University of Alberta

Survival and movement behaviour of resident and translocated wapiti (*Cervus elaphus*): Implications for their management in west-central Alberta, Canada

by

Jacqueline Leigh Frair ©

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"Science is organized knowledge. Wisdom is organized life."
-- *Immanuel Kant*

"It's hard to make predictions, especially about the future"
-- *Yogi Berra, also attributed to*
Niels Bohr (Nobel Laureate in Physics)

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Survival and movement behaviour of resident and translocated wapiti (*Cervus elaphus*): Implications for their management in west-central Alberta, Canada submitted by Jacqueline Leigh Frair in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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This work is dedicated to my parents,
Dan and Sue Frair and Sue and Jim Dekay,
who have an unwavering faith in my ability to do great things
despite having no idea what I do.

ABSTRACT

Much of our knowledge of wapiti ecology has been acquired from predator-free systems. Restoration of large carnivores and rapid landscape changes from industrial activities are changing the environmental conditions for this important ungulate species in western forests. The goals of this research were two-fold: 1) increase our understanding of the consequences of competing mortality risks and continued landscape changes on wapiti, and 2) put tools into the hands of managers trying to balance competing demands on the forest ecosystem.

Because my research relied heavily on wapiti location data collected by global positioning system (GPS) collars, I first conducted a simulation study to test the effects of collar bias on habitat selection patterns and the efficacy of two bias-correction techniques – sample weighting and simulation via multiple imputation – both of which effectively removed the effects of bias from inferences of habitat selection.

Between Jan 2000-Dec 2004, I conducted a translocation study, releasing wapiti from 4 different source populations into the central Rocky Mountain foothills of Alberta, Canada and compared movements and survival to that of resident wapiti in the area. In so doing, I observed spatial and temporal trade-offs associated with the risk of mortality from aboriginal hunters and wolves in the area that have implications for managing the resident wapiti population as well as for improving translocation programs. Roads played a defining role in the survival patterns of wapiti in this system.

Using a technique called first-passage time, I detected different scales of movement by resident wapiti that reflected patterns of landscape heterogeneity caused by timber harvest in the central foothills. Based on this information, I divided wapiti trajectories into behavioural "states", which fluctuated diurnally and responded to local variation in vegetation and terrain conditions, predation risk by wolves, and the proximity of roads and trails. Ultimately, I devised a state-based movement model for wapiti, using a correlated random walk to evaluate the combined effects of habitat amount, alternative road development schemes, and increasing road density on habitat effectiveness for wapiti in the central Rocky Mountain foothills of Alberta.

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TABLE OF CONTENTS

CHAPTER 1

CHAPTER 2: APPROACHES FOR REMOVING GPS-COLLAR BIAS IN HABITAT-SELECTION STUDIES

CHAPTER 3: LESSONS FROM WAPITI TRANSLOCATIONS INTO RISKY LANDSCAPES

CHAPTER 4: SCALES OF MOVEMENT BY WAPITI (*Cervus elaphus*) IN RESPONSE TO HETEROGENEITY IN FORAGE RESOURCES AND PREDATION RISK

CHAPTER 5: LINKING MOVEMENTS, ROADS AND HABITAT EFFECTIVENESS FOR A LARGE UNGULATE

CHAPTER 6

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

1.1 GENERAL INTRODUCTION

North American wapiti (*Cervus elaphus*) are majestic creatures, valued by recreational hunter, wilderness photographer, and sight-seer alike. Similar to other large, migratory and herding ungulates such as caribou (*Rangifer tarandus*) and bison (*Bison bison*), wapiti are an important component of ecosystems. Indeed, wapiti affect key ecological functions – they compete with other ungulates (Johnson *et al.* 2000; Stewart *et al.* 2002), provide food resources for predators and scavengers (Wilmers *et al.* 2003; Anderson & Lindzey 2003; Wilmers & Getz 2004; Kunkel *et al.* 2004), and modify vegetation communities (Kay 1990; Bailey & Whitham 2002; Palmer *et al.* 2003; Schoenecker *et al.* 2004). Yet wapiti play other roles in the context of ecosystem management – roles more social than ecological (Cooperrider 2002). Being popular and charismatic, wapiti qualify as a "flagship" species (Simberloff 1998). Given their propensity for large movements they might also be thought of as "umbrella" species (Schrader-Frechette & McCoy 1993), but as Cooperrider (2002) points out this is a risky proposition given that wapiti prospered in Pacific Northwest forests as populations of spotted owl (*Strix occidentalis*), marbled murrelet (*Brachyramphus marmoratus*), pine marten (*Martes americana*), and Pacific fisher (*Martes pennanti pacifica*) dramatically declined. Nonetheless, wapiti are sensitive to human activities similar to other large and potentially less tractable mammals such as the grizzly bear (*Ursus arctos*), which, combined with their popularity, has secured wapiti the role of "featured" species in ecosystem management plans across western North America.

There are several advantages to working with an abundant and well-known species like wapiti. First, the techniques have largely been worked out for their efficient capture and handling. Being large-bodied, wapiti can carry sophisticated tracking equipment, such as Global Positioning System collars, with little consequence on their behaviour. Second, their general habitat requirements are relatively well known (Skovlin, Zager & Johnson 2002; Cook 2002; Hudson & Haigh 2002) and can be measured. Third, given their abundance and status as a game species, they can be experimentally manipulated (Cook *et al.* 1998). The latter may be crucial considering that the "threshold" conditions under which animals might fail to persist may not be detectable by observing wapiti where they currently exist. Although much research and information synthesis has taken place on wapiti, our knowledge of their habitat ecology comes largely from predator-free systems. Attempts to restore functioning ecosystems by recovering large predator populations are changing the living conditions for wapiti and other ungulates (Hebblewhite *et al.* 2002; Wolff & Van Horn 2003; Ripple & Beschta 2004; Fortin *et al.* 2005). Moreover, in parts of the Rocky Mountains and associated foothills – the stronghold for wapiti populations in North America – the footprint from forest, oil, and gas industries is increasing at an exponential rate (Timoney & Lee 2001). The linear clearings, roads, and other infrastructure associated with these industries can result in habitat loss (Dyer *et al.* 2001; Papouchis *et al.* 2001; Nellemann *et al.* 2003), increased human-caused mortality (Basile & Lonner 1979; Lyon & Burcham 1998; McCorquodale *et al.* 2003), and altered predator-prey dynamics (James & Stuart-Smith 2000; Kunkel & Pletscher 2003). When the effects of ever-increasing human populations, encroachment of "civilization" into formerly wild areas, and improved motorized access to wapiti range are considered, our prospects for maintaining wapiti, and populations of other large mammals, becomes less certain. Securing wapiti populations in light of these changes might only be achieved by gaining a greater understanding of how individuals cope with competing mortality risks and changing landscape conditions.

In addition to managing habitat and mortality risks, translocations have played a large role in the history of wapiti management across North America (O'Gara & Dundas 2002). The originally vast range of wapiti, spanning from the west to the east coast of North America at their maximal extent, was reduced to remnant herds in the inter-mountain west and Pacific northwest by the turn of the 20th century following European settlement (O'Gara & Dundas 2002). Attempts to reestablish populations via translocation have been undertaken in at least 33 U.S. states and 5 Canadian provinces (O'Gara & Dundas 2002). Gunson (1997) documented the translocations of 2,391 wapiti in Alberta between 1900-1995, which were designed to augment remnant or reestablish lost herds throughout the province. With protection and prudent management, wapiti rebounded in Alberta (Figure 1.1). As wapiti numbers grew, translocations became increasingly used to control burgeoning park populations and, in the 1980s, were added to the list of tools used to control animals at the agricultural fringe (Gunson 1997). For all of these reasons, translocations continue today in Alberta and across North America (Didier & Porter 1999; Rosatte *et al.* 2002; Larkin *et al.* 2004).

Multiple, concurrent herd reduction programs around the province provided the unique opportunity to study the competing mortality risks facing wapiti from two different perspectives – animals naive to versus those knowledgeable of local conditions.

In so doing, the factors associated with mortality risk could be more thoroughly elucidated (Armstrong *et al.* 1994). In recent years, the central foothills region of west-central Alberta (Figure 1.2) was identified as a suitable recipient area for wapiti translocations in part because the forest industry had created new foraging habitats that remained un- or under-utilized by resident animals (James Allen, Alberta Fish & Wildlife, personal communication). The opportunity to work with translocated animals rooted this study in the central foothills, also known as "David Thompson" country – a popular destination for campers, hunters, hikers, off-highway vehicle recreationists, and horseback riders. The region is also home to a suite of large predators including wolves (*Canis lupus*), mountain lion (*Puma concolor*), grizzly and black bear (*Ursus arctos* and *U. americanus*). Importantly, the region is undergoing rapid landscape change due to the combined effects of the forestry and oil & gas industries (Timoney & Lee 2001). Thus, the area provided the unique opportunity to study wapiti movements, habitat use, and survival where wapiti face hunting, predation (Lima & Dill 1990), disturbance from humans (Frid & Dill 2002), and broad-scale habitat changes. Concurrent research on wolves and involvement by the forest industry in the area set the stage for a rich study. The goal of this research was not only to increase our understanding of the consequences of competing mortality risks and continued landscape changes on wapiti but to put tools into the hands of the managers trying to balance competing demands on the forest ecosystem.

In this dissertation, I first assessed the potential for bias in estimates of habitat use determined from Global Positioning System collars and developed tools to correct for these biases (Chapter Two). From these assessments, I observed that the particular collars I used were little affected by habitat bias. Thus, despite developing techniques to correct for bias when it is a problem, I did not need to employ corrections for the resource selection models I produced for wolves and wapiti in this dissertation. In Chapter Three, I evaluated the efficacy of wapiti translocations to the central foothills, identified critical factors predicting wapiti mortality, and highlighted options for improving the success of future translocations. In Chapter Four, I turned my focus solely to resident animals to understand the movement strategies by which wapiti mediated their mortality risk in the central foothills. I quantified wapiti movement behaviour and how forage resources, predation risk, and human infrastructure affected movement decisions. In Chapter Five, I developed a simulation model to explore the movement and mortality consequences associated with an increasingly industrialized landscape (Chapter Five). These chapters are organized as independent papers, two of which have already been published (Chapters Two and Four). The format of these chapters, except where specific University of Alberta requirements dictated, follows the convention of the *Journal of Applied Ecology*. Besides this introductory chapter, I also provide a synthesis and discuss management implications for wapiti in the central Rocky Mountain foothills (Chapter Six).

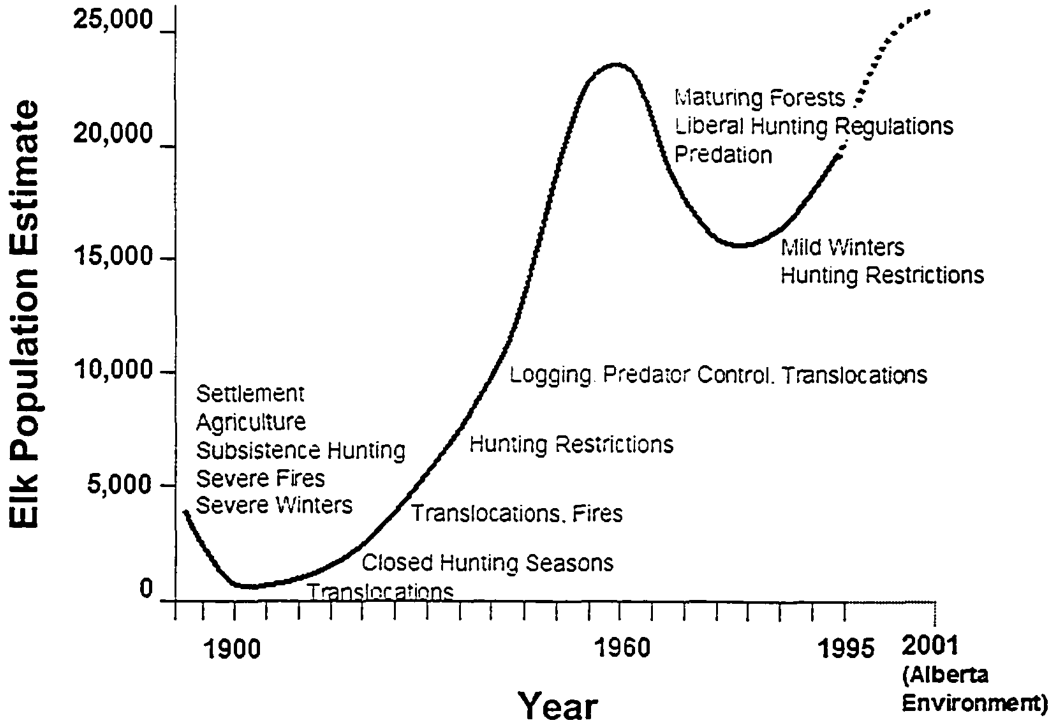

Figure 1.1. Elk population trend in Alberta with the factors considered responsible for declines and increases in elk numbers (adapted from Gunson 1997).

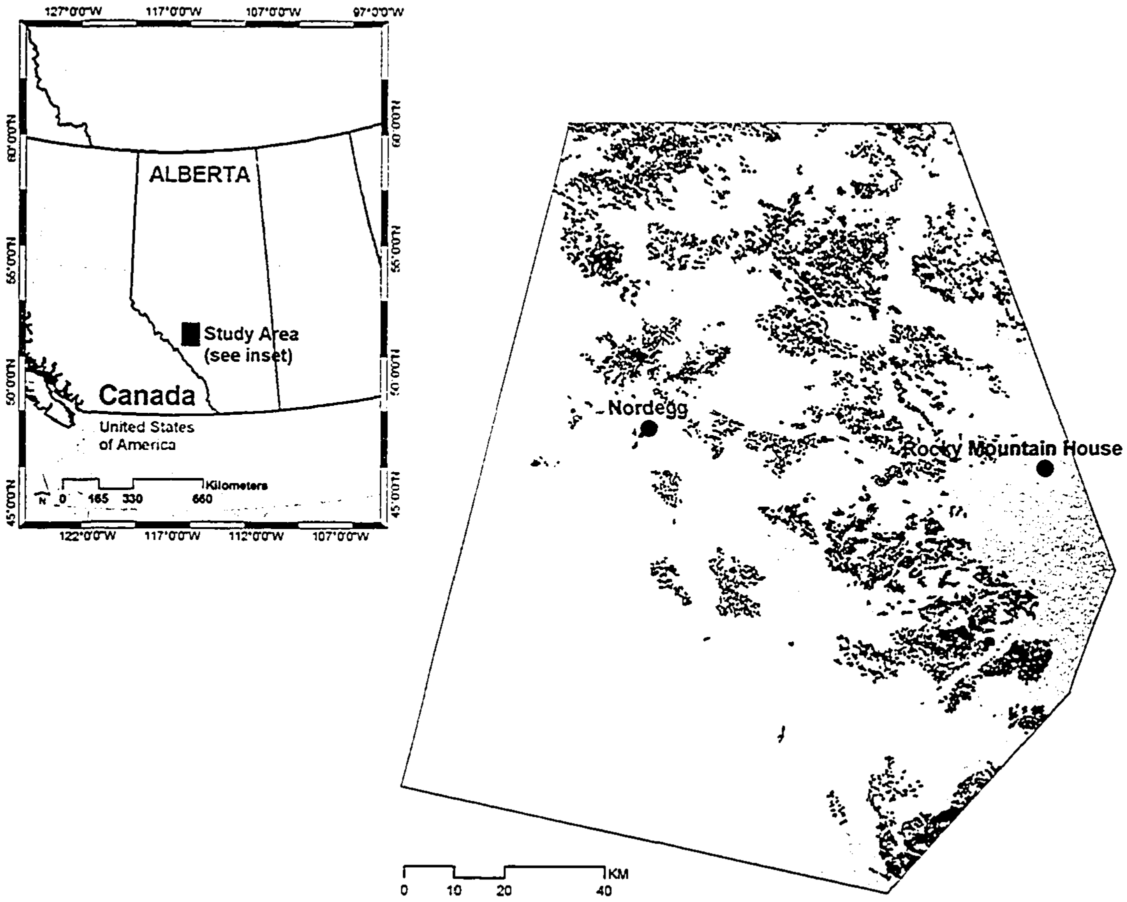

Figure 1.2. Study area in the central Rocky Mountain foothills of Alberta, Canada. The map at right shows the extent of potential foraging habitats for elk, specifically cutover forst (cutblocks; black) and natural meadows (white).

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CHAPTER 2

APPROACHES FOR REMOVING GPS-COLLAR BIAS IN HABITAT-SELECTION STUDIES[1]

2.1 INTRODUCTION

Recent integration of global positioning systems (GPS) into devices for tracking animals has extended our ability to monitor movements of free-ranging species over a broad range of spatial and temporal conditions. Despite improvements in this technology two types of errors remain inherent in animal location data collected by GPS telemetry, specifically, *spatial inaccuracy* in the locations acquired and *missing data* in the form of failed location attempts. The first type of error is not unique to GPS telemetry and its effect on apparent habitat selection has been well considered (White & Garrott 1986; Nams 1989). In particular, location inaccuracy can lead to misclassification of habitat use dependent upon the magnitude of location error and the degree of landscape heterogeneity. Location inaccuracy may be of less concern since the intentional degradation of satellite signals (selective availability) ceased in May 2000 because errors are reported to be ≤ 31 m 95% of the time (D'Eon *et al.* 2002), which is comparable to the resolution of most habitat maps. To counteract potential misclassification problems, one might re-sample locations within error polygons (Nams 1989; Samuel & Kenow 1992; Kenow *et al.* 2001) or replace point data with areas (buffers) around points (Kufeld *et al.* 1987; Rettie & McLoughlin 1999).

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[1] This chapter was originally published in April 2004 (volume 41, pages 201-212) in the *Journal of Applied Ecology* by J.L. Frair, S.E. Nielsen, E.H. Merrill, S.R. Lele, M.S. Boyce, R.H.M. Munro, G.B. Stenhouse, and H.L. Beyer. Reprinted with kind permission of Blackwell Publishing.

The second type of error, missing data, has largely been ignored even though it may have a more profound effect on inferences of habitat selection than inaccurate locations (Johnson *et al.* 1998). Missing locations equate to a loss of information, the implications being reduced efficiency and potential bias in the parameters estimated by habitat selection models (Little & Schenker 1995). Bias is likely in GPS telemetry studies because failed location attempts do not occur randomly but systematically. Previous work has shown that canopy type (Moen *et al.* 1996; Moen *et al.* 1997), percentage canopy cover (Rempel *et al.* 1995; Rumble & Lindzey 1997; D'Eon *et al.* 2002), tree density (Rumble & Lindzey 1997), tree height (Rempel & Rogers 1997; Dussault *et al.* 1999), and tree basal area (Rempel *et al.* 1995; Rumble & Lindzey 1997) can affect the acquisition of GPS locations. For example, GPS collars have been shown to be 3.8 times less likely to acquire a location under a tall forest canopy (> 15 m height) than in treeless areas (Rempel & Rogers 1997). In mountainous study areas, terrain conditions can interact with forest canopy cover to further reduce location acquisition (D'Eon *et al.* 2002). There also are predictable temporal effects due to the presence or absence of deciduous leaves (Moen *et al.* 1997; Dussault *et al.* 1999) and a changing satellite constellation throughout the day (Moen *et al.* 1997). A simulation experiment demonstrated that animal locations biased to approximate GPS error lead to Type II errors (failure to detect significant selection) and incorrect conclusions of selection versus avoidance (Rettie & McLoughlin 1999). The magnitude of effects observed by Rettie and McLoughlin (1999) depended on the level of data loss, how often the animal used biased vegetation types, and the degree of spatial association among vegetation types.

Despite documentation of GPS bias, and strong recommendations for bias corrections (Rumble & Lindzey 1997; Johnson *et al.* 1998; Dussault *et al.* 1999), most statistical analyses of habitat selection continue to ignore the effects biased data may have on subsequent inferences. One suggested method for reducing these effects, in addition to the effects of spatial inaccuracy, is to measure the areal extent of each habitat type within buffers around point locations rather than the habitat type at each location (Kufeld *et al.* 1987; Rettie & McLoughlin 1999). Using this approach, Rettie and McLoughlin (1999) were better able to accurately identify selection versus avoidance because buffers captured portions of biased habitat types that the acquired set of locations did not. However, buffers added sampling error by including "noise", habitats that may not affect animal behaviour, and thus their power to detect significant selection of certain habitats was reduced. Buffers, therefore, fail to solve the problems caused by biased missing data. Because missing GPS locations may be largely predictable, a more direct approach is to model the missing data mechanism and correct for bias statistically.

In this paper, I modelled the effects of collar brand, forest structure, season, terrain, and time of day on the probability of acquiring a GPS-collar location using field data. Using this model, I removed locations incrementally from an unbiased set of animal locations at two temporal sampling intensities (six- and one-hour locations). I identified the level of data loss at which coefficients in habitat selection models differed from unbiased estimates. Resource selection functions (RSFs; Manly *et al.* 2002) were used to quantify selection patterns. Alternative methods exist for assessing selection, e.g. compositional analysis (Aebischer *et al.* 1993), but I am most familiar with RSF techniques and focus solely on these. I chose a sampling design consistent with a third-order selection process (Johnson 1980), where used sites (animal locations) are compared to available sites (random locations) within the animal's home range, because this design is common to selection studies. I compared model coefficients produced using unbiased and biased data to determine how habitat-induced data loss affected the direction (selection versus avoidance), magnitude (coefficient value), and strength (significance level) of selection. Finally, I evaluated the effectiveness of two bias-correction methods, sample weighting and iterative simulation, at removing bias from RSF coefficients. Sample weighting is a deterministic process in which the influence of each location in the dataset is weighted by the inverse probability of having acquired that location (Little 1986; Kish 1992; Pfeffermann 1993). The alternative approach, iterative simulation, involves repeatedly simulating plausible spatial coordinates for each missing location and using multiple imputation methods to combine simulation results into a single model (Rubin 1987; Schafer 1999). Both techniques require a bias estimate for every location in the landscape, which I produced using field trials and data held in a geographic information system (GIS).

2.2 MATERIALS AND METHODS

2.2.1 GPS-BIAS MODEL

I modelled the probability of acquiring a GPS location using data from GPS collars recorded during 194 trials in the eastern-central Rocky Mountains and foothills of Canada (52° 27′ N, 115° 45′ W). I used 10 Lotek GPS 2200 collars (2001 production; Lotek Wireless, Ontario, Canada) at 143 sites, seven Televilt GPS Simplex collars (1999 production; Televilt International, Sweden) at 33 sites, and six ATS GPS collars (2000 production; Advanced Telemetry Systems, Minnesota, USA) at 24 sites (Table 2.1). Logistical constraints led to uneven sample sizes among collar types. Trials were conducted from July to December 2000 and during July 2001 and consisted of placing a GPS collar approximately 1-m above ground, with the antenna directly upright, and leaving the collar to collect locations at 30- or 60-minute intervals for ≥ 22 hours. Trials took place across a range of conditions from gently rolling to mountainous terrain in open and forested areas. Forests were dominated by lodgepole pine *Pinus contorta* Dougl. *ex* Loud., black spruce *Picea mariana* (Mill.) B.S.P., white spruce *Picea glauca* (Moench) Voss, Engelmann spruce *Picea engelmannii* Parry *ex* Engelm., trembling aspen *Populus tremuloides* Michx., and balsam poplar *Populus balsamea* L.

At each trial site I recorded percentage canopy closure as the average spherical densiometer estimate across five site readings, directly over the collar and 10-m distant in the four cardinal directions. Tree height, diameter at breast height (dbh), and density was recorded within a 2 × 10 m transect centered over the collar. A 100-m digital elevation model with a 30-m cell size was used to calculate terrain indices for each location using Arc/Info software (Environmental Systems Research Incorporated, California, USA). Terrain indices included percentage slope at the test site, terrain ruggedness of the area (standard deviation in elevation within a 500-m radius), and percentage visible sky (the amount of a hemispherical dome centered over the location that was not obstructed by terrain). Percentage visible sky was analogous to the "available sky" index described by D'Eon *et al.* (2002). The effects of time of day have not been apparent using consecutive 4-hour classes (D'Eon *et al.* 2002), most probably because various optimal and sub-optimal satellite configurations can occur throughout the day. As an alternative, I pooled trials, plotted percentage location acquisition by hour, and assigned each location attempt to one of three time classes: (1) location acquisition rates > 90%: early morning (0300–0600), early afternoon (1200–1300), and evening (1800–2000); (2) acquisition rates from 87–90%: late morning (0700–1100) and night (2100–0200); and (3) acquisition rates ≤ 86%: late afternoon (1400–1700). I excluded two trials (one each for Lotek and Televilt collars) because the collars acquired < 1% of the attempted locations and I would not apply corrective measures to such obvious incidences of collar malfunction.

I used logistic regression to model the probability of a location attempt being successful (1) or unsuccessful (0) as:

eqn 1
$$P_{ACQ} = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}$$

where β_0 is the regression constant and $\beta_1 \dots \beta_n$ are coefficients estimated for variables $x_1 \dots x_n$ (Hosmer & Lemeshow 2000). Because successive location attempts at a site were not independent, I used a clustering technique that recognized the unit of replication to be the trial site rather than each observation (Pendergast *et al.* 1996; STATA Corporation 2001a). Using the techniques of Pregibon (1981), I identified several trials having high leverage but considered none to be outliers. Thus, all trials (n = 192) were retained for model development. I considered candidate models to be all possible combinations of non-correlated variables (Pearson r < 0.5 when $P < 0.05$) and appropriate interaction terms. Therefore, potential covariates included collar brand (Televilt, ATS, Lotek), season (leaf-on, leaf-off), time class, mean tree height (m), mean tree dbh (cm) or percentage canopy closure, tree density (number of trees per ha) or percentage canopy closure, vegetation class (open conifer forest, closed conifer forest, deciduous forest, mixed forest, non-forested) or overstorey canopy type (open, closed, no canopy) or percentage canopy closure, and percentage slope or terrain ruggedness or percentage visible sky. For all categorical variables, I used indicator coding and selected as a reference category the class least likely to influence location acquisition.

Akaike's information criterion with a small-sample bias adjustment (AIC_c) and Akaike weights (w_i) were used to identify a set of parsimonious models that best explained my data (Burnham & Anderson 2002). From these I selected the best-supported model to calculate the probability of acquiring a GPS location across the landscape. I assessed overall model classification accuracy by using the area under the receiver operating characteristic (ROC) curve (Hanley & McNeil 1982) and model fit by the Hosmer & Lemeshow goodness-of-fit statistic ($\hat{C}$; Hosmer & Lemeshow 2000).

2.2.2 EFFECTS OF GPS BIAS ON RESOURCE SELECTION FUNCTION (RSF) COEFFICIENTS

I evaluated the effects of GPS bias on habitat selection using data from a free-ranging, female wapiti *Cervus elaphus* L. inhabiting the central east slopes of the Rocky Mountains in Alberta. Actual animal locations were used to include realistic spatial and temporal autocorrelations in habitat use patterns. I took a resource selection function (RSF) approach to model habitat selection where an RSF is any statistical model that yields values proportional to the probability of resource use by an organism (Manly *et al.* 2002). The design I used for RSF estimation is commonly employed in radiotelemetry studies where characteristics of sites "used" by animals are compared to those "available" using logistic regression. The relative probability of animal occurrence is assumed to take the form:

eqn 2 $$w^*(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

where $\beta_1 \ldots \beta_n$ are logistic regression coefficients estimated for environmental variables $x_1 \ldots x_n$ (Manly *et al.* 2002).

The wapiti selected for this analysis wore a Lotek collar that achieved a 96% location acquisition rate given a one-hour sampling interval over a period of five months despite the animal occupying a landscape that was over 70% forested. Using the original data ($n = 2986$) and a re-sampled set of six-hour locations ($n = 497$), I estimated RSFs using three environmental variables, two of which, vegetation type and percentage slope, were variables in the best GPS bias model (P_{ACQ}). The third variable, distance to nearest trail, was included to explore the effects of both GPS bias and my corrections on variables that do not directly influence location acquisition. Vegetation type was derived from Alberta Vegetation Inventory data produced through air-photo interpretation using a 0.5 ha minimum-mapping unit and converted to a 30-m resolution grid. A grid format was required to make spatially explicit predictions of GPS error and the 30-m cell size is consistent with the resolution of Thematic Mapper satellite imagery, which is commonly used for studies on large mammals. Because the grid cell size was below the resolution of the original data there was no loss of information due to format conversion. Percentage slope was derived from the digital elevation model. Trails included 5–9-m wide, recreation trails and seismic exploration transects. In this area, trails occurred in each vegetation type and terrain condition proportionate to their occurrence.

For both sampling intensities I compared RSF coefficients based on the full (unbiased) data set to subsets of these data after removing 10–40% of the locations in a biased manner. The reduction process involved randomly selecting locations for evaluation and removing a subset of selected locations according to their probability of being acquired using the P_{ACQ} model. Because the data reduction process was stochastic, I created 10 independent sets of biased data for each level of data loss. To represent resource availability I generated 2986 random locations within a minimum convex polygon (Mohr 1947) that enclosed the complete set of one-hour locations and 497 random locations within the polygon enclosing the set of six-hour locations. The same set of available locations was used for all models produced at a given sampling intensity. Following RSF estimation I considered the Type II error rate to be the percentage of biased model coefficients that were falsely detected as non-significant when compared to the unbiased model coefficient using $\alpha = 0.05$. Likewise, Type I error rates (failure to correctly detect non-significance) were determined by comparing biased to unbiased coefficients using $\alpha = 0.05$. Coverage, defined by the proportion of unbiased coefficient values that fell within the confidence intervals of the coefficients derived from biased data, was used to assess if GPS bias caused a significant change in the apparent magnitude of selection.

2.2.3 CORRECTIONS FOR GPS BIAS

A data loss of 30% falls at the upper end of the range of data loss reported for collars recovered from free-ranging animals (Edenius 1996; Merrill *et al.* 1998; Dussault *et al.* 1999; Biggs *et al.* 2001). Thus, I applied two bias correction approaches given a

30% data loss to the biased six- and one-hour location data. In the first approach, sample weighting, I applied $1/P_{ACQ}$ as a weight to each acquired location, and 1 as a weight to each available location, while estimating RSF coefficients. To calculate standard errors for coefficients I used a Huber/White sandwich estimator that is based on White's heteroskedastic-consistent estimator (White 1980; Winship & Radbill 1994; STATA Corporation 2001b).

In the second approach, iterative simulation, I "filled in" the locations missing from each biased dataset prior to estimating RSF models. The simulation process required a plausible, finite spatial domain within which each missing location was likely to have occurred (Figure 2.1). For simplicity, I defined that domain to be a square centred over the last and next known animal locations. Iterative simulations required the spatial domain to contain > 2 cells; therefore, when the square domain had side length < 100 m I placed the missing location midway between the last and next known locations. I filled in each remaining missing location in a random but weighted manner using the P_{ACQ} model. Thus, I generated 30 "complete" datasets for each biased dataset. I calculated a RSF for each of the 30 datasets and plotted the mean coefficient against the number of simulations conducted to discern how many iterations were needed to achieve stable estimates (Rubin 1996; Robins & Wang 2000). After selecting the necessary number of iterations, *n*, I calculated final coefficients as the average across the first *n* RSF models (Rubin 1987). The total variance associated with each coefficient was calculated as a function of the within- and between-simulation variance using multiple imputation techniques (Rubin 1987; Schafer 1999). Standard errors and significance levels for each coefficient were calculated using a *k*-component, Student-*t* reference distribution (Barnard & Rubin 1999).

2.3 RESULTS

2.3.1 COLLAR PERFORMANCE AND GPS-BIAS MODEL

The mean rates of successful location attempts ranged from 67.6 ± 8.2% (SE) to 99.7 ± 0.3% across collar brands, vegetation types, and terrain conditions (Table 2.1). Initial univariate models indicated that collar brand (Wald $\chi^2 = 11.48$, $P = 0.022$), vegetation class ($\chi^2 = 11.48$, $P = 0.022$), season ($\chi^2 = 8.54$, $P = 0.004$), tree density ($\chi^2 = 5.84$, $P = 0.016$), mean tree height ($\chi^2 = 7.92$, $P = 0.005$), percentage canopy ($\chi^2 = 3.97$, $P = 0.046$), and time class ($\chi^2 = 29.42$, $P = 0.005$) significantly affected the probability of acquiring a GPS location. The AIC_c-selected, multiple logistic regression model included collar brand, vegetation class, percentage slope, and interaction terms for vegetation class × percentage slope, although there was also support for a similar model that included season (Table 2.2). Televilt collars had a lower probability of acquiring a GPS location than Lotek collars (the reference category), whereas ATS and Lotek collars did not differ (Table 2.3). Both closed conifer and deciduous forest had large and negative effects on the probability of acquiring a GPS location compared to the non-forested, reference class. The effects of open canopy conifer and mixed forest did not differ from non-forested areas. After controlling for collar brand and vegetation effects, an increasing percentage slope further reduced the likelihood of acquiring a location. However, the probability of acquiring a location under closed conifer and deciduous forest was better on steep slopes than on flatter terrain.

Overall my bias model was significant (Wald $\chi^2 = 43.70$, $P < 0.001$) and discriminated between successful and unsuccessful location attempts moderately well for Televilt (ROC area = 0.713) and ATS collars (ROC area = 0.664). In comparison, the model poorly classified location attempts for Lotek collars (ROC area = 0.535) because these collars were highly successful at acquiring locations across the range of conditions I tested. Model predictions ranged from 0.63–0.98, consistent with the mean location acquisition rates observed in my trials, but did not predict the very low success observed in several trials as reflected by the Hosmer and Lemeshow (2000) goodness-of-fit test ($\hat{C} = 73.76$, groups = 10, n = 6,693, $P < 0.001$). For my simulations I solved the P_{ACQ} model for Televilt collars and recognize that my estimates for the amount of bias affecting these collars may be conservative.

