudson and Morgantini 1988). Similarly, reported speeds for other North American cervids vary from "slow" (e.g. mountain caribou, Edwards and Ritcey 1956) to "fast" (black-tailed deer, Harestad 1979; tundra caribou, Fancy et al. 1989). While some of this discrepancy may be due to inter-specific and inter-population differences, it is also possible that it is in part an artifact of observation technique. Actual calculation of speed of travel requires the type of continuous data usually only available from individually radio-tracked animals.

The fastest cervid migration speed I have found in

the literature is 40 km·day<sup>-1</sup> for tundra caribou (Fancy et al. 1989). They reported pregnant cows averaged 7-24 km·day<sup>-1</sup> while migrating. This is similar to the speeds observed for elk during my study (2-25 km·day<sup>-1</sup>).

The rapid migrations made by some cervids are not consistent with the view that migrants follow the growth of their food plants upslope in the spring (Harestad 1979). However, if familiarity with specific ranges (summer and winter) is an advantage to individuals (knowledge of food patches, escape routes etc.), then rapid migrations may serve to minimize time spent in relatively unfamiliar or unfavorable territory. Relative energy costs

Migrant cows may give birth on either summer or winter ranges, or on route between ranges. Newborn elk do not migrate immediately after birth (Knight 1970, Adams 1982, Boyce 1989). By late June or July, calves have more than doubled their weight and reduced their relative energy investment in migration (Figure 7). If they are born on the winter range or between ranges, they then accompany their mothers to the summer range.

Energy investment in migration decreases relative to body size (Figure 7) suggesting that relative mobility might increase with body size. However, adult cows are usually accompanied by young (Woods 1990) and their mobility should be thus constrained. Therefore, mobility as predicted by relative energy investments,

would predict adult bulls, non-lactating adult cows, 2-year-olds, and 1-year-olds to be the most mobile groups.

In BRV elk, the majority of adult bulls followed in this study were migrants whereas most adult cows were residents (Chapter 2). Furthermore, the most complex migration patterns (up to 3 cycles per year) were seen in adult bulls. Migration distance did not vary significantly between the sexes. Although it is poorly documented, dispersal in elk is thought to be most prevalent in 1- and 2-year-old males (Flook 1970).

Table 12. Horizontal and vertical distances<sup>a</sup> reported for migrating elk and other North 

m j	igra	ting	elk	and	other	North	Temperate	e cervi	ds.
-----	------	------	-----	-----	-------	-------	-----------	---------	-----

Species Area	Av.	Later Max.	al(km Min.	l) Vei Av	tical Max.	(m) Min.	Source
Elk CND Rockies CND Rockies CND Rockies	32 50 -	74 69 100	14 26 -	951 1000 -	1432	392 _ _	this study Morgantini1988 Woods and
USA Rockies Norway	-	129 150	2 -	800 -	1067	610 -	Adams 1982 Langvatn and Albon 1986
USA Nevada	-	150	-	<del>.</del>	1219		Gruell and Papez 1963
Black-tailed D CND BC	2	3	1	200	400	0	Harestad 1979
White-tailed D USA, Various	eer 6	89	13	-	-	-	Marchinton and Hirth 1984
<u>Caribou</u> USA, Alaska, T	'undı -	a 2500		-	-	-	Fancy et al. 1989
CND, AB, Woodl	and 15	26	5	-	-	-	Edmonds 1988
CND BC Mount	67	134	33	-	-	-	Edmonds 1988
CND, BC, Mount	.a.m -	-	-	-	1067	-	Edwards and Ritcey 1959
Moose CND, AB	-	20+	-	-	-	-	Hauge and Keith 1981
CND, BC	-	64	-		1372	-	Edwards and
USA Alaska	-	100	-	-	-	-	Van Ballenberghe
Europe Sweden	-	150 14	_ 60	-	-	-	Pullianen 1974 Sandegren and Bergstrom 1983

<sup>a</sup> one-way

#### CHAPTER 5. DIET COMPOSITION AND QUALITY

# Introduction

Altitudinal migration is a common behavior amongst North American ungulates living in mountainous areas (Fryxell and Sinclair 1988). Several possible benefits have been proposed for these migrations, the most favored being a nutritional advantage over residency (Klein 1965, Hebert 1973, Morgantini and Hudson 1983). Since forage quality generally peaks in young, rapidly growing plants and then declines as the plants mature (Johnston et al. 1968, Nelson and Leege 1982), animals could benefit from tracking early growth stages as spring advances from valley bottom to alpine. In this case, then at any time during the growing season, migrant animals should have access to more nutritious forage than if they had remained on low elevation ranges.

Empirical data for various North American ungulates on forage quality, animal condition, and animal movements, do not consistently support the hypothesis that migrants have access to better quality food. In bighorn sheep ranges in Western North America, forage quality may be higher (Hebert 1973), lower (Festa-Bianchet 1988), or similar (Krausman et al. 1989) in high elevation sites compared to low elevation sites at the same time. On elk summer ranges differing substantially in altitude, plant species, and vegetation

structure, Baker and Hobbs (1982) found consistency in diet quality and suggested that elk can generalize their choice of feeding habitats without incurring a loss in diet quality.

Langvatn and Albon (1986) observed that migrant elk returning to low elevation ranges were heavier than residents in a partially migratory Scandinavian population. However, as Morgantini (1988) noted in his study of elk in the Canadian Rockies, even in populations where a nutritional advantage for migrants is suspected, the coexistence of healthy non-migratory elk suggests that non-migratory individuals may be able to compensate (e.g. dietary changes, increased intake, increased selectivity).

Poor correlation with nutritional quality is suggested by Brazda's (1953) observation that most migrant elk in a Rocky Mountain population did not arrive on high elevation ranges until plants were in later stages of development. Radio-tracking studies showing rapid (1-3 days) spring migration by black-tailed deer on Vancouver Island (Harestad 1979) and by elk in this study (Chapter 4), do not suggest that these species follow the phenological progression of green-up between low and high elevation ranges.

Demonstration of a nutritional advantage for migrant individuals requires some estimation of what their diet composition and quality would have been, had

they not migrated. However, if all animals migrate (e.g. Hebert 1973), or if only the migratory component is studied (e.g. Morgantini 1988), then comparisons rely on assumed diets of "residents". Simultaneous comparison of the diet composition and quality for migrant and resident elk within a partially migrant population, offers a more direct method of investigating the nutritional advantage hypothesis.

In this study, I followed migrant and resident elk from a single population and compared diets and forage quality on low and high elevation ranges. I addressed the question: during the part of year when migrants are separate from residents, do migrants have higher quality forage in their diets?

#### Methods

### Fecal collections

Fresh elk feces were collected at 2-4 week intervals from October 1985 through December 1988. Each collection consisted of at least 3 pellets from 15 pellet groups. Collection sites included 5 locations within the montane zone (representing ranges used by resident elk) and 2 areas in the upper subalpine (representing ranges used by migrant elk).

Samples for diet analysis were air dried and diet composition was assessed through fragment analysis at the Composition Laboratory, Colorado State University, Fort Collins, Colorado. Estimates of percent dry weight were obtained using the technique described by Sparks and Malechek (1968). Each field sample was sub-sampled by making 3-5 slides and examining 20 fields per slide. Although this technique may under-represent forbs and leaves (Leslie et al. 1983, Putnam 1984), I assume that any bias is constant for comparison of diets of migrant and resident elk.

This analysis could not discriminate between <u>Shepherdia</u> (buffaloberry) and <u>Eleagnus</u> (wolf-willow). However, <u>Eleagnus</u> was restricted to mesic sites in the lowest areas of the montane within the BRV. <u>Shepherdia</u> <u>canadensis</u> was widespread in dry sites in the montane and occurred through to upper subalpine elevations. Since elk were frequently observed eating <u>Shepherdia</u>

leaves and since <u>Shepherdia/Eleagnus</u> occurred as a major diet item in montane and subalpine sites, all collections were assumed to be <u>Shepherdia</u> rather than <u>Eleagnus.</u>

Forages were grouped into 4 classes: 1) grasses (grasses and sedges), 2) deciduous trees and shrubs, 3) evergreen trees and shrubs, and 4) forbs and miscellaneous items. Major forage items were identified as any genus (or group) constituting more than 5% of a sample (Collins et al. 1978). Seasonal differences in diet composition in the montane and subalpine were examined by partitioning the data into 4 seasons: 1) winter (December-February), 2) spring (March-May), 3) summer (June-August); and, autumn (September-November).

Crude nitrogen was used as an estimate of protein content in fecal samples (crude protein = 6.25 x nitrogen, Nelson and Leege 1982). Samples for chemical analysis were frozen and shipped to Norwest Laboratories, Edmonton, Alberta or to Crossfield Laboratories, Crossfield, Alberta. Organic nitrogen was determined on a dry weight basis using the semi-automated Kjeldahl technique (A.O.A.C. 1965).