2.3.2 EFFECTS OF GPS BIAS ON RSF COEFFICIENTS

The unbiased selection patterns of the wapiti were the same whether six- or one-hour locations were used, although RSF coefficients for the one-hour data were more significant ($P \leq 0.001$ excluding percentage slope) because of the larger sample size. Relative to non-forested areas, the animal avoided both closed conifer and open conifer forest and selected both deciduous and mixed forest (Table 2.4). The animal also selected areas close to trails while areas with varying percentage slope were used in proportion to their availability. Although percentage slope was not a significant variable in my unbiased RSFs, I retained it to observe whether Type I errors occurred due to GPS bias or my bias corrections.

No Type I errors or changes in coefficient sign were observed regardless of the GPS sampling intensity or level of data loss. Likewise, for the one-hour sampling intensity, no Type II errors were observed regardless of the level of data loss. For the six-hour sampling intensity, random data loss caused Type II errors in the mixed forest variable once data losses reached 30%. However, Type II errors due to GPS bias were prevalent in the deciduous forest and distance to nearest trail variables given as little as a 10% data loss (Table 2.4). A marginally significant interaction term between closed conifer forest, a biased vegetation type, and distance to nearest trail ($\beta = -2.37$, SE = 1.37, $P = 0.085$) indicated that areas close to trails were used more often under dense conifer canopy (all other interaction terms $P \geq 0.218$) and, thus, GPS bias indirectly affected the apparent selection of other covariates.

Biased data loss increased the magnitude of avoidance of closed conifer forest, which was significantly avoided in the unbiased model. At the six-hour sampling interval, closed conifer coefficients derived from biased data became significantly different from the unbiased coefficient given data losses of ≥ 30% (Figure 2.2). Increasing the sampling intensity from six- to one-hour locations increased the effect of bias on the closed conifer forest variable such that 100% of the coefficients derived from biased data differed from the unbiased coefficient given a data loss of ≥ 20%.

2.3.3 EFFECTIVENESS OF BIAS CORRECTIONS

Mean coefficients for the closed conifer forest variable stabilized after 15 simulations for 6-hour locations and after 25 for the one-hour locations (Figure 2.3). Simulation results for the six-hour data yielded a 10 and 40% reduction of Type II errors in the distance to trail and deciduous forest coefficients, respectively (Table 2.5), and 100% coverage of the unbiased coefficients for closed conifer forest (Figure 2.4A). Sample weighting reduced Type II errors by 30 and 0% for the distance to trail and deciduous forest coefficients, respectively (Table 2.5), and also achieved 100% coverage of the unbiased closed conifer forest coefficient (Figure 2.4A). Either technique combined with $\alpha = 0.10$ rather than 0.05 nearly eliminated Type II errors in all variables without causing Type I errors (Table 2.5). For the one-hour locations, simulation achieved 100% coverage and sample weighting 80% coverage of the unbiased closed conifer forest coefficient, even though coefficients were consistently underestimated (Figure 2.4B). All other variables retained 100% coverage at both sampling intensities when biased and following bias corrections.

2.4 DISCUSSION

The results from my collar tests generally agreed with previous studies in that acquisition of GPS locations was lowest under dense forest canopies, taller trees, and during the summer months (Moen *et al.* 1997; Rempel & Rogers 1997; Dussault *et al.* 1999; D'Eon *et al.* 2002). Unlike D'Eon *et al.* (2002), I found significant differences by time of day. Nevertheless, time was not a variable in my highest-ranked models and its effect on habitat selection therefore was not evaluated by my tests. I did not detect an effect of open canopy forests (< 60% canopy closure) or mixed deciduous-coniferous forest cover on location acquisition possibly because the latter type tended to have a layered canopy with an "open" overstorey. Terrain variables were not significant by themselves possibly due in part to the coarse resolution of my digital elevation model.

However, interactions between closed canopy forest types and percentage slope suggested that the reduction in canopy interference down-slope outweighed the potentially increased blockage of satellites upslope due to terrain. Uncertainty among my highest-ranked models indicated that season also had important effects on GPS bias. For simplicity I did not include an effect of season in my tests but I have observed acquisition rates to vary by season for collars recovered from free-ranging wapiti and, therefore, a model including season may be necessary to appropriately compensate for GPS bias in field studies. Finally, differences in acquisition rates between collar brands may reflect, in large part, different years in which the collars were manufactured, i.e., Televilt collars were produced in 1999 and Lotek collars produced in 2001, because other researchers have reported that collar performance has improved over the years (Rempel & Rogers 1997; Dussault *et al.* 1999).

I conclude that a GPS bias model should be produced specific to the collars employed in a given study, the specific conditions and seasons under study, and preferably produced using a sampling interval consistent with that of the free-ranging collars to be corrected. Further, animal behaviour has been shown to affect collar performance (Moen *et al.* 1996; Bowman *et al.* 2000) and collars that provide information on animal activity may additionally improve my ability to model acquisition error. I caution against extrapolating my GPS bias model to areas outside the east-central Rocky Mountains and foothills of Alberta because poorly fit models may introduce bias or cause excessive variation in parameter estimates (Robins *et al* 1994). I concur with D'Eon *et al.* (2002) that unexplained or random error is a large cause of the data missing from GPS collars but, nevertheless, I demonstrated that even a small bias resulting in small losses of data can influence my assessment of resource selection by animals.

Habitat-induced bias in animal locations acquired by GPS collars can result in Type II errors and biased RSF coefficients. Several factors influenced the extent of these errors. First, *rarity* of certain vegetation types made them susceptible to Type II errors. Similar observations have been reported by White and Garrott (1986) and Rettie and McLoughlin (1999). The two rare types, deciduous and mixed forest, were similar in extent (11 and 8% of the landscape, respectively) but deciduous forest was used slightly less (16 vs. 21%). The lower apparent strength of selection for deciduous forest (P = 0.042) compared to mixed forest (P = 0.008), combined with the large and negative effect of deciduous forest cover on GPS location acquisition, was sufficient to cause Type II errors in this type given relatively small data losses (10%). Second, *interactions* among variables indicated that GPS-induced bias in one variable may influence conclusions about an animal's selection of another resource. For example, I observed that the biased loss of locations from closed conifer forest probably caused Type II errors in the distance to trail variable because the wapiti more frequently used areas near trails when under a closed conifer canopy compared to other vegetation types. Third, even though closed conifer and deciduous forest had similar coefficients in the GPS bias model (see Table 2.3), I did not observe an equivalent bias in RSF coefficients for these variables because the *magnitude of use* of each type of forest by the wapiti differed. My understanding of this effect, however, differs from the simulations conducted by Rettie and McLoughlin (1999). Here closed conifer forest was the most extensive vegetation type (58% of the landscape) and was used 2.3 times more than deciduous forest, thus, bias related to wapiti use of conifer forest occurred at least twice as often as for use of deciduous forest. Therefore, the magnitude of the modelled bias alone may not be sufficient to anticipate the full influence of biased data loss.

How well my corrections reduced the effects of GPS bias depended on how effectively each approach "replaced" missing locations. Simulation increased sample sizes to their original level thereby reducing Type II errors in the rare deciduous forest type and, when combined with $\alpha = 0.10$, reducing more Type II errors overall than sample weighting. However, simulation placed locations on the landscape randomly with respect to trails and was thus less effective than sample weighting at removing Type II errors from the distance to nearest trail variable. Sample weighting effectively "re-sampled" existing animal locations, which in this case were not distributed randomly with respect to trails. Refinements to the spatial domain for imputations, e.g., limiting location replacements to within a buffer around the straight-line displacement between the last and next known locations, may better conserve the selection patterns of the animal under study and are worthy of further investigation. Further, the GPS sampling intensity affected both the magnitude of coefficient bias and how well corrections performed. Both techniques effectively eliminated bias from closed conifer forest coefficients without introducing bias into any other variables. The extreme condition I tested of frequent sampling (one-hour locations) and large data losses (30% reduction) limited my ability to correct coefficients. However, I have observed that location rates generally increase as relocation intervals shorten and thus this extreme is unlikely to be achieved in field studies.

The approach most suitable for bias correction will depend on the design for assessing resource selection. For widely roaming animals or infrequent location schedules, sample weighting may be preferable because simulating locations within a large spatial domain may introduce an unreasonable amount of sampling error especially in heterogeneous landscapes. Further, sample weighting may perform better than simulation when covariates are distance-based (e.g. Conner *et al.* 2003). Note that when sample weights are applied, a weight of one should be assigned to all influential and outlying data points to avoid unduly inflating the influence of these locations when estimating coefficients (Little & Schenker 1995). However, sample weighting may not be applicable for certain designs such as conditional fixed-effects logistic regression where weights cannot be applied to individual observations (STATA Corporation 2001a). For designs that temporally constrain availability (e.g., Arthur *et al.* 1996; Cooper & Millspaugh 1999; Hjermann 2000; Compton *et al.* 2002), iterative simulation may be more desirable as corrections are constrained to the time and area of the missed location. Further, location inaccuracy may be of concern to sample weighting as weights are applied to the GPS location rather than the true location of the animal. My simulation routine could be adapted as part of a re-sampling method similar to Kenow *et al.* (2001) to account for GPS bias due to both location uncertainty and failed location attempts. Using multiple imputation techniques to combine simulation results would also be appropriate when correcting for inaccurate locations. Note that simulations should not be conducted on long sequences of missing data that occur due to random malfunction rather than GPS bias. For example, I rarely observed gaps between successful locations of greater than eight hours for Lotek collars and, thus, I used eight hours as a cutoff for corrections. Finally, both techniques support the use of point data, which overcomes the limitations imposed by the use of buffers (Rettie & McLoughlin 1999). However, I have not tested the effects of bias or my corrections under any sampling design other than using logistic regression to detect a third-order selection process. I encourage exploration of bias and corrections when using any other sampling design.

Despite the increased sample sizes and increased spatial accuracy of animal locations obtained by GPS collars, inherent biases in this technology remain an evolving challenge for their users. Large-scale studies across heterogeneous landscapes may suffer unequal sample sizes among individuals due to the local effects of GPS bias. Rarification of data to investigate resource selection for specific behaviours, e.g. small- versus large-scale movements (Johnson *et al.* 2002), or for certain time periods, e.g. day versus night, will restrict sample sizes potentially to within the range for which I observed pervasive Type II errors and coefficient bias. Further, researchers will adapt their questions to take advantage of improving technologies and, thus, sampling intervals will become increasingly shorter to the extent allowed by battery capacity. In so doing, coefficient bias may become more problematic rather than less so over time. The bias correction techniques I present can be used to overcome many of these issues, however, large sample tests across a broad range of conditions may be necessary to understand the stability of the patterns I observed.

Table 2.1. Landscape characteristics of sites where GPS collar trials were conducted and the percentage of location attempts that were successful for three types of collars. Collars attempted locations every 30–60 minutes for ≥ 22 hours per trial.

Vegetation Category	Number of trial sites	Percentage canopy mean ± SE	Percentage slope mean ± SE	Percentage location Success	
				Range	Mean
Televilt GPS Simplex Collars					
Non-forested	8	0.1 ± 0.0	5.8 ± 0.2	48.9 – 100.0	91.6 ± 6.4
Open Conifer Forest	8	36.8 ± 0.8	13.2 ± 0.8	53.2 – 98.9	85.5 ± 5.9
Closed Conifer Forest	11	89.7 ± 0.2	17.7 ± 0.7	12.8 – 92.6	67.6 ± 8.2
Deciduous Forest (leaf-on)	3	83.0 ± 1.2	28.7 ± 1.0	70.2 – 100.0	84.4 ± 8.6
Mixed Forest (leaf-on)	3	87.0 ± 0.1	15.6 ± 0.5	72.6 – 93.6	85.9 ± 6.7
ATS Collars					
Non-forested	7	0.0 ± 0.0	13.4 ± 1.0	97.9 – 100.0	99.7 ± 0.3
Open Conifer Forest	7	29.5 ± 0.9	8.3 ± 0.3	33.3 – 100.0	88.0 ± 9.2
Closed Conifer Forest	8	90.3 ± 0.3	20.8 ± 0.7	59.4 – 100.0	89.5 ± 4.8
Deciduous Forest (leaf-on)	1	90.0	13.7		89.6
Mixed Forest (leaf-on)	1	86.0	22.2		84.4
Lotek GPS2200 Collars					
Non-forested	28	5.1 ± 0.3	12.7 ± 0.6	58.3 – 100.0	94.9 ± 2.6
Open Conifer Forest	11	47.2 ± 0.5	6.4 ± 0.4	70.8 – 100.0	86.7 ± 3.8
Closed Conifer Forest	37	84.1 ± 0.3	16.7 ± 0.5	70.2 – 100.0	93.5 ± 1.9
Deciduous Forest (leaf-on)	11	82.7 ± 0.3	8.5 ± 0.2	50.0 – 100.0	87.5 ± 4.6
Deciduous Forest (leaf-off)	25	83.9 ± 0.3	13.3 ± 0.4	62.5 – 100.0	94.3 ± 2.1
Mixed Forest (leaf-on)	5	74.6 ± 1.0	3.7 ± 0.2	91.7 – 100.0	97.5 ± 1.7
Mixed Forest (leaf-off)	22	80.2 ± 0.6	13.1 ± 0.3	60.9 – 100.0	96.1 ± 2.0

Table 2.2. Comparison of the 10 highest ranked, logistic regression models for GPS bias in the eastern-central foothills of the Rocky Mountains, Alberta. The models are shown, in order of decreasing rank, with the model log-likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion for small sample sizes (AIC_c), AIC difference (Δ_i), and AIC weight (w_i). An * indicates interaction terms for the specified variables.

Rank	Variables	LL	K	AIC_c	Δ_i	w_i
1	BRND[1], VEG[2], SLP[3], VEG*SLP	−2042.97	12	4111.66	0.00	0.55
2	BRND, VEG, SLP, VEG*SLP, SEAS[4]	−2042.02	13	4112.06	0.40	0.45
3	BRND, CAN[5], SLP, CAN*SLP	−2068.41	6	4149.27	37.61	0.00
4	BRND, VEG, SLP, SEAS	−2073.91	8	4164.60	52.94	0.00
5	BRND, VEG, SLP	−2075.79	8	4168.36	56.70	0.00
6	BRND, CAN, SLP	−2099.08	5	4208.48	96.82	0.00
7	BRND, OVER[6]	−2102.12	4	4212.45	100.79	0.00
8	STEM[7], HGHT[8], SLP	−2129.79	3	4265.70	154.04	0.00
9	STEM, HGHT	−2133.20	3	4272.53	160.87	0.00
10	BRND, VEG, SLP, VEG*SLP, HOUR	−2121.45	14	4273.25	161.59	0.00

[1] collar brand (ATS, Televilt, Lotek), [2] vegetation class (closed conifer, open conifer, deciduous, mixed forest, non-forested), [3] percentage slope, [4] season (leaf-on, leaf-off), [5] percentage canopy, [6] overstorey canopy class (closed, open, no canopy), [7] stem density, [8] tree height, [9] hour class (early morning, early afternoon, and evening; late morning and night; late afternoon)

Table 2.3. Highest-ranked logistic regression model for predicting the probability of acquiring a GPS location (P_{ACQ}) in the in the central Rocky Mountains and foothills of Alberta, Canada (N_{obs} = 6,763, Wald $\chi^2 = 43.70$, $P < 0.001$, ROC area = 0.683). Standard errors were adjusted because data were clustered by trial site (n = 192).

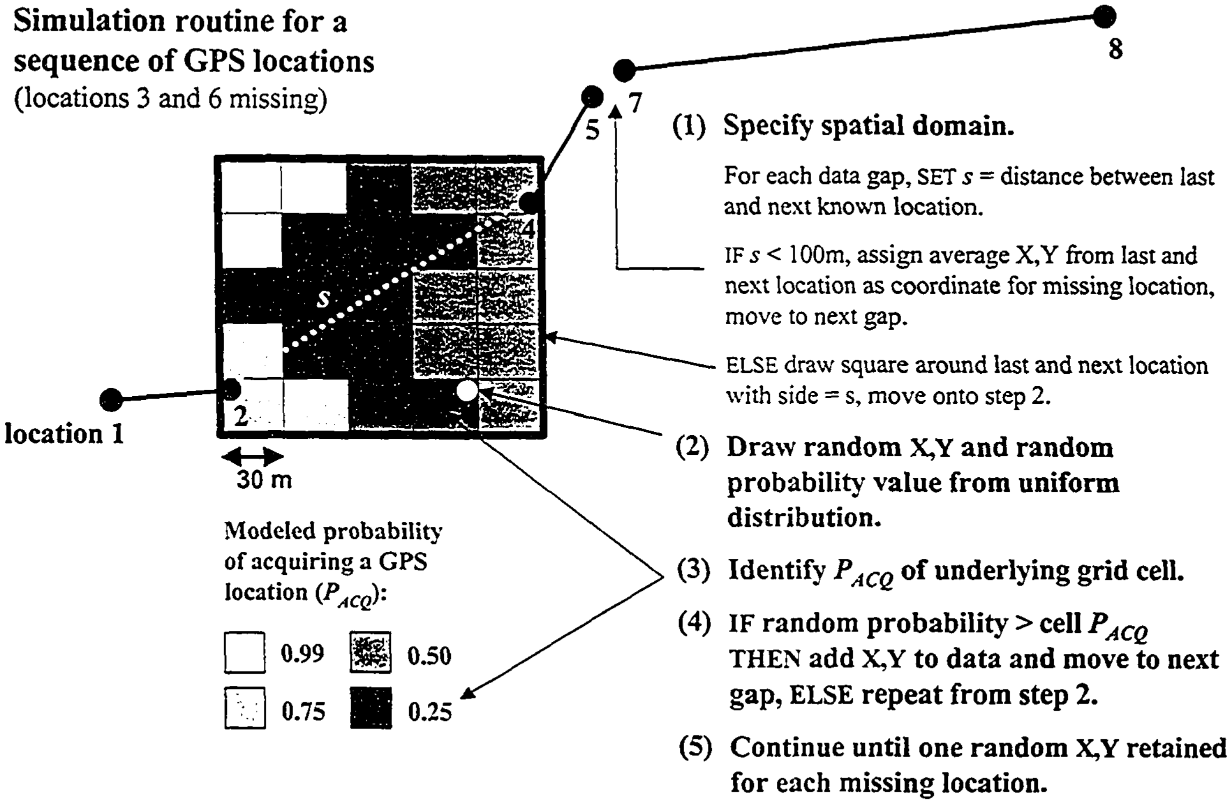
Variable	β	Adjusted S.E.	*z*	*P*
Vegetation Type				
open conifer forest (<60% canopy)	−0.8515	0.6349	−1.34	0.180
closed conifer forest (>60% canopy)	−1.8304	0.6683	−2.74	0.006
deciduous forest (>60% canopy)	−1.7097	0.6379	−2.68	0.007
mixed forest (>40% canopy)	−0.2673	0.6906	−0.39	0.699
reference = non-forested				
Collar Brand				
ATS (2000 model)	−0.4544	0.4173	−1.09	0.276
Televilt GPS Simplex (1999 model)	−1.0969	0.2847	−3.85	<0.001
reference = Lotek GPS2200 (2001 model)				
Percentage Slope	−0.0316	0.0151	−2.10	0.036
Interaction Terms				
percentage slope × open conifer forest	0.0087	0.0171	0.51	0.610
percentage slope × closed conifer forest	0.0459	0.0232	1.97	0.048
percentage slope × deciduous forest	0.0565	0.0195	2.89	0.004
percentage slope × mixed forest	−0.0137	0.0305	−0.45	0.654
Constant	3.8585	0.5829	6.85	<0.001

Table 2.4. The effects of GPS-biased data loss on the detection of resource selection by a female wapiti in the Rocky Mountain foothills, Alberta. Coefficient values (β), standard errors (SE), and significance levels (*P*) are shown for the RSF estimated using unbiased locations collected every six hours for five months (n = 497). Also shown are Type II error rates calculated as the percentage of RSF coefficients (n = 10 for each level of data loss) that were falsely identified as non-significant compared to the unbiased coefficient using α = 0.05.

	Unbiased Model:			Type II error rate after the level of data loss specified:			
Variable	β	SE	*P*	10%	20%	30%	40%
Vegetation Type							
closed conifer forest	−0.543	0.177	0.002	0	0	0	0
deciduous forest	+0.534	0.263	0.042	30	20	50	40
mixed forest	+0.639	0.243	0.008	0	0	20	70
open conifer forest	−0.907	0.239	<0.001	0	0	0	0
reference = non-forested							
Distance to nearest trail (km)	−1.138	0.523	0.029	40	60	70	100
Percentage Slope	+0.003	0.015	0.862	0	0	0	0

Table 2.5. The effects of sample weighting and iterative simulation on detecting resource selection given a 30% biased data loss and a six-hour sampling interval. Type II error rates were calculated as the percentage of RSF coefficients (n = 10) that were falsely identified as non-significant when compared against the unbiased coefficient using $\alpha = 0.05$ ($\alpha = 0.10$ shown in parentheses).

Variable	Biased	Weighted	Simulated
Vegetation Type			
closed conifer forest	0 (0)	0 (0)	0 (0)
deciduous forest	50 (10)	50 (10)	10 (0)
mixed forest	20 (10)	20 (10)	20 (0)
open conifer forest	0 (0)	0 (0)	0 (0)
reference = non-forested			
Distance to Nearest Trail (km)	70 (40)	40 (10)	60 (20)
Percentage Slope	0 (0)	0 (0)	0 (0)



Simulation routine for a sequence of GPS locations
(locations 3 and 6 missing)

(1) Specify spatial domain.

For each data gap, SET s = distance between last and next known location.

IF s < 100m, assign average X,Y from last and next location as coordinate for missing location, move to next gap.

ELSE draw square around last and next location with side = s, move onto step 2.

(2) Draw random X,Y and random probability value from uniform distribution.

(3) Identify P_{ACQ} of underlying grid cell.

(4) IF random probability > cell P_{ACQ} THEN add X,Y to data and move to next gap, ELSE repeat from step 2.

(5) Continue until one random X,Y retained for each missing location.

Figure 2.1. Iterative simulation framework for replacing the locations missing from GPS collars.

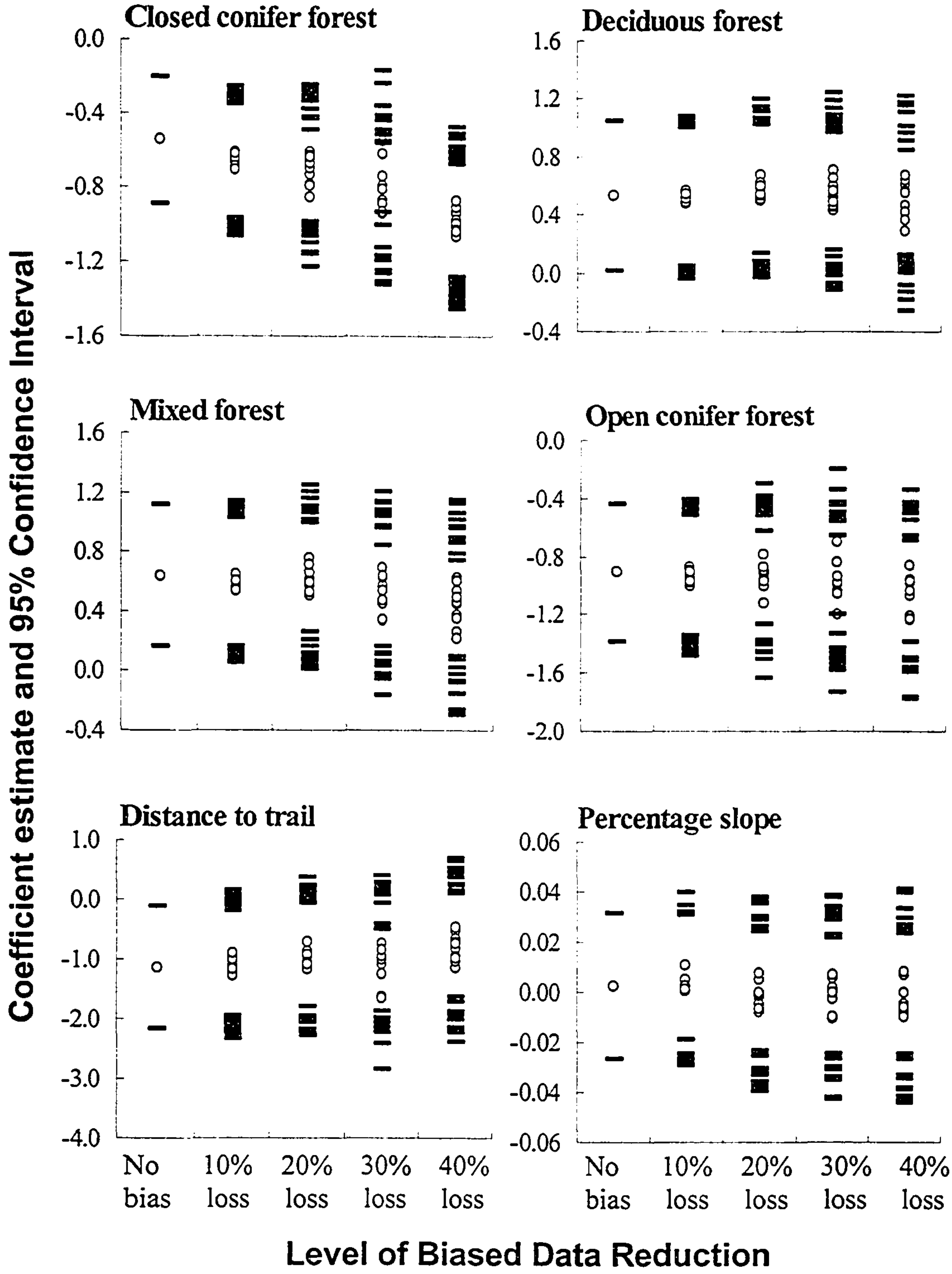


Figure 2.2. The effects of biased data loss on resource selection function coefficients given a six-hour GPS location interval. Coefficient values (open circles) and 95% confidence intervals (solid lines) are shown for the unbiased data model and each model produced using biased data (n = 10 models for each level of data reduction).

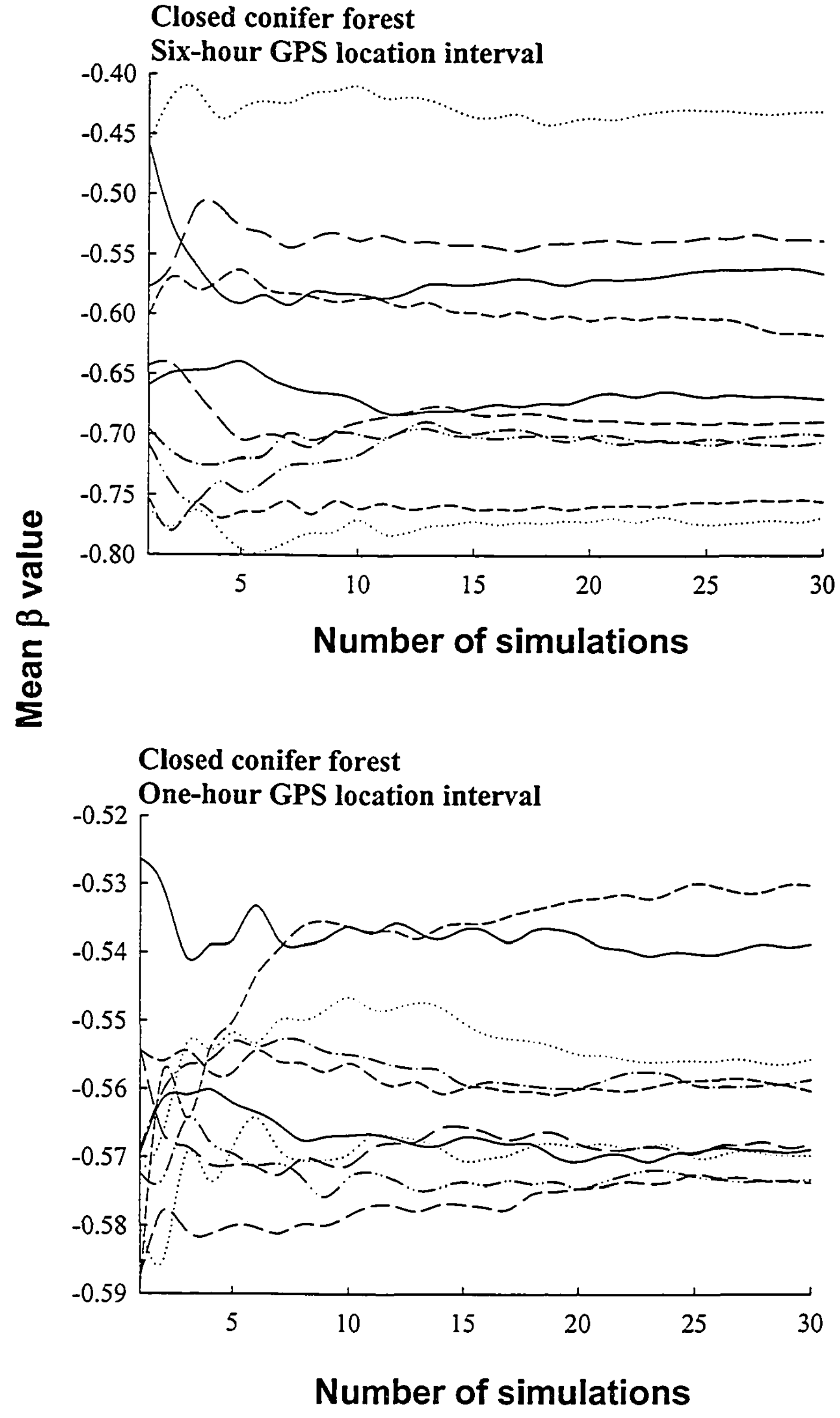


Figure 2.3. Changes in the mean coefficient value for the closed conifer forest variable given the number of simulations conducted. Each line represents one of 10 sets of data, given a 30% biased data reduction, for the six-hour sampling intensity (top) and one-hour sampling intensity (bottom).

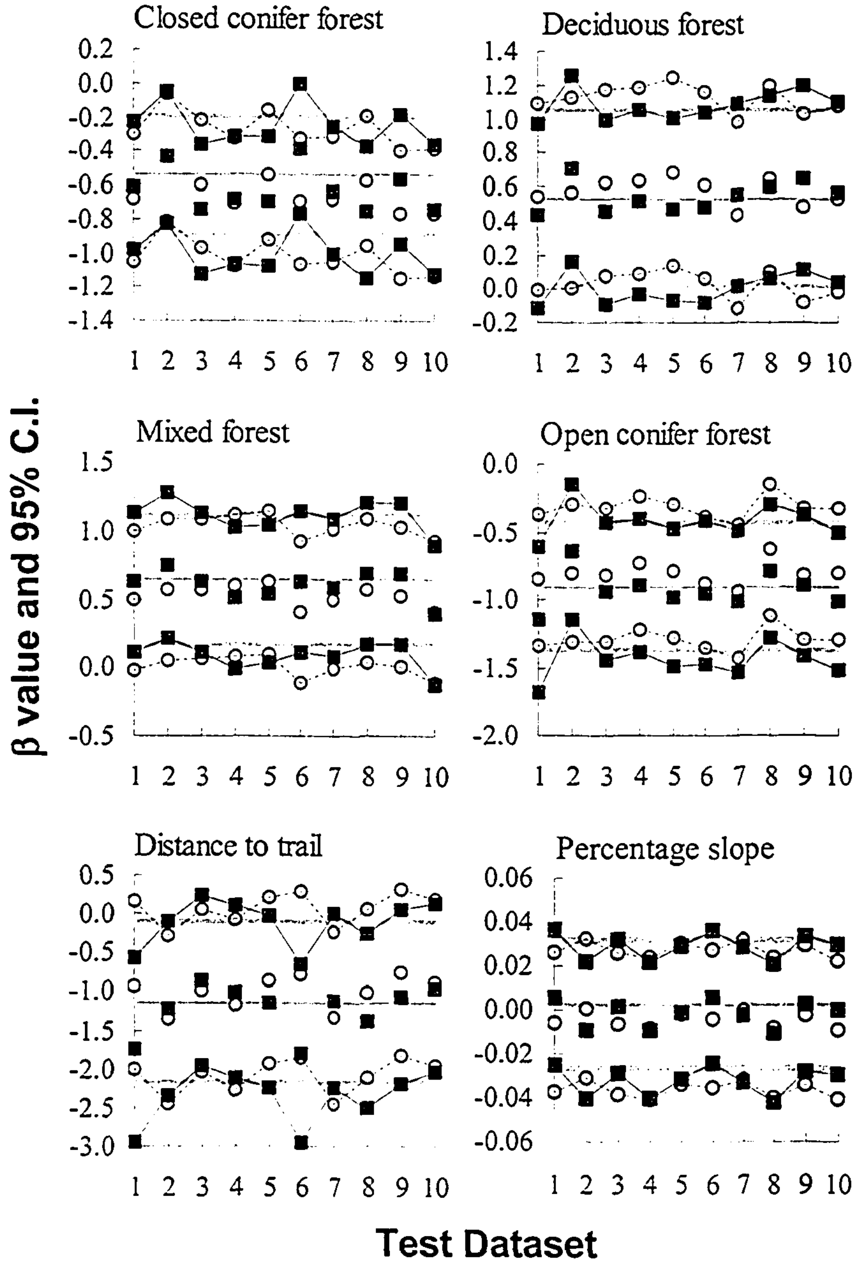


Figure 2.4A. The effects of sample weighting and iterative simulation on resource selection function coefficients given a 30% biased data loss and a six-hour sampling interval. Coefficient values are shown after applying sample weights (squares) and combining simulation results (open circles), with their respective 95% confidence intervals (connected squares and circles, respectively). The unbiased coefficient (thin grey line) and 95% confidence intervals (heavy grey lines) are shown for reference.

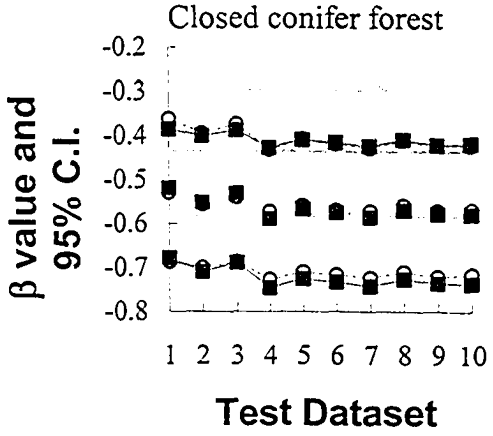


Figure 2.4B. The effects of sample weighting and iterative simulation on resource selection function coefficients given a 30% biased data loss and a one-hour sampling interval for the biased closed conifer forest type. Coefficient values are shown after applying sample weights (squares) and combining simulation results (open circles), with their respective 95% confidence intervals (connected squares and circles, respectively). The unbiased coefficient (thin grey line) and 95% confidence intervals (heavy grey lines) are shown for reference.

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CHAPTER 3

LESSONS FROM WAPITI TRANSLOCATIONS INTO RISKY LANDSCAPES

3.1 INTRODUCTION

Translocation, the "mediated movement of wild individuals or populations from one part of their range to another" (IUCN-The World Conservation Union 1995), is one of the main tools used by biologists to recover critically small or extirpated populations. Specific objectives of a translocation program may vary – e.g. re-establish extinct sub-populations, numerically supplement small populations, or increase genetic variability – but the principal goal is to establish viable, free-ranging populations that require minimal long-term management (IUCN 1995). Despite conducting translocations world-wide, the important factors affecting the success of different programs remain poorly understood, often because studies are short-term, too few animals are released, and releases are not designed to critically assess potentially influential factors (Armstrong *et al.* 1994; Owen-Smith 2003). Nevertheless, meta-analyses provide guidelines to follow: select release areas within the core of the historic distribution of the species, limit release sites to those having high habitat quality, and release at least 20 individuals (Griffith *et al.* 1989; Wolf *et al.* 1996; Wolf *et al.* 1998; Fischer & Lindenmayer 2000; Komers & Curman 2000). Additional criteria may be important to specific taxonomic groups or areas (Hodder & Bullock 1997; Duncan *et al.* 2001), but the amount and quality of habitat in the release area remains an over-riding consideration.

While suitability of habitat is an essential pre-requisite for all programs, there are several reasons why information on habitat suitability derived from observations of historic or extant populations may fail to predict the success of translocated individuals

(Johnson & Swift 2000; Harig & Fausch 2002; Matson *et al.* 2002). First, the original cause of decline may not be known, or the detailed studies necessary to determine whether the cause has been controlled or eliminated may not be feasible given the high costs associated with such assessments (Armstrong & McLean 1995). Second, past information on habitat use may reflect preferences rather than requirements (Gray & Craig 1991) and the relevance of past habitat-use patterns to unoccupied areas may be difficult to understand where a species historic range has been reduced considerably, or where novel risks now occur (Stanley Price 1989; Armstrong & McLean 1995). Third, past experience of the source populations may not be adequate to efficiently exploit available resources (Owen-Smith 2003) or to cope with novel threats that may exist in an area (O'Bryan & McCullough 1985; Kenward & Hodder 1998). As a result, assessing habitat suitability alone may not suffice for ensuring translocation success because success might depend on the interaction between individuals' past experience and conditions at the release site. However, few studies have addressed the importance of previous experience of the source population (Warren *et al.* 1996; Kenward & Hodder 1998) except when captive-reared individuals are released.

In this study, I used information from translocated wapiti (*Cervus elaphus*) to improve our understanding of how important the experience of a wild-caught source of animals might be for improving the success of translocations (Fischer & Lindenmayer 2000). Specifically, I addressed two pertinent questions. First, does previous experience with habitat conditions and mortality risks present in release areas play an important role in the survival and retention of translocated individuals? Second, can past experience be matched with local variation in habitats and mortality risks to identify optimal release areas, i.e., areas having a high probability of retention and survival? Wapiti offer several advantages for this kind of investigation. First, wapiti are a game species in Alberta and, as a result, a sufficiently large sample of individual animals could be translocated to assess fitness in the release area. Second, habitat requirements for wapiti and potential mortality risks in the release area were relatively well known and could be measured. Third, sources of wapiti with differing backgrounds were available relative to habitat and predator exposure. Finally, individuals resident in the release area (the control population) allowed us to better distinguish the effects of habitat conditions and source population (Sarazzin & Barbault 1996; Armstrong *et al.* 1994).

My general approach was to release individuals from two or more sources in the same areas and to monitor their retention and survival relative to direct exposure to forage resources and mortality risks. Source populations came from different habitat conditions and included wapiti habituated to humans but wary of predators, familiar with hunting but inexperienced with predators, and naive to both. Hunters and large carnivores were prevalent in the study area these wapiti were released into. I measured wapiti encounters with forage resources because high-quality foraging areas were limited in this largely forested environment (Jones & Hudson 2002) and forage availability has been found to be important for the success of various ungulate species (Singer *et al.* 2000; Owen-Smith 2003; Mésochina *et al.* 2003; Matson *et al.* 2004). In contrast, the presence of predators in release areas, including humans, has not been a consistent predictor of translocation failure (Griffith *et al.* 1989; Wolf *et al.* 1996; Wolf *et al.* 1998; Fischer & Lindenmayer 2000). However, predation risks and the experience of source populations with predators typically have not been well quantified and may have differed among translocations (Compton *et al.* 1995; Matson *et al.* 2004). Generally, managers choose release sites where predators are absent or can be controlled (Truett *et al.* 2001; Armstrong & McLean 1995). Yet control of a primary predator alone may fail to lower mortality rates where animals face multiple competing risks (O'Bryan & McCullough 1985; Priddel & Wheeler 2004). As a result, I used a competing risks formulation of the Cox proportional hazards model (Lunn & McNeil 1995) to model the risk of dying from different causes or, alternatively, of dying versus dispersing away from release sites. Using these models I map mortality and dispersal hazards to highlight areas inherently low in mortality risks for future translocations and those areas where management of one or more risks might be required.

3.2 MATERIALS AND METHODS

I tracked the movements and fate of adult female wapiti both translocated to and resident within the central Rocky Mountain foothills of Alberta, Canada (52°27′ N, 115°45′ W) from Jan 2000 – November 2004 (Table 3.1; Appendix IA, IB). Adult females were monitored because maximizing initial population growth rates may be critical for translocation success (Komers & Curman 2000) and, for wapiti, survival of the breeding female component has the greatest effect on growth rates (Nelson & Peek 1982; Gaillard *et al.* 1998). Prior to release, individuals were fitted with LMRT4 VHF collars or GPS2200 collars (Lotek Wireless, Ontario, Canada). The location of each radio-collared animal was recorded via aerial telemetry approximately every two weeks until radio-contact was lost, the animal died, or GPS collars were retrieved via breakaway device (11 months post-release). All collars were equipped with mortality sensors that activated after 7 hr of immobility. Condition of femur marrow (Sinclair & Arcese 1995), wapiti remains, and the mortality site were used to classify cause of death (accidental, vehicle strike, malnutrition, harvest, predation, unknown). Deaths from unknown causes occurring within 1 month of release were considered a result of capture myopathy (Beringer *et al.* 1996).

3.2.1 STUDY AREA AND RELEASE SITE SELECTION

The study area ranged in elevation from 790-3300 m (Figure 3.1). The area was dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) forests (~70% forested overall), with aspen declining in prevalence along a generally east to west axis. Interspersed throughout the forested matrix were scattered natural meadows (~7% of the area) and cutover areas following timber harvest (~4%). The remaining areas consisted of bare soil/rock, rivers and lakes, and urban/agricultural areas the latter limited largely to the eastern-most edge. Approximately 2000 non-migratory wapiti inhabited the area with annual trend counts indicating the population to be growing or at least stable prior to this study (Allen 2005). The regulated fall harvest of wapiti was limited to 3- or 6-point bulls but harvest of both sexes and all age classes was allowed year-round for First Nations people by treaty right. The area also supported harvested populations of wolves, cougars, grizzly bears and black bears.

To identify suitable release sites, I used a 10 × 10 km moving-window analysis (Van Deelen *et al.* 1997; Didier & Porter 1999) and selected sites based on three criteria. First, areas where forest cover exceeded approximately 85% were excluded because they were unlikely to support wapiti (Jones & Hudson 2002). Second, I stratified the remaining areas to capture variation in the amount of natural meadows versus areas regenerating after timber harvest. Third, within each habitat stratum, I identified areas as having relatively high or low human access indexed by the density of linear features, which are typically 5-15 m wide recreation trails, seismic exploration transects, and utility line right-of-ways. Spatial variability in predation risk was not considered due to insufficient information at the time releases were planned. Several potential release areas were rejected due to their proximity to human settlements and only those sites accessible by a truck and livestock trailer were used.

3.2.2 SOURCE POPULATIONS AND ANIMAL HANDLING

I captured 14-24 wapiti resident in the study area during each winter using a net gun fired from a helicopter (Province of Alberta permit #1432GP and University of Alberta #300 401) with individuals released at their capture location after ~15 minutes handling time. No two animals were collared in any local group during the first two years but to maintain desired sample sizes a second animal may have been collared in a given herd in subsequent years.

Source populations for translocations came from 4 areas within 106-267 km of release sites (Figure 3.1). In all areas, animals were captured in corral traps baited with hay, transported in livestock trailers that held between 9-16 animals depending on the sex and age class composition, and were released directly from the trailers into the study area (Province of Alberta animal care permit #1432GP and University of Alberta #300 401). A total of 38 releases occurred in 16 different areas (Figure 3.1; Appendix I and II). In some cases, partial trailer loads (4-6 individuals) were released ~5 km apart in an attempt to maintain independence among collared individuals. Individuals from different source populations were released at the same site only in separate years. Details pertinent to each source population follow.

Banff and Jasper National Parks

In the mountain parks, wapiti populations are restricted by extreme terrain conditions to montane habitats in valley bottoms (Achuff & Corns 1982), areas they share with wolves, cougars, grizzly bears, and black bears (Gloyne & Clevenger 2001; Hebblewhite *et al.* 2003; Chruszcz *et al.* 2003; Huggard 1993; Whittington *et al.* 2005). Wapiti use urban habitats around the town sites of Banff and Jasper where they remain year-round, have habituated to human activities, and occasionally act aggressively towards humans (McKenzie 2001). As part of the plan to reduce human/wapiti conflicts, a total of 115 and 69 wapiti were translocated from the Banff (Tom Hurd, Banff National Park, personal communication) and Jasper town sites (Wes Bradford, Jasper National Park, personal communication), respectively, and were used in this study (Table 3.1; Appendix I). Banff animals were quarantined for 30 days to screen for tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*) and to administer treatment for liver fluke (*Fascioloides magna*) prior to translocation. No disease tests or epizootic treatments were required in Jasper and releases occurred within 10 days of capture. Animals from Jasper and Banff were pooled into a single "Mountain Park" source due to the small sample size from Jasper and the similar natural histories between these source populations.

Elk Island National Park

Elk Island Park lies within the productive aspen parkland ecoregion (Bork *et al.* 1997). This relatively small park (102 km^2) is enclosed by a 2.2-m tall fence preventing wapiti and other large mammals from moving into or out of the area and is subdivided by a major highway with the southern portion closed to the public. Despite being protected from hunting, wapiti in the park avoid areas visited regularly by people and do not appear to have habituated to human activities in the park (Rob Kay, Elk Island National Park, personal communication). In further contrast to the mountain parks, no large predators occurred in Elk Island Park prior to this study. Translocations of wapiti have been implemented since 1937 to prevent "over-grazing" and disease outbreaks (R. Kay, personal communication). A total of 135 wapiti were translocated for use in this study (Table 3.1; Appendix I). Animals were held 30-45 days to screen for tuberculosis and brucellosis while administering treatment for winter tick (*Dermacentor albipictus*) and liver fluke prior to translocation.

Cross Area

Approximately 20 km southwest of Calgary, a major metropolitan center in southern Alberta, a wapiti herd using the Cross Conservation Area (co-managed by the Sandy Cross Foundation and the Province of Alberta) was targeted for reduction. The region is a transition zone between dry prairies and rugged mountains with gently rolling topography, extensive aspen forest habitats, and pastures of introduced and native prairie grasses (Gilson & Pittaway 1996). Aside from the conservation reserve, the area is a mixture of private farms and ranches. Cougars are occasionally observed in the area but wolves and bears are not. The regulated harvest of wapiti – limited to an archery only season but with special rifle hunts held in 1986, 1988 and 1996 – has not been sufficient to maintain the herd at the level desired (Pat Young, Alberta Fish and Wildlife, personal communication). A total of 159 wapiti were translocated for use in this study (Table 3.1; Appendix I). No testing or epizootic treatments were required and animals were released within approximately 8-24 hours following capture.

3.2.3 QUANTIFYING EXPOSURE TO RESOURCES AND RISKS

Following release, I quantified an individual's exposure to resources and risks at each location (17.3 ± 0.4 SE days apart on average) over 3 scales. First, I quantified spatial variables within a 1 × 1 km window, the area potentially experienced by each individual over a few days based on the observed daily displacements of wapiti ($\bar{x}$ = 361 ± 54 SE m/day; N =223). For any potentially delayed effects from exposure I quantified spatial covariates within the 1-km^2 window around the preceding wapiti location (at time t-1) and, for potential cumulative effects, I calculated a running mean of values over the current and preceding 5 locations (~2–3 months). The spatial variables recorded are summarized below.

Forage Resources

I established 14–17 transects in each of 10 vegetation classes that were revisited approximately every 15 days throughout summer during 2001 and 2002. Total standing herbaceous biomass along each transect was modeled as a function of julian day, landcover class, and elevation (Visscher *et al.* 2004; Frair *et al.* 2004) and extrapolated to each 28.5 m cell in the landscape using the vegetation classification of Beyer *et al.* (2004) and a digital elevation model. Using data from an additional set of 159 transects in cutover forest areas, I predicted herbaceous biomass at peak for each of three regeneration classes – 0-3, 4-14, and 15-37 years post-harvest (Visscher *et al.* 2004; Frair *et al.* 2004). For all vegetation classes, winter loss in herbaceous biomass was calculated as a linear decline from 10 October to 28 May. I retained mid-summer (15 July) and mid-winter (15 January) estimates of herbaceous biomass for each year after accounting for landscape changes due to wildfire, timber felling, and infrastructure development.

I also recorded the species and basal diameter of shrubs within a 0-2.5-m stratum along the vegetation transects. For species used by wapiti (Cook 2002), I calculated the total biomass of leaves and stems to 7-mm diameter and applied the mean browse biomass along transects to each of the 10 landcover classes (Visscher *et al.* 2004; Frair *et al.* 2004). For the winter period, only estimates of woody biomass were used.

Potential Encounters With Predators

I focused on wolves because they were the primary predator of translocated wapiti. I considered the probability of an wapiti encountering a wolf to be related to the relative probability of wolf occurrence across the landscape (Hebblewhite, Merrill & McDonald 2005) adjusted for annual variation in wolf population size. To do this, I estimated a resource selection function (RSF; Manly *et al.* 2002) to predict the relative probability of wolf use across the landscape. The wolf RSF was derived using 2-3 hour GPS collar locations from wolves in 4 packs collected December 2003 – November 2004.

I partitioned the data into winter (15 October – 15 May) and summer (15 May – 15 October) to account for differential habitat-use patterns when movements were constrained by den and rendezvous sites (Jedrzejewski *et al.* 2001). Availability of landscape measures was sampled randomly from within a minimum convex polygon enclosing the locations for a given wolf using a 1:1 ratio of used to available points. The average wolf territory (536.1 ± 110.8 SE km^2) contained 672,500 landscape cells of which 0.3% were used by wolves on average, thus, I considered sampling contamination to be low (Keating & Cherry 2004). I estimated RSF coefficients using a generalized linear mixed model with a logit link, selected among candidate models using the conditional Akaike's Information Criterion (AIC; Burnham & White 2002), and evaluated the predictive ability of my top-ranked models using 5-fold cross-validation (Boyce *et al.* 2002).

The RSF models indicated that wolves selectively used "open" landcover types in both seasons – specifically dry and wet meadows, shrublands, and bogs – as well as areas close to trails. During winter they also selectively used newly cut forest, reclaimed areas and frozen lakes. In both seasons wolves avoided rugged terrain conditions, areas having a high road density, and areas adjacent to major rivers – each of which tended to define territory boundaries for these packs. These selection patterns are consistent with other wolf telemetry studies (Kunkel & Pletscher 2000; Hebblewhite *et al.* 2005a) and model predictions were robust (cross-partioning $\bar{r}$ = 0.96 ± 0.02 SD and 0.85 ± 0.06 SD during winter and summer). I weighted RSF values annually by the estimated number of wolves harvested during the October-January hunting and trapping period (9-56 wolves). Harvest records may not reflect true population sizes, but they do represent the minimum number of wolves removed from the area immediately preceding wapiti releases each winter. Annual harvest adjustments were used to weight wolf RSF values such that in years when more wolves were removed from the system, wolf RSF values decreased. The annual harvest index, wolf RSF, and annually weighted RSF were potential covariates in the candidate models for wapiti survival and retention.

Potential Encounters With Hunters

Because humans typically use roads for access when hunting (Lyon & Burcham 1998), I calculated the distance to the nearest road of any type, and alternatively the distance to the nearest primary gravel or paved road, as well as the density of roads within the 1-km^2 area around each wapiti location. Terrain and vegetation might provide refuge for wapiti close to roads (Unsworth *et al.* 1993; McCorquodale *et al.* 2003), thus, I additionally calculated how many road cells (each 28.5 m cell containing a road) within 1 km of each wapiti location were actually visible to an wapiti. Finally, anthropogenic linear clearings provide off-road vehicle access, thus, I calculated the distance from the nearest linear clearing as well as the density of linear clearings around each wapiti location.

Geophysical Obstacles

For use in retention models, I identified terrain obstacles as those conditions receiving no use by the resident population (>40° slope or >2100 m elevation). Using a 28.5-m digital elevation model I calculated the percentage of the 1-km^2 area around wapiti locations that contained terrain obstructions as well as the mean proximity of terrain obstructions. Additionally, I used a 1:50K hydrology map to calculate the proximity of major rivers (those that remain open during winter).

Additional Variables

I calculated March-May snowfall (9.3 – 119.2 cm) as an index to winter severity and June-July rainfall (86.4 – 303.6) as an index to vegetation growing conditions (Environment Canada 2004) because annual climatic variation may confound differences among source populations. Annual snow and precipitation data were acquired for Nordegg in the upper foothills (1320 m) and Rocky Mountain House in the lower foothills (969 m; Figure 3.1) with values assigned to telemetry locations by year and region. Rather than control for variation in wapiti density at the time of release I added release group size and annual estimates of wapiti density to each wapiti location, the latter derived for 24 wildlife management units using winter wapiti survey data (range 0.06–3.00 wapiti/km^2; Allen 2005). Lastly, to account for covariation between movement tendencies and survival probability I included as a covariate the individual's rate of movement (m/day) over each telemetry interval.

3.2.4 STATISTICAL ANALYSES

Prior to estimating survival and retention rates, I addressed several potential biases arising from my sampling design. First, I identified potential pseudo-replication among collared individuals (Hurlbert 1984) by exploring post-release spatio-temporal associations using ASSOC1 software (Weber *et al.* 2001). I considered animals to be associated when they spent >50% of their time within 1 km of each other because this definition identified meaningful groups, from which I retained only one collared individual at random. Second, given that the actual timing of death was uncertain, I selected a mortality date at random from the final telemetry interval. Lastly, and specific to harvest mortalities, where the mortality location was unknown, i.e. no carcass was found, I considered the animal to have died where I last recorded it alive.

Annual survival rates for each source population were calculated using Kaplan-Meier hazard functions (Kaplan & Meier 1958; Kalbfleisch & Prentice 1980). The effects of spatial covariates on hazard functions were estimated using Cox regression (Cox 1972; Andersen & Gill 1982). Cause-specific failure rates – death due to wolves, hunters, and "other" causes – and covariates associated with each type of failure were analyzed using the competing risks approach detailed by Lunn and McNeil (1995). Here, the data for each individual were replicated 3 times and a categorical variable, denoted by δ_m, was used to assign each observation to one of the 3 failure types (Tai *et al.* 2001). A series of model specification tests were conducted to evaluate if covariates met the proportional hazards assumption following Lunn and McNeil (1995), Therneau and Grambsch (2000), and Cleves *et al.* (2004). Where assumptions were violated, I assessed whether variable re-specification (e.g. an x^2 term was added), the inclusion of temporal variables, or truncation of analysis time was required. Failing that, I employed a stratified model that estimated a separate baseline function for either each source population or each failure type and included strata by covariate interactions to allow the effect of covariates to vary across strata; (Kay 1986; Tai *et al.* 2001; Clark *et al.* 2003). For the competing risks models, I employed a sandwich variance estimator to obtain robust standard errors for the estimated coefficients (Thernaeu & Grambsch 2000). For categorical variables, I report risk ratios (RR) following Riggs and Pollack (1992).

Estimating Retention Probabilities

Wapiti status was recorded as within (0) or beyond (1) distance bands ranging 10–180 km from the release site. Using a time-to-first-failure approach, I calculated Kaplan-Meier hazard rates for each distance band. To evaluate covariate effects on retention probabilities, I used the distance band at which retention rates exceeded 0.50 for at least 1 source population (30 km). Given that death might confound my ability to observe covariates pertinent to dispersal, I evaluated death and dispersal beyond 30 km as opposing events in a competing risks analysis as detailed previously for survival.

Model Selection

My model selection process followed three stages. First, I used AIC_c (Burnham & Anderson 2002) to rank alternative models for the main components of risk – forage resources, wolf encounters, and human encounters. To the number of estimable parameters, I added 1 for each baseline hazard and 1 for each stratum. The effective sample size was set as the number of failure events (Hosmer & Lemeshow 1999). In the second stage, I created a pooled model by combining the variables from each top component model and adding potentially confounding variables. Lastly, I followed the principle of parsimony by retaining variables only when their inclusion yielded an improvement in AIC by > 2 units from the model excluding only that term (Burnham & Anderson 2002).

Model Validation

I employed 5-fold cross-validation (Harrell & Mark 1996; Hastie *et al.* 2001) to evaluate the predictive capacity of my top survival and retention models. For each iterations 20% of the individuals were withheld and the model was refit using the remaining 80%. The hazard an individual encountered on a per day basis was quantified as the sum of the daily hazard ratios ($\exp^{\beta X}$) divided by the number of days alive. For each iteration, I created 10 bins of hazard/day values such that an equal number of individuals in the estimation sample occurred in each bin and, for each bin, I tallied the number of individuals in the validation sample that failed. I expected the frequency of failures to increase linearly with the ranked hazard/day values (bin number; Boyce *et al.* 2002).

Model Application

The best-supported models were used to create risk surfaces by applying $\exp^{\beta X}$ to each 28.5 m pixel of the landscape. Map values were grouped by quantiles to identify relatively high versus low risk and the results were combined to identify areas where the probability of survival and retention were both high.

3.3 RESULTS

3.3.1 SURVIVAL RATES

I documented a total of 104 mortalities of collared wapiti (14 resident, 90 translocated) between January 2000 and October 2004 (Figure 3.2; Appendix III).

Predators (wolves, cougars, grizzly bear and black bear) and hunters (treaty right and poaching) were the largest causes of mortality for translocated wapiti and accounted for a similar number of total mortalities (37.8% and 34.4%). Resident wapiti died more from hunters (42.9%) than predators (14.3%). Of the predation-related fatalities, wolves accounted for 82 and 100% for translocated and resident wapiti. Accidental deaths, i.e. hit by vehicle, mired in mud, falls in steep terrain and other major injuries, were observed only among translocated animals.

The magnitude and pattern of mortalities differed between the first-year following release and subsequent years (Figure 3.2), thus, I estimated survival rates separately for these periods. After exploring animal associations in the first year, I excluded 12 animals (6, 4, and 2 from the Mountain Park, Cross Area, and Elk Island populations) from all analyses to follow. Additionally, I excluded all suspected capture myopathies (3 each from the Elk Island and resident populations). Kaplan-Meier survival estimates for the first-year following release were significantly lower for all translocated source populations than for residents with Elk Island animals exhibiting the lowest overall survival rate (Table 3.2). Exploring the incremental hazard over time indicated two peaks in mortality risk during the first year (Figure 3.3). Accounting for differences in the timing of releases (Appendix I), peaks coincided with spring (3 April-24 May) and late summer/fall (21 August-3 December). Cross-referencing Figures 3.2 and 3.3 indicates that the early peak was largely driven by predation whereas the second peak was largely hunter-caused.

In the second and subsequent years following release I excluded 1 individual from each of the Resident, Mountain Park, and Cross Area populations due to animal associations. Elk Island animals were also excluded due to small sample sizes. During their second year in the study area, survival rates ($\phi_{365\text{-}730\text{ days}}$) tended to remain lower for Mountain Park animals than for Cross Area and resident wapiti although no significant differences were observed (Table 3.2). The smoothed hazard estimates for animals during their second year indicated a single peak for all source populations that occurred late in the year (Figure 3.3) and reflected a higher component of hunter- versus predator-caused mortalities (Figure 3.2).

3.3.2 VARIABLES INFLUENCING SURVIVAL

During the first year, the risk of dying from hunters, wolves, or other causes remained proportional over time and, consequently, risk type (δ_m) was entered as a categorical covariate. In contrast, the differential hazard functions among source populations required model stratification. The first-year model also required a seasonal variable differentiating between the two peaks in mortality hazard (December-May separate from June onwards). The final model met all assumptions (Schoenfeld residuals test: global $\chi^2_{15} = 11.78$, $P = 0.696$) and had good predictive power (Figure 3.4).

Encountering areas used by wolves and humans negatively affected survival rates during the first year (Table 3.3; Appendix IV). Areas likely to be used by wolves carried a high mortality risk for animals inexperienced with wolves (Cross Area and Elk Island), but not for animals familiar with them (Mountain Park and Resident). For all wapiti, wolf-caused mortalities occurred closer to trails and further from roads than was accounted for by the resource selection pattern of wolves. The competing risks model identified a dynamic in mortality risk with respect to roads and linear clearings. Pooling all causes of mortality together revealed that predation by wolves masked the mortality risk associated with wapiti use of areas adjacent to roads during the first year (Table 3.3). Even though a greater proportion of wapiti was taken by hunters versus wolves or other causes (Table 3.4), wolf predation preceded hunter take in time (Figures 3.2, 3.3) and the two types of mortality traded-off in space with respect to the proximity of roads (Table 3.3), the latter likely due to wolves avoiding humans. Alternative road and trail variables, e.g., road density, were not supported (ΔAIC = 2.90 – 7.52).

The most supported index to predation risk during the first year was the annually weighted wolf RSF. However, the effect appeared to be largely spatial because substituting the annual harvest index produced a larger difference (ΔAIC = 10.12) than substituting the wolf RSF alone (ΔAIC = 4.54). The effects of all covariates appeared to occur on a local spatial and temporal scale because I did not observe support for either a lagged or cumulative effect of any variables other than forage biomass during the first year (substituting these variables into the final model yielded ΔAIC = 11.68 – 20.64). Although the cumulative forage biomass encountered appeared to affect survival, forage was not retained in the highest ranked first-year model.

Sample sizes in the second and subsequent years were too limited for a competing risks analysis and, consequently, I produced an all-causes model stratified by population source (excluding Elk Island). As observed during the first year, a seasonal variable to differentiate winter months (Jan-Apr) from the remainder of the year was required to meet proportional hazards assumptions (Schoenfeld residuals test: global $\chi^2_9 = 2.02$, $P = 0.991$; Appendix V). Also consistent with the first-year model, higher rates of movement coincided with a higher risk of mortality (Table 3.4) even though overall movement rates declined for translocated animals between the first ($\bar{x}$ = 449.74, SE = 22.78, N = 136) and subsequent years ($\bar{x}$ = 243.83, SE = 13.80, N = 49; one-tailed $t = 5.293$, $P < 0.001$). Cumulative encounters with browse biomass and the local proximity of a road were important spatial covariates after the first year. Here again, substituting the proximity of high use roads, the density of roads, or the road visibility index into the final model yielded lower model support (ΔAIC = 3.00 – 8.60) as did considering road effects to be lagged or cumulative (ΔAIC = 4.40 – 9.34). Mortalities were too few to employ cross-validation techniques but Cox-Snell residuals plotted against the Nelson-Aalen cumulative hazard indicated good model fit except at the extreme right tail of the plot where sample sizes became limiting.

3.3.3 RETENTION RATES

Only data from translocated animals were entered into the retention analysis. Retention rates were consistently highest for Mountain Park animals (Figure 3.5) regardless of the spatial extent considered. Very few animals remained within 10 km of their release areas even though the width of resident wapiti home ranges in this area rarely exceeded 10 km. Differences in retention among source populations emerged for dispersals ≥ 30 km from the point of release, and < 50% of each source population was retained at smaller spatial extents. Using a 30-km spatial definition, I observed that the majority of wapiti dispersed mid-May to mid-August with the peaks for different source populations within 10-15 days of each other.

3.3.4 VARIABLES INFLUENCING RETENTION

All but one dispersal occurred within the first year following release, thus, I limited the Cox model to the first year. The risk of dispersing > 30 km or dying remained proportional over time and, consequently, failure type (death or dispersal) was added as a categorical covariate. Here again, it was necessary to stratify the model by population source. In contrast to considering survival alone, distinguishing among seasons was not required to meet the assumption of proportionality for the final model (Schoenfeld residuals test: global $\chi^2_{10} = 11.01$, $P = 0.357$; Appendix VI). The effect of movement rate on dispersal did not differ from its effect on survival during the first year (Table 3.6). Individuals were more likely to disperse (and less likely to die) during wetter summers. I observed some evidence that individuals released in larger groups were less likely to disperse but were perhaps more likely to die. However, the group-size variable appeared to be influenced inordinately by the first set of releases of animals from the mountain parks (Appendix I). Excluding 3 releases where group sizes exceeded 30 individuals indicated that the relationship of group size with mortality was unstable ($\beta = -0.0413$, SE = 0.0569, $P = 0.468$) whereas its relationship with retention was fairly stable but less significant ($\beta = -0.0777$, SE = 0.0476, $P = 0.103$).

Spatial covariates influencing retention included cumulative encounters with forage biomass and local encounters with wolves (Table 3.6). In contrast to the survival models, forage biomass was the primary spatial predictor of retention (Appendix VI) and the effect of forage was clearly cumulative rather than lagged or local (substituting either into the final model yielded $\Delta\text{AIC} \geq 263.24$). Although wapiti were less likely to disperse away from areas having a high herbaceous biomass, they were more likely to die in those areas (Table 3.6). A similar pattern was observed for areas likely to contain wolves. Here again the effect of wolves was largely spatial rather than numerical because the un-weighted wolf RSF received more support in the final model than annually weighted RSF values (ΔAIC = 12.28) or the wolf harvest index alone (ΔAIC = 13.12). The effect of wolf encounters on dispersal also was local rather than lagged or cumulative (ΔAIC = 4.46 – 5.46). No geophysical variables were retained in the final model. The analogous "retention only" model was consistent with the competing risks model, but generally had attenuated coefficients and reduced coefficient significance (Table 3.6).

Although sample sizes precluded cross-validating the model solely for dispersal failures, model predictions for all failures (dispersal or mortality) were robust ($r = 0.834$, $P = 0.003$) and the model predicted a higher hazard/day for animals that dispersed versus those that stayed in release areas (one-tailed $t = -3.057$, $P = 0.001$).

3.3.5 MODEL APPLICATION

Taken together, the relative probability of an wapiti being retained and surviving either wolves or hunters illuminated hot spots of high risk as well as islands of inherently low risk (Figure 3.6). Due to spatial trade-offs in the risk of dying from wolves and hunters, few areas of the central foothills were low in both mortality risks.

3.4 DISCUSSION

The competing risks approach was integral to uncovering the relative magnitude and important variables associated with the survival and retention of wapiti in this study.

Forage resources, while important to the retention and long-term survival of wapiti, were not directly related to wapiti survival during the first year following release when ~70% of all mortalities were observed. Instead, survival during this initial period was a function of encounters with wolves and hunters. In fact areas having high herbaceous biomass, where wapiti were most likely to stay following release, carried a high risk of mortality potentially setting an "ecological trap" for animals naive to local risks (Schlaepfer *et al.* 2002; Kristan 2003). A separate study of wapiti in this area indicated that resident wapiti spend the majority of their time in areas with low-intermediate forage biomass, low wolf use, and close to cover (Frair *et al.* 2004), behaviours that might explain in part the relative invulnerability of resident wapiti to wolf predation that I observed. During the second year following release, the survival rates of translocated and resident animals did not differ statistically indicating that animals released into the central foothills had learned to mediate their mortality risk (Lima & Dill 1990). However, the habituated animals from the mountain parks tended to remain more vulnerable to hunters/poachers than other wapiti during their second and subsequent years in the study area indicating that learning about hunting risk may be a slower process than learning about predation risk (Frid & Dill 2002). Although hunters/poachers accounted for the greatest proportion of overall wapiti mortality, I suspect that more frequent and non-lethal encounters with recreational and industrial users of the central foothills confounds the ability of wapiti to learn about the risks imposed by hunters (Lima & Bednekoff 1999). Given that translocated wapiti in this study were likely to settle areas that initially carried a high overall mortality risk, releasing animals already experienced with mortality risks or alternatively controlling mortality risks in the release landscape may be crucial to improving translocation success.