Although fecal nitrogen has been criticized as an indicator of diet quality (Robbins et al. 1987), it has been widely used in elk studies (e.g. Gates and Hudson 1981, Merrill et al. 1987, Morgantini 1988) and is positively correlated with dietary nitrogen. Holechek et

al. (1982) reviewed the use of fecal indices and concluded that they are useful in the study of relative differences (such as my study), rather than absolute values.

### Forage collections

Based on major diet items identified in fecal samples during 1986-87, 3 diet items were selected for forage analysis in 1988: 1) mixed grasses (Gramineae); 2) Salix spp.; and 3) Shepherdia.

At 1 subalpine and 2 montane areas (A and B), habitat patches actively used by elk were identified by direct observation of feeding elk or fresh feces, or by the presence of radio-tagged elk (Chapter 2). Forage samples were collected as close as possible to these patches. Observers walked across the patch (typically less than 100 m) and hand-plucked 50 sub-samples (approximately 1 gm each). These samples were fresh frozen and sent to Crossfield Laboratories, Crossfield, Alberta for analysis. For grasses, cured stems and leaves were picked only if green material was not available. For shrubs, current year stem growth was picked only if leaves were not available. Although the observers may not have been as selective as feeding elk, the same observers made all collections and I assume that this bias was constant between areas.

Forage quality was assessed on the basis of parameters commonly used in range studies: nitrogen,

cell solubles, lignin, phosphorus, and calcium (Nagy and Haufler 1980). Nitrogen was used as an index of crude protein and is recognized as a critical nutrient for herbivores. Cell solubles are 98% digestible and lignin inhibits cellulose digestibility. Phosphorus and calcium are important for growth (especially of antlers) and phosphorus is often a limiting nutrient. Organic nitrogen, phosphorus, and calcium were determined using the semi-automated Kjeldahl technique (A.O.A.C. 1965). Neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin were assayed as described by Robbins and Moen (1975). Cell solubles were calculated as 1-NDF.

Differences in forage and fecal quality parameters were compared using the Wilcoxon signed ranks matched pairs test.

# Estimates of diet quality

Diet quality in the subalpine and montane was estimated by assuming that 100% of the diets were composed of <u>Shepherdia</u>, <u>Salix</u> spp., and grasses. These forage components constituted approximately 92% of all subalpine elk diets and 94% of all montane diets. For each site and forage component, a monthly diet quality estimate was calculated by multiplying the percentage occurrence of a forage type represented in elk diets, by the diet quality parameter for that site. The results for the 3 forage components were then added together.

#### Results

### Diet composition

Grasses and sedges were major components of elk diets in both subalpine and montane habitats throughout the year (Table 13). However, in both habitats grasses and sedges were eaten more during the winter, spring, and autumn, than during the summer (Figure 8). There was no significant difference in the relative use of grasses and shrubs between the habitats at any season. The relative use of grasses and sedges in the subalpine (mean=38.5%, S.E.=4.75) during the summer was considerably greater than relative use in the montane (mean=13.8%, S.E.=4.14), although this was not quite statistically significant (P=0.06).

Deciduous shrubs were major components of elk diets during spring, summer, and autumn in the subalpine and during all seasons in the montane (Table 13). Use of <u>Salix</u> spp. was high in both habitats during the summer and moderate in the montane during the autumn. <u>Shepherdia</u> was used frequently in the subalpine during the summer and in the montane during the spring, summer and autumn. In both habitats, use of shrubs peaked during the summer months when shrubs were in leaf (Figure 8). There were no significant differences in the relative use of shrubs between habitats during any season. The relative use of shrub leaves in the subalpine (mean=55.4%, S.E.=8.34) during the summer

months, was considerably less than the relative use in the montane (mean=83.1%, S.E.=5.02), although this was not quite statistically significant (P=0.06).

Coniferous trees and shrubs were not eaten by elk in the subalpine during any season, and were only lightly used by elk in the montane during winter, spring, and autumn (Table 13). <u>Equisetum</u> use was light to moderate during spring and autumn in the subalpine, and during winter, spring, and autumn in the montane. Legumes and mosses were lightly used during the spring in the montane, but their use did not exceed 5% during other seasons in the montane, or during any season in the subalpine. Table 13. Major<sup>a</sup> components of elk diets during 4

seasons<sup>b</sup> on subalpine and montane ranges.

Plant	Subalpine					Montane		
	W	Sp	Su	Α	W	Sp	Su	A
Grasses and sedges								
Agropyron	••		• •	• •	L	L	••	L
Carex	H	Н	М	М	н	н	••	М
Festuca	L	М	L	н	М	М	L	M
Juncus		• •	• •	• •	L	••	••	••
Koeleria	L	$\mathbf{L}$	••	L	• •	L	••	• •
Poa	M	L		М	L	М	L	L
Stipa/Oryopsis	••	L	••	••	L	H	L	L
Deciduous trees and	sh	rub	5					
Populus	••	••		••		L	••	• •
Rubus	• •	L	• •	• •	••	••		••
Salix	• •	••	Н	••		L	H	М
Shepherdia		••	H	L	L	H	H	н
Coniferous trees and	d si	hrul	bs					
					L	L	••	• •
Picea	• •	• •			-			_
Picea Pinus	••	••	••	••	L	L	• •	L
Picea Pinus Pseudotsuga	••• •••	•••	••	••	L L	L L	••	L L
Picea Pinus Pseudotsuga Other plants	•••	•••	•••	••	L L	L L	••	L L
Picea Pinus Pseudotsuga Other plants Equisetum	•••	  L	•••	  M	L	L L L	•••	L L L
Picea Pinus Pseudotsuga Other plants Equisetum Medicago-Melilotu	· · · · ·	  L	•••	 M	L L L	L L L L	· · · · ·	

 a food component constituting >5% of any sample
 b symbols: W=winter, Sp=spring, Su=summer, A=autumn, H=maximum occurrence 75-100%, M=maximum occurrence 25-74%, L=maximum occurrence 6-24%

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Figure 8. Grass and deciduous shrubs in elk diets collected in subalpine and montane habitats, 1988. (□ — □ subalpine grass; •---• montane grass; △--△ subalpine deciduous shrubs; ○--- ○ montane deciduous shrubs; horizontal bars indicate period between median migration dates)

#### Forage quality indicators

## Nitrogen

Fecal nitrogen values in both the subalpine and the montane peaked during the summer (Figure 9). In 1988, paired samples from the subalpine and montane tracked each other closely (Figure 9) and were not significantly different.

Forage nitrogen in <u>Shepherdia</u>, <u>Salix</u> spp., and grass in the subalpine and the montane peaked in June (Figure 10). Mean forage nitrogen values during the period May-September in <u>Shepherdia</u> and <u>Salix</u> spp. were similar in subalpine and montane habitats (Table 14). At Montane B site, the forage nitrogen in grass was significantly less than the corresponding value from the subalpine site in this period but not significantly different from Montane A.

Estimated nitrogen in elk diets in subalpine and montane environments peaked in June and was lowest in April and November (Figure 10).

# Phosphorus

Phosphorus content in <u>Shepherdia</u>, <u>Salix</u> spp., and grass in the subalpine and the montane peaked in June and declined through November (Figure 11). Mean forage phosphorus during the period May-September for <u>Shepherdia</u> was similar in subalpine and montane habitats (Table 14). Mean forage phosphorus during this period for Salix spp. and grass was significantly lower at site

Montane A than in the subalpine site. Phosphorus in Montane site B was similar to Montane site A, but not statistically different from phosphorus in the subalpine site (P=0.05).

Estimated phosphorus in elk diets peaked in June-July and was lowest in April and November in both subalpine and montane environments. Phosphorus levels were generally higher in estimated subalpine diets (Figure 11).

## Calcium

Forage calcium in <u>Shepherdia</u>, <u>Salix</u> spp., and grasses in the subalpine and the montane generally increased from spring through autumn (Figure 11). Mean forage calcium during the period May-September for <u>Salix</u> spp. and grass was similar in subalpine and montane habitats (Table 14). <u>Shepherdia</u> calcium estimates were significantly greater in sites Montane A and B then in the subalpine site.

Estimated calcium in elk diets in the subalpine and montane were lowest in May (Figure 11).

# <u>Cell</u> Solubles

Estimates of cell solubles (1-NDF) in <u>Shepherdia</u> were lowest in the early spring twigs and generally higher in leaves throughout the summer and early autumn in the subalpine and montane (Figure 10). <u>Salix</u> spp. cell soluble estimates had less obvious seasonal fluctuation than other nutrient parameters (Figures

10,11). In grasses, cell solubles were generally highest in mid-June. Mean forage cell solubles were significantly higher in <u>Salix</u> spp. samples from site Montane A and significantly less in grass samples from site Montane B compared to the subalpine site.

Estimated cell solubles in elk diets were consistently higher in montane diets than in subalpine diets throughout the period June-September (Figure 10). Lignin

Lignin in 3 forage classes differed markedly in its seasonal pattern of occurrence. In <u>Shepherdia</u>, twigs were relatively high in lignin (mid-May, early June) but low in lignin throughout the leaf period (Figure 10). In <u>Salix</u> spp., lignin concentrations were variable with no consistent difference between twig and leaf samples. In grasses, lignin was consistently low throughout the sampling period. Mean forage lignin was similar for all 3 forage classes in the subalpine and montane (Table 14).