To my knowledge this is the first study of a large ungulate where the effect of previous experience on the post-release survival of animals has been quantified. Interestingly, even though wapiti were 4.5 times more likely to die from hunters than from wolves in my study area, familiarity with either of these risks prior to release increased survival rates to a similar degree – 2.2 and 1.9 times, respectively. Should no other options be available, utilizing source populations partially experienced with risks present in release areas may yield survival rates sufficient to establish a local population albeit it at a slower rate than might occur in the absence of such risks (e.g., Gogan & Barrett 1987; Larkin *et al.* 2003). For captive-reared stocks or those living in predator-free areas, operant conditioning might effectively be used to familiarize animals with potential risks prior to release (McLean *et al.* 1994; Griffen *et al.* 2000). But faced with naive animals where conditioning is infeasible, managers must necessarily shift their focus to controlling mortality risks in release areas and my models provided various insights into options for doing so.

Areas where wapiti died from hunters and wolves were largely predictable from local landscape features. Extrapolating the local mortality hazard across the landscape revealed large-scale variation in risks and exposed "islands" of high retention/low mortality risk – areas potentially suitable as release sites. Particular to hunter-caused mortalities, the proximity of roads and trails ultimately identified areas having a high density of these features as being most risky for wapiti. This pattern is consistent with previous studies of wapiti hunting mortality elsewhere in North America (Unsworth *et al.*

1993; Hayes *et al.* 2002; McCorquodale *et al.* 2003). Thus, when seeking to restore wapiti to portions of their former range, efforts to find release areas having little motorized access are appropriate (VanDeelen *et al.* 1997; Didier & Porter 1999; Larkin *et al.* 2001; McClafferty & Parkhurst 2001). Indeed, a long-term investment by managers to restrict road access or enforce harvest restrictions may be needed to insure population persistence (Cole *et al.* 1997; Gratson & Whitman 2000a,b).

In addition to a temporal trade-off between wolf and hunter-caused mortality risks, I observed a spatial trade-off in these two risks given the proximity of roads. Wolves consistently avoid highly roaded areas across North America (Mladenoff *et al.* 1995; Arjo & Pletscher 2004; Whittington *et al.* 2005) indicating that such a trade-off in mortality hazard might exist wherever wolves and humans share the landscape (e.g. Hebblewhite *et al.* 2005b). Spatial trade-offs in primary mortality hazards also may occur with respect to other landscape features, such as terrain conditions, where multiple predators coexist (Husseman *et al.* 2003; Arjo & Pletscher 2004). Given the trade-off in mortality risks faced by wapiti in the central foothills of Alberta, the alternatives for increasing the success of wapiti translocations, besides or in addition to selection of an experienced source stock, include selection of areas where one or both of the primary mortality risks are low or potentially controllable either through harvest restrictions, limits to motorized access, or control of predator populations.

An important finding from this study was that the mortality risk imposed by wolves was of short duration, largely limited to the winter period immediately following wapiti releases. As a result, control programs for wolves to improve wapiti translocations may only be required immediately preceding wapiti releases. However, I caution that predator control programs may not necessarily increase the survival of released animals. For example, after effectively removing introduced red foxes (*Vulpes vulpes*), the primary predator of brush-tailed bettongs (*Bettongia penicillata*) in parts of Australia, translocated bettongs died extensively from feral cats (*Felis catus*), birds, and other non-fox predators (Priddel & Wheeler 2004). Likewise, if the wolf-implicated mortalities observed in this study were largely compensatory, i.e. something else would have killed wapiti in the absence of wolves, suppression of wolf numbers alone would not increase wapiti survival rates. All non-hunter causes of death (malnutrition, accidents, and unknown causes) observed in this study were also most common during the winter period following release suggesting the potential for predation-related mortalities to have been compensatory to some degree. In light of this, a potentially more effective approach to improving wapiti survival might be to delay releases until summer when forage resources are more abundant, wapiti condition is greater, and wapiti vulnerability to predation by wolves may be lower (Huggard 1993; DelGuidice *et al.* 2002). Delaying releases in this fashion mimics head-starting programs, which are commonly employed for translocations of species vulnerable to predators at young developmental stages (Alberts & Phillips 2004). Given that I observed the greatest risk of dispersal away from release areas during the summer months, I further suggest the use of holding facilities at release sites, with supplemental feed to carry wapiti through the winter, rather than capturing and transporting wapiti during the summer months. Such "soft-release" techniques may result in an increased fidelity to release sites (Davis 1983; Bright & Morris 1994) but additional experimentation is required to determine the effects of soft-releases on large ungulate dispersal and survival patterns.

Faced with the challenge of large ungulate habituation to human activities (Thompson & Henderson 1998), where translocations are increasingly being used to reduce human/ungulate conflicts (Conover 2001), and given efforts to restore large carnivores to wild systems (Bangs *et al.* 1998; Mladenoff & Sickley 1998), it is likely that ungulate translocations to risky landscapes will become increasingly common in North America. Moreover, the long-term persistence of critically endangered species, such as many flightless birds in New Zealand, may require establishing populations in areas containing novel mortality risks such as introduced predators (Armstrong & McLean 1995). My study indicates that improving the success of translocations to risky areas may depend upon what knowledge can be gained of the type, magnitude, and spatio-temporal variability of potential risks in release areas. If the goal of a translocation program is to minimize the long-term management intervention required to secure viable populations (IUCN 1995), then a greater up-front investment to gain as much knowledge of the local system as possible may be a priority. I suggest that experimental translocations, or trial releases, may provide the best opportunities for uncovering critical information where multiple risks are present (Armstrong *et al.* 1994). When source populations are deemed too small for experimentation, useful insights might be gained instead from releases of a related but more abundant species (Wallace & Temple 1987; Zwank & Wilson 1987; Powell & Cuthbert 1993; Miller *et al.* 1994; Toone & Wallace 1994). Should experimental releases not be an option, my results indicate that studies of the habitat-use patterns of predators in release areas may help guide releases and management interventions. Additional research is required to assess to what degree animal conditioning, soft-releases, manipulation of predator numbers, or manipulation of release group sizes might further improve the success of translocations to risky landscapes (Armstrong & McLean 1995; Fischer & Lindenmayer 2000).

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Table 3.1. Summary of elk releases in the central Rocky Mountain foothills of Alberta, Canada, 2000–2004.

		Risk Familiarity		Release Group Sizes		Sample Sizes	
Source Population	Release Dates	Hunters	Wolves	Mean	(SD)	First yr	Second yr
Banff town site	January–March 2000, February 2001	no[a]	Yes	28.9	(26.7)	37	17
Jasper town site	January 2000	no[a]	yes	34.5	(34.6)[b]	10	3
Cross Area	December 2000–January 2001, December 2001–January 2002	yes	no	15.9	(9.0)	60	25
Elk Island National Park	January–February 2002, January 2004	no	no	14.8	(5.7)	29	3
Resident (not translocated)	February 2000, December 2000, February 2001, December 2001, February 2002, December 2002, March 2003, March 2004	yes	yes	9.2	(6.8)	87	29

[a] These populations considered to be habituated to human activities.

[b] All individuals from this source released at one site in two separate release events 21 days apart.

Table 3.2. Kaplan-Meier survival estimates for adult-female elk during the first and second years following release into the central Rocky Mountain foothills of Alberta, Canada from 2000-2004. Superscripts indicate significant differences among source populations (log-rank $\chi^2 \geq 3.97$, $P < 0.05$).

Source Population	First Year Surival $\phi_{1-365 \text{ days}}$	95% Confidence Interval		Second Year Survival $\phi_{365-730 \text{ days}}$	95% Confidence Interval	
		Lower	Upper		Lower	Upper
Foothills Resident	0.912^{abc}	0.823	0.957	0.857	0.663	0.944
Mountain Park	0.455^{ad}	0.292	0.604	0.655	0.357	0.840
Cross Conservation Area	0.502^{bc}	0.362	0.626	0.855	0.613	0.951
Elk Island National Park	0.157^{cde}	0.032	0.370	--	--	--

Table 3.3. Covariates affecting the survival of adult-female elk during their first-year post release into the central foothills of the Rocky Mountains in Alberta, Canada ($N_{\text{subjects}} = 211$, $N_{\text{failures}} = 71$, $N_{\text{obs}} = 3160$). Shown are the model coefficients (*β*) with standard errors (SE) and significance levels (*P*). Negative coefficients indicate a positive effect of the covariate on survival probability (negative effect on the hazard function). Interaction terms are indicated by "x". The first set of coefficients corresponds to the AIC$_c$-selected, competing risks model (LL = −276.23, LR $\chi^2_{15} = 96.53$, $P < 0.001$) and the second set corresponds to the analogous pooled, or "all causes", model (LL = −220.42, LR $\chi^2_9 = 32.88$, $P < 0.001$).

	Competing Risks Model Robust			All-Causes Model		
Variable	*β*	SE	*P*	*β*	SE	*P*
Risk Type:						
Hunters (hunting/poaching)	1.5596	0.5427	0.004			
Wolves	−0.0616	0.4360	0.889			
Other = reference						
Annually Weighted Wolf RSF	−0.4706	1.3244	0.722	−0.2980	1.3246	0.822
Cross Area x Weighted Wolf RSF	5.6975	1.8627	0.002	5.6530	1.8891	0.003
Elk Island x Weighted Wolf RSF	13.8406	5.7048	0.015	15.4472	5.6590	0.006
Proximity of Road (km)	−0.3400	0.1636	0.038	0.0038	0.0905	0.966
Wolves × Proximity of Road	0.5812	0.1835	0.002			
Proximity of Linear Clearing (m)	0.0004	0.0009	0.651	−0.0013	0.0007	0.055
Hunters × Proximity of Linear Clearing	−0.0024	0.0018	0.167			
Wolves × Proximity of Linear Clearing	−0.0038	0.0016	0.014			
March–May Snowfall (cm)	0.0085	0.0051	0.093	0.0096	0.0049	0.053
Residents × Snowfall	−0.0389	0.0117	0.001	−0.0398	0.0120	0.001
Rate of Movement (km/day)	0.5840	0.2415	0.016	0.5954	0.2399	0.013
Period:						
First Winter/Spring (December–May)	2.0456	0.8328	0.014	1.0659	0.7760	0.170
June into following winter = reference						
Hunters × First Winter	−3.3581	0.8022	<0.001			

Table 3.4. Risk ratio estimates and 90% confidence intervals for the death of an adult-female wapiti due to competing risks in the first-year post-release into the central Rocky Mountain foothills of Alberta, Canada.

		90% Confidence Interval	
Competing Risk	Risk Ratio	Lower	Upper
Wolves versus Other	1.0634	0.3464	1.7806
Hunting versus Other	4.7568	3.8641	5.6495
Hunting versus Wolves	4.4729	4.1926	4.7532

Table 3.5 Covariates affecting the survival of adult-female wapiti during the second and subsequent years following release into the central Rocky Mountain foothills of Alberta, Canada (LL = −33.72, LR $\chi^2_7 = 37.21$, $P < 0.001$). Shown are the estimated coefficients (*β*) with standard errors (SE) and significance levels (*P*). Interaction terms are indicated by "x". Negative coefficients indicate a positive effect of the covariate on survival (negative effect on the hazard function).

Variable	*β*	SE	*P*
Browse Biomass (g/m^2)	−0.0296	0.0116	0.011
Proximity of Road (running mean; km)	−1.5059	0.6826	0.027
Cross Area × Proximity of Road	1.6565	0.9409	0.078
March–May Snowfall (cm)	0.0444	0.0311	0.154
MP × Snowfall	−0.0643	0.0344	0.062
Move Rate (km/day)	3.1700	1.1621	0.006
Period:			
Winter (January – April)	−3.4939	1.5392	0.023
May – December = refererence			

Table 3.6. Covariates affecting translocation failure (death or dispersal beyond 30-km of the release location) for adult-female elk in their first-year following translocation to the central Rocky Mountain foothills of Alberta, Canada ($N_{subjects} = 134$, $N_{dispersal} = 40$, $N_{mortality} = 67$, $N_{obs} = 1{,}609$). Shown are the estimated coefficients (*β*) with standard errors (SE) and significance levels (*P*). Negative coefficients indicate a positive effect of the covariate on retention (negative effect on the hazard function). Interaction terms are indicated by "x". The first set of coefficients corresponds to the AIC$_c$-selected, competing risks model (LL = –231.87, LR $\chi^2_{10} = 318.95$, $P < 0.001$) and the second set corresponds to the analogous "retention only" model (LL = –94.04, LR $\chi^2_5 = 41.12$, $P < 0.001$).

	Competing Risks Model			Retention Only Model		
Variable	*β*	SE	Robust *P*	*β*	SE	*P*
Risk Type:						
Mortality	–0.2792	0.7849	0.722			
Dispersal (reference)						
Herbaceous Biomass (running mean; g/m^2)	–0.0548	0.0122	<0.001	–0.0303	0.0165	0.066
Mortality x Herbaceous Biomass	0.0761	0.0058	<0.001			
Wolf RSF	–5.4817	1.6574	0.001	–3.4764	1.8316	0.058
Mortality x Wolf RSF	5.7018	1.7509	0.001			
June–July Rainfall (mm)	0.0138	0.0033	<0.001	0.0115	0.0036	0.002
Mortality x Rainfall	–0.0115	0.0035	0.001			
Release Group Size	–0.0441	0.0123	<0.001	–0.0323	0.0128	0.012
Mortality x Group Size	0.0370	0.0134	0.006			
Move Rate (km)	0.6522	0.2164	0.003	1.4912	0.4015	<0.001

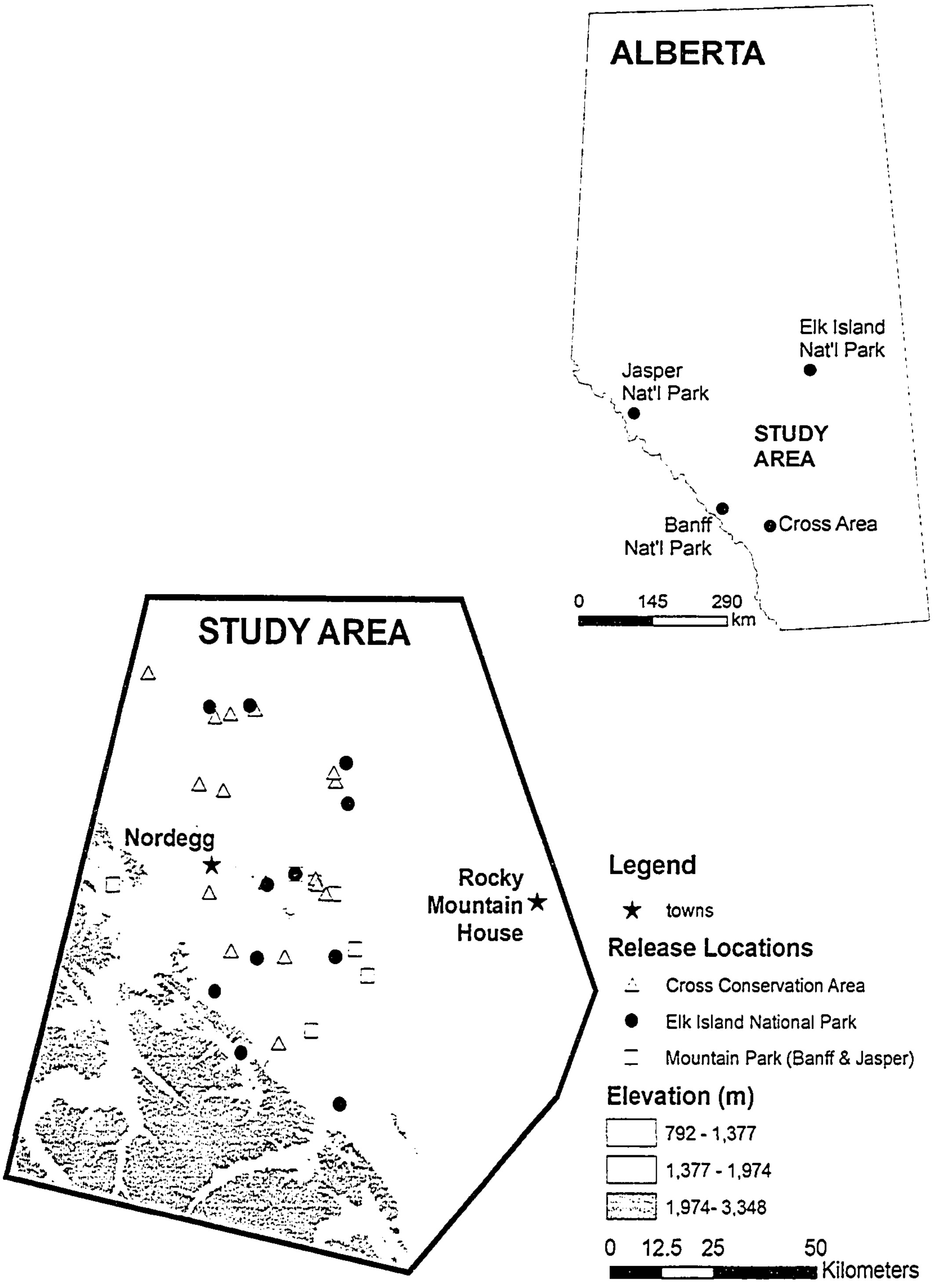

Figure 3.1. Location of the study area, wapiti source populations and release sites in west-central Alberta, Canada.

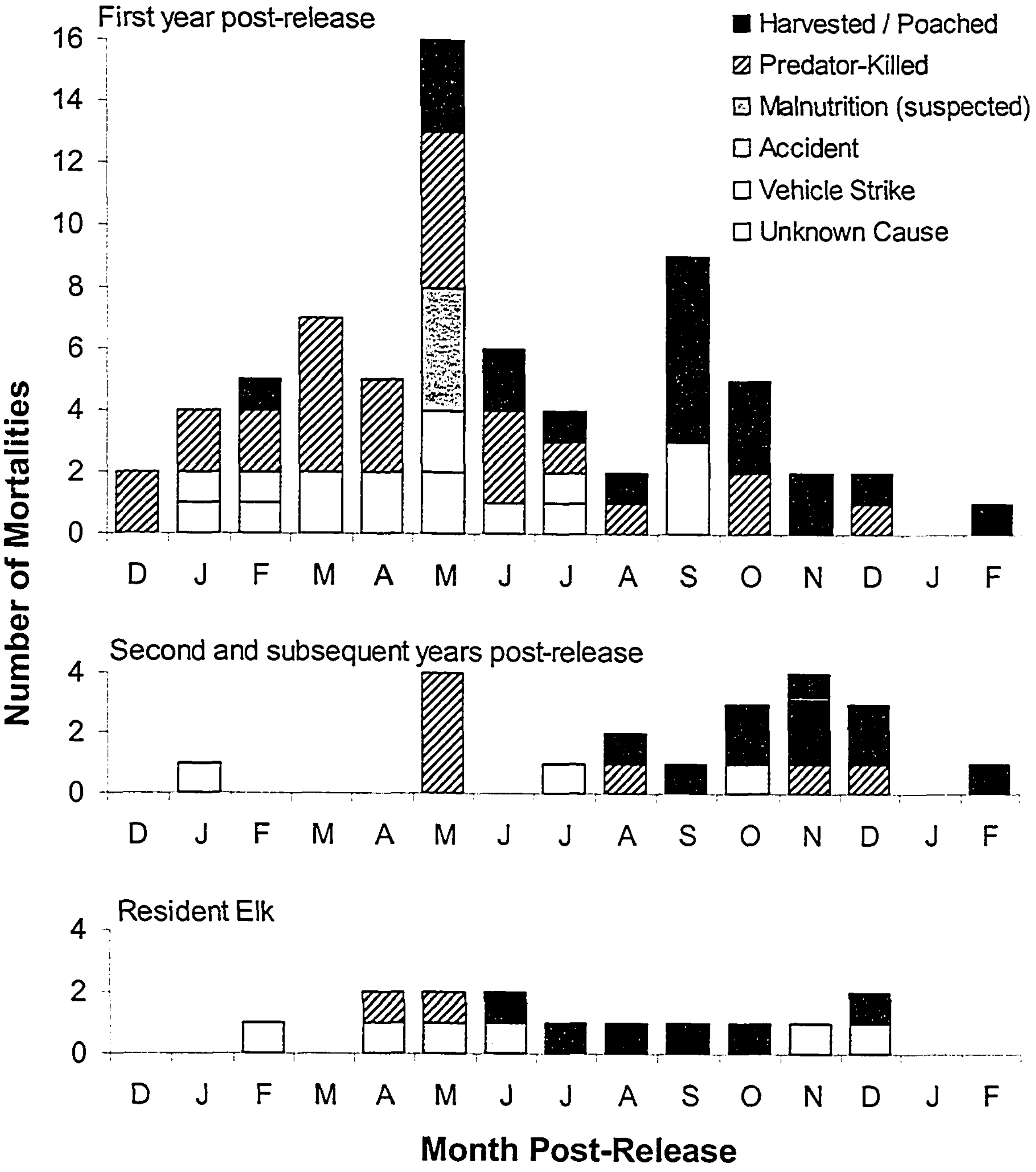

Figure 3.2. Number and cause of mortalities for translocated wapiti during the first-year post-release (top panel), subsequent years (middle panel), and for resident wapiti (bottom panel) in the central Rocky Mountain foothills of Alberta, Canada from 2000-2004.

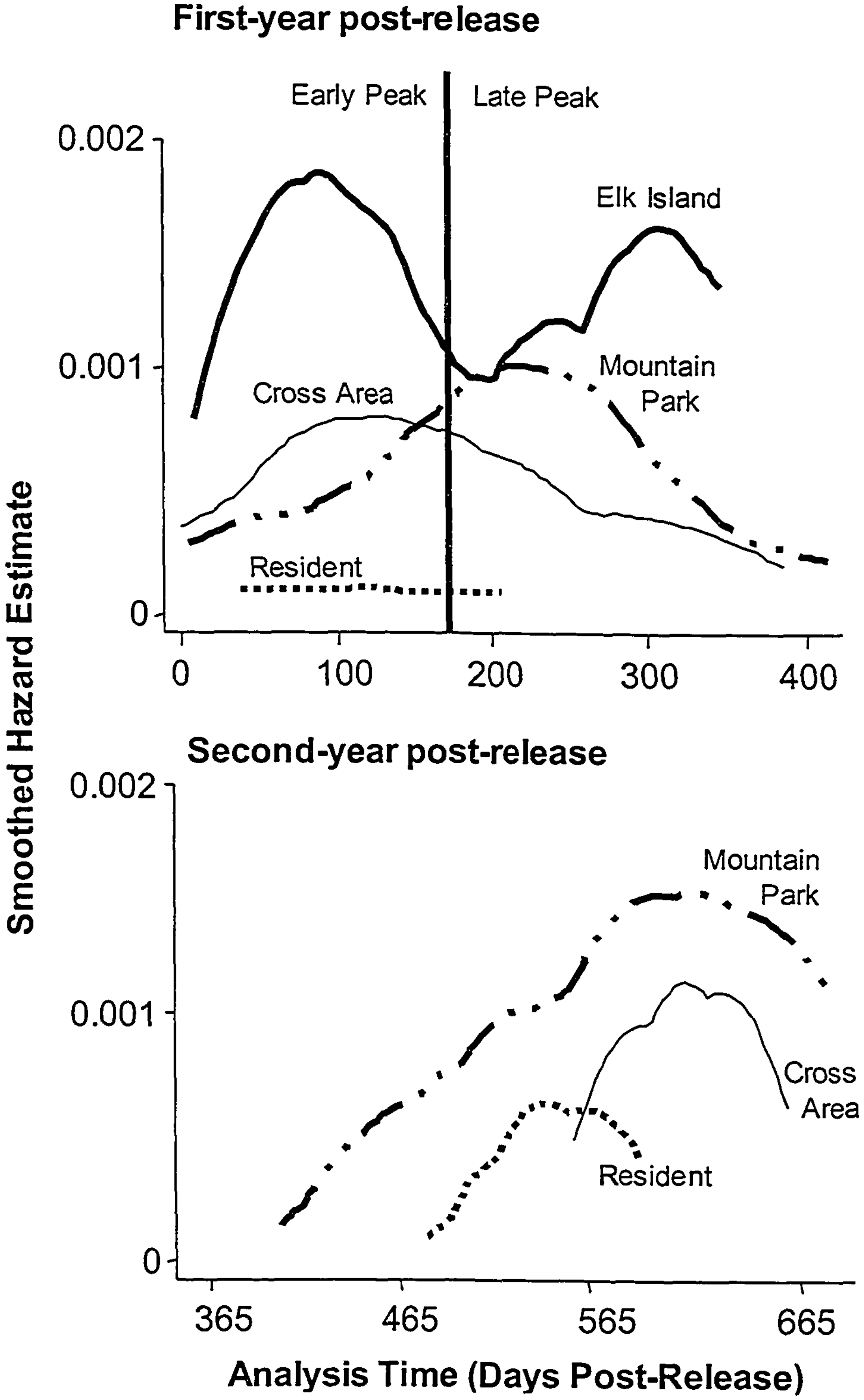

Figure 3.3. Smoothed mortality hazard estimates for wapiti released into the central foothills of Alberta, Canada from 2000-2004. Separate estimates are shown for the first-year following release (top panel) and the subsequent year (bottom panel).

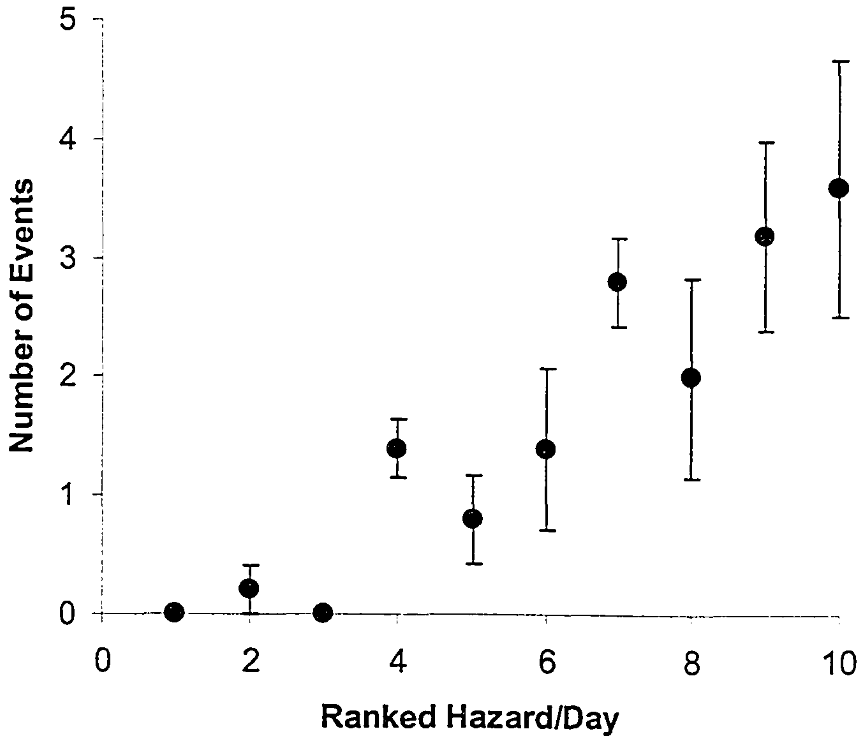

Figure 3.4. The mean (with SE) number of wapiti in withheld validation samples that died plotted against the ranked daily mortality hazard for individuals as predicted from the first-year survival model (Pearson $r = 0.941$, $P < 0.001$).

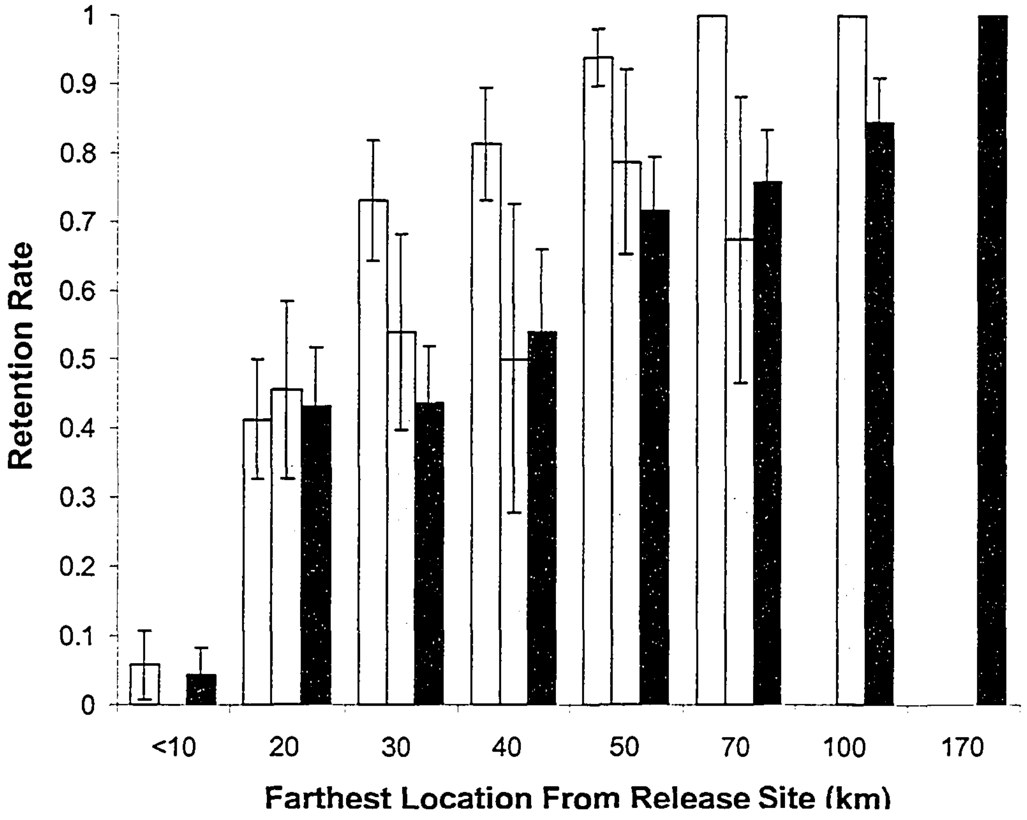

Figure 3.5. Retention rates (with SE) for wapiti translocated from the Mountain Parks (white bars), Elk Island (gray bars), and the Cross Area (black bars) to the central foothills of the Rocky Mountains in Alberta, Canada from 2000-2004 given alternative circle radii defining the extent of the retention area.

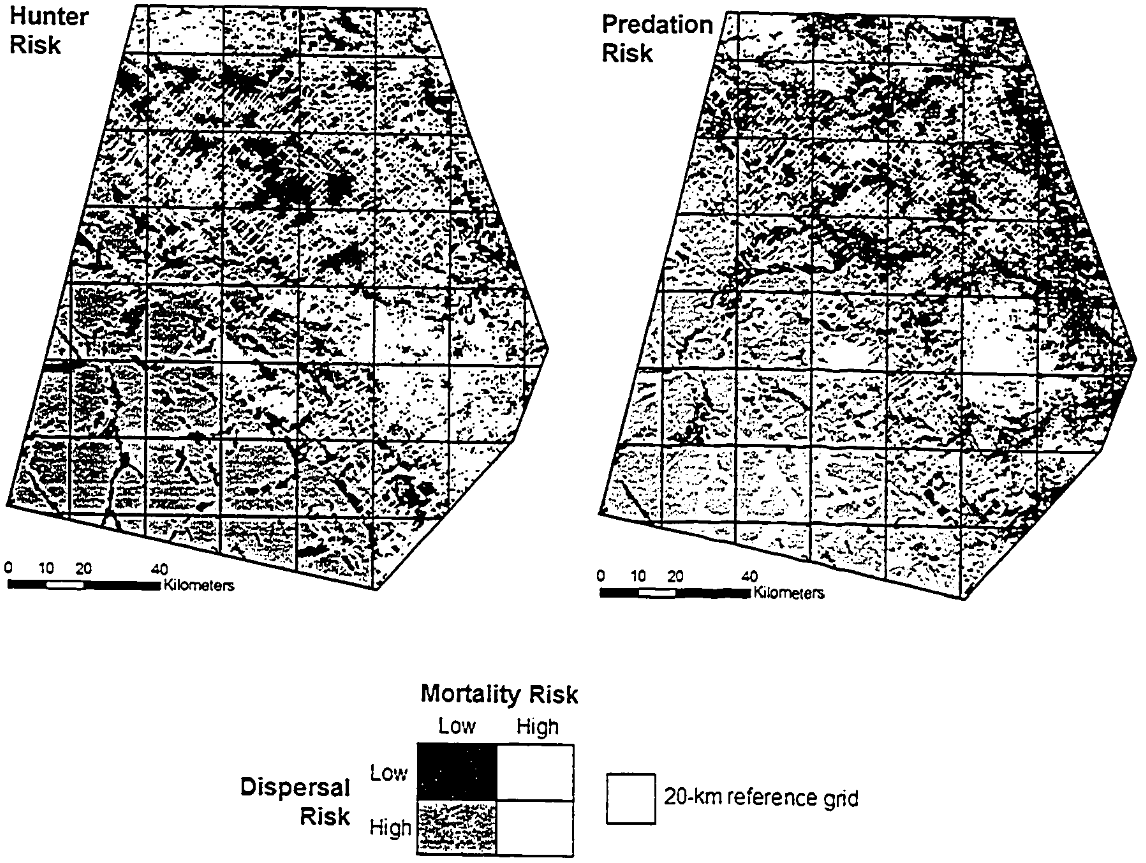

Figure 3.6. Spatial predictions for the relative probability of a translocated wapiti dispersing > 30 km and being killed by a hunter (left panel) or wolf (right panel) in the central foothills of the Rocky Mountains in Alberta, Canada.

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CHAPTER 4

SCALES OF MOVEMENT BY WAPITI (*CERVUS ELAPHUS*) IN RESPONSE TO HETEROGENEITY IN FORAGE RESOURCES AND PREDATION RISK[1]

4.1 INTRODUCTION

Movement is a fundamental process underlying animal distributions (Turchin 1998) and simple movement models, e.g. correlated random walks (CRW; Kareiva & Shigesada 1983), are being applied increasingly to the study of movements by large herbivores (e.g., Ward & Saltz 1994; Bergman *et al.* 2000). Although CRW models can effectively predict the redistribution pattern of animals over short time scales they tend to fail over longer time horizons likely because behaviours change when different habitat conditions are encountered (Jonsen & Taylor 2000) or different activities are undertaken (Firle *et al.* 1998; Van Dooren & Matthysen 2004). For example, a wide variety of taxa alter their movement rates and/or frequency of turns in response to local resource abundance by adopting an area-concentrated search pattern that results in slow, sinuous trajectories within patches and fast, directed trajectories between patches (Ward & Saltz 1994; Haskell 1997; Vernes & Haydon 2001; Nolet & Mooij 2002). Further, long distance migrations may occur in response to large-scale environmental gradients (Fryxell & Sinclair 1998; Mysterud 1999) irrespective of small-scale heterogeneity. Understanding the scales at which animals alter their movements in response to landscape heterogeneity should help us identify the underlying processes involved and ultimately facilitate my ability to model animal movements. In particular, identifying discrete

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movement states and relating those states to landscape structure could help extend the applicability of CRW models to larger spatio-temporal domains (Skalski & Gilliam 2003).

Approaches to identify distinct states or modes of movement from animal trajectories range from methods based on the distance and direction moved between consecutive locations (Johnson *et al.* 2002; Franke *et al.* 2004; Morales *et al.*, 2004) to path-based metrics such as tortuosity (Haskell 1997; McIntyre & Wiens 1999), fractal dimension (With 1994; Bascompte & Vilà 1997; Mårell *et al.* 2002; Fritz & Weimerskirch 2003), and first-passage time (Fauchald & Tveraa 2003). Based on Fickian diffusion, first-passage time was originally defined as the time required for a walking animal to first move out of a circle centered on the origin of the walk (Johnson *et al.* 1992). For a simple random walk, first-passage time scales proportionately to the square of the radius of the circle in a homogeneous environment (Johnson *et al.* 1992) and to the spectral and spatial dimensions of a fractal environment (d'Auriac *et al.* 1983). In contrast, Fauchald and Tveraa (2003) demonstrated that an area-concentrated search process results in a quadratic response of the variance in first-passage time to increasing circle sizes with curve maxima disclosing spatial scales at which movements are concentrated. Although Fauchald and Tveraa (2003) identified nested spatial scales at which migrating shorebirds altered their movement patterns, they did not relate those scales to specific indices of landscape heterogeneity nor did they investigate local movement responses to resources along the migration route. Indeed, studies relating movement trajectories to landscape heterogeneity have been largely limited to controlled settings where both animal trajectories and forage resources can be directly observed.

However, the coupling of global positioning system (GPS) collars with remotely-sensed imagery now allows us to track both animal movements and resources within the large spatio-temporal domain over which wild animals roam (e.g., Johnson *et al.* 2002).

I used first-passage time to explore the movement behaviours of GPS-collared wild wapiti (*Cervus elaphus*) in a northern temperature ecosystem in western Canada. I focus on three specific questions. First, do non-migratory wapiti exhibit distinct scales of movement? Second, are the scales of different movement behaviours related to landscape patterns within individual wapiti home ranges? Third, is the occurrence of path segments belonging to different movement behaviours related to local environmental variables? Past research in this region indicates that wapiti distributions are influenced by the distribution of forage resources, terrain conditions, and predators (Morgantini & Hudson 1989; Jones & Hudson 2002; Hebblewhite *et al.* 2002; White *et al.* 2003). In my study area, landscape heterogeneity originates from a diverse topographic relief that affects the distribution of soils and microclimatic conditions associated with elevation, aspect, and drainage. In this otherwise forested landscape, heterogeneity in forage resources is created by the interspersion of natural meadows and anthropogenic habitats, specifically large areas regenerating after timber harvest and extensive linear clearings resulting from the exploration for oil and gas resources. I hypothesized that patterns in wapiti movements would reflect spatial characteristics of forage patches. Also, I expected spatial heterogeneity in the risk of predation by wolves (*Canis lupus*), the major predator of wapiti in the region, to be largely related to encounter rates (Lima & Dill 1990), thus, I hypothesized that wapiti movement behaviours would be related to the relative probability of wolf occurrence across the landscape.

4.2 METHODS

4.2.1 STUDY AREA AND ANIMAL DATA

I conducted my research in an area of 15,800 km^2 along the eastern slopes of the Rocky Mountains in central Alberta, Canada (Figure 4.1). Approximately 2000 wapiti inhabited the area during the period of this study (James Allen, Alberta Sustainable Resource Development, unpublished data). Elevation ranged from approximately 500-1500 m and the area was largely forested (68.7% of the total area). Dominant tree species included lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*) and aspen/poplar (*Populus tremuloides* and *P. balsamea*). Interspersed throughout the forested matrix were wet and dry meadows (7.1%), cutover forest following timber harvest (4.3%), bare soil/rock outcrops (12.3%), rivers and lakes (2.1%), and areas regenerating from wildfire or site reclamation (< 1%). Anthropogenic linear clearings were extensive (≥ 28,000 linear km; Figure 4.1) and included typically 5-15 m wide trails and seismic exploration transects. Concentrated human use areas (e.g. urban, roaded, and agricultural areas) accounted for only 4.1% of the area.

I captured 18 adult, female wapiti during two winters (2000-01 and 2001-02) using a net gun from a helicopter. Each animal was fitted with a Lotek GPS2200 collar (Lotek Wireless, Ontario, Canada) that collected locations every 2 hours for up to 11 months. Although home ranges of collared wapiti overlapped between years (Figure 4.1), only one animal was collared per herd during any given year to insure independence among animals. I focused on movements during summer (1 Jun–30 Sep) when wapiti were most active and snow was absent. Although collars were active for the duration of each summer, the number of locations obtained per animal ranged from 797–1324 with a mean of 1154 (SD = 160). The four collars collecting < 1000 locations suffered intermittent periods of obvious collar malfunction rather than systematic bias (Frair *et al.* 2003). Collar tests across the range of cover and terrain conditions encountered within the study area indicated positional accuracy of ≤ 50 m 80% of the time (J. Frair, unpublished data).

4.2.2 IDENTIFYING SCALES OF MOVEMENT

Following Fauchald and Tveraa (2003), I calculated first-passage time as:

eqn 1 $$t(r)_i = \mathbf{FPTB}_i + \mathbf{FPTF}_i$$

where FPTB_i (first-passage time backward) was the number of minutes it took the animal to move from the edge of a circle having radius r to the center of the circle at location i (technically calculated backwards from location i) and FPTF_i (first-passage time forward) was the time it took to move from location i forward along the path to the edge of the circle. Because path segments were bisected at circle edges, I assumed a straight-line path and a constant rate of movement between locations to determine the remaining proportion of the path (converted to time in minutes) that occurred within each circle. Variation in $t(r)$ increases with increasing circle sizes as progressively more of the movement trajectory is captured. For this reason, I expressed variance in $t(r)$ on a per unit area basis as:

eqn 2 $$\sigma_r^2 / A_r = \text{Var}[t(r)] / \pi r^2$$

Peaks or asymptotes in the plot of σ_r^2 / A_r against r coincide theoretically with the spatial extent of the underlying dynamical process (Rand & Wilson 1995; Haydon *et al.* 2000).

In this application, such points identified the circle size that best isolated tortuous path segments from more directed movements. I fit second or higher order polynomials to the plots of σ_r^2 / A_r against r to identify the circle radius corresponding to peaks or asymptotes (hereafter rv_{max}).

Relating Movement Scales to Heterogeneity in Home Ranges

I regressed rv_{max} for each individual against the total amount and arrangement of foraging habitat, density of linear clearings, mean predation risk, and terrain ruggedness within wapiti home ranges (see *Environmental Variables*). Home ranges were delineated by a minimum convex polygon enclosing the set of all locations for an individual during the period of study. The samples sizes ($\geq$ 797 locations / wapiti / summer) far exceeded those required for an unbiased, seasonal MCP estimate (Girard *et al.* 2002). Linear regression was used to detect a linear, quadratic, or loglinear response in rv_{max} to each home range variable. Five individuals did not have cutover forest habitat within their home range, thus, sample sizes were not equivalent among analyses and model selection via Akaike's Information Criterion (AIC) would be invalid (Burnham & Anderson 2002). Thus, I compared univariate models using likelihood ratio tests between the model containing a given variable and the intercept-only model. Likelihood ratio tests were also conducted for models containing multiple, non-correlated variables ($r < 0.5$ when $P < 0.05$) for nested models.

Relating Movement Behaviour to Local Heterogeneity

I classed each path segment, i.e., the displacement between consecutive 2-hour locations, as belonging to one of three movement behaviours — largely "inactive/resting" when the distance moved was < 50 m (see *Results*), "active/foraging" when distances were ≥ 50 m but $< rv_{max}$, and "active/relocating" when distances were $\geq rv_{max}$. To better understand these behavioural classes, I first evaluated whether or not greater move distances corresponded to increased activity levels as determined by sensors in GPS collars. Prior to estimating the animal's location, tip-switches stored in the GPS collars counted the number of head up/down and side/side transitions within a 4 or 10-minute sampling frame depending upon the year of collar deployment. I summed the two counts, standardized values by the sampling duration (transitions/min), and estimated a Pearson correlation coefficient between counts and move distances. Second, I split the data by time of day (0400-0800, 0800-1800, 1800-2200, and 2200-0400 hours) to determine if wapiti were more often active (foraging or relocating) versus inactive during crepuscular periods. Third, I evaluated if relocating behaviour was indeed less tortuous than foraging behaviour by summarizing the turn angle distributions. For each behaviour, I calculated the mean vector direction and length (Batschelet 1981) to determine how concentrated turns were around 0° (straight-ahead).

To discriminate between movement behaviours based on local environmental variables, I employed multinomial logistic regression and chose foraging as the reference category. Given this model, the probability of exhibiting a given movement behaviour is calculated as:

eqn 3 $$\mathbf{Pr(y = 1) = 1 / 1 +} e^{X\beta(2)} + e^{X\beta(3)}$$

eqn 4 $$\mathbf{Pr(y = 2) = e^{X\beta(2)} / 1 + e^{X\beta(2)} + e^{X\beta(3)}}$$

eqn 5 $$\mathbf{Pr(y = 3) = e^{X\beta(3)} / 1 + e^{X\beta(2)} + e^{X\beta(3)}}$$

where X and $\beta(i = 2,3)$ are vectors equal to $(x_1, x_2, \ldots x_n)$ and $(\beta_{i1}, \beta_{i2}, \ldots \beta_{in})'$, respectively, y is the movement behaviour (1 = foraging, 2 = inactive, 3 = relocating), and $\sum_{y=1}^{3}(\mathrm{Pr}) = 1$ (Hosmer & Lemeshow 2000). Model covariates included forage resources (herbaceous and browse biomass), distance to the nearest linear clearing, terrain conditions (aspect, steepness, and net change in elevation), predation risk, and distance to cover (see *Environmental Variables*).

Before producing multinomial models, I tested for autocorrelation in my data using the continuous variable step length. Autocorrelation and partial autocorrelation plots indicated an AR-1 process and low-level periodicity. To control for these effects, I added the previous step length (SL_{t-1}) as a covariate in my multinomial models and fit a wave function to time of day as:

eqn 6 $$\mathbf{SIN_t = \sin(2\pi t / 12) \text{ and } COS_t = \cos(2\pi t / 12)}$$

where t is time of the location expressed to the closest hour. Thus, candidate models were identified as SIN_t, COS_t, and SL_{t-1} in addition to all plausible combinations of non-correlated environmental variables. When estimating standard errors for coefficients, I employed a clustering algorithm to account for the individual wapiti (N = 18) rather than the GPS location (N = 17,692) as the unit of replication (Pendergast *et al.* 1996; Nielsen *et al.* 2002). Sample sizes were identical among all models, thus model selection proceeded using the difference in AIC values (ΔAIC) and model weights (Burnham and Anderson 2002). For all categorical variables, classes having similar effect sizes were pooled and alternative categorizations were tested within the AIC framework. After identifying the best-supported model, I estimated binary logistic models for each comparison (Begg & Gray 1984; Hosmer & Lemeshow 2000) to report the overall classification accuracy as the area under the receiver-operating characteristic curve (AUC; Hanley & McNeil 1982).

4.2.3 ENVIRONMENTAL VARIABLES

Landcover Classes

Using ArcGIS (Environmental Systems Research Institute, Redlands, California), I derived 27 landcover classes from a Thematic Mapper (TM) satellite image acquired in September 2001 and GIS data on terrain, hydrology, and anthropogenic features. The landcover classification had a resolution of 28.5 m (cell size 0.08 ha) and an overall classification accuracy of 82.7% (based on an out-of-sample set of 513 random locations; Beyer 2004). I considered natural foraging habitats to include wet or dry meadows and shrublands while anthropogenic foraging habitats included cutover forests. The boundaries of cutover forest were delineated using timber harvest records and the TM image. Fragstats (McGarigal & Marks 1995) was used to calculate the total area, mean patch size and Euclidean nearest-neighbor distance between natural and anthropogenic foraging habitats as well as for both foraging habitats combined. I considered all forested cover types and tall shrublands (> 2 m height) to provide security cover for wapiti (Hillis *et al.* 1991). For the multinomial model, I calculated the minimum distance to security cover from the start location of each 2-hour path segment.

Herbaceous Biomass

To predict forage abundance, I first reduced the 27 landcover classes to 10 attempting to minimize within- while maximizing between-class differences in forage resources. With the exception of one rare class, recent burn, I established 14–17 transects in each class, split evenly between high- (≥ 1300 m) and low-elevation (< 1300 m) areas. Transects were revisited approximately every 15 days throughout summer for 2001 and 2002. I recorded the resting height of a 0.25 m^2 plastic disc on 16 plots along each transect. Total biomass underlying the disc was predicted from disc height, vegetation class, and sampling period (Visscher *et al.* 2004). This disc-calibration model was derived from ≥ 50 0.25 m^2 plots in each vegetation type (N = 638) that occurred adjacent to transects, were clipped to ground level, and were dried to a constant weight at 50°C for 48 hours (Vartha & Matches 1977). To extrapolate the mean biomass along transects to each 28.5-m cell across the landscape, I modeled herbaceous biomass as a function of julian day, landcover class, and elevation (N = 139). Cutover areas were handled separately to account for time since cut with data from an additional set of 159 transects (D. Visscher, unpublished data). These data yielded herbaceous biomass at peak for each of three regeneration classes, which I adjusted throughout summer with a phenology model derived from 15 long-term transects (Visscher *et al.* 2004). For the multinomial analysis, I calculated the total herbaceous biomass within a 100 x 100 m moving window (to account for potential errors in both wapiti locations and landscape layers) for each month and assigned month-specific values to the starting point of each 2-hour path segment.

Browse Biomass

Within a 0–2.5 m browse stratum (Bobek & Bergstrom 1978; Newton *et al.* 1989), I measured the species and basal diameter of each shrub in 4 8-m^2 plots along each transect. For species utilized by wapiti (Cook 2002), I calculated the total biomass of leaves and stems to 7-mm diameter (Lundberg & Danell 1990) using species-specific basal diameter to browse weight regressions (Visscher *et al.* 2004). Regression models were derived from 20–60 individuals per species in each landcover type clipped adjacent to transects and dried at 100°C for 72 hours (Brown 1976; MacCracken & Van Ballenberghe 1993). Browse biomass on each transect was calculated as the sum of the estimates for individual species and was not influenced by julian day, elevation, slope, or aspect. To extrapolate browse across the landscape I applied the mean biomass to each of the 10 landcover classes. I calculated the total browse biomass within a 100 x 100 m area around the starting point of each 2-hour path segment.

Linear Clearings

Linear clearings typically had a width less than the minimum mapping unit of my TM image and, thus, were not included in my forage biomass estimates. The central line of all linear clearings was mapped using Indian Radar Satellite Imagery having a 5-m resolution. I calculated the density of linear clearings within home ranges and the minimum distance to a linear clearing at the start of each 2-hour path segment. To determine if there was a threshold distance at which linear clearings affected wapiti movements, I recoded distance to linear feature as a series of binomial variables using cutoffs of 50, 75, 100, or 150 m and substituted each for the continuous distance variable in the model selection process.

Terrain

Terrain variables were derived from a 30-m digital elevation model. To determine if rv_{max} was constrained by terrain conditions, I calculated the standard deviation in elevation within home ranges as an index to overall terrain ruggedness. As an index to the energetic costs of local movements, I measured the degree slope at the start of each 2-hour path segment and calculated the net difference in elevation across the path segment. Aspect at the start of each path segment was categorized as belonging to 1 of 8 45° classes with south identified as the indicator contrast.

Predation Risk

The relative probability of wolf occurrence was modeled as a resource selection function (RSF; Manly *et al.* 2002) using telemetry locations from two wolf packs acquired from 1984-1986 in my area (John Gunson, Alberta Fish and Wildlife, unpublished data). I used these data to develop a RSF specific to the area because more recent data was available only for adjacent, mountainous areas where wolf distributions are largely determined by a strong elevation gradient (Callahan 2000) that does not occur in my study area. However, by using these data I assumed that the habitat use patterns of wolves have remained stationary over time. I believe this to be a reasonable assumption because both trend counts of the major ungulate species – deer (*Odocoileus virginianus* and *O. hemionus*), moose (*Alces alces*), and wapiti – and trapping records of wolves indicate that the spatial distribution and relative abundance of these species have not changed substantially since the 1980s (James Allen, Alberta Fish and Wildlife, personal communication). In contrast, land uses have changed and I adjusted my existing landcover and linear clearings data to the conditions present in 1985 based on archived aerial photos. Using logistic regression, I developed a wolf RSF based on 107 independent wolf locations and 191 locations selected at random within 95% kernel ranges for two adjacent wolf packs. Kernel ranges were produced using a fixed smoothing factor determined by least-squares cross-validation (Hooge & Eichenlaub 1997) and were used in lieu of MCPs, which tended to overestimate the area potentially utilized by these wide-ranging animals. Although the locations were divided roughly equally among the packs, I employed a clustering algorithm to appropriately identify the pack as the sample unit (Pendergast *et al.* 1996). To account for uncertainty in the placement of wolf telemetry locations I re-sampled landscape data to a 250-m cell size by taking the average of terrain variables and using a majority rule for landcover classes. The relative probability of wolf occurrence was modeled as a function of landcover class, degree slope, aspect, proximity of pipeline right-of-ways (> 10 m wide linear clearings), and the density of roads. I applied this model to the 2001-02 landscapes and considered predictions to be adequate based on a visual comparison to contemporary telemetry records and known wolf-killed wapiti locations, which were too few to conduct a formal evaluation. To represent predation risk, I calculated the mean wolf RSF value within wapiti home ranges and the RSF value at the start of each 2-hour path segment.

4.3 RESULTS

4.3.1 SCALES OF MOVEMENT

Patterns of σ_r^2 / A_r varied among individuals but I consistently observed a peak or asymptote at intermediate circle sizes (Figure 4.3a). I estimated rv_{max} (Figure 4.2b) from 550-1650 m depending on the individual with an average of 1033 m (SD = 314, N=18) for the population. Animals also consistently showed a tendency towards a second, very small-scale peak potentially below the resolution of GPS locations (~50 m) and some showed tendencies toward additional, larger scales of movement.

4.3.2 MOVEMENT SCALES AND HOME RANGE HETEROGENEITY

The spatial patterning of foraging habitat within a home range depended on the dominant habitat type (meadows versus cutover forest) because the total amount of cutover forest and natural meadows within a home range were inversely correlated ($r = -0.543$, $P = 0.020$, N = 18), and the mean patch size and nearest neighbor distances of cutover forest patches (9.6 ha, SD = 8.4 and 427.1 m, SD = 374.7, respectively, N = 18) were greater than those observed for meadows (1.25 ha, SD =1.43 and 132.5 m, SD = 28.7, respectively, N = 18). I observed rv_{max} to correspond most closely to the mean patch size of cutover areas ($r^2 = 0.743$, $P = 0.001$, N = 18; Table 4.1), but the relationship was quadratic rather than linear (Figure 4.3). The inverse relationships between the amount of cutover area and meadows precluded us from testing the relative effects of each foraging type in a multivariable model, but combining meadows and cutover forest into one foraging habitat did not improve model fit (Table 4.1). Although the total area of foraging habitat was not correlated with the mean patch size of cutover forest ($r =$

0.168, $P = 0.542$, N = 18), no improvement in fit was achieved by including total foraging habitat in the model with mean patch size (LR = 2.93, $P = 0 .0870$, N = 18). Nearest neighbor distances between foraging patches, terrain ruggedness, and the mean level of predation risk within wapiti home ranges also did not improve model fit.

4.3.3 MOVEMENT BEHAVIOUR AND LOCAL HETEROGENEITY

Due to GPS error, I could not determine whether or not an animal was active when path segments were < 50 m in length. However, activity sensor counts at the start of each path segment were highly correlated with the distances moved in 2 hours (r = 0.778, $P = 0.003$, N = 17,692), thus, very short segments coincided with low activity levels. More inactive path segments were observed during the day/night period (0800-1800 and 2200-0400 hrs; 65.2%, SD = 5.7; two-sided binomial $P < 0.001$, N = 18) whereas more foraging segments occurred during crepuscular hours (0400-0800 and 1800-2200 hrs; 56.1%, SD = 4.2; $P < 0.001$, N = 18). Temporal patterns in relocating were the most consistent with 77.6% (SD = 6.4) of these path segments occurring during crepuscular hours ($P < 0.001$, N = 18). With respect to turn angle distributions, the mean vector was ≤ 5.5° for all movement behaviours and differences in vector strength indicated that the distribution of turns was more concentrated around the mean direction when relocating than when foraging (Table 4.2).

After accounting for time of day (SIN_t, COS_t) and autocorrelation in path segments (SL_{t-1}), all autocorrelation and partial correlations in the residuals from the multinomial model were low (≤ 0.071, $P < 0.001$). The highest ranked multinomial model indicated that movement behaviour could be discriminated best by terrain, predation risk, forage, and linear clearings (Table 4.3). Little support was observed for the model including distance to cover (Table 4.3). Overall, the effect of linear clearings was best explained as a threshold effect with a distance cutoff of 50 m because I observed considerably more support for models containing the variable in this form compared to larger cutoffs or to distance entered as a continuous variable (ΔAIC ≥ 12.46, $\omega_i < 0.01$; Table 4.3). I observed more support for the model including the net difference in elevation, i.e., discriminating between moves directed up-slope (positive values) versus down-slope (negative values), versus the absolute value of the difference in elevation (Table 4.3). There was also more support for a quadratic versus linear relationship between movement behaviour and net difference in elevation, degree slope, and herbaceous biomass (Table 4.3). As a result, wapiti were most likely to be foraging versus relocating or remaining inactive in moderately steep areas (~10-25°), when moving down-slope, and in areas having intermediate levels of herbaceous biomass (~220-270 g/m^2; Table 4.4, Figure 4.4). When a net loss of up to100 m elevation occurred, the model predicted foraging and resting behaviours to be equally likely (Figure 4.4). Grouping the data by month indicated that when relocating wapiti incurred a net gain in elevation (positive mean for the net difference in elevation) during June-August (with a peak in July) and a net loss in elevation (negative mean) during September. The multinomial model additionally indicated that wapiti were more likely to relocate rather than forage in areas with abundant herbaceous biomass, high predation risk, close to linear clearings, and where slopes exceeded ~30° (Table 4.4; Figure 4.4). In contrast, wapiti were more likely to remain inactive versus forage on north to east-facing slopes and in areas of low herbaceous biomass, high browse biomass, low predation risk, and farther than 50 m from a linear clearing (Table 4.4; Figure 4.4). Binomial logistic models indicated moderate classification accuracy for both the inactive versus foraging and relocating versus foraging comparisons (AUC = 0.665, N = 14,133 and AUC = 0.676, N = 11,972, respectively).

4.4 DISCUSSION

Identifying scales of movement patterns in free-ranging animals may be an important step in understanding the processes that lead to animal distributions (Turchin 1998; Turner *et al.* 2001). Although several studies have addressed how environmental heterogeneity influences scales of habitat selection (e.g. Ward & Saltz 1994; Schaefer & Messier 1995; Wallace *et al.* 1995; Fortin *et al.* 2003; Boyce *et al.* 2003), few studies have shown how landscape heterogeneity influences scales of movement in free-ranging ungulates (e.g. Johnson *et al.* 2002).

In my study, distinguishing no movement associated with complete bouts of inactivity was limited by error in GPS locations (~50 m). However, segments ≤ 50 m likely reflected bouts of inactivity (bedding and ruminating) because these observations coincided with periods of low activity counts recorded in the collars and the majority of small segments occurred during the times of day I would have expected wapiti to be inactive (Ager *et al.* 2003; Wolff & Van Horn 2003). Areas where wapiti were inactive reflected choices for secure (low wolf use) and potentially cooler locations (north- to east-facing slopes, high shrub biomass). In contrast, wapiti used areas of high herbaceous biomass and moderately steep slopes when foraging. These patterns are consistent with previous studies of habitat selection by wapiti (see review by Skovlin *et al.* 2002). Similar to what Jones and Hudson (2002) observed, I also found that wapiti were more likely to be foraging rather than resting when close to linear clearings. Choosing to bed farther than 50 m from linear clearings may reflect responses to predation risk at a scale finer than that captured by my wolf RSF model, which had a minimum mapping unit of 6.25 ha. Wolves selectively use linear features in winter (Gehring 1995) and their rates of travel on linear features can be up to 3 times faster than through adjacent habitats (James 1999). As a result, encounter rates may increase if ungulates also use linear clearings or areas adjacent to them as foraging habitat (Kunkel & Pletscher 2000; James & Stuart-Smith 2000). Similar behaviour by wolves in summer is likely but has not been documented. Alternatively, humans readily use linear clearings in summer to access remote areas and wapiti may equate disturbance by humans to the risk of predation (Lima & Dill 2002).

The scale (rv_{max}) separating relocating and foraging path segments appeared to be related most to the size of cutover forest patches in wapiti home ranges. The nonlinear response I observed may reflect the tendency for wapiti to readily use all areas within small patches but to restrict their movements to smaller areas within large patches (McIntyre & Wiens 1999). Contrary to my expectations, I did not observe a relationship between rv_{max} and the mean predation risk within wapiti home ranges. I expected that a high mean predation risk in an wapiti's home range might result in more frequent relocating moves and a greater overall scale of movement, but I did not find this to be the case. Alternatively, wapiti might reduce their overall scale of movement to avoid detection by wolves as overall predation risk in a home range increases, but I did not detect this either. However, I may have failed to capture heterogeneity in predation risk at the scale of the home range, because wolves use areas close to territory boundaries less than core areas (Mech & Harper 2002). I have observed wolf sign in all areas occupied by wapiti and daily movements by wolves even in summer, when tied to a den (see review and data in Jedrzejewski *et al.* 2001), exceed the average width of the home ranges of the wapiti I studied (7.06 km, SD = 1.8). Indeed, at the scale of individual path segments, wapiti were more likely to relocate than forage or remain inactive in areas of high predation risk.

Contrary to my observations, relocating or "inter-patch" movements by mountain caribou were associated with areas away from the habitats used by wolves (Johnson *et al.* 2002). Spatial separation from wolves may be achieved to some degree by a species like caribou where their habitat use patterns do not overlap greatly with alternative prey species (James 1999; Kojola *et al.* 2004). Wapiti share the central foothills of Alberta with several, more abundant, ungulate species whose space-use patterns overlap those of wapiti. Thus, spatial separation from wolves is likely unattainable for wapiti in a landscape like ours and modifying group sizes (Hebblewhite & Pletscher 2002) or remaining close to cover (Kunkel & Pletscher 2000; Woff & Van Horn 2003) may be more profitable strategies. I was limited in my ability to document group sizes because the area is largely forested. While it was not clear that wapiti modified their movements depending on their proximity to cover, wapiti were found within ~30 m of cover, on average, irrespective of their movement behaviour. In fact, remaining close to cover at all times would restrict wapiti use of large open areas to the patch perimeter and this could explain the quadratic response of rv_{max} to the mean patch size of cutover forest. As a result, an indirect interaction between the spatial pattern of human activities and wolf predation may determine the scale of wapiti movements in the area.

Consistent with previous studies, I observed foraging behaviour to dominate wapiti activity during summer (Green & Bear 1990; Merrill 1994). Because wapiti in my study were non-migratory, relocating moves were only 6 times larger than foraging moves and likely reflected transitions between resting and foraging areas (Collins *et al.* 1978; Green & Bear 1990; Ager *et al.* 2003). Similar to my observations, crepuscular transitions between resting and foraging areas for wapiti on the Starkey Experimental Forest and Range in Oregon, USA coincided with both a sharp increase in movement rates and upslope movements (Ager *et al.* 1993). I suspect that changes in relocating moves with respect to elevation gains reflected foraging responses by wapiti to differences in plant phenology across an elevation gradient (Albon & Langvatn 1982; Mysterud 1999; Mysterud *et al.* 2001). That the average elevation of foraging path segments increased by up to 224 m over the summer, depending upon the individual, supports my observations. Because movements reflecting relocation were associated with high rates of movement, steep slopes, and tended to be directed upslope, they potentially incur high movement costs (Parker *et al.* 1985). Little research has focused on specific landscape features other than cover or terrain that might facilitate such prolonged or directed movement by wapiti (Skovlin *et al.* 2002; Fortin *et al.* 2005). Traveling along linear clearings may alleviate movement costs to some degree (James 1999), and I observed wapiti to be 24 times more likely to be relocating rather than foraging when close to linear clearings. However, the fitness costs of encounters with wolves or humans, both of which also use linear clearings, may potentially offset the energetic benefits of using linear features or habitats adjacent to them.

4.5 SUMMARY

I have shown that non-migratory wapiti inhabiting the central east slopes of Alberta, Canada exhibited distinct scales of movement. Broad-scale movement patterns were strongly and nonlinearly related to the mean size of cutover forest patches in wapiti home ranges, likely reflecting limitations to movements within and among foraging patches as they become large. Local changes in wapiti movements were related to heterogeneity in forage resources and perceived predation risk. My research suggests that anthropogenic "habitats", including cutover forest and linear clearings, pose a trade-off situation for wapiti in Alberta by creating potential foraging opportunities and travel lanes that may incur high risks imposed by wolves, humans, or both.

Table 4.1. Relationship between rv_{max} and home range metrics. Shown is the likelihood ratio test statistic (LR) with significance level (LR *P*) for the given model versus the null model (intercept only), the F-test statistic (F) with significance level (*P*), and model fit (r^2).

Variable	LR	LR *P*	F_{df}	*P*	r^2
Cutover MPS[1] (quadratic)	17.646	<0.001	$14.43_{2,10}$	0.001	0.743
Foraging habitat[2] TA[3] (linear)	4.419	0.036	$4.45_{1,16}$	0.051	0.218
Foraging habitat ENN[4] (linear)	4.003	0.045	$3.99_{1,16}$	0.063	0.199
Meadow ENN (linear)	3.252	0.071	$3.17_{1,16}$	0.094	0.165
Meadow TA (linear)	1.927	0.165	$1.81_{1,16}$	0.198	0.102
Line density[5] (quadratic)	3.123	0.210	$1.42_{2,15}$	0.272	0.159
Cutover TA (linear)	0.976	0.323	$0.89_{1,16}$	0.359	0.053
Cutover MPS (linear)	0.528	0.468	$0.46_{1,11}$	0.514	0.039
Cutover ENN (linear)	0.275	0.600	$0.25_{1,16}$	0.627	0.015
Terrain ruggedness[6] (linear)	0.118	0.732	$0.10_{1,16}$	0.750	0.007
Predation risk[7] (linear)	0.034	0.853	$0.03_{1,16}$	0.863	0.002
Foraging habitat MPS (linear)	0.007	0.933	$0.01_{1,16}$	0.937	<0.001
Meadow MPS (linear)	0.005	0.944	$0.00_{1,16}$	0.948	<0.001

[1] Mean patch size (ha), [2] Cutover forest and natural meadows combined, [3] Total area (ha), [4] Mean Euclidean nearest neighbor (m), [5] Density of linear clearings (km/km^2), [6] Standard deviation in elevation, [7] Mean value of wolf RSF

Table 4.2. Movement behaviours by adult female wapiti in west-central Alberta, Canada identified using first-passage time and 2-hour location intervals. The mean values across animals are given for percent occurrence and distances moved with standard deviations in parentheses (N = 18). The vector strength indicates how concentrated turn angles are around the mean direction (~0° in all cases).