In estimated elk diets, lignin peaked in mid-July in both the subalpine and montane diets (Figure 10).

Table 14. Comparison of 6 measures of forage quality means during the period May-September, 1988<sup>a</sup> for 1 subalpine (A) and 2 montane (B,C) sites.

Plant Parameter	Subalpine (Elk Meadows)		Monta: (Duth	ne B il)	Montane A (Hillsdale)	
Salix spp. Nitrogen Phosphorus Calcium NDF ADF Lignin	2.49 0.40 1.02 46.28 29.80 14.60	(0.36) (0.06) (0.13) (2.63) (2.77) (1.36)	2.67 0.28 1.14 37.99 29.77 14.48	(0.20) (0.05) (0.10) (2.75) (1.79) (1.16)	2.59 0.29 <sup>b</sup> 1.08 36.88 34.81 16.72	(0.34) (0.05) (0.11) (3.57) (3.12) (1.17)
Shepherdia Nitrogen Phosphorus Calcium NDF ADF Lignin	3.51 0.25 0.77 36.79 25.32 8.75	(0.20) (0.03) (0.11) (4.96) (2.61) (1.77)	3.27 0.21 0.91 <sup>b</sup> 33.68 23.61 7.58	(0.23) (0.04) (0.08) (3.61) (1.99) (1.15)	3.33 0.24 0.87 <sup>b</sup> 30.37 24.03 6.79 <sup>b</sup>	(0.19) (0.03) (0.11) (2.79) (2.08) (0.94)
Grasses Nitrogen Phosphorus Calcium NDF ADF Lignin	2.25 0.23 0.70 56.16 31.66 3.58	(0.27) (0.03) (0.05) (3.99) (1.26) (0.47)	1.43 <sup>b</sup> 0.13 <sup>b</sup> 0.63 67.07 <sup>b</sup> 34.59 4.14	(0.13) (0.02) (0.07) (1.62) (1.96) (0.45)	2.13 0.17 <sup>b</sup> 0.60 60.01 34.96 4.00	(0.31) (0.03) (0.04) (4.65) (1.94) (0.30)

<sup>a</sup> mean % dry weight (standard error) of 9 paired samples from each site, May 15, June 1, June 15, July 1, July 15, August 1, August 15, September 1, September 15

15, August 1, August 15, September 1, September 15 <sup>b</sup> significantly different from corresponding subalpine measurement (Wilcoxon signed rank test, P<0.05); no significant differences for any Montane A - Montane B comparison



Figure 9. Nitrogen in elk fecal samples from montane and subalpine sites in Banff National Park, 1985-88. (horizontal bars indicate period between median migration dates)



MONTH (1988)

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Figure 10. Nitrogen, cell solubles, and lignin in montane and subalpine forages and estimated diets, Banff National Park, 1988. (horizontal bars indicate period between median migration dates of females (F) and males (M))



MONTH (1988)

Figure 11. Calcium and phosphorus in montane and subalpine forages and estimated elk diets, Banff National Park, 1988. (horizontal bars indicate period between median migration dates of females (F) and males (M))

#### Discussion

# Diet composition

BRV elk in both subalpine and montane environments relied on grasses, sedges, and shrubs during 1 or more seasons, consistent with the view that elk are "generalist" (Gates and Hudson 1981) or "intermediate" (Hobbs et al. 1983) feeders. Although some elk populations (migrants) eat a high percentage of forbs during the summer and grass during the winter (Schuerholz 1984, Merrill et al. 1987), others eat primarily shrubs in summer and grass in the winter (Morgantini 1988). The importance of forbs in Banff elk summer diets suggested by Flook (1970) was not confirmed by my study or by Morgantini (1988).

The prevalence of <u>Shepherdia</u> <u>canadensis</u> in elk diets was surprising since plants rarely appear browsed and the twigs are known to contain high levels of phenolics (Sinclair et al. 1982). However, elk use was almost entirely restricted to the period when <u>Shepherdia</u> was in leaf in the summer and autumn. The phenolic content of these leaves is unknown as is the relative phenolic content of montane and subalpine plants. High use of <u>Shepherdia</u> has recently been found in Kootenay National Park elk (D. Poll, Canadian Parks Service, pers. comm.) and is noted in summer elk diets by Murie (1951) and Martinka (1969).

## Forage quality

As found by Morgantini (1988) and Merrill et al.(1987), fecal nitrogen of elk in my study generally tracked forage nitrogen. In all 3 studies, estimated spring and summer peaks in fecal nitrogen were approximately 4%. Fecal nitrogen winter minima were lowest in Morgantini's study along the Red Deer river (<1%), highest in Merrill et al.'s Mt. St. Helens study (1.6%), and intermediate in my study (1%).

Although the Red Deer River population also was partially migratory, most animals were migrants and fecal nitrogen values were not obtained for resident animals during the summer (Morgantini 1988). Fecal data thus described the diets of migrant elk as they moved from low elevation winter ranges to high elevation summer ranges. Fecal nitrogen on these summer ranges peaked at the same time (July) as did those on both montane and subalpine ranges in the nearby BRV.

Nitrogen levels in grass forage samples from high elevation ranges of Red Deer River elk were significantly higher than in grasses on low elevation ranges at corresponding times (Morgantini 1988). This agrees with my comparison of Montane site B and the subalpine. However, unlike Morgantini (1988), I could detect no differences in mean <u>Salix</u> spp. nitrogen levels during the summer between the low and high elevations. Summer values for Salix spp. nitrogen in the BRV montane

were higher than the corresponding low elevation Red Deer River values, perhaps due to drier conditions in that area.

Differences between the nutritive values of forage classes appeared to be more significant than differences between ranges within a forage class. This is illustrated by the generally low protein content of grasses throughout the summer compared to both <u>Shepherdia</u> and <u>Salix</u> spp. leaves. Forage lignin was lowest in grasses and <u>Shepherdia</u> leaves, and much higher in <u>Salix</u> spp. leaves. Since lignin decreases the digestibility of hemicellulose and cellulose (Nagy and Haufler 1980), this may explain Morgantini's (1988) observation that summer samples of <u>Salix</u> spp. were higher in protein but less digestible than grass samples.

# Diet quality

Although Bobek et al.(1983) suggested that non-browse food was higher in nutritional value for BRV elk than browse during the growing season, they assumed a hypothetical elk diet that contained many species (e.g. <u>Astragulus</u>, <u>Artemisia</u>) which have not been identified as major foods in BRV elk. When actual diet data are combined with nutritional estimates, the leaves of shrubs are superior foods to grasses in several ways (e.g. nitrogen content).

Levels of nitrogen, calcium, and lignin in the

estimated diets of migrant and resident elk were similar. Migrant elk had consistently more phosphorus in their diets. A notable exception to the similarities is the higher level of cell solubles estimated for low elevation elk during the summer. Since these solubles are estimated to be 98% digestible (Robbins and Moen 1975), resident elk diets were superior to diets of migrant elk in this respect.

In a study of summer food composition and diet quality of elk in Colorado, Baker and Hobbs (1982) noted consistency in elk diet quality from year-to-year, and between plant communities which varied substantially in altitude, plant species composition, and vegetation structure. Their hypothesis, that elk can generalize their choice of foraging habitats without suffering nutritional disadvantage, is consistent with the results I obtained for migrant and resident BRV elk.

# Nutritional advantage hypothesis

These results do not support the hypothesis that migrants universally gain access to better quality food, even by moving to higher elevational ranges. Considering the extremely large geographical range of the species and the diverse habitats occupied by elk (Geist 1982), it is likely that that the nutritional pay-offs for migration will vary widely between populations. In areas where summers are hot and dry on the winter ranges, large differences in forage quality may exist between

low and high elevation sites. In more mesic and cooler situations such as the BRV, the nutritional benefits of migration could be reduced or non-existent. Although Geist (1982) considered elk in the Rockies to be migratory and to follow melt lines of snow, more recent evidence has shown that a substantial portion of several populations, particularly cows, may neither migrate nor follow snow melt lines if they do migrate (Morgantini 1988, Woods and Hlady 1988, Chapter 2). As Morgantini (1988) pointed out, migration as such may not be a species characteristic of elk, as has been implied by many authors, but rather a "versatile" response to a given environmental situation. This is consistent with Geist's (1982) "opportunism" theory of elk behavior and the observation that no one variable (e.g. diet quality, previous experience, harassment by predators) is likely to explain the range of foraging and movement behaviors seen in the species.

# CHAPTER 6. CHANGES IN THE ELK POPULATION

# Introduction

In the study of wildlife populations, any management action can be treated as an experimental perturbation. Macnab (1983) discussed how the infrequent application of this approach has impeded progress in separating educated guesses from tested hypotheses. The experimental approach requires that the appropriate data be collected systematically, which is difficult and expensive for all large mammals. However, as Burk (1973) outlined in his review of predator-prey lessons from the Kaibab deer herd, the absence of experimental rigor can lead to the acceptance of ideas not supported by facts.