Movement Mode	Percent Occurrence Mean (SD)	Distance Moved (m) Mean (SD)	Vector Strength
Inactive / resting	21.4 (5.3)	25.3 (2.2)	0.192
Active / foraging	71.3 (6.0)	265.7 (42.5)	0.250
Active / relocating	7.3 (4.6)	1518.7 (388.8)	0.326

Table 4.3. Multinomial logistic regression models for the probability of a 2-hour path segment belonging to the inactive (N = 3,798), foraging (N = 12,569), or relocating behavioural state (N = 1,325). The top control + environmental component models are shown with the model log-likelihood (LL), number of estimable parameters (K), change in AIC (ΔAIC), and model weight (ω_i). All models include three variables that control for autocorrelation (SL_{t-1}) and periodicity (SIN_t, COS_t).

Rank	Model Components	LL	K	ΔAIC	ω_i
1	Terrain[1], Risk[2], Forage[3], Lines[4]	−11077.1	29	0.00	0.60
2	Terrain[1], Risk[2], Forage[3], Lines[4], Cover[5]	−11076.5	31	2.70	0.16
3	Terrain[6], Risk[2], Forage[3], Lines[4]	−11080.9	27	3.44	0.11
4	Terrain[7], Risk[2], Forage[3], Lines[4]	−11081.4	27	4.62	0.06
5	Terrain[1], Risk[2], Forage[3], Lines[8]	−11081.6	27	4.94	0.05
6	Terrain[9], Risk[2], Forage[3], Lines[4]	−11084.7	25	7.18	0.02
7	Terrain[1], Risk[2], Forage[3], Lines[10]	−11083.9	27	9.58	0.01
8	Terrain[11], Risk[2], Forage[3], Lines[4]	−11085.2	27	12.20	0.00
9	Terrain[1], Risk[2], Forage[12], Lines[4]	−11089.0	25	15.72	0.00
10	Terrain[1], Forage[3], Lines[4]	−11089.9	25	17.46	0.00
11	Terrain[1], Risk[2], Forage[3], Lines[13]	−11088.1	27	17.86	0.00
12	Terrain[14], Risk[2], Forage[3], Lines[4]	−11092.1	27	22.08	0.00
13	Terrain[15], Risk[2], Forage[3], Lines[4]	−11092.5	25	22.66	0.00

[1] Difference in elevation over segment (m), difference in elevation^2, slope (°), slope^2, north to east-facing aspect at start location (binary), [2] Wolf RSF value at start location, [3] Mean herbaceous biomass at start location (g/m^2), herbaceous biomass^2, mean browse biomass at start location (g/m^2), [4] Linear clearing within 50 m (binary), [5] Distance to security cover (m), [6] Remove squared term for difference in elevation, [7] Substitute southwest to southeast facing slopes for north to northeast facing slopes, [8] Substitute linear clearing within 75 m (binary) for linear clearing within 50 m (binary), [9] Remove north to east-facing aspect at start location (binary), [10] Substitute linear clearing within 100 m (binary) for linear clearing within 50 m (binary), [11] Substitute absolute value of the net difference in elevation for the net difference in elevation, [12] Remove herbaceous biomass^2, [13] Substitute continuous distance to linear clearing for linear clearing within 50 m (binary), [14] Remove squared term for net difference in elevation, [15] Remove squared term for degree slope

Table 4.4. The highest-ranked multinomial model for the probability of a 2-hour path segment being associated with resting or relocating versus foraging behaviour (LL = –11077.13, LR(15) = 1424.87, $P < 0.001$). The estimated coefficients (β) are given with robust standard errors (SE) and significance levels (*P*).

	Inactive vs. Foraging			Relocating vs. Foraging		
Variable	β	SE	*P*	β	SE	*P*
Time of day (sine function)	–0.0899	0.0342	0.009	0.0127	0.0406	0.756
Time of day (cosine function)	0.7574	0.0496	<0.001	–0.6522	0.0568	<0.001
Previous step length (m) / 100	–0.0291	0.0090	0.001	0.0599	0.0079	<0.001
Net difference in elevation (m) / 50	–0.0516	0.0468	0.053	0.1771	0.0583	0.002
Net difference in elevation^2	–0.0516	0.0192	0.007	–0.0142	0.0113	0.210
Slope (°)	0.0018	0.0149	0.904	–0.0800	0.0352	0.023
Slope^2	–0.0005	0.0006	0.480	0.0032	0.0011	0.003
North to east-facing aspect (binary)	0.1431	0.0618	0.021	–0.1130	0.1263	0.371
Herbaceous biomass (g/m^2) / 100	0.5321	0.2955	0.072	–0.6998	0.3580	0.051
Herbaceous biomass^2	–0.2478	0.1046	0.018	0.2585	0.1335	0.053
Browse biomass (g/m^2)	0.0018	0.0008	0.019	–0.0016	0.0016	0.304
Relative predation risk	–0.1721	0.0616	0.005	0.0842	0.0354	0.017
Linear clearing within 50 m (binary)	–0.2785	0.1039	0.007	0.2121	0.0999	0.036
constant	–1.5062	0.3109	<0.001	–1.8495	0.3538	<0.001

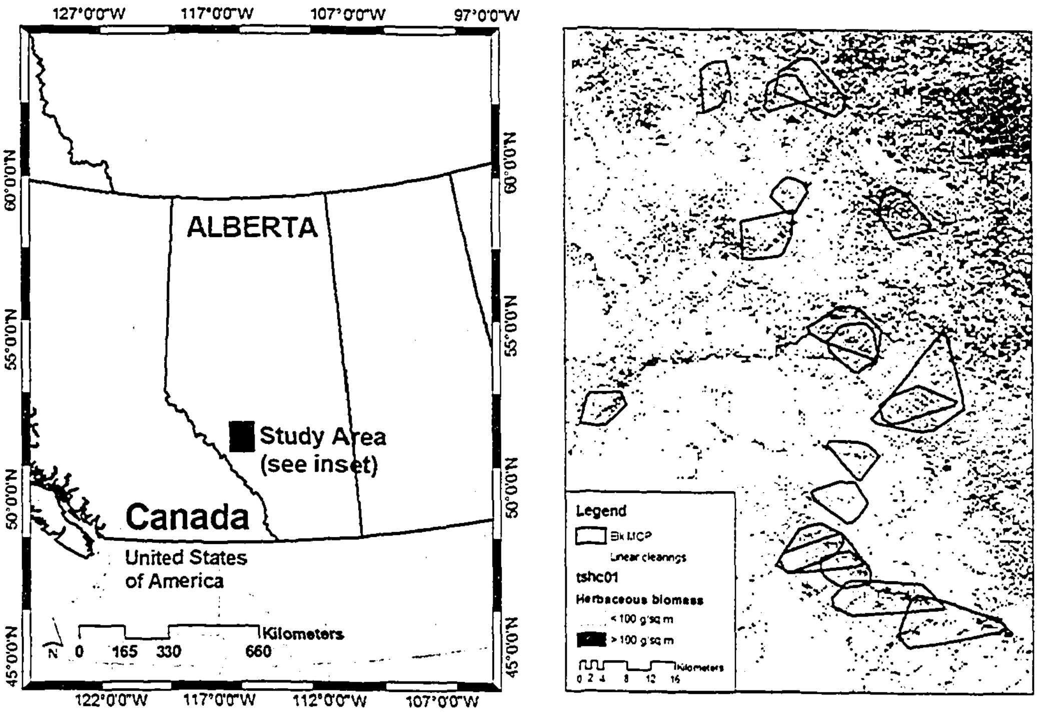

Figure 4.1. Location of the study area in west-central Alberta, Canada. The inset shows heterogeneity in herbaceous biomass, the distribution of linear clearings, and the MCP home ranges of wapiti used in this study.

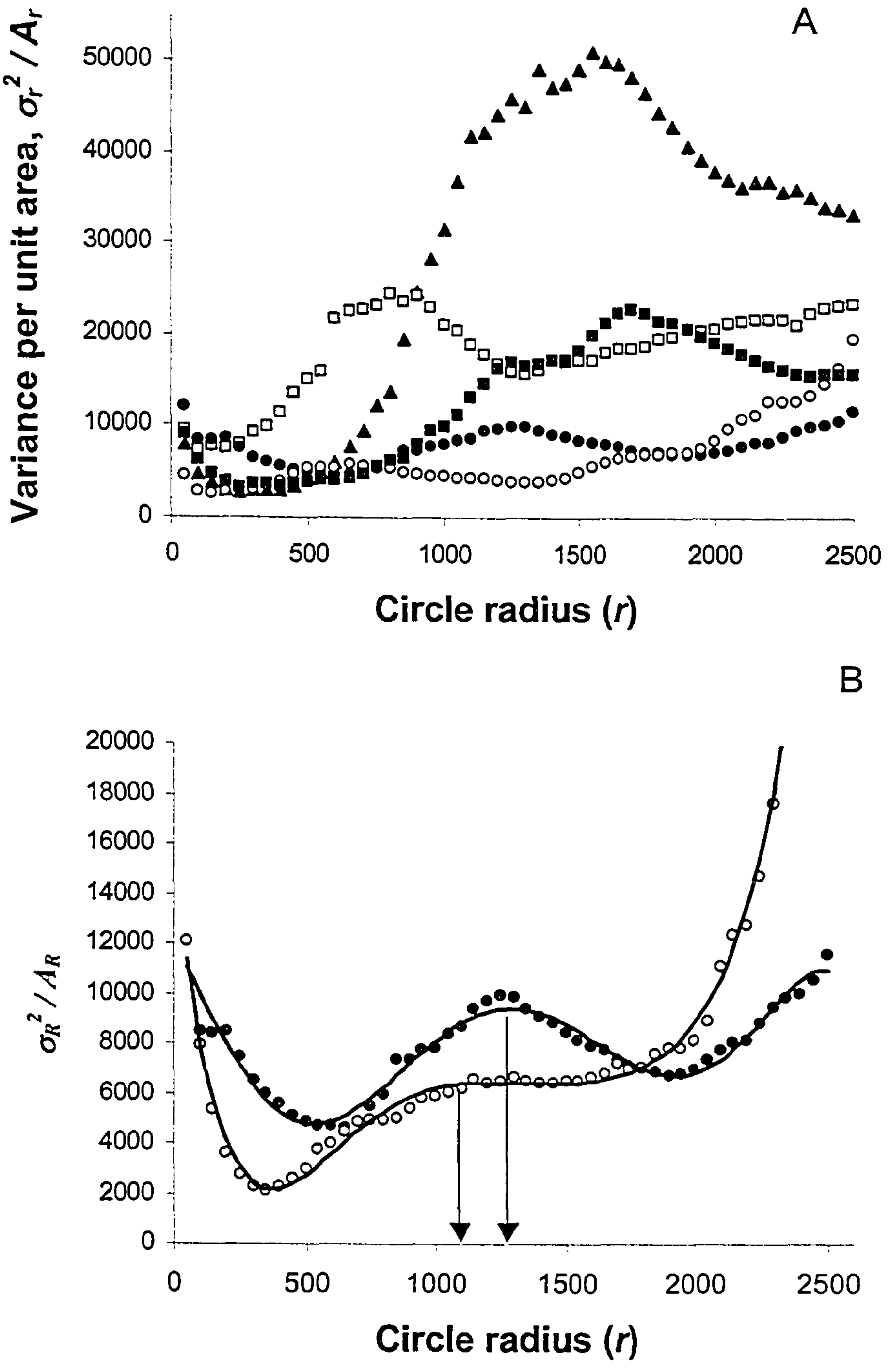

Figure 4.2. Variance in first-passage per unit area, σ_r^2 / A_r, given an increasing circle radius, r, for a sample of wapiti demonstrating the various patterns observed among individuals (A). Fitted polynomials were used to identify curve maxima or asymptotes that correspond to the circle size at which movement patterns change, rv_{max} (B).

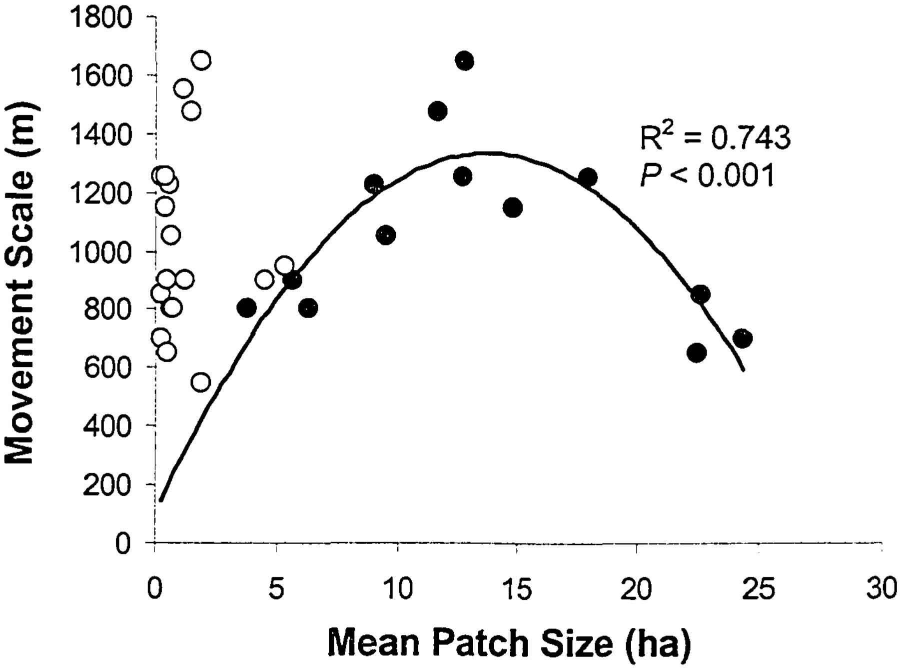

Figure 4.3. Relationship between the circle size separating foraging and relocating behaviours, rv_{max}, and the mean patch size of cutover forest (black circles) and natural meadows (open circles) within wapiti home ranges.

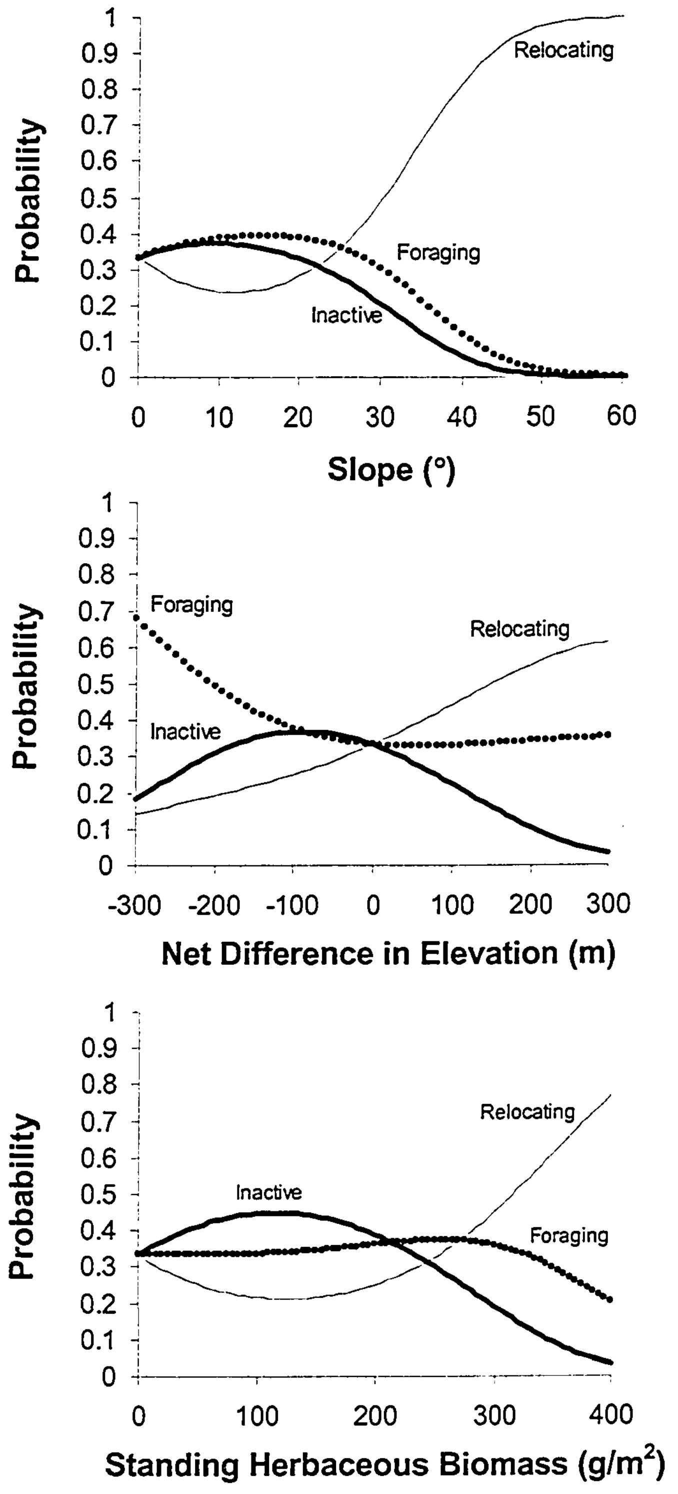

Figure 4.4. The predicted probability of an wapiti foraging, relocating, or remaining inactive as a function of degree slope at the start of the path segment, the net difference in elevation across the segment, and herbaceous biomass at the start of the segment after setting the effects of all other covariates (including the intercept) to zero.

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CHAPTER 5

LINKING MOVEMENTS, ROADS AND HABITAT EFFECTIVENESS FOR A LARGE UNGULATE

5.1 INTRODUCTION

Resource extraction industries are rapidly changing the face of wildlife habitat in the Rocky Mountains of western North America. Outside the boundaries of national parks and wilderness areas in Canada, the footprint of forestry and oil & gas operations is increasing at an exponential rate (Timoney & Lee 2001). Together these industries create an increasingly pervasive and dense network of roads. As road networks grow worldwide so do concerns over their ecological ramifications including the loss and fragmentation of natural habitats (Forman & Alexander 1998; Trombulak & Frissell 2000; Spellerberg 2002; Jaeger *et al.* 2005). In the southern Rocky Mountains, the cumulative impact of forestry roads was shown to have a greater effect on landscape structure (mean patch size, edge density, and core area) over a 40-year period than timber harvest per se (McGarigal *et al.* 2001). Yet, for large herbivores, changes in landscape structure due to roads may be less important than the functional loss of habitat due to avoidance of roads and associated infrastructure (Barnes *et al.* 1991; Czech 1991; Forman & Alexander 1998; Dyer *et al.* 2001; Papouchis, Singer & Sloan 2001; Nellemann *et al.* 2003; Jaeger *et al.* 2005) or an increased vulnerability of animals to hunters using roads (Basile & Lonner 1979; McCorquodale, Wiseman & Marcum 2003; Frair 2005).

North American elk, or wapiti (*Cervus elaphus* L.) are sensitive to disturbance by humans and, as a surrogate to human presence in the landscape, the proximity or density of roads has been correlated with wapiti movements (Cole, Pope, & Anthony 1997), habitat use (Morgantini & Hudson 1989; Jones, Hudson, & Farr 2002; Licoppe & De Crombrugghe 2003), and survival (Unsworth *et al.* 1993; Cole *et al.* 1997; Hayes, Leptich, & Zager 2002; McCorquodale, Wiseman, & Marcum 2003; Frair 2005). Studies across western North America have recorded wapiti avoidance of areas close to roads (Rost & Bailey 1979; Witmer & deCalesta 1985; Czech 1991; Rowland *et al.* 2000; Jones, Hudson, & Farr 2002). These studies do not indicate nonuse, or direct habitat loss, but rather use that is lower than might be expected in the absence of any road effect. The concept of "habitat effectiveness" has been invoked to account for the lost habitat potential for wapiti due to roads (Thomas *et al.* 1979; Lyon 1983; Lyon *et al.* 1985). Habitat suitability indices (HSI) and their variants typically discount the expected habitat value of an area by the density of open roads (Leege 1984; Wisdom *et al.* 1986; Thomas *et al.* 1988). Such models have been widely applied for timber harvest planning where wildlife habitat is an important consideration (Edge, Olson-Edge, & Irwin 1990). However, in a rigorous test of road-based HSI models conducted at the Starkey Experimental Forest and Range in Oregon, Rowland *et al.* (2000) observed that while the underlying premise of the road density model was valid – wapiti avoided areas near roads – there was no relationship between HSI values and wapiti abundance. Model failure may result in large part from manipulation of the empirical relationship, i.e. pellet group density by distance from road, into a largely untested effect of road density (Rowland *et al.* 2000; Gautestad & Mysterud 2005). Road configuration partly accounted for model failure, which Rowland *et al.* (2000) explored via landscape simulation. They found that given an equal road density, a uniform distribution of roads resulted in smaller residual habitat patches and, by extension, lower wapiti habitat effectiveness. Differences in habitat configuration, forage quality, and terrain conditions may further confound how local responses to roads affect wapiti redistribution (Rowland *et al.* 2000). Moreover, differential human uses of the road network and wapiti habituation to human activities are likely important but have rarely been considered (Millspaugh 1999; Roloff *et al.* 2001). Rather than discard the oversimplified model, a revisitation of the habitat effectiveness / road density paradigm is warranted because the concept of declining wapiti habitat effectiveness with increasing road density has propelled forest management in a direction that has benefited wapiti and other large ungulate populations (Lyon & Christensen 2002).

Herein, I develop a spatially-explicit, individual-based simulation model to explore how biased movements by wapiti with respect to habitat and roads might scale up to the overall distribution of wapiti in a managed forest landscape. A simulation approach based on movements is appealing for several reasons. Foremost, the approach allows us to control habitat amount and configuration to isolate the effect of roads (Boutin & Hebert 2002; Frankhauser & Enggist 2004), which would be difficult to achieve in a large landscape study. Of equal importance, movement models inherently account for the accessibility of habitats contingent upon starting conditions and movement constraints. In contrast, statistical models of habitat effectiveness may identify highly suitable areas that remain unused due to intervening barriers or inhospitable habitats (Matthiopoulos 2003). HSI models further assume that animals will shift their distribution away from roaded areas without consideration of traditional patterns of use or site fidelity behaviour (Van Dyke *et al.* 1998). A simulation approach allows us to test the effects of different assumptions regarding wapiti movement behaviour. Third, stochasticity can be built into movement decisions or introduced randomly to reduce determinism in model predictions, uncover a range of plausible outcomes, and extend the generality of the model. Fourth, movement models require few inputs – the distribution of step lengths and turn angles at a minimum – but can meaningfully recapture complex animal paths (Blackshaw & Goodwin 2004) and the spread of individuals over space and time (Bergman, Schaefer, & Luttich 2000; Firle *et al.* 1998). Detailed mechanistic models, such as those based on foraging energetics (Moen, Pastor, & Cohen 1997; Turner *et al.* 1993, 1994), are useful to determine optimal strategies under given set of constraints but such models can become exceedingly complex, require many parameters that cannot be measured empirically, and because of their complexity can be difficult to interpret (Van Nes & Scheffer 2005). Moreover, this level of detail may not be required to meaningfully recreate observed animal distribution patterns or to assess the consequences of fixed behavioural strategies under alternative landscape management scenarios (Zollner & Lima 1999; Frankhauser & Enggist 2004).

My approach was to parameterize a correlated random walk (CRW; Kareiva & Shigesada 1983) using the movement trajectories of female wapiti collected by global positioning system (GPS) collars during the summers of 2001-2004 in the central Rocky Mountain foothills of Alberta, Canada (52° 27′ N, 115° 45′ W). I evaluated competing model structures to identify the simplest formulation that accurately redistributed wapiti with respect to roads and habitat (Caswell 1988). I then explored the effect of increasing road density on 1) the time wapiti spent near roads when constraining wapiti movement to within a fixed "home range", and 2) the rate at which animals might leave unfavorable landscapes. In the first case, I evaluated how the rate of increase in wapiti use of areas close to roads changed under alternative scenarios where I varied road density, the road development scheme, and the amount of cutblock habitat available to wapiti. Based on my previous study of wapiti in the central foothills (See Chapter Three), I related the use of areas close to roads to the potential mortality risk accrued by wapiti under the different scenarios. In the second case, I used the model to assess changes in the accessibility of habitats for wapiti. To do so, I first quantified habitat accessibility as a function of how difficult it was for an wapiti to find a suitable place to move to (Knaapen, Scheffer, & Harms 1992). I then varied wapiti tolerance for different levels of landscape resistance to quantify how rapidly wapiti might abandon the area as it becomes increasingly roaded and whether the overall amount of cutblock habitat or road development scheme mediated emigration rates. Thus, I broaden the wapiti/road density/habitat effectiveness paradigm to include changes in habitat accessibility, mortality, and potential emigration rates as a function of increasing road density. I discuss limitations to the generality of my findings and implications for managing wapiti habitat in multiple use forests.

5.2 METHODS

5.2.1 EMPIRICAL DATA AND STUDY AREA

I collected movement data from 23 adult-female wapiti during June–September, 2001–2004, in the Lower Foothills Natural Subregion (Beckingham, Corn & Archibald 1996) of the central Rocky Mountains in Alberta, Canada (Figure 5.1). The ~2,800 km^2 study area ranged in elevation from 870-1800 m and was predominantly forested (~84% of total area) by lodgepole pine (*Pinus contorta* Dougl. ex Loud), white spruce (*Picea* *glauca* [Moench] Voss), aspen (*Populus tremuloides* Michx.) and balsam poplar (*P. balsamifera* L.) species. The remainder of the study area consisted of areas regenerating after timber harvest (cutblocks; 8.9%), scattered natural meadows (dry/mesic or wet herbaceous or shrub-dominated; 2.6%), reclaimed herbaceous areas, such as pipelines (0.6%), and baresoil/rock outcrops, fen/bog areas, and lakes or rivers (0.9% collectively). Approximately 1000 wapiti were estimated to occupy this region for a density of ~0.19 wapiti/km^2 (Allen 2005). Annual trend counts indicated the wapiti population to be stable or growing at the time of this research (Allen 2005). Throughout this study the regulated fall harvest of wapiti was limited to 3-point bulls but aboriginal hunting of both sexes and all age classes occurred year-round. The area also supported harvested populations of wolf (*Canis lupus* L.), cougar (*Felis concolor* L.), grizzly bear (*Ursus arctos* L.) and black bear (*U. americanus* Pallus).

Individual wapiti were captured using a net gun from a helicopter such that only one animal was collared per local herd in a given year although additional animals may have been collared in the same herd in alternate years (Figure 5.1; Table 5.1). Although the capture technique was restricted to open areas, I attempted to minimize potential biases in the habitat types that animals were captured within (cutblocks versus natural meadows). Animal relocations were acquired using GPS2200 collars (Lotek Engineering, NewMarket, Ontario, Canada) set to collect a location every 2 hours for 11 months and then to drop from the animal. In formal tests across the range of canopy and terrain conditions encountered in this region, these collars achieved a high fix rate, 92.8% (± 3.7 SE, n = 142; Frair *et al.* 2004) and positional accuracy ≤ 50 m 80% of the time (mean error 57.9 m ± 8.9 SE; J. Frair, unpublished data). Although prone to random malfunction, which created an imbalance in sample sizes among individuals, the collected set of locations were considered to be unbiased by vegetation and terrain conditions (Frair *et al.* 2004). From these 2-hr data I derived the step length (*l*) originating from each animal location as the straight-line distance between consecutive locations and turning angle (ω) as the angular difference between two consecutive steps (scaled between –180 and +180°) using Hawth's Tools (www.spatialecology.com). I recovered 879 (± 47 SE) step lengths and 735 (± 50 SE) turning angles on average across animals. The models developed in the following sections were parameterized using data from 11 independent wapiti having largely non-overlapping home ranges (Figure 5.1). The remaining individuals were withheld for model validation.

5.2.2 SIMULATION MODEL DEVELOPMENT

My simplest model was a CRW where correlation was inherent in the empirical distributions of *l* and ω from which random draws were made. The distribution of step lengths ranged 0 – 6308 m (median = 154 m; n = 11,671) and the mean vector direction from the distribution of turns was 0.38° (n = 9,983). Being neither uniform (Kuiper V = 2.577, $P < 0.001$) nor unimodel (Rayleigh $P = 0.105$), the distribution of turn angles showed discernable peaks around 0 and 180° (Figure 5.2, top panel). Random and independent draws from the *l* and ω distributions were used to redistribute wapiti across the landscape using an object-oriented model developed within the ArcGIS 9 (Environmental Systems Research Institute, Redlands, California, USA) framework. One hundred *x,y* locations were selected at random from the GPS collar data for each wapiti, which I used as the starting locations for the simulation yielding a total of 1100 paths. At each 2-hr time step, one l and ω pair was drawn at random to determine the next location of the wapiti. At the end-point of each step I recorded the *x,y* coordinates, vegetation type (see below), and the distance to the nearest road. In the event that a chosen step crossed the landscape boundary, defined by a minimum convex polygon (MCP; Mohr 1947) around the empirical data for each wapiti, the step was rejected and another l and ω were drawn at random until a suitable step was identified. Individuals were moved for 120 days (1,440 steps of 2-hour duration).

My alternative model structure was a state-based CRW, where different l and ω distributions were used for each of three states: inactivity, foraging, and traveling. States were assigned to the empirical data using a first-passage time approach (see Frair *et al.* 2005). I considered wapiti to be inactive where $l < 50$ m. The distribution of "turns" associated with these short steps was unimodal (Rayleigh $P < 0.001$) with a mean vector direction of 182.8° (Figure 5.2, second panel). Foraging step lengths ranged from 50 – 1241 m (median = 154.2 m) and were associated with a distribution of turns that was neither uniform (Kuiper V = 2.116, $P < 0.001$) nor unimodal (Rayleigh $P = 0.192$) but "W" shaped with peaks at 0 and 180° (Figure 5.2, third panel). In contrast, traveling step lengths ranged from 200 – 6308 m (median = 718.6 m) and had an associated distribution of turns that was unimodal (Rayleigh $P < 0.001$) with a mean vector direction of 0.60° (Figure 5.2, bottom panel). The simulation routine for the state-based CRW started with the same 1100 initial *x,y* coordinates as detailed previously with time initialized at midnight and state initialized as inactive. At each time step the state of the simulated animal was determined stochastically by comparing a randomly generated number (P_r; range 0-1) to the probability of being in each state (inactive, P_i, foraging, P_f, or traveling,

P_t) as determined by predictive models (see below). At each time step, the wapiti was considered to be inactive if $P_r < P_i$. When active, a new probability was drawn to determine if the wapiti was foraging ($P_r < P_f$) or traveling. Consistent with the simple CRW model, the only constraint on the end-point of a move was that it not extend beyond the MCP of the assigned individual.

Predictive Models of Wapiti State

I developed statistical models to predict wapiti state based on the time of day and environmental characteristics at the animal's location using cross-sectional time-series, logistic regression. Models were fit using the XTLOGIT function in Stata v8.2 (StataCorp, College Station, Texas) to account for the inherent time-dependent structure of wapiti trajectories and differences among individuals in the proportion of time they spent in different states. Following Frair *et al.* (2005), diurnal activity patterns of wapiti were incorporated by fitting a sine wave to time of day (in 2-hour intervals having period $2\pi = 12$) and including this function as a set of fixed covariates. Environmental covariates used to predict state included vegetation type, slope (°), aspect (bearing), predation risk, the proximity of a linear clearing, and the proximity of a road at each wapiti location. Vegetation type was derived from a Landsat Thematic Mapper (TM) 5 image classification having a 28.5 m resolution (see Frair *et al.* 2004). Terrain conditions were derived from a 28.5 m resolution digital elevation model. Predation risk was derived from a resource selection function (Manly *et al.* 2002) for wolves that was shown to have good predictive power for the likelihood of wolf occurrence as well as being inversely correlated with wapiti survival in the region (see Chapter Three). Linear clearings, 5-9 m wide seismic exploration transects and recreational trails, were mapped using 5-m resolution Indian Remote Sensing satellite imagery. All roads passable by passenger vehicle were compiled from vector GIS data provided by Alberta Fish and Wildlife, Sunpine Forest Products, and Weyerhaeuser Ltd. and verified using TM satellite images and field reconnaissance. Candidate models predicting state were ranked using Akaike's Information Criterion (AIC), the change in AIC (ΔAIC), and model weights (Burnham & Anderson 2002). For parsimony, variables were retained in the highest ranked models only when their inclusion yielded ΔAIC of <2 units from the model excluding only that covariate. Data from the 12 withheld wapiti were used to validate model predictions using a non-parametric receiver operating characteristic (ROC) curve (Hanley & McNeil 1982) comparing observed states to model predictions.

Incorporating a Habitat Bias

The simple and state-based CRW models detailed thus far predicted how far and in what direction an animal would move from a given location without consideration of the spatial context of the move. Herein, I bias movements to reflect habitat selection by wapiti. Following (Manly *et al.* 2002:47) I estimated selection ratios for 6 vegetation types as:

$$\hat{R}_i' = \sum_{j=1}^{n} (y_j / x_j) / n$$

where y_j is the frequency of use of type i by individual j and x_j is the availability of type i within the MCP of individual j. The vegetation types repesented natural meadows (dry/mesic/wet herbaceous or shrub-dominated), lowland forests and bogs, non-forested riparian areas (largely sand bars along major rivers), cutblocks, forests having >40% of the canopy cover comprised of deciduous species, and conifer-dominated forests. A 1:1 ratio of used:available locations was set for each individual and availability was sampled at random within each MCP. Standard errors were calculated following Manly *et al.* (2002:48).

Several simplifying assumptions of animal cognition are involved when assigning rules for habitat biased movements, which may be difficult to test empirically and for which model output is quite sensitive (Ruckelshaus, Hartway, & Kareiva 1997; Kramer-Schadt *et al.* 2004). I attempted to match the habitat bias in my simulations as closely as possible to its empirical measurement. Therefore, I scaled $\hat{R}_i'$ values from 0-1 to represent the relative probability of use (P_{use}) of any given vegetation type and the cell at the end-point of any given l and ω pair was rejected at a rate of $1 - P_{use}$. When rejected, another l and ω were drawn until a suitable end-point was identified. In this way, I biased wapiti movements towards selected habitat types without consideration of the intervening areas (Schippers *et al.* 1996) and without evaluating adjacent cells in the neighborhood of the end-point (Ruckelshaus, Hartway & Kareiva 1997) – complications that could be included at a later date if necessary. One additional complication that I did consider was whether selection of habitats remained constant given the proximity of roads. To assess this, I divided the landscape into areas > 1 km from the nearest road and, for areas within 1 km of a road, into 10 intervals each having a width of 100-m (e.g., <100 m, 101-200 m, ... , 901-1000 m). Assigning each of the 6 vegetation types to each road proximity interval yielded 66 potential road proximity by habitat combinations. As above, I calculated $\hat{R}_i'$ for each of the 66 new classes, rescaled values from 0-1, and used these values as an alternative habitat bias (referred to as the road-adjusted habitat bias).

Comparison of Model Structures

I compared the results of the simple and state-based CRW models without a habitat bias, with a bias for the six vegetation types, and with a road-adjusted habitat bias for a total of six candidate models. Summary statistics excluded data from the first 24 times steps (2 days), which allowed patterns of habitat use to achieve a steady state. For each simulation I calculated the mean use (across animals) of areas within 50-m distance intervals from roads to 1km, of all areas > 1 km from a road, and of two key vegetation types – cutblocks and conifer forest. Confidence intervals were constructed using a sample size of 11 individuals. I sought consistent overlap between the simulated and empirical wapiti data (Rykiel 1996). In the event that two models redistributed wapiti well with respect to habitat and roads, I favored the model producing the tightest confidence intervals (Rykiel 1996).

Model Validation and Sensitivity

To test the validity of the model, I simulated movements within the MCPs of the 12 individuals with-held from model development. As before, I selected 100 start locations at random from each wapiti, moved individuals for total of 120 days, and constrained movements to occur within the boundaries of their respective MCP. Plots of the empirical and predicted wapiti distribution with respect to habitat and roads were compared as above. To test the sensitivity of the state-based model to the variables in the predictive models for state, I compared simulations where state was predicted as a function of time of day and environmental covariates to those where I zeroed out the effects of all environmental covariates.

5.2.3 MODEL APPLICATION

I explored the consequences of increasing road density on wapiti habitat effectiveness using two measures that reflected (1) the mortality hazard resulting from the use of areas close to roads and (2) the ability of an wapiti to find suitable habitat in an area. For this application, I selected an area approximating the size of the average MCP for wapiti in my study (10 x 10 km). The area used also was representative of the average habitat conditions with respect to the extent of clearcuts within wapiti MCPs (~20% of the landscape cut). I simulated increasing road density in a pattern consistent with existing roads in the central foothills of Alberta. First, I represented baseline conditions by considering the landscape to contain no cells within 1 km of any road (Scenario 1; Figure 3a). Second, I "developed" the main access road, which I identified from the existing road network (Scenario 2: 0.10 km/km^2; Figure 3a). From this point onwards, roads were developed according to two alternative schemes. Under the first scheme, roads created by the forest industry, which remain open and accessible year-round to travel by passenger vehicles, were developed (Scenario 3: 0.31 km/km^2; Figure 3a). These roads were identified from the existing road network for this area and I refer to this scenario as the "minimal forestry roads" scheme. Under the second scheme, all roads required to remove timber from cutblocks were developed (0.92 km/km^2; Figure 3b). Most of the roads in this scheme were identified from the existing road network and, where necessary, I added the miminum road length required to extend the network to each cutblock. This scenario is referred to as the "maximal forestry roads" scheme.

These additional roads generally are reclaimed, blocked, or become otherwise impassable after the completion of harvest operations and I included this scheme as a worst-case scenario should all developed roads remain open. On top of these two base networks I added roads to mimic the ever-expanding operations of the gas industry in the central foothills (Scenarios 3a-3e: 0.63-2.08 km/km^2 and Scenarios 4a-c: 1.34-2.33 km/km^2; Figures 3a,b). Oil and gas roads were added so as to capitalize on existing infrastructure where possible but were otherwise located independently of the location of cutblocks. Road development was restricted only by the location of rivers in the northeast and southeast corners of the landscape, with the maximum density approximating that currently observed in the central foothills (1.74 km/km^2). To test the sensitivity of model predictions to overall habitat amount, I used these same road networks after randomly replacing 50 and 75% of the existing cutblocks with conifer forest leaving 11 and 5% of the landscape cut (Figure 4). I randomly selected 100 *x,y* coordinates, which were used as the start locations for all scenarios, and moved simulated individuals for 120 days.

I used two measures of habitat effectiveness assuming different wapiti behaviours: 1) stay in the home range and use available habitats in accordance with the selection ratios even as values decay due to road encroachment, or 2) leave the landscape when suitable habitat becomes inaccessible. Following the first assumption, I tracked the rate of increase in both the proportional availability and wapiti use of areas at different road proximities given an increasing road density under the alternative road development schemes and habitat amounts. I then converted the use of areas within 1 km of roads to the mean mortality hazard (*H*) accrued by wapiti under scenario *j* as:

$$H_j = \sum_{k=1}^{100} \left(\sum_{l=1}^{10} nh \right) / 100$$

where the frequency of locations (n) for wapiti k occurring in distance bin l was multiplied by the relative mortality hazard (h) associated with use of that distance bin. I tallied the frequency of wapiti locations within 50-m distance bins to 1 km from roads and calculated the mortality hazard as $h = e^{-1.5059x}$, where x was the midpoint of each bin expressed in km (0.025, 0.075, ... , 0.975). This relationship was derived from a Cox proportional hazards model developed for adult-female wapiti in this region (See Chapter Three: Table 3.5).

Under the alternative assumption that wapiti would leave the area when suitable habitat was difficult to find, I considered the relative accessibility of suitable habitat (Knaapen, Scheffer, & Harms 1992) to be reflected by the "potential number of moves" required to find a suitable end-point for a given move. As roads encroach into the landscape, an increasing amount of the landscape will be closer to roads and consequently more areas will have low P_{use} values. As a result, a greater number of step attempts (draws from the distributions of l and ω) will be required before an acceptable end-point is identified. Consequently, I quantified habitat accessibility as the inverse of the mean number of attempted moves at each time step integrated over the duration of the simulation and across individuals. Moreover, I allowed individuals to "emigrate" from the landscape when the number of attempted moves exceeded a set tolerance level (T). I compared habitat accessibility and emigration rates across road densities, road development schemes and cutblock amounts.

5.3 RESULTS

5.3.1 STATISTICAL MODELS FOR ACTIVITY STATES

Foraging was the dominant activity state of wapiti (55.9 ± 0.04% SE) followed by bouts of inactivity (22.4 ± 0.01% SE) and traveling (21.7 ± 0.03% SE). Time of day and local environmental conditions were significantly correlated with wapiti state (Table 5.2). Wapiti were most likely to be inactive during midday and at night as well as in areas of higher predation risk or potentially cooler locations (north to easterly facing slopes). In contrast, wapiti were most likely to be traveling during crepuscular periods and when within 50 m of a linear clearing or 300 m of a road. Foraging was likely throughout the day but was most likely to coincide with cutblock habitat and areas that were not flat. Time of day explained the majority of the variation in wapiti state as evidenced by a large change in AIC values when time variables were removed from the active versus inactive (ΔAIC = 654) and foraging versus traveling (ΔAIC = 348) models reported in Table 5.2. In contrast, removal of any given environmental covariate yielded $\Delta\text{AIC} \leq 34$. ROC analysis for the 12 out-of-sample wapiti indicated a classification accuracy of 65% for the prediction of active versus inactive states (n = 8,298 locations) and 61% for prediction of foraging versus traveling (n = 6,579 locations). The low ROC values indicated a high degree of overlap among the conditions associated with wapiti states.

5.3.2 HABITAT SELECTIVITY

I pooled wapiti locations across states to quantify selectivity patterns because the proportional use of the six habitat types did not differ by state (Figure 5.5). Wapiti selectively used meadow and cutblocks habitats, avoided lowland/bog, open riparian, and coniferous forest habitats, and used deciduous forests in proportion to their availability (Table 5.3). Selectivity patterns varied with the proximity of roads, most notably for cutblocks (Figure 5.6). Wapiti used cutblock habitat within 100 m of a road largely in proportion to its availability but became increasingly selective for cutblocks as a function of increasing distance away from roads. For open riparian and deciduous forest habitats, wapiti switched from a pattern of avoidance at close proximity to roads to proportional or even selective use at intermediate distances (Figure 5.6). In contrast, wapiti consistently avoided lowland/bog and conifer forest regardless of road proximity.

5.3.3 SIMULATION MODEL DEVELOPMENT AND VALIDATION

The CRW and state-based CRW models redistributed wapiti reasonably with respect to roads but showed a tendency to deviate from the empirical distribution at very close proximities to roads (Figure 5.7 top, left panel). However, both models failed to redistribute wapiti meaningfully with respect to habitat (Figure 5.7 top, right panel). The addition of a habitat bias based on habitat selection ratios (Table 5.3) exaggerated the deviation between model predictions and the empirical distribution of wapiti in close proximity to roads (Figure 5.7 center, left panel), indicating a reduction in the use of habitats close to roads. However, both models with a habitat bias meaningfully recovered the proportional use of habitats by wapiti. Only by incorporation of the road-adjusted habitat bias were wapiti redistributed well with respect to both roads and habitats (Figure 5.7 bottom panels).

The wapiti in the with-held sample used areas >1 km from a road 15% more and cutblocks 10% less on average than did the wapiti used to parameterize the simulation models. Regardless, the state-based CRW with road-adjusted habitat bias redistributed the 12 out-of-sample wapiti well with respect to roads and habitat (Figure 5.8). Zeroing out the effect of all variables except time in the state-based movement model yielded tighter confidence intervals around wapiti redistribution patterns but still provided a high degree of overlap between the simulated and empirical redistribution patterns. Thus, I used this simplified version of the state-based model to assess the effects of road density on wapiti habitat effectiveness.

5.3.4 MODEL APPLICATION: REVISITING HABITAT EFFECTIVENESS

When wapiti were constrained to their home range, the number of simulated wapiti locations occurring within a given proximity of a road increased largely as a function of the areal extent of the landscape coinciding with that road proximity (Figure 5.9). However, the use of areas very close to roads (<250 m) was affected by the road development scheme, with use of this distance band up to two times greater when every cutblock contained a road. The overall amount of area cut had less effect than the road development scheme on use of areas within 250 m of a road (Figure 5.10). Both the availability and use of any given distance band from a road saturated as road density increased (Figure 9) due to overlapping distance bands from adjacent roads (road redundancies). Given these non-linear patterns of use, the estimated mortality risk accrued over the 120-day simulation initially increased as a saturating function of road density (Figure 5.10). However, the function switched to an accelerating accrual of mortality risk at greater road densities as areas further than 500 m of a road became increasingly scarce (Figures 5.9, 5.11). The shape of this relationship was largely insensitive to the overall amount of cutblock habitat in my simulations (Figure 5.11).

However, as the amount of cutblock habitat increased, wapiti incurred a higher mortality risk under the maximal forestry roads scheme than under the minimal scheme (Figure 5.10).

Controlling for differences in habitat amount, I observed a 30% reduction in habitat accessibility given a road density of 0.34 km/km^2 and a 50% reduction by a density of ~2 km/km^2 (Figure 5.12). Maintaining a road to every cutblock had a pronounced effect – causing a reduction in habitat accessibility equivalent to the effect of reforesting 50% of the existing cutblocks. The potential rate of loss of wapiti from the landscape was strongly affected by the amount of cutblock habitat available and wapiti tolerance for decreasing habitat accessibility (Figure 5.13). The majority of tolerant animals ($T \geq 60$ step attempts) remained in the landscape across all habitat and road density scenarios. In contrast, sensitive animals ($T \leq 50$ step attempts) left the landscape at a rapid rate depending upon the amount of cutblock habitat and the road development scheme (Figure 5.13).

5.4 DISCUSSION

5.4.1 MODEL DEVELOPMENT

Net displacement of individuals or properties of the distribution of steps or turns are the metrics by which random walk and CRW models are typically compared to empirical data (Firle *et al.* 1998; Morales & Ellner 2002). Generally, the CRW is used as a null model of animal movement (Turchin 1998) – what might be expected by random chance constrained only by the movement ability of individuals (the distribution of observed step length and turn angles). But heterogeneity in the distribution of resources and risks insures that animals are not distributed randomly across space (Wiens *et al.* 1993) and, in my simulations, using a CRW as a null model was potentially misleading as to the effect of roads on wapiti distribution patterns. Indeed, wapiti appeared to be distributed largely at random with respect to roads until I controlled for their responses to habitat. By incorporating a habitat bias into wapiti movement decisions, I observed that wapiti use of areas within ~200 m of a road was less than expected given the road-adjacent habitats. This trade-off in wapiti use of space was apparent as well in the relationship between wapiti state and environmental variables, which indicated wapiti were likely to move more quickly through areas within 300 m of a road. The trade-off was further apparent in the road-adjusted habitat bias, where wapiti became increasingly selective of cutblock habitat as the distance away from roads increased. Other large mammals share this trade-off behaviour with respect to habitats and human infrastructure (Rempel *et al.* 1997; Mysterud, Lian & Hjermann 1999; Rothley 2002; Jepsen & Topping 2004). Only by incorporating this trade-off behaviour in the simulation model – by allowing habitat selectivity to vary as a function of the proximity of roads – were wapiti reliably redistributed with respect to both roads and habitats in my study area.

Generally, the state-based models provided a better qualitative agreement with the empirical data and, in some cases, tighter confidence intervals indicating a higher degree of accuracy in the predictive ability of the model (Rykiel 1996). With respect to predictions of animal state, I observed considerable variation among animals in their responses to environmental conditions (indicated by low ROC scores) and in the overall amount of time they spent in different states (indicated by high variation around the random intercept; Table 5.2). In my simulations, statistical predictions of state suited the sample they were derived from, but resulted in greater variation in the responses of wapiti to roads and habitat when applied to new animals in the area (see also Frankhauser & Enggist 2004). Whether this variability arose from individual preferences or local differences in environmental conditions is the focus of ongoing research. Nevertheless, state responses among wapiti were consistent by time of day. Using time of day as the only predictor of state reliably redistributed wapiti in both the estimation and validation samples despite differences between these "populations" in the potential scale of their movements (reflected by larger MCPs; Table 1), their responses to cutblocks, and their proportional use of areas away from roads (Figure 5.8). Using the simplified model also provided for easier interpretation of the results from the simulation experiment (Van Nes & Scheffer 2005).

5.4.2 REVISITING HABITAT EFFECTIVENESS FOR WAPITI

I used the model to evaluate alternative hypotheses regarding potential behavioural responses of wapiti to increasing road density. First, wapiti and red deer are resistant to dispersing away from their natal ranges (Morgantini & Hudson 1998; Van Dyke *et al.* 1998; Conradt, Clutton-Brock & Guinness 1999), even when they might increase their fitness by doing do (Conradt *et al.* 1999). For this reason, I considered the mortality consequences of remaining within a "home range" as road densities increased. Although wapiti continued to use areas away from roads selectively, increased use of areas close to roads was inevitable because areas away from roads became increasingly scarce as road densities increased. Based on a survival model for adult-female wapiti in this region, the mortality risk from aboriginal harvest decreased ~14% for every 100 m increase in the distance away from a road (See Chapter Three: Table 3.5). However, the accrual of mortality risk by wapiti in my simulations was non-linear as a function of increasing road density for two reasons. First, the amount of use by wapiti of areas close to roads increased as a saturating function given increasing road density due to "redundancies" caused by overlap in the spatial extent of distance buffers from two or more adjacent roads (see Figure 5.9). This resulted in an initially saturating function for mortality risk to a road density of ~1 km/km^2 (see Figure 5.10). Second, a shift from a saturating to an accelerating accrual of mortality risk at road densities > 1 km/km^2 coincided with a shift in the landscape to one where ≥ 85% of the landscape occurred within 1 km from a road (see Figure 5.9). In addition, wapiti use of areas close to roads was greatest under the maximal forestry roads scheme because cutblocks were selected more strongly than any other habitat type at all road distances, which translated to a greater mortality risk for wapiti when cutblocks were both abundant and closely associated with roads. The overall shape of the mortality function arose from simple properties of the road network, being affected to only minor degree by the amount of cutblock habitat, and is thus likely to be general even though absolute amounts of mortality risk may differ for wapiti in other landscapes. However, regenerating trees might provide security cover within older cutblocks, which might offset the risk of mortality to some degree.

My alternative hypothesis was that wapiti might shift their distribution away from roaded areas (Frid & Dill 2002), a basic assumption of existing wapiti habitat effectiveness models. In my simulations, increasing the overall amount of habitat available (cutblocks) mediated the effect of increasing road density to some degree by slowing the potential rate of loss of individuals from the landscape. Documenting such shifts in nature may prove difficult given the long time frame over which such shifts might occur. For example, a gradual shift in the distribution of caribou away from infrastructure associated with a hydroelectric facility in Norway was observed only by conducting monthly surveys for 10 consecutive years before and after development of the facility (Nellemann *et al.* 2003). Proper replication of road density treatments over various habitat amounts and road configurations is impossible using such "natural experiments" and unlikely even under more controlled conditions. Although the mechanisms leading to the response curves shown in Figure 5.13 are simple, the curves hypothetically reflect plasticity in wapiti responses to roads potentially within a given population or between populations occupying different areas in response to traffic volumes or human activities along roads (Edge & Marcum 1985; Van Dyke & Klein 1996), wapiti habituation patterns (McKenzie 1999), or fidelity to traditionally used areas (Van Dyke *et al.* 1998). Importantly, I show that a wide range of potential responses can arise from the same fixed pattern of road avoidance behaviour. In so doing, the seemingly contradictory patterns observed in previous studies (Millspaugh 1999; Roloff *et al.* 2001; Rowland *et al.* 2000) might be better understood.

Although the simulation model redistributed wapiti well with respect to roads and habitat, my application of it required simplifying assumptions regarding wapiti behaviour (Lima & Zollner 1996). Foremost, I assumed selection patterns to remain constant as landscape conditions changed. Changes in use of a resource given changes in the availability of that resource, termed a functional response, have been observed for various species (Mysterud & Ims 1998; Mauritzen *et al.* 2003). One might reasonably expect wapiti to become increasingly selective of areas away from roads as such areas become increasingly rare, causing a non-proportional increase in the use of areas close to roads and a more rapidly decreasing habitat accessibility with increasing road density. Moreover, I assumed that the decision of whether to move from one area to another depended only upon the quality (accessibility) of the location at the end-point of each potential move. Increasingly, researchers are recognizing the importance of the quality of the "matrix", i.e. areas between suitable patches of habitat, on movement decisions (Ricketts 2001; Revilla *et al.* 2004; Tishendorf *et al.* 2005; but see also Goodwin & Fahrig 2002). Yet such transition behaviours are difficult to measure empirically, especially for wide-ranging individuals moving across a continuous rather than discrete landscape (Schippers *et al.* 1996; Cramer & Portier 2001; Kramer-Schadt *et al.* 2004). Importantly, the results of movement models depend critically on how such transitional behaviours are incorporated (Ruckeshaus *et al.* 1997; Russel, Swihart & Feng 2003). The step-selection function (SSF) of Fortin *et al.* (2005) provides a promising tool for empirically deriving movement rules in complex landscapes. The SSF allows estimation of the relative effects of conditions around the start location, around various potential end locations, and along the path leading to potential end-points, on the subsequent movement decision. As such, the approach allows inclusion of multiple landscape effects, like variable topography (Kie, Ager & Bowyer 2005), as well as the proximity of roads and habitats (Fortin *et al.* 2005), into movement decisions. However, additional work is required to effectively translate patterns from the SSF to movement rules in a simulation model.

5.4.3 CONCLUSIONS AND IMPLICATIONS

Individually-based movement models provide insights that may be difficult or impossible to derive empirically (Turchin 1998; Matthiopoulos 2003). For example, non-linearities arising from road adjacencies, while conceptually understood, may have led to improper extrapolation of a distance-based measure of wapiti use to an effect of road density in the original models of Lyon (1979). Moreover, maintaining roads that lead to every cutblock, while having a strong and negative effect on habitat accessibility, led to increased use of areas close to roads by wapiti with an increasing effect on wapiti mortality risk becoming apparent as cutblocks became more abundant. Perhaps most importantly, the simulation modeled allowed me to explore plasticity in the behavioural responses of wapiti under controlled conditions. My empirical analyses concur with previous research on wapiti in areas where cutblocks are the primary foraging habitat and where roads carry a mortality risk from hunters (Basile 1979; Unsworth *et al.* 1993; Hayes *et al.* 2002; McCorquodale *et al.* 2003). By varying assumptions of elk behaviour, my simulation model provides a potentially unifying framework for considering wapiti habitat effectiveness under contrasting ecological conditions.

With respect to road management I provide the following additional insights from this research. Although how roads were developed – in close association with cutblocks versus randomly located with respect to cutblocks – had measurable effects on the use of space and survival patterns of wapiti, the differences between these two road development schemes were small in comparison to the effect of increasing road density, and in particular, to the effect of adding any roads to an unroaded landscape. I observed a rapid decrease in habitat accessibility, and a rapid increase in wapiti mortality risk, when road densities were still relatively "low" (≤ 0.5 km/km^2). The average road density within wapiti MCPs (~0.4 km/km^2), which I believe to be representative of wapiti in the region, combined with the observations of road avoidance behaviour by wapiti in this study, leads me to conclude that wapiti in the central foothills of Alberta are quite sensitive to the changing conditions imposed by a growing road network. The projected consequences of such sensitivity is a potential shift in wapiti distributions away from roaded areas as road densities increase or, alternatively, increased wapiti mortality rates from aboriginal harvest. While not considered here, a shift away from roaded areas may also negatively affect wapiti survival rates should wapiti density increase in the ever-shrinking refuges away from roads potentially leading to increased competition for forage resources (Stewart *et al.* 2005) or increased predictability for wolves (Hebblewhite & Pletscher 2002), the major predator of wapiti in this system (see Chapter Three). While road construction practices may alleviate road effects to some degree (see Lyon and Christensen 2002), maintaining effective wapiti habitat in the central foothills might better be accomplished by 1) minimal construction of new roads either by excluding road development in areas traditionally used by wapiti or by encouraging cooperation among the different industries creating roads, 2) reclaiming roads that are no longer needed by industry shortly after completion of industrial activities, and 3) restricting recreational access to roads in areas used by wapiti.

Table 5.1. Description of wapiti data used to assess road effects on habitat effectiveness.

ID	Year	N	Summer MCP (km^2)	Percent of MCP cut	MCP road density (km/km^2)	Sample Assignment
1026	2001	1320	29.3	0.21	0.37	estimation
1029	2001	1204	53.1	0.30	0.88	estimation
1032	2001	1159	62.3	0.22	0.74	estimation
1049	2002	1195	30.9	0.23	0.48	estimation
1056	2002	1167	44.7	0.37	0.67	estimation
1057	2002	797	22.0	0.04	0.18	estimation
1059	2003	1139	27.4	0.49	0.51	estimation
1067	2003	1115	46.6	0.25	0.32	estimation
1072	2003	1312	49.5	0.21	0.13	estimation
1077	2003	1088	81.1	0.28	0.41	estimation
1078	2004	954	47.1	0.24	0.57	estimation
		average	44.9	0.26	0.48	
1027	2001	1294	61.6	0.20	0.23	validation
1040	2002	1324	45.9	0.27	0.46	validation
1046	2002	913	44.3	0.05	0.71	validation
1051	2002	968	128.7	0.06	0.31	validation
1062	2003	797	44.4	0.16	0.43	validation
1063	2003	1027	25.2	0.11	0.14	validation
1066	2003	1052	30.5	0.21	0.42	validation
1075	2003	1138	129.9	0.25	0.13	validation
1079	2004	1218	36.8	0.34	0.62	validation
1080	2004	971	83.8	0.16	0.27	validation
1081	2004	764	54.1	0.27	0.34	validation
1089	2004	692	23.1	0.17	0.26	validation
		average	60.4	0.19	0.34	

Table 5.2. The AIC-selected, logistic regression models predicting whether an wapiti was active versus inactive ($N_{obs} = 11{,}615$, $N_{groups} = 11$, Wald $\chi^2 = 663.8$, $P < 0.001$) and, when active, foraging versus traveling ($N_{obs} = 9{,}024$, $N_{groups} = 11$, Wald $\chi^2 = 406.38$, $P < 0.001$) at a given time and location in the central foothills of Alberta, Canada, 2001-2004. The estimated coefficient (*β*) with standard error (SE) and significance level (*P*) are given for each model along with the standard deviation of the random intercept (σ) and the intraclass correlation (ρ) or total residual variance due to residual variability among subjects.

	Active versus Inactive			Foraging versus Traveling		
Variable	*β*	SE	*P*	*β*	SE	*P*
Time of Day						
sin(hour)	0.0801	0.0328	0.015	−0.0335	0.0355	0.346
cos(hour)	−0.8522	0.0349	<0.001	0.6732	0.0369	<0.001
Vegetation						
reclaimed herbaceous	0.8676	0.4086	0.034			
bare soil / sandbar	0.9504	0.5333	0.075	−0.9382	0.3417	0.006
herbaceous meadow				−0.5076	0.1793	0.005
cutblock				0.2111	0.0517	<0.001
other = reference						
Slope (°)				0.0230	0.0068	0.001
Aspect						
N-NE-E facing	−0.2024	0.0542	<0.001			
other = reference						
Predation risk	−0.4242	0.2367	0.072			
Proximity of seismic line						
≤ 50 m	0.4409	0.0745	<0.001	−0.1727	0.0703	0.014
other = reference						
Proximity of road						
≤ 100 m	0.2285	0.1040	0.028	−0.5308	0.0954	<0.001
100 – 200 m				−0.3627	0.0936	<0.001
200 – 300 m				−0.2179	0.0962	0.024
other = reference						
Constant	1.5255	0.1188	<0.001	0.8465	0.0495	<0.001
	σ = 0.3258 ρ = 0.0313			σ = 0.5261 ρ = 0.0776		

Table 5.3. Selection ratios ($\hat{R}'$; Manly *et al.* 2002: 47) from 11 adult-female wapiti for vegetation classes in the lower foothills of central Alberta, Canada, 2001-2004.

Vegetation Class	$\hat{R}'$	Lower 95% CI	Upper 95% CI	Vegetation Types Included
1 (Meadow)	1.62	1.18	2.08	Dry/mesic/wet graminoid and forb meadows, reclaimed herbaceous areas, shrub-dominated meadows
2 (Lowland / Bog)	0.45	0.28	0.63	Treed riparian areas, open and forested bogs/fens
3 (Open Riparian)	0.51	0.39	0.64	Sandbars along rivers
4 (Cutblock)	2.32	2.20	2.44	Regenerating cutover forest areas
5 (Deciduous Forest)	1.03	0.66	1.40	Deciduous or mixed deciduous/coniferous forest
6 (Coniferous Forest)	0.56	0.41	0.71	Pine or spruce dominated forest

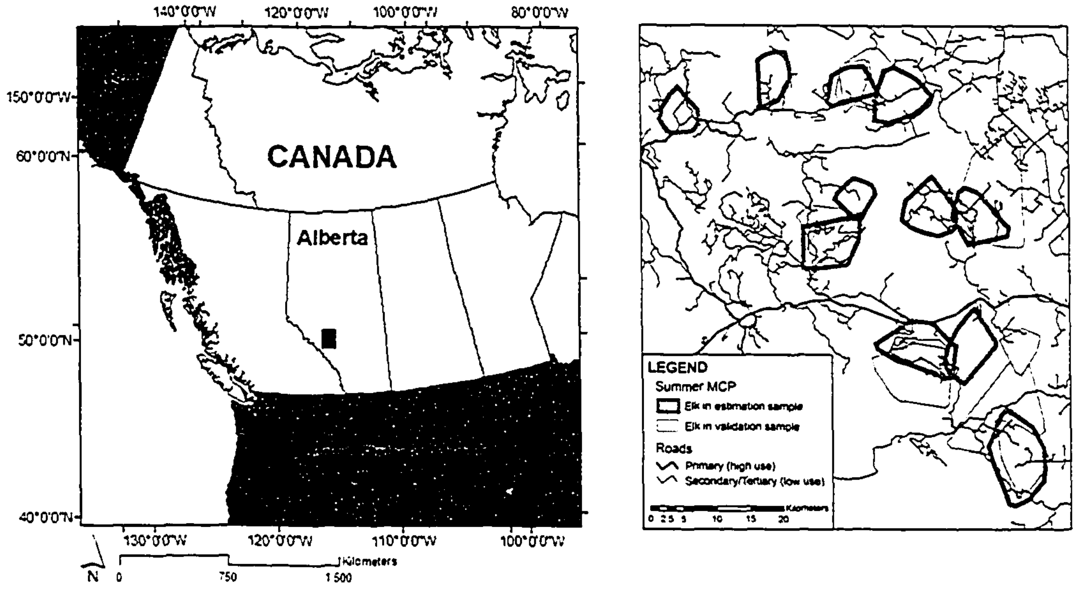


Figure 5.1. Study area in the foothills of the Rocky Mountains, west-central Alberta, Canada. The panel on the right shows the distribution of wapiti and roads used in this study.

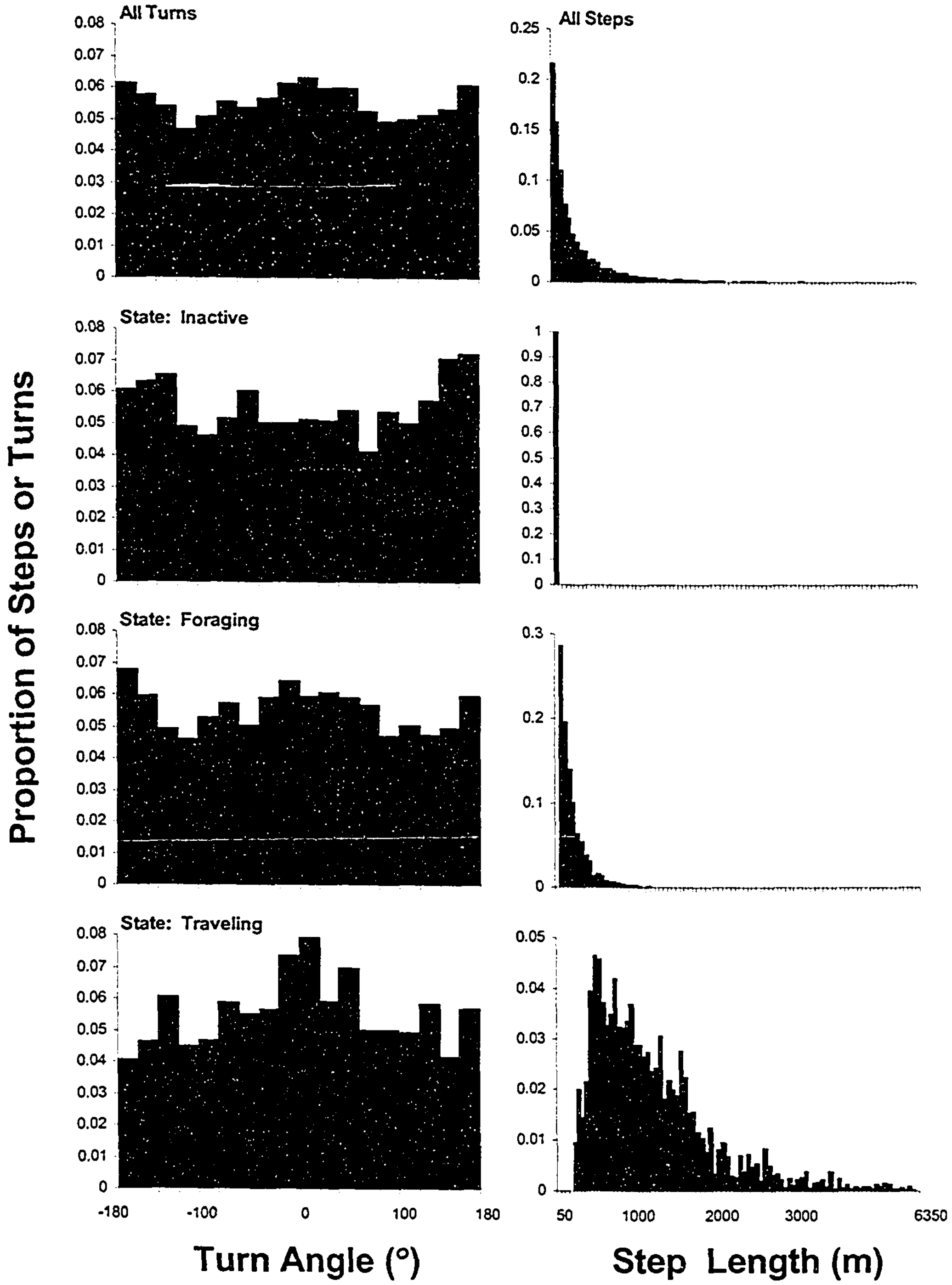


Figure 5.2. Distributions of all turn angles and step lengths and by activity state for the 11 adult-female wapiti in the central foothills of Alberta, Canada used to parameterize movement models.