The BRV elk population of Banff National Park has been of management interest for more than a century. Although the park was established in 1885, elk disappeared from the BRV early in the 1900's. The cause of the disappearance was not identified. Candidate explanations included disease, severe winters, and over-harvest (Banfield 1958, Holroyd and Van Tighem 1983).

During 1915-20, native elk reappeared in the park area and additional elk were transplanted into the BRV from Yellowstone National Park, Wyoming (Lloyd 1927, Banfield 1958, Holroyd and Van Tighem 1983). By the 1940's, the BRV was considered to be "over-stocked" and an elk population control program instituted, which

lasted until 1969 (Holroyd and Van Tighem 1983). The Canadian Parks Service (CPS), in conjunction with the Canadian Wildlife Service, studied the elk population throughout the cull period (Cowan 1950, Green 1950, Green 1957, Banfield 1958, Flook 1967, Flook and Stenton 1969, Flook 1970, Holroyd and Van Tighem 1983).

In the 1970's, management attention shifted to the numbers of elk killed in collisions with automobiles and trains within the BRV. Highway traffic and elk road-kills increased dramatically throughout the 1970's and there was concern that the additive effects of man-caused elk mortalities would result in the collapse of the population (Holroyd and Van Tighem 1983). In addition, accidents caused by elk-vehicle collisions posed a human safety problem. For these reasons, an ungulate-proof fence was constructed along an expanded portion of the highway between 1983-87 (Klenavic 1979, Paradine 1982, Woods 1990). During the period 1983-89, CPS, in conjunction with Public Works Canada, studied the elk population and the impact of the fence, and concluded that the fence had successfully reduced the number of elk road-kills (Woods 1990).

The history of the BRV elk population suggests several implicit management hypotheses, including: 1) that the transplant was necessary in order to re-establish the population (1917-20); 2) that the range was "over-stocked" (1940-69); and, 3) that partial
highway fencing would prevent the collapse of the elk population and allow it to increase (1983-87).

Despite the historic and continuing interest in BRV elk, data on population size are scant. This is of interest both for the management of elk in the park, and for the analysis of density-dependence. In this study, I measured several population characteristics (e.g. size, condition, parasites) and compared them with similar data gathered during the population control period (1940-69). I address the general null hypothesis that these characteristics have not changed. Methods

#### Historical data

The data files maintained by the park warden service in Banff were reviewed and summarized by year. Unless otherwise noted, data for the period 1944-54 are from H. U. Green (Green 1949, 1957) and data for the period 1958-66 from Flook (1967, 1970).

# Population estimates

I used 3 methods to estimate the elk population: direct ground counts, mark-recapture estimates, and aerial counts. Ground counts were conducted each autumn (late October-early November) and spring (late April-early May). Autumn counts coincided with post-rut herd formation and spring counts with the first visible "green-up" of grasses in the BRV. Aerial counts and mark-recapture estimates were made at the same time as the spring ground counts. This reference time was chosen because elk were more visible than at any other time of the year and because it precedes recruitment into the population (late May-early June) (R. Kunelius, CPS, pers. commu.).

Ground counts were made from roadways (estimated length 200 km) during the early morning and late afternoon. To minimize duplication caused by elk movement, adjacent areas were surveyed either at the same time (2 teams) or as shortly (<1 day) after one another as possible. Ground counts approximated the survey

technique used in elk counts before 1985 except that previous BRV counts were confined to the park and occasionally were conducted as early as late September.

During the ground counts, radio transmitters were not used to locate elk, but were noted in the herds surveyed. After the ground count was completed, all radio-tagged elk were located (radio-tagging methods described in Chapter 2). Using the number known to be within the BRV used as the marked sample and the number seen during the count as the "recapture" sample, a Chapman estimate was calculated using the methods presented by Pollock et al.(1990).

Aerial counts were made by the park warden service using a standardized methodology and experienced observers (R. Kunelius, CPS, pers. comm.). Each year from 1985-90, the BRV was surveyed by helicopter following a predetermined flight path which covered the entire BRV from Canmore to Lake Louise. The flights were scheduled to complete the counts on three consecutive mornings, covering approximately one-third of the area per flight. The resulting count gave a minimum number of elk within the BRV. In 1988, the aerial count was repeated 3 times. Radio transmitters were not used to locate elk during these flights. Because collars could not be readily observed from the air, Chapman indices of population size and aerial visibility biases based on collared elk were not determined.

Samuel et al.(1987) found that percent vegetation cover and group size were primary factors influencing observability in aerial elk counts. Group size bias in aerial and ground counts was minimized in spring counts by standardizing the count date at the start of the green-up. Group sizes estimated from 5 spring ground counts averaged 11.98 (S.E.=1.03) and group sizes estimated from 6 autumn ground counts averaged 14.45 (S.E.=1.35). Percent vegetation cover was a constant.

Concurrent ground counts and aerial counts during 5 springs (1986-90) allowed an estimate of the ground-aerial bias. The assumption that similar biases occur in the autumn allowed the autumn ground counts for all years (1944-90) to be corrected and directly compared. I did not use historic population estimates and cull data to calculate an index-manipulation-index estimate (Caughley 1977) because the interval between repeated indices (6-12 months) violated the assumption of a closed population.

## Recruitment

The pregnancy rate was estimated by determining <u>in</u> <u>utero</u> pregnancies of 45 salvaged road- or rail-killed elk during the period November-May.

Classified counts were made each autumn and spring in conjunction with ground counts. Elk were observed either at very close range (<100 m) through binoculars, or through a 20-25x spotting scope. Animals were

classified into 4 categories: calf (either sex <1-year-old), adult cow (1-year-old and older), spike bull (1-year-old), and adult bull (2-years-old and older). Calf, spike bull, and adult bull results were expressed as a ratio per 100 adult cows. Confidence intervals were established using the formula presented by Sinclair and Grimsdell (1983) with elk herds as sub-samples.

Survival of cohorts of young bull elk from conception to 2-year-olds was estimated from the <u>in utero</u> pregnancy rate and the successive changes in ratios observed in sequential classified counts. This estimate assumed a 1:1 sex ratio <u>in utero</u> and negligible adult cow mortality.

#### Mortality

Most elk road-kills were located by members of the park warden service and cooperating agencies. Animals hit on roadways but dying out of sight were located during other work, or by mortality mode signals from radio-tagged elk (Chapter 2). I think that most road-kills were found because warden patrols were frequent and because 4 of 5 road-killed radio-tagged elk were found by park wardens without the use of radio signals. Elk killed in collisions with trains were much more difficult to locate because much of the rail-line was not observable from park roads. Rail-kills were located by following up incidental reports, and by

bimonthly helicopter flights along the entire rail-line from March 1987 to March 1989. A concurrent study of radio-tagged wolves started in February 1987 and provided information on elk killed by wolves.

Elk deaths were classified as highway or railway mortalities if evidence was found indicating a collision, and wolf kills if there was evidence of struggle. Other categories (e.g. parasites, hunting) were determined from either incidental reports or necropsies.

Calf and 1-year-old elk were aged by tooth replacement patterns (Larson and Taber 1980). Older elk were aged from cementum analysis of either the lower central incisor or the upper canine by Matson's Laboratory, Milltown, Montana. May 1st was the assumed birthday for all elk.

Relocating radio-tags broadcasting on mortality mode allowed an independent estimate of mortality. Survival rates were calculated from the number of deaths in the radio-tagged sample using the Kaplan-Meier procedure as modified for staggered entry and censored data (Pollock et al. 1989). Differences in survival between years and between sexes were compared using the log-rank test as described by Pollock et al.(1990).

# Animal condition indices

Data on morphology and parasite loads were gathered from salvaged carcasses of elk killed in collisions with vehicles on roads and the rail-line. The lungs and liver

were frozen and sent to Alberta Fish and Wildlife in Edmonton, Alberta., where they were examined by M. Pybus for the presence of giant liver fluke (<u>Fascioloides</u> <u>magna</u>), lungworms (<u>Dictyocaulus viviparus</u>) and hydatid cysts (<u>Echinococcus granulous</u>). Livers were thinly sectioned in entirety and the major lung passageways cut open and examined visually. The prevalence of parasites was expressed as a percentage of animals with a particular parasite within a specific age class.

Body weights were obtained from intact carcasses weighed whole on a spring balance located in a central abattoir. Bull weights included antlers. Antler weights were obtained by sawing one side of an an intact antler from the skull just below the burr and drying the antler at room temperature for six months (Clutton-Brock et al. 1982). In a trial comparing fresh to dry antlers, the average weight loss was 7% (N=21). The two-sided, fresh antler weights presented by Flook (1967) were reduced by 7% and divided in half to provide a comparable dry, single-sided antler weight.

#### Results

# Population estimates

During 1985-90, aerial counts in spring ranged from 795-955 elk and were within contemporaneous mark-recapture confidence intervals (Table 15). Ground counts in spring were consistently smaller than aerial counts and not within the mark-recapture confidence intervals (Table 15). Results from all 3 census methods suggested little change in elk numbers from 1985-90.

Autumn counts corrected for aerial-ground bias were higher and more consistent for 1985-90 than during 1944-53 or 1959-68 (Table 16, Figure 12, Appendix I). During these earlier periods, autumn census data suggested unlikely yearly increases during 3 intervals (57%, 1952-53; 80%, 1962-63; and 180%, 1967-68).

During 1944-48, spring counts combined with known numbers of elk culled during the winter, consistently exceeded the preceding autumn count (Appendix I). During the 18 years with population control programs and autumn population estimates, the average cull was 21.7% of the corrected autumn count (range 0.2-55.8%)(Figure 12, Appendix I).

### Recruitment

All 29 pregnant elk examined in this study carried a single fetus. One case of twins was recorded during the 1944-54 elk culls (N=571).

The pregnancy rate during 1985-89 was 67% (N=45).

This was significantly lower (Chi-square=7.449, P=0.006, d.f.=1) than the 1958-67 rate of 83% (N=736) but not significantly different (Chi-square=0.103, P=0.748, d.f.=1) from the 1944-54 rate of 69% (N=823). Flook (1970) reported that 21% of 1-year-old cows (N=82) were pregnant during 1958-67. There were no pregnant 1-year-olds in this study (N=4).

The numbers of calves per 100 adult cows in autumn during 1985-90 were higher and more uniform (42-57) than those observed during 1944-54 (13-45) (Table 17). The single ratio reported for 1958-66 (55) was within the range of recent counts. The highest ratio reported for the population was 63 (1976) and the lowest 18 based on pooled observations 1975-80 (Holroyd and Van Tighem 1983).

Classified counts showed a significant reduction in the numbers of calf elk between autumn and spring counts during 1985-90 (Table 17). Assuming a 1:1 ratio of bull to cow calves, there was a further significant reduction in the relative number of bulls to cows between their 2nd and 3rd winters (Table 18). The effective recruitment of bull elk entering their 3rd year was 8 per 100 adult cows (range 7-12).

The sex ratios of calf and 1-year-old elk killed in road and rail collisions were not significantly different from 1:1 (Table 18). However, the bull/cow ratio for age classes older than 1-year-olds was significantly lower

(45). These results parallel those observed during 1944-54 and 1957-64 (Table 18).

### Survival

During the period February 1986 to April 1989, 300 deaths of adult elk were reported, including 17 radio-tagged elk (Table 19). Significantly more adult elk were classified as natural deaths in the radio-tagged sample than in the total sample. Of the radio-tagged sample, road-kills were the leading cause of death (N=5), followed by wolf-kills (N=3), unidentified natural causes (N=3), rail-kills (N=2), parasites (N=2), hunting (N=1), and human-related accidents (N=1).

Although average adult cow survival (0.90) exceeded bull survival (0.83) during 1986-89, this difference was not significant (Table 20). Cumulative survival of young elk from conception through 23 months averaged 0.23 (Table 21).

The calf:cow ratio of highway kills was significantly higher (106:100) than the pregnancy rate (67:100). The calf:cow ratio in rail-kills (27:100) was slightly larger than the late winter classified counts for the population (21:100). In a sample of 53 wolf kills, the ratio of calves per 100 adult cows (154) was significantly greater than the elk pregnancy rate, and the ratio of bull elk per 100 adult cows (227) in wolf kills was significantly greater than the assumed 1:1 ratio in utero.

During both 1957-64 and 1985-90, the oldest cows (21- and 22-year-olds respectively) outlived the oldest bulls (14- and 13-year-olds respectively). In this study, the average age for elk older than calves killed on the highway and railway was 5.8 years (N=130) for cows and 3.4 years (N=82) for bulls. Although it was not possible to calculate average ages from data reported by Flook (1967, 1970), 4-year-old and older cow elk comprised 57.3% (N=131) of the adult cows in this study and 55.7% (N=531) of the 1957-64 sample. Four-year-old and older bull elk comprised 73.8% (N=42) of all bulls older than 1-year-olds in this study, and 66.7% (N=225) during 1957-64.

## Parasites

Giant liver flukes, lungworms, and hydatid cysts in BRV were found in the BRV elk population (Table 22). Both giant liver flukes and hydatid cysts had peak prevalence in older age class elk (>2-year-olds), whereas lungworm prevalence was highest in age class 1-year-olds.

Liver flukes were first reported in BRV elk in 1959 (Flook 1967). Between 1959-89 they increased from 0-89% prevalence in elk >2-year-olds (Table 22). The prevalence of liver flukes in elk >2-year-olds during 1985-89 was significantly greater than reported for this age class during 1959-65 (Table 22). The only elk deaths attributed to parasites were the 2 adult radio-tagged elk found dead during my study. They had massive liver damage resulting

from giant liver fluke infestations.

Although both hydatid cysts and lungworms are known from this population since the 1940's, the prevalences I observed in >2-year-old elk were significantly greater than in earlier years (Table 22).

# Body and antler weights

Age specific body weights were obtained from 129 intact road and rail-killed elk (Table 23). Bulls >2-year-olds were significantly heavier (mean=339 kg, N=22, range=230-471) than cows in the same age class (mean=238 kg, N=29, range=168-311). Confidence intervals for mean weights of bull and cow elk 3- to 10-years old during 1985-89 overlapped with the corresponding data from Banff culls in 1960-63 with exception of 6-year-olds.

Dried antler weights were obtained from 68 road- and rail-killed elk (Table 24). Antlers from 4-year-old elk were significantly heavier those than from 1- to 3-year-olds and significantly lighter than antlers from 8- to 9-year-old elk. Confidence intervals for 1960-63 overlapped 1985-89 confidence intervals in all cases.

Table 15. Early spring elk population estimates based on ground counts (GC), aerial counts (AC), and mark-recapture (MR), BRV, 1985-90

Year	GC	ACa	MR <sup>b</sup>	95% CIb	
1984-85	n.a.	795	n.a.	n.a	<u>.</u>
1985-86	488	955	926	652-1200	
1986-87	487	891	951	673-1229	
1987-88	440	942°	860	620-1100	
1988-89	531	860	979	694-1264	
1989-90	523	894	1222	776-1668	

a early spring total count from helicopter

<sup>b</sup> early spring Chapman estimate and confidence intervals based on radio-tagged adult elk (Pollock et al. 1990) <sup>c</sup> highest of three counts (933, 939, 942)

Table 16. Autumn elk population estimates based on ground counts corrected for ground-aerial bias during 3 periods: 1944-53, 1959-68, and 1985-90.

Period	N(years)	Average Correctedª Count	S.E.	
1944-53	10	648	66	
1959-68	10	725	92	
1985-90	6	978 <sup>b</sup>	54	

a ground-aerial bias 0.55 based on 5 paired spring counts, 1985-89

b significantly greater than 1944-53 average (t-test, P=0.004) Table 17. Classified elk count ratios and 95% confidence intervals (CI) of calf (C), 1-year-old bull (YB), and mature bull (MB) elk in the BRV expressed per 100 adult cows, 1943-90.

							<u> </u>	
Year	Season	_		Class	ratio	s_(CI	)	
		С		ΥB	M	В		Nª
1990-91	Autumn	47.1	(6.6)	11.5	(2.9)	22.5	(13.4)	442
1989-90	Autumn Spring	43.1 28.2	(3.3) (4.2)	13.1 7.9	(4.8) (1.3)	18.3 17.6	(10.3) (3.8)	506 523
1988-89	Autumn Spring	42.2 24.5	(2.4) (4.5)	9.1 7.7	(1.9) (2.3)	14.8 7.9	(3.3) (3.9)	618 531
1987-88	Autumn Spring	44.4 21.8	(2.6) (3.6)	7.4 7.4	(2.2) (2.0)	20.1 11.9	(4.8) (5.0)	624 440
1986-87	Autumn Spring	42.8 29.8	(4.0) (4.2)	13.6 7.0	(3.5) (1.6)	24.0 17.4	(8.5) (5.2)	489 487
1985-86	Autumn Spring	57.4 23.8	(2.1) (3.0)	13.6 11.9	(1.5) (2.0)	35.1 17.2	(5.0) (5.3)	546 488
$1976-77 \\ 1963-64 \\ 1953-54 \\ 1951-52 \\ 1950-51 \\ 1949-50 \\ 1948-49 \\ 1947-48 \\ 1946-47 \\ \end{array}$	Autumn <sup>b</sup> Autumn <sup>c</sup> Autumn <sup>d</sup> Autumn <sup>d</sup> Autumn <sup>d</sup> Autumn <sup>d</sup> Autumn <sup>d</sup>	63.0 54.6 28.8 35.1 13.0 44.9 13.3 36.8 14.5		n.a. 12.4 12.5 5.2 10.2 5.1 5.1 3.2 4.8		n.a 28.5 16.3 20.1 26.9 25.0 13.9 12.9 15.8		n.a. 567 126 215 162 273 496 523 387
1945-46	Autumn <sup>d</sup> Spring®	34.6 15		3.7 n.a	•	18.9 n.a	•	341 n.a.
1944-45	Autumn <sup>d</sup> Spring®	39.9 21		5.5 n.a	•	21.6 n.a	•	456 n.a.
1943-44	Spring®	20		n.a	•	n.a	•	n.a.

<sup>a</sup> sample size

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<sup>b</sup> Holroyd and Van Tighem (1983)
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c Flook (1967)

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<sup>d</sup> Green (1957)
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• Cowan (1950)

Table 18. Bull/cow ratios of BRV elk during 1985-89ª,  $1957-64^{b}$ , and  $1944-54^{c}$ .

Age	Time Period						
	1944-5	4 (N)	192/-0	4 (N) 	1985-6	59 (N)	
Calf	1.10	(197)	1.25	(146)	0.77	(106)	
1-year	1.15	(151)	1.04	(145)	1.57	(59)	
2-year	n.a.	n.a.	0.47ª	(134)	0.35ª	(23)	
>1-year	0.22ª	(928)	0.49 <sup>d,e</sup>	(685)	0.45 <sup>d,f</sup>	(154)	

a present study, rail- and road-kills

b calculated from Flook (1967), culled elk c calculated from Green (1957), culled elk

<sup>d</sup> significantly different from 1:1

oldest bull 14 years, oldest cow 21 years
f oldest bull 13 years, oldest cow 22 years

Table 19. Deaths<sup>a</sup> of adult elk reported from all sources and from radio-tagged animals only, February 1986 - April 1989.

Cause	<u>All sour</u> Number	Ces %	<u>Radio-t</u> Number	elemetry %	y only
Man-related	212	80	8a	47 <sup>b</sup>	
Natural	53	20	9	53 <sup>b</sup>	
Total	265	100	17	100	

a excludes deaths of unknown cause (N=19) and of uncertain age (N=16)

<sup>b</sup> significantly different from deaths reported from all sources

Tabl	le 2	20. A	nnual	surv	ival	rate	s (S)	and 95	90 00	
conf	Eide	ence	interv	vals	(CI)	for	radio-	-tagged	adult	elk
in t	he	BRV,	1986-	-89.						

Class Year	N	S	CIª	
Adult cow				
1986-87	34	0.86	0.75-0.98	
1987-88	33	0.94	0.86-1.02	
1988-89	31	0.90	0.80-1.01	
Average	33	0.90	0.80-1.00	
Adult bull				
1986-87	16	0.74	0.52-0.97	
1987-88	14	0.85	0.66-1.03	
1988-89	12	0.91	0.74-1.08	
Average	14	0.83	0.64-1.03	
Pooled cow	and bull			
1986-87	50	0.83	0.72-0.93	
1987-88	47	0.91	0.83-0.99	
1988-89	43	0.91	0.82-0.99	
Average	47	0.88	0.79-0.97	

a calculated following Pollock et al. (1989)

Table 21. Cumulative survival estimates from birth to age 24 months for 6 cohorts of bull elk based on classified counts, 1985-90<sup>a</sup>.

Year	·····	Age (months)					
	0-6	7-12	13-18	19-24			
<b>_</b>							
1985-86	0.86	0.36	0.41	0.21			
1986-87	0.64	0.45	0.22	0.22			
1987-88	0.66	0.33	0.27	0.23			
1988-89	0.63	0.37	0.39	0.24			
1989-90	0.65	0.42	0.34	-			
1990-91	0.71	-	-	-			

\* based on data presented in Table 17

Table 22. Prevalence of giant liver flukes, lungworms, and hydatid cysts in BRV elk during 3 periods: 1944-54<sup>a</sup>, 1958-66<sup>b</sup>, and 1985-89<sup>c</sup>.

Parasite		Prevale 00	ence %	by age 01	class (san 02	nple size) >02
Liver flukes 1985-89 1958-66 1944-54	3 0	( 69) (138) (197)	57	(30) (126) (147)	69 ( 16) 13 (117)	89 <sup>d</sup> (70) 13(462) 0(906)
Hydatid cysts 1985-89 1958-66 1944-54	5 2 0 0	(51) (154) (197)	0 4 4	(24) (142) (147)	0 ( 12) 18 (130) n.a.	31°( 52) 24 (523) 9 (906)
Lungworms 1985-89 1958-66 1944-54	8 1 15	(51) (204) (83)	44 6 8	(25) (192) (72)	25 ( 12) 5 (181) n.a.	10 <sup>f</sup> ( 52) 2 (517) 2 (228)

a calculated from Green (1957)

<sup>b</sup> calculated from data presented by Flook (1967); liver fluke sample period 1959-65; lungworm data from the BRV, Kootenay National Park, and the Ya-Ha Tinda Ranch, Alberta

<sup>c</sup> source present study, road- and rail-killed elk

<sup>d</sup> significantly different from and 1944-54 and 1958-66 prevalence (2x2 Contingency table P<0.001)</p>

 significantly different from 1944-54 prevalence (P<0.001) but not the 1958-66 prevalence

f significantly different from 1944-54 and 1958-66 prevalence (P=0.003 and P=0.030 respectively)

Table 23. Mean body weights (BW) (kg) and 95% confidence intervals (CI) for rail-killed and road-killed elk, BRV, 1985-89.

		Bull	L		Cows	
Age	N	BW	CI	N	BW	ĊĪ
0	23	105	88-122	23	94	80-108ª
1	16	170	150-190ª	5	147	118-176ª
2	5	221	185-257	6	186	159-213ª
3	7	280	250-310	4	221	188-254
4	0	-	-	5	234	197-271
5	3	351	305-397	5	225	195-255
6	4	403	363-443ª	4	255	222-288
7	5	351	315-387	3	234	196-272
8	2	341	285-397	3	209	171-247
9	1	401	<b>_</b>	2	265	218-312
10	0	_	-	3	285	247-323

<sup>a</sup> CI's do not overlap with corresponding CI's presented by Flook (1970)

Age	N	Average Weight	CI	
1	14	0.20	0.00-0.48	
2	2	0.61	0.00-1.35	
3	12	1.01	0.71-1.31	
4	3	2.28	1.68-2.88	
5	7	2.66	2.27-3.05	
6	8	2.65	2.28-3.04	
7	8	2.98	2.61-3.35	
8	7	3.41	3.01-3.81	
9	5	3.60	3.13-4.07	
10	2	3.19	2.45-3.93	

Table 24. Antler weights (kg) and 95% confidence intervals (CI) for rail-killed and road-killed elk, BRV, 1985-89.



Figure 12. Autumn elk population estimates based on ground counts corrected for ground-air bias and percent of this estimate subsequently culled during the autumn or early winter, BVER, 1944-89.

### Discussion

# Population estimates

Accurate estimates of population size or trend are required to test density hypotheses for BRV elk. The autumn ground counts employed during most of the culling period (1944-69), consistently underestimated the population and included biologically unlikely increases (e.g. 180%, 1967-68). Some of the estimates of post census annual cull rates were also impossibly large (>100%). During years when both autumn and spring counts were available, fewer elk were seen in the autumn than can be accounted for by adding the winter culls to the counts the following spring. Further, simultaneous ground and aerial counts in this study illustrated that ground counts consistently underestimated the population.

Recent radio-telemetry data for BRV elk (Chapter 2) confirm earlier observations that only part of the wintering population is in the BRV during the period of the late autumn censuses (CPS, unpubl. data, Flook 1970). After 5 years of intensive culling (1944-48), elk delayed their return to the valley. This may have contributed the large (45%) drop in autumn counts between 1947-48 (Figure 12).

The enhanced observability of elk during the early spring green-up and the concentration of elk within the BRV at that time likely explain the paradox of elk

numbers increasing over the winter, and show that early spring is the best census time. The general agreement between mark-recapture estimates and aerial counts, and the close agreement of the replicated aerial counts in 1987, suggest that the more recent aerial count procedures employed by the park warden service have produced more consistent elk population data. However, confidence intervals cannot be applied to these direct counts, and like ground counts, they represent a minimum population estimate.

I conclude that the autumn is an unreliable census time for BRV elk and thus, that the apparent increase in the elk population from 1944-53 to 1985-90 is suspect. Sex ratios and longevity

Flook (1970) considered the apparent disparity in elk sex ratios in BRV (1957-64) and in other elk populations in the Canadian Rockies, and noted an abrupt change in the sex ratio between 1-year-olds and 2-year-olds. Data presented in this paper for the periods 1944-54 and 1985-90, also showed this ratio change at the same age interval. Furthermore, during both 1957-64 and 1985-90, the oldest elk sampled were cows.

In an analysis of population dynamics of the Jackson Hole elk herd, Boyce (1989) demonstrated cow-biased sex ratios and greater longevity amongst cows. These observations were consistent with a higher

over-winter survival of adult cows in that population. Flook (1970) suggested that unequal dispersal, unequal survival, or both could account for the unbalanced sex ratios observed in the BRV.

Although the present study did not demonstrate significant differences in survival of adult bull and adult cow elk, the survival estimates had wide confidence intervals. In addition, the radio-tagged sample consisted primarily of adult elk and therefore would not have detected differences in survival between the ages of 1 and 2 years. Since more adult bulls migrate than adult cows in the BRV population, and since the sex ratio disparity does not appear until after age 2, decreased survival associated with migration or dispersal provides a reasonable, but untested explanation of the data.

### Body and antler weights

Caughley (1979) noted that although population condition parameters such as body size are not directly related to "over-population", they would be expected be change with population densities. McCorquodale et al. (1989) found that antler weights from a colonizing (low density) elk population in Washington State were significantly heavier than those observed either by Flook (1970) or in the present study in the BRV. While this between-population comparison is consistent with the density-dependence hypothesis that antler size

decreases with increasing elk density, more convincing evidence would come from 1 population observed at different densities. This may be possible in the future if BRV elk numbers increase.

## Parasites

The significant increase in giant liver fluke prevalence was the only clear change in the elk population condition between the start of the elk population control program in the 1940's and the present study. Since specific efforts were made find parasites throughout the cull program (Green 1957, Flook 1967, 1970), and giant liver flukes are conspicuous parasites, I believe that this increase is real. Hydatid cysts and lungworms are more difficult to detect, and for these species I consider the statistically significant increases suspect.

Pybus (1990) discussed the recent distribution of the giant liver fluke in Alberta, and noted that it had a higher prevalence (89%) in elk in Banff National Park (Alberta) and adjacent Kootenay National Park (British Columbia) than in Alberta generally (29%). This abundance pattern may be related to the original dispersal pattern of the parasite from British Columbia (Pybus 1990).

The two parasite-related mortalities observed in this study were the first deaths of free-ranging elk attributed to giant liver flukes in the park and

possibly the first deaths of free-ranging elk attributed to giant liver flukes anywhere (M. Pybus, pers. comm.). However, these deaths (2/17) may under-represent the true mortality from these parasites because intact livers from natural deaths are rarely available for necropsy.

#### Recruitment and survival

In a recent study of <u>in utero</u> pregnancies amongst elk on ranges immediately north of the BRV, the rate for all elk older than calves was 0.66 (N=417) (Morgantini 1988). This rate was within the values observed for BRV elk during the past 50 years and within values observed for many North American elk populations (Taber et al. 1982).

No simple conclusion can be drawn from BRV pregnancy rates other than they appear to have increased and more recently declined again. The percent of older cows (>3-year-olds) was similar in the 1960's and in this study. However, the large number (21%) of breeding 1-year-olds during the 1958-67 suggests that the high pregnancy rate may have been the consequence of more breeding participation by younger age classes.

Reliable calf:cow estimates taken over a variety of population densities have been used to demonstrate density-dependent recruitment in elk populations (Houston 1982, Boyce 1989). Appropriate data for this analysis in the BRV were lacking.

Bobek et al.(1983) used classified count data from the BRV (1944-70) to illustrate highly variable calf:cow ratios, an inverse relationship between snowfall and calf production, and an inverse relationship between snowfall and bull:cow ratios. However, these data should be used with caution because confidence intervals were not determined prior to 1985. During the present study, I found that 1-year-old bulls with slender spike antlers could be easily mistaken for adult cows, as could large bull calves. For this reason, elk classifications were only made by practiced observers with the aid of a spotting scope or binoculars at close range. Although Green (1957) was an experienced observer, details on the 1944-54 classification methods are lacking and the highly variable annual results at that time should be viewed with some caution. For the same reason, I lack confidence in the extremely low ratio (18:100) for Banff elk calculated from pooled incidental observations made over three months by various observers during 1975-80 (Holroyd and Van Tighem 1983). During the same period (November 1976), a single classified count in the BRV estimated 63 calves:100 cows, the highest ratio ever reported (Holroyd and Van Tighem 1983).

Paired autumn/spring classified counts for the BRV during 1985-90 illustrated the importance of count timing. Classified counts described as "winter" counts could contain a great deal of variability due to count

date.

Low 1st year survival rates have been previously documented in this elk population (Cowan 1950, Green 1957, and Flook 1967) and in the Upper Red Deer River valley elk population (Morgantini 1988). Similar results were found in my study. Cowan (1950) presented low juvenile survival as a characteristic of this population on "over-stocked" range. Since current juvenile survival rates are similar to those presented by Cowan (1950), and since rates have not been observed over a range of densities, I doubt that these survival rates indicate a range at or above "carrying capacity".

Holroyd and Van Tighem (1983) reviewed mortality sources for Banff elk, suggesting a predominance of human-caused mortalities. My comparison of reports from all sources, with deaths of radio-tagged elk, suggests that incidental mortality reports are highly biased. Elk dying on the highway and railway are much easier to find than natural deaths. There have been no previous estimates of survival rates for adult elk in the BRV. The Future of the BRV Elk Population

Although "carrying capacity" is a frequently used term in wildlife ecology, much ambiguity surrounds the concept. Caughley (1979) distinguished between "ecological" carrying capacity (K<sub>i</sub>), the unaided equilibrium resulting from the interaction of a population and its environment, and alternative carrying

capacities defined by human objectives (e.g. K<sub>e</sub>, maximum sustained yield). It follows that the concept of "over-population" (i.e. exceeding carrying capacity) must be explicitly defined. Macnab (1985) noted that although ungulate numbers may naturally fluctuate about K<sub>i</sub>, chronic and episodic mortality may be viewed as "a bad thing" by some people.

For some 30 years, the BRV elk population was considered to be "over-stocked" or "excessive", based on the observed condition of the range, the suspected depression of other ungulate species, and the potential for a major elk die-off in the event of a harsh winter (Cowan 1950, Banfield 1958, Flook 1970, Holroyd and Van Tighem 1983). Since recent population estimates are at or above values observed during the population control period, and since the fence may result in a stable or increasing elk population, the topic of "over-abundance" is of continuing interest.

Elk and other large ungulates are frequently involved in K<sub>i</sub> discussions, and concern for the welfare of these populations has resulted in anticipatory intervention such as cull programs. Houston (1985) outlined such a case in Yellowstone National Park and tracked population characteristics after population control was discontinued. Observations of recruitment rates at comparatively low and high densities, illustrated density-dependent recruitment for calf and

1-year-old bulls in the Yellowstone population after the culling stopped.

In the BRV, cessation of the cull program was coincidentally followed by a substantial increase in highway traffic. Elk road-kills also increased and the population did not expand markedly. Therefore, recruitment, migration rates and other potentially density-dependent characteristics (Boyce 1984) have not been measured over a wide range of population sizes. If management interventions such as highway fencing reduce mortality, elk densities may increase. However, isolation of the cause and effect may be complicated by simultaneous changes in several factors such as mortality from other sources (road-kills on unfenced portions of the highway, rail-kills, predation, parasites, hunting) and a change in the K, of the BRV resulting from forest succession, landscape alienation, or climate change.

# CHAPTER 7. CONCLUSION

In this study I set out to understand the nature of seasonal movements in a population of elk. My goals were to describe these movements and to reach some understanding of their causes.

I found a complex set of annual movement behaviors including migration and residency (Chapter 2). If these movement behaviors are considered to be alternate strategies, then demonstration of a mixed ESS would require that migrant and resident morphs have equal fitness (Maynard Smith and Price 1973) and that individuals would have fixed strategies. Although I did not measure fitness, I documented individuals "switching" between resident and migrant status from year-to-year, and a mixture of residents and migrants during the rut. Qualitative observations of this population during former years also illustrated flexibility in seasonal movement behavior related to disturbance by humans. These data support the hypothesis (1) that partial migration in elk is a conditional ESS and are consistent with the conclusions of Morgantini (1988) and Boyce (1991) for elk, Sandegren and Bergstrom (1983) for moose, and McCullough (1985) for long range movements of terrestrial mammals in general.

Given the ecological plasticity of elk, and the diversity of documented movement behaviors, it would be surprising to find a strict genetic linkage with

annual movement behavior. Versatility would allow a species to optimize its response to a given set of environmental variables and to change this response as conditions dictate. Not only would elk populations from environmentally different areas be expected to vary in movement patterns, but within an area, movement patterns could vary with environmental fluctuation (e.g. density, predator disturbance, snow depth).

The complexity of elk seasonal movement behavior is further illustrated by the preponderance of male migrants which contradicts the hypothesis (2) that adult males and adult females in this population are equally likely to migrate. The asymmetries in morphology and ecology between the sexes in this species (Clutton-Brock et al. 1982), suggest that male and female elk evaluate their environment differently, and therefore might have different migrant/resident ratios. In addition, if juvenile males are the predominant dispersers in elk (currently unproven), they would be the sex most likely to develop experience with alternate ranges. Return migration behavior could develop from "exploratory" dispersals.

The hypothesis (3) of equal numbers of migrants and residents was rejected by the significantly greater number of residents in the BRV population. In contrast, migrants outnumber residents in most other elk populations in the Rockies. The BRV population also is

unusual in being largely unhunted. It is possible (but untested) that if they were hunted, the migrant/resident ratio would change in favor of migrants.

Since seasonal movements of elk are population-specific, it is important to recognize inter-population differences. For example, although the BRV and Red Deer River valley elk populations in Banff National Park occupy adjacent drainages of the Canadian Rockies, these populations have different migrant/resident ratios and distinct migration patterns and timing (Morgantini 1988, this study Chapter 1). As Boyce (1991) discussed for the Jackson elk herd, knowledge of these factors can play an important role in species management.

Although migration has the potential of uncoupling predator-prey relationships (Fryxell and Sinclair 1988), this was unlikely to be the case for elk and wolves in the BRV. The hypothesis (4) that migration takes prey beyond the foraging range of their predators was inconsistent with the observation that most BRV elk and wolves were sympatric throughout the year.

Despite individual versatility in movement behavior within BRV elk, they were not nomadic, and most adults showed philopatry to both their movement strategy and their occupancy of winter, summer, and rutting ranges (Chapter 3). Although BRV elk were philopatric relative to a random model, I could not reject the hypothesis (5)

that the relative philopatry of cows and residents was equal to that of bulls and migrants. Most adults used the same areas at the same times from year-to-year. Exceptions to this pattern were shown by the few animals that switched migration strategies (although their use of winter range remained constant) and the single instance of adult dispersal.

During this study environmental conditions in the BRV were relatively constant (no extreme snow years, no cull program, presence of timber wolves) and the elk were philopatric. However, in the mid-1940's, the simultaneous initiation of an elk cull program and the reappearance of timber wolves may have caused both the migrant/resident ratio and migration timing to change relative to earlier years. This suggests that while elk are generally philopatric, they remain versatile enough to adopt new movement patterns and ranges if faced with major changes in their environment (e.g. initiation of a hunting season, appearance of a major predator, extreme snowfall).

There is need for additional research on migration and dispersal of young elk (from calves through to 3-year-olds), particularly of young from cows of known movement history. The dramatic drop in the proportion of 2-year-old bulls first observed by Flook (1967), continues to be shown by this population (Chapter 6). As Flook (1967) suggested, this may be the result of

differential dispersal, differential mortality, or both.

Calculation of net time and energy costs of migration by BRV elk did not support the hypothesis (6) that these investments of time and energy are significant relative to other life history costs (Chapter 4). This result could suggest that net rewards resulting from migration (e.g. avoidance of predation, better quality food) need not be large to produce net benefits. The short-term visits to alternate ranges (e.g. winter ranges during the summer) made by several radio-tagged BRV elk during this study, could be interpreted as low-cost "tests" of environmental quality on these alternate ranges.

Data on forage quality on resident and migratory ranges of BRV elk did not demonstrate a consistent difference between ranges. However, I could not reject the hypothesis (7) that the nutritional quality of low and high elevation ranges was equal (Chapter 5). This similarity in the food quality of different ranges corroborates evidence from other areas that high elevation ranges can be high, low, or equal in nutritional quality compared to low elevation ranges used by the same populations. Such variability in food quality underscores the value of flexibility in seasonal movements.

In most respects, the hypothesis (8) that population characteristics have not changed since the
cull program, was upheld. Although the incidence of giant liver flukes increased, in most other respects (e.g. population size, body weight, antler weight, sex ratios, major predators), the elk population either has changed relatively little, or the data are inadequate to demonstrate a change (Chapter 6). Unfortunately, measurements of these characteristics have not been made at different populations levels. Finally, further work also is needed on natal dispersal, density-dependence processes, and carrying capacity.

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Period	AUT	SP	R CUL	L RAIL	ROAD	Source		
1885-1903	+	+	0	?	0	CPSª		
1903-14	0	0	0	0	0	CPS		
1915-16	+ <sup>b</sup>	+	0	?	0	CPS		
1918-19	41+°	?	0	?	0	Lloyd (1927)		
1920-21	194+°	?	0	?	0	Lloyd (1927)		
1923-24	+	282	0	?	0	Lloyd (1927)		
1929-30	+	+	0	18	0	Holroyd and Van Tighem (1983)		
1930-31	+	+	0	12	0	Holroyd and Van Tighem		
1931-32	+	+	0	10	0	Holroyd and Van Tighem		
1932-33	+	+	0	121	0	Holroyd and Van Tighem (1983)		
1933-34	+	+	0	18	0	Holroyd and Van Tighem (1983)		
1940-41	+	+	+	?	?	CPS		
1941-42	+	+	+	?	?	CPS		
1942-43	+	+	+	?	?	CPS		
1943-44	+	570	175ª	?	?	CPS		
1944-45	456	592°	200	50	4	CPS		
1945-46	341	535	352	50	4	CPS, Flook (1970)		
1946-47	387	343	309	50	4	CPS, Flook (1970)		
1947-48	523	394	254	50	4	CPS, Flook (1970)		
1948-49	496	+	103 <sup>f</sup>	50	4	CPS, Flook (1970)		
1949-50	273	+	270 <sup>±</sup>	50	4	CPS, Flook (1970		
1950-51	190	+	143 <sup>±</sup>	50	4	CPS, Flook (1970)		
1951-52	244	+	102 <sup>±</sup>	50	4	CPS, Flook (1970)		
1952-53	255	+	0	50	4	CPS, Flook (1970)		
1953-54	400	+	53	50	4	CPS, Flook (1970)		
1954-55	+	+	7	?	?	CPS, Flook (1970)		
1955-56	+	÷	10	?	?	CPS, Flook (1970)		
1956-57	+	+	?	13	?	CPS		
195/-58	+	+	91	26	?	CPS		
1958-59	+	+	99	9	?	CPS		

Appendix I. Autumn (AUT) and spring (SPR) ground counts, numbers removed for population control (CULL), numbers of rail-kills (RAIL), and numbers of road-kills (ROAD) for elk in the BRV, 1885-1990.

Appendix I. (page 2) Autumn (AUT) and spring (SPR) ground counts, numbers removed for population control (CULL), numbers of rail-kills (RAIL), and numbers of road-kills (ROAD) for elk in the BRV, 1885-1990.

Period	AUT	SPR	CULL	RAIL	ROAD	Source	
1959-60	669	+	300	?	?	CPS	
1960-61	459	+	151	?	?	CPS	
1961-62	434	+	199	?	?	CPS	
1962-63	340	+	100	?	?	CPS	
1963-64	613	+	73	?	?	Flook (1970	)
1964-65	360	+	67	?	?	Flook (1970	)
1965-66	250	+	1	?	?	Flook (1970	)
1966-67	260	+	32	?	?	Flook (1970	)
1967-68	158	+	0	?	?	CPS	
1968-69	442	+	9	?	?	CPS	
1969-70	+	+	132	?	20	CPS	
1970-71	+	+	0	3h	12 <sup>h</sup>	CPS	
1971-72	+	+	0	25 <sup>h</sup>	21 <sup>h</sup>	CPS	
1972-73	+	+	0	80 <sup>n</sup>	8 <sup>n</sup>	CPS	
1973-74	+	+	0	6 <sup>n</sup>	7 <sup>n</sup>	CPS	
1974-75	+a	+	0	10 <sup>n</sup>	17 <sup>n</sup>	CPS	
1975-76	+	+	0	17 <sup>n</sup>	29 <sup>n</sup>	CPS	
1976-77	372	+	0	4n	26 <sup>n</sup>	CPS	
1977-78	+	+	0	6" 17b	3/1	CPS	
19/8-/9	+	+	0	1 7 "	40"	CPS	
19/9-80	+	+	0	115	59" 60h	CPS	
1980-81	+	+	0	41" 10h	00" 44b	CPS	
1901-04	+	+	0	10" 11b	44 10h	CPS	
1002-03	+	+	0	Oh	40** /Qh	CPS	
1001_05	<b>T</b>	+ +	ů č	9 25h	40" 56h	CPS	
1985-86	546	188	0	30	90		
1986-87	189	487	0	10	88	CPS	
1987-88	624	407	Ő	22	45	CPS	
1988-89	618	531	õ	26	32	CPS	
1989-90	506	523	Õ	11+	39	CPS	
1990-91	442	559	õ	79	53	CPS	
a Canadia	n Parks	Service	unpuk	lishe	d data,	Warden Off:	ice,
Banff,	data for	1944-5	54 from	n Gree	n (195 <sup>°</sup>	7)	
<sup>b</sup> native	elk note	d in pa	rk sup	perint	endent	reports	
<sup>c</sup> number	of elk t	ranspla	nted i	n BRV	from Y	ellowstone I	National
Park		_					
<sup>d</sup> aggrega	te culle	d 1940-	43				
° warden	estimate	of 150	0 cite	ed by	Banfiel	.d (1958)	
f include	d BRV and	d Casca	de Riv	ver va	lley		
<pre>g estimat probabl</pre>	e publis Le error	hed in	Bobek	et al	.(1982)	of 30 excl	uded as

h based on calendar year of first year

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