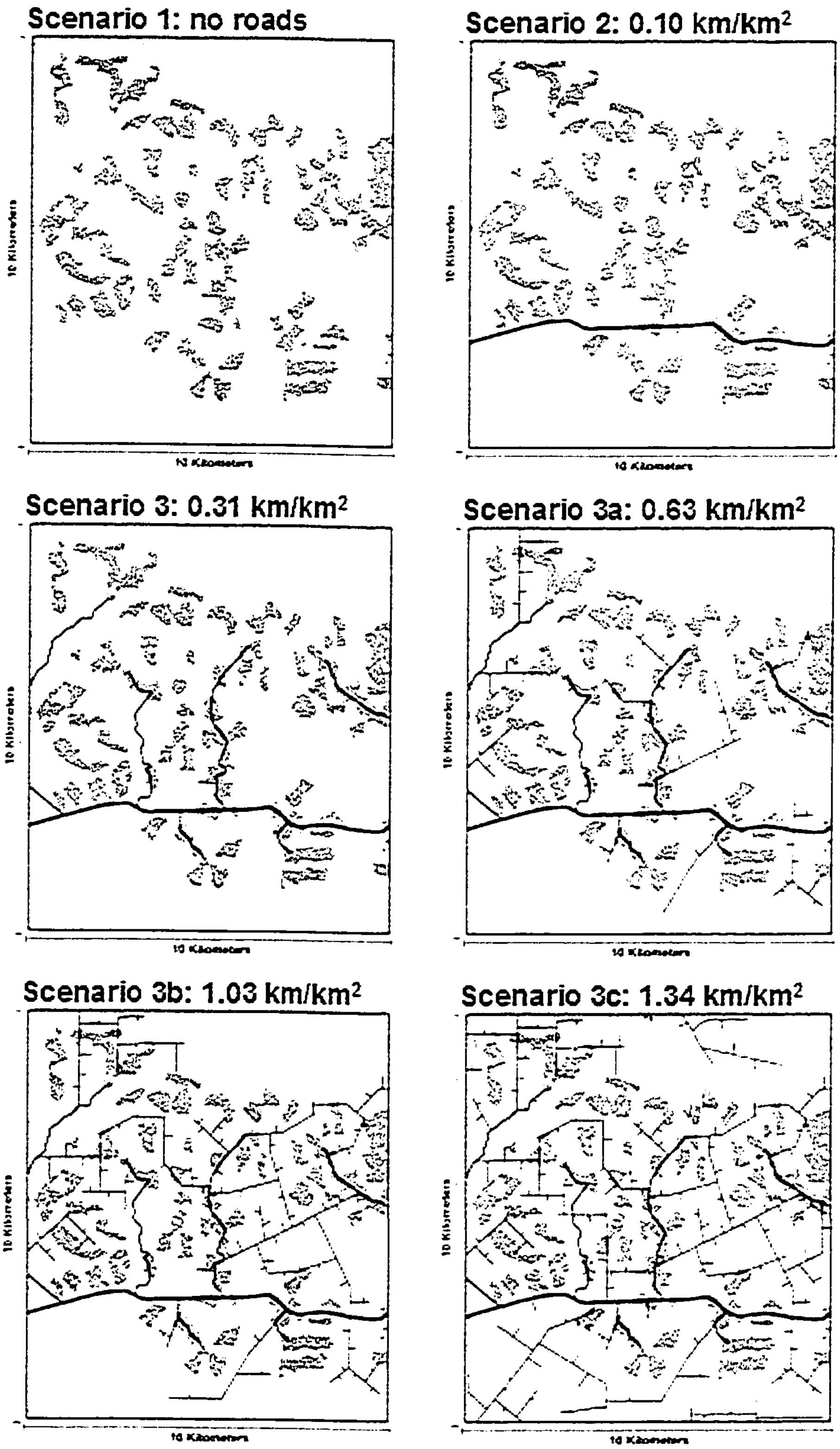
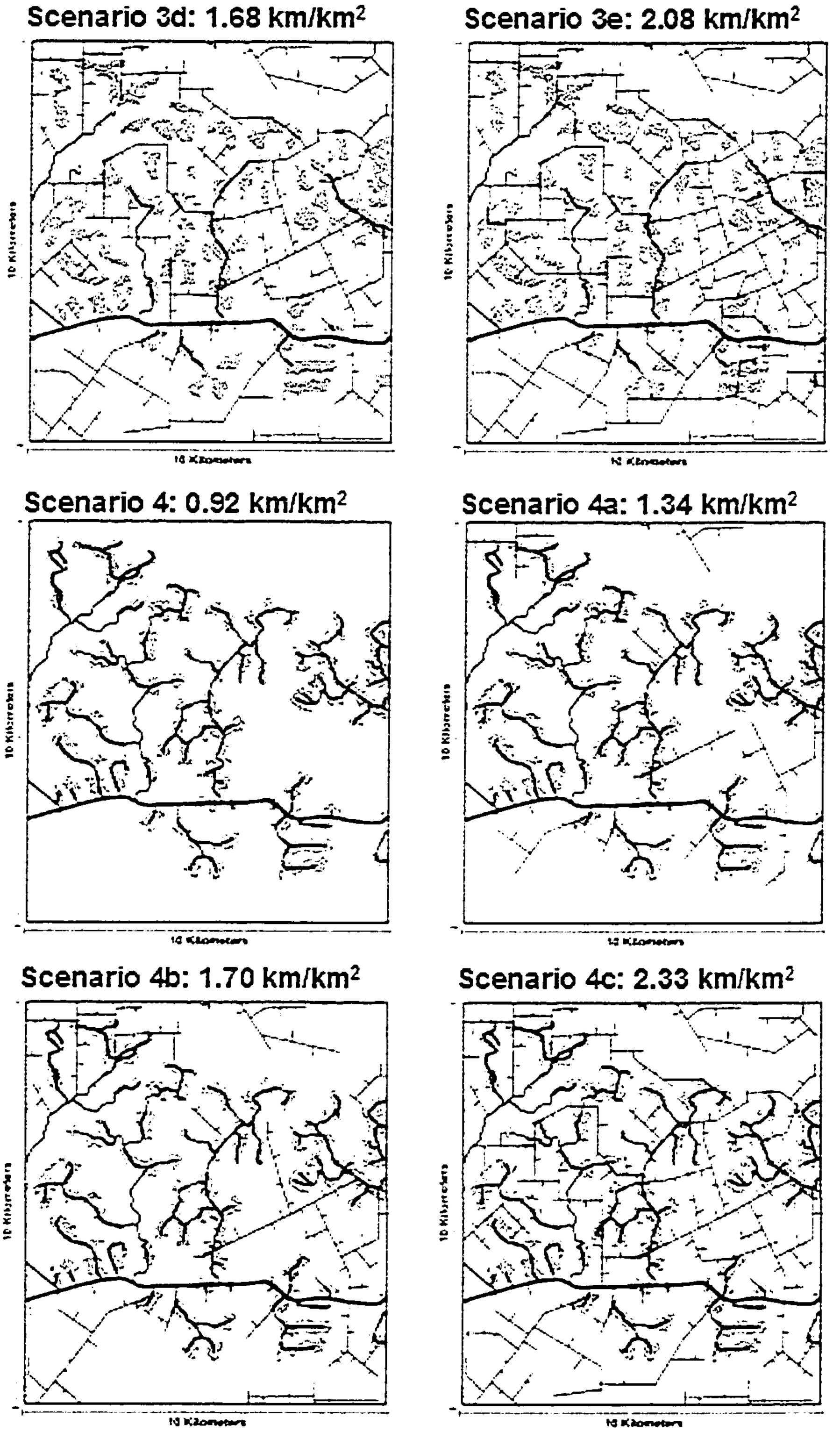


Figure 5.3A. Landscapes showing roads (black lines) and vegetation types used in the scenarios of modeling habitat effectiveness. Cutblocks are shaded in dark gray, meadows, deciduous forest and rivers in light gray, and all areas in white represent avoided vegetation types.


Scenario 3d: 1.68 km/km^2

Scenario 3e: 2.08 km/km^2

Scenario 4: 0.92 km/km^2

Scenario 4a: 1.34 km/km^2

Scenario 4b: 1.70 km/km^2

Scenario 4c: 2.33 km/km^2

Figure 5.3B. Landscapes showing roads (black lines) and vegetation types used in the scenarios of modeling habitat effectiveness. Cutblocks are shaded in dark gray, meadows, deciduous forest and rivers in light gray, and all areas in white represent avoided vegetation types.

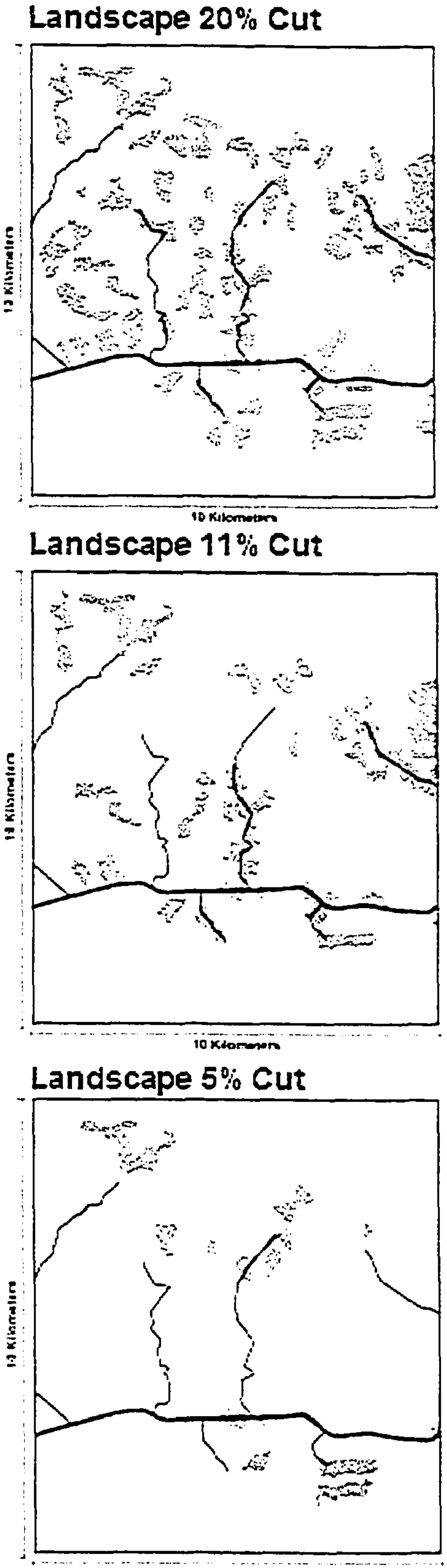


Figure 5.4. Landscapes used in the scenarios to model habitat effectiveness when 20, 11, and 5% of the area was cut.

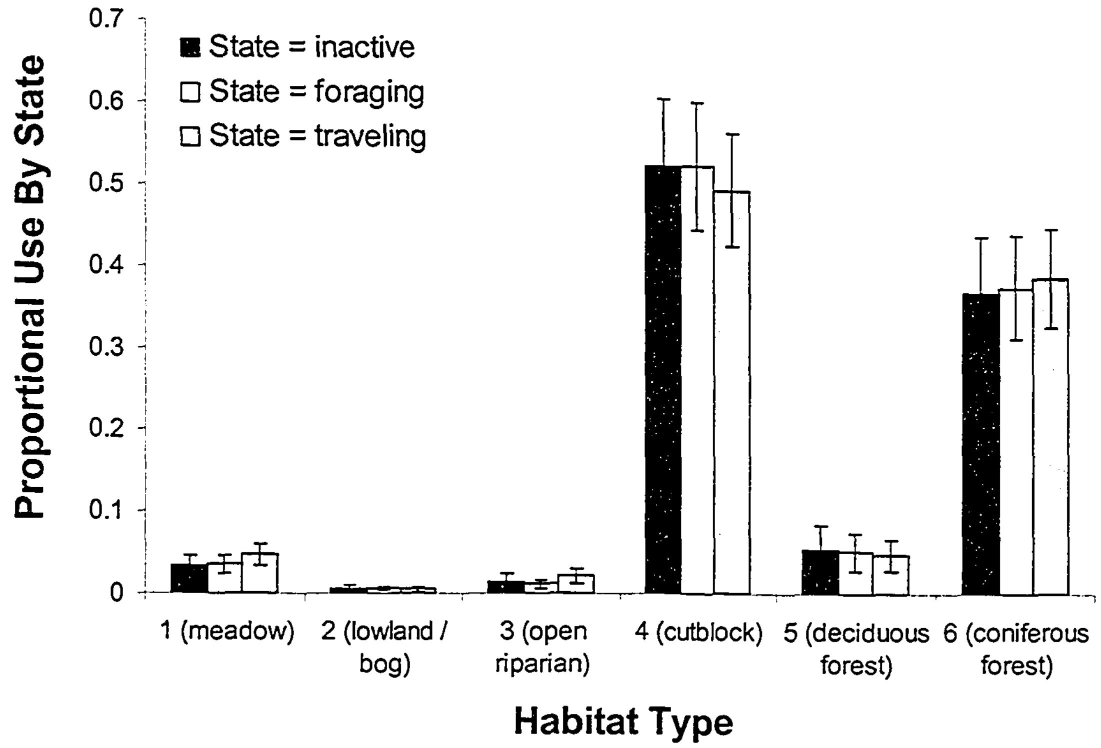


Figure 5.5. Mean (±SE) proportion of locations of 11 GPS-collared wapiti in each of six vegetation types when wapiti were inactive (n_{locs} = 2,596), foraging (n_{locs} = 6,489) or traveling (n_{locs} = 2,586) in the central foothills of Alberta, Canada 2001-2004.

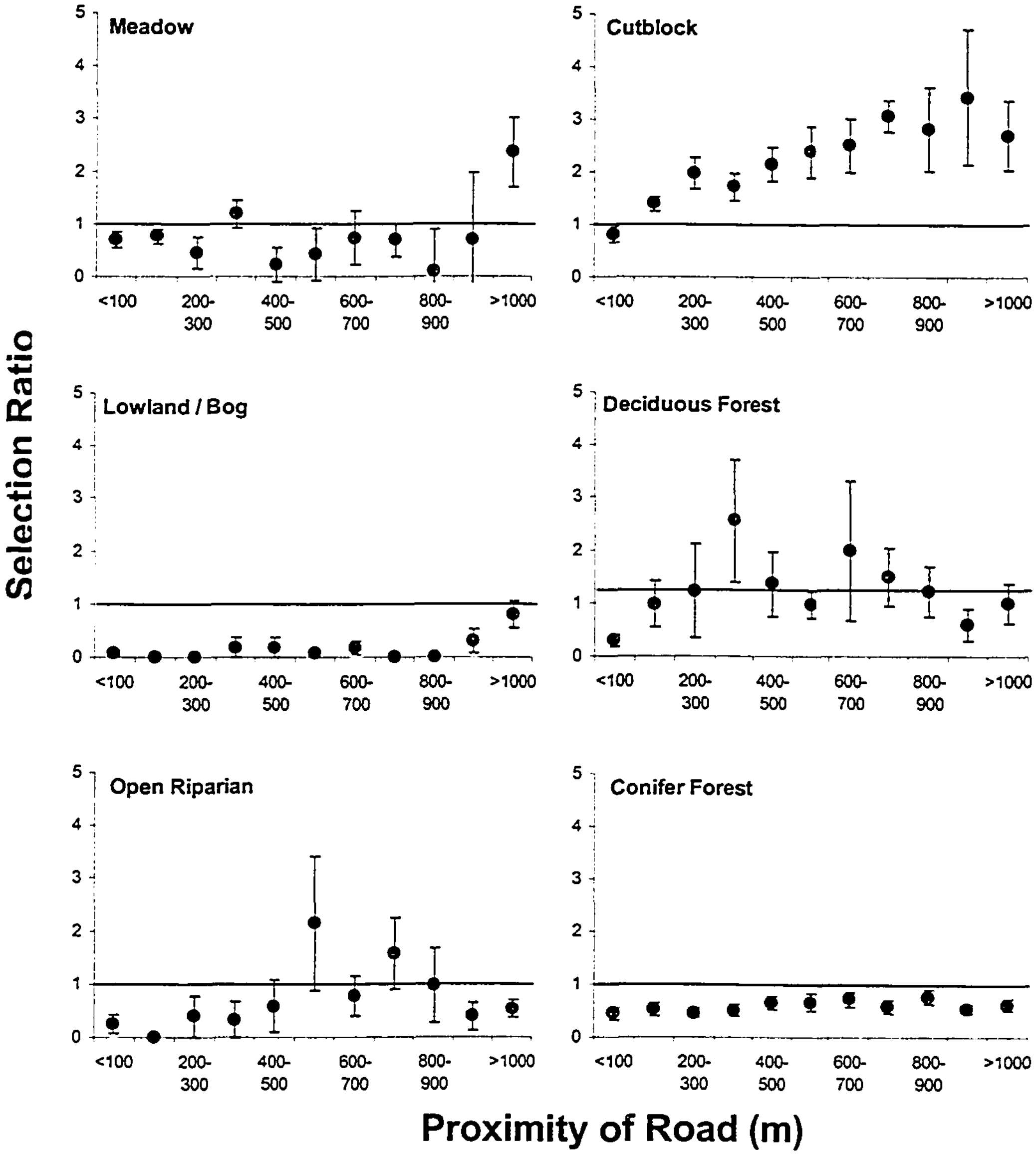


Figure 5.6. Mean selection ratios (±SE) derived for 11 adult-female wapiti and six vegetation types by road proximity in central Alberta, Canada. Values near 1 indicate use of the vegetation type proportional to availability.

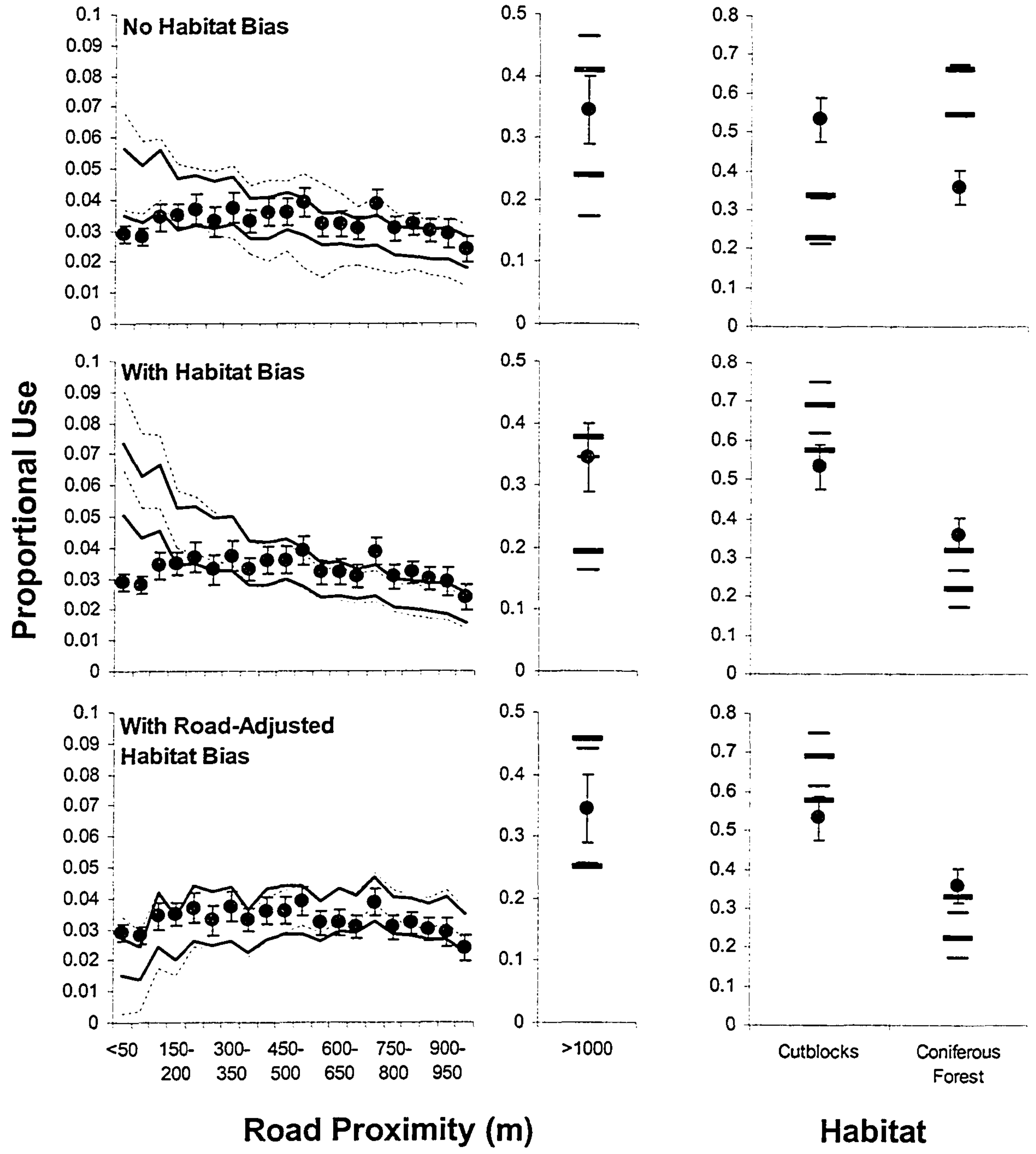


Figure 5.7. Model development results. The proportional use of areas close to roads and key vegetation types by the wapiti in the estimation sample (mean±SE; filled circles) and simulated individuals following a simple CRW (thin, dashed lines) or state-based CRW (thick lines) without a habitat bias (top panel), with a habitat bias (middle panel), and with a road-adjusted habitat bias. Simulation results are shown as 95% confidence intervals.

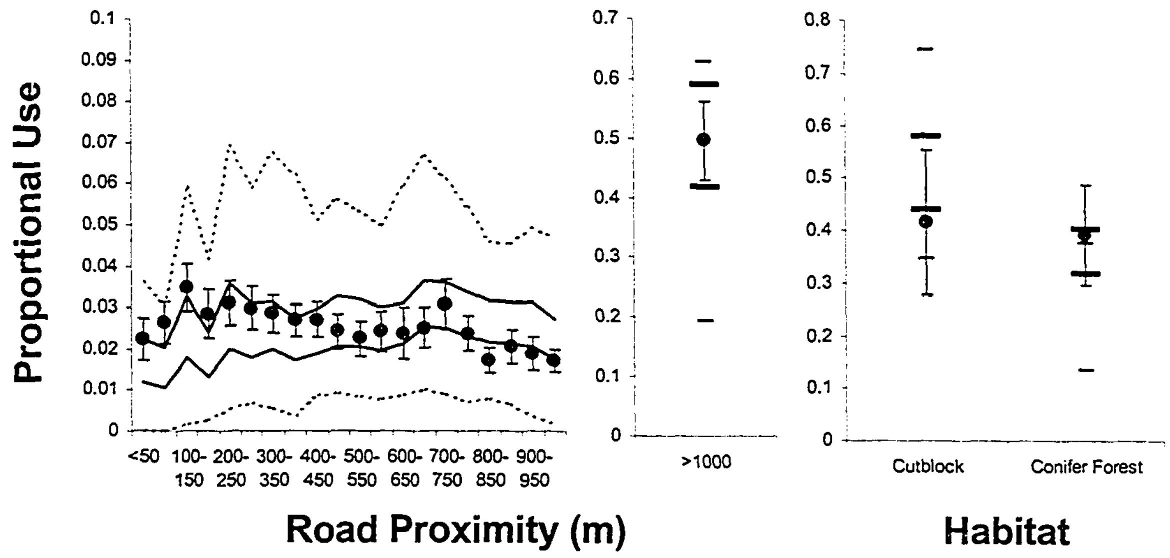


Figure 5.8. Model validation results. The proportional use of areas close to roads and key vegetation types by wapiti in a with-held validation sample (mean±SE; filled circles) and simulated individuals following a state-based CRW with state predicted by time of day and local environmental conditions (dashed lines) or a state-based CRW with state predicted by time of day only. Simulation results are shown as 95% confidence intervals.

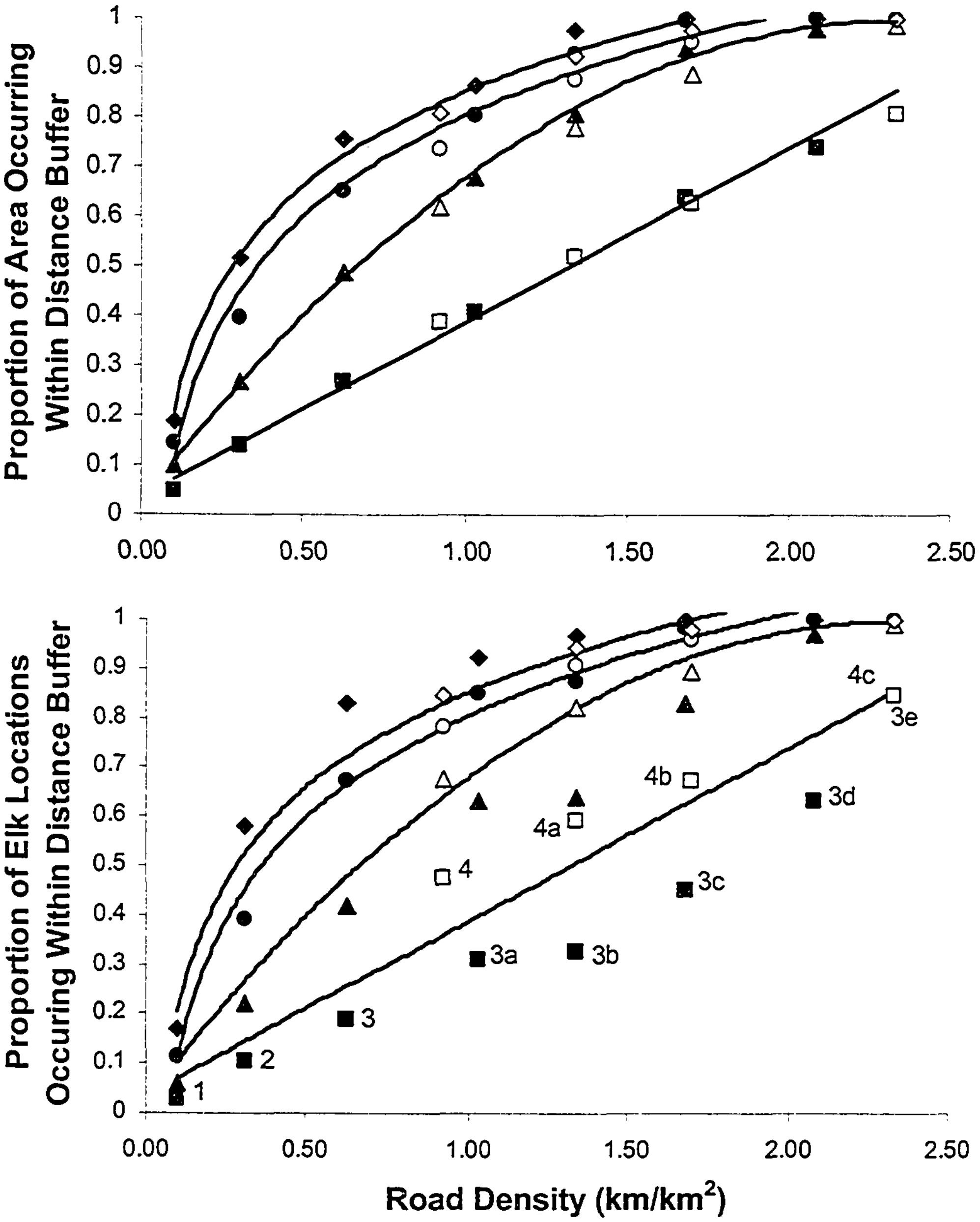


Figure 5.9. Increases in the proportion of area available (top) and used by wapiti in the simulations (bottom) within 250 (squares), 500 (triangles), 750 (circles), and 1000 m (diamonds) of a road given an increasing road density when 20% of the landscape was cut. Lines were fit to the increase in the availability of areas near roads given a minimal forestry roads scheme (filled symbols) but the maximal forestry roads scheme is also shown (open symbols). These same lines were redrawn in the bottom panel for reference against the proportional use of areas close to roads by wapiti. Scenario labels are given in the bottom panel to aid cross-referencing with Figures 3a,b.

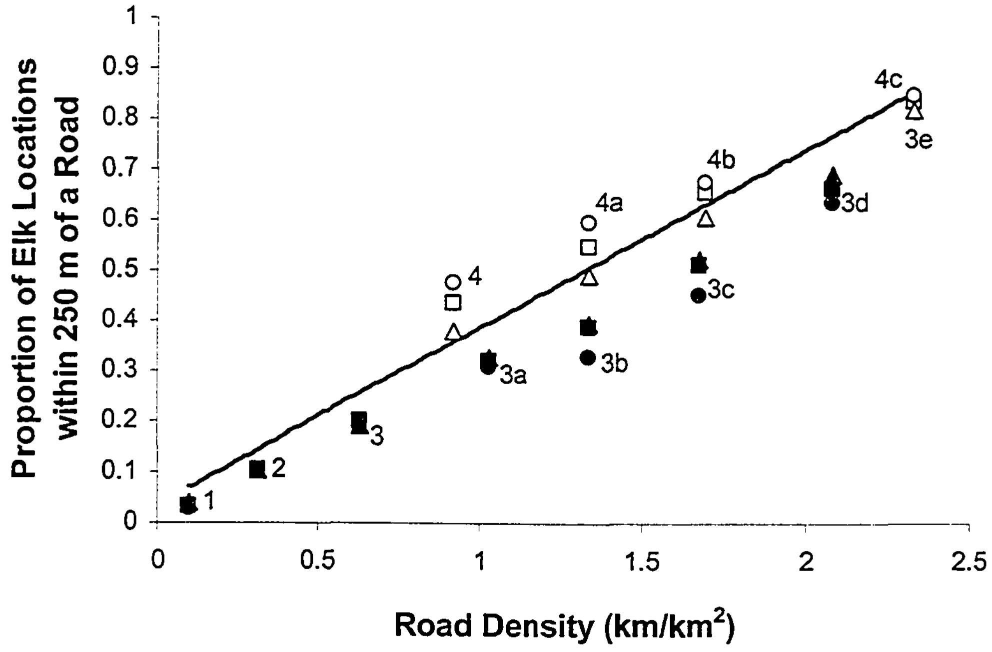


Figure 5.10. Differences in the proportional use of areas by simulated wapiti within 250 m of a road when 20% (circles), 11% (squares), or 5% (triangles) of the landscape was cut and roads developed under a minimal (filled symbols) or maximal forestry roads scheme (open symbols).

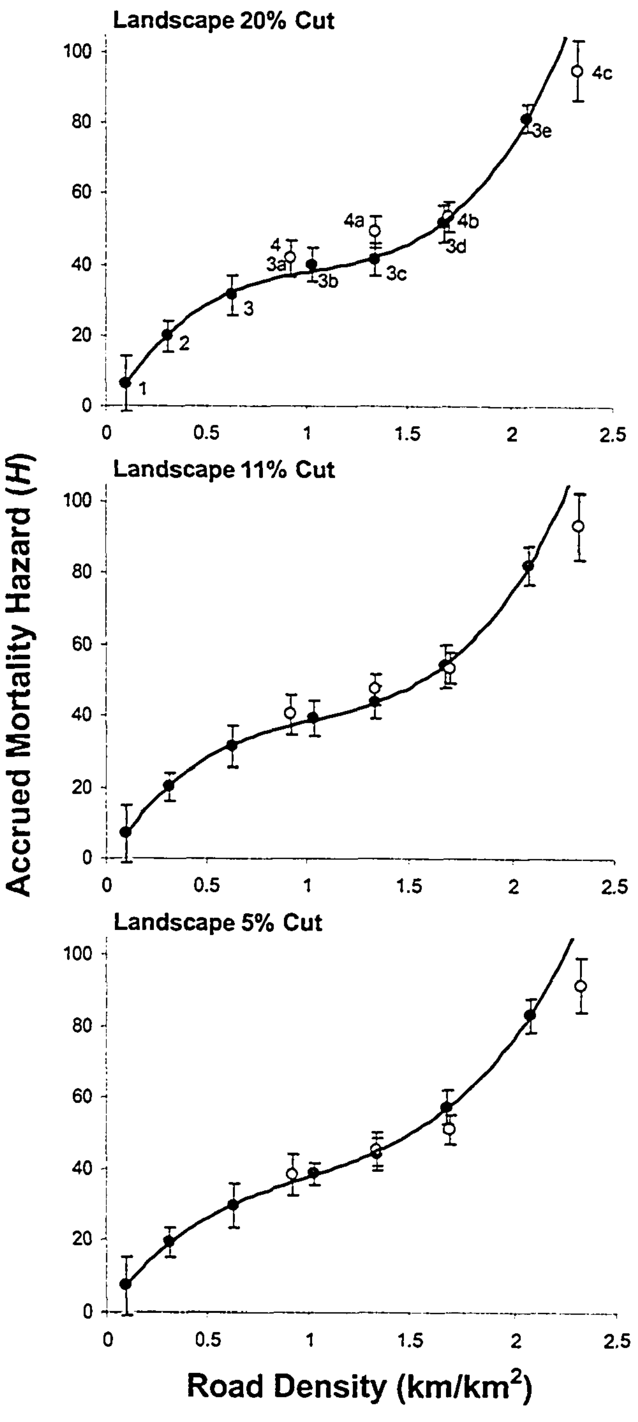


Figure 5.11. The estimated mortality hazard (mean±SD) accrued by simulated wapiti over the 120-day period given an increasing road density and differing amounts of cutblock habitat based on a survival model for adult-female wapiti in the central foothills developed by Frair (2005; see text). Polynomial curves were fit to the minimal forestry roads scheme (Scenarios 3-3e; filled circles) but the maximal forestry roads scheme is also shown (open circles). Scenario labels are provided in the top panel to aid cross-referencing with Figures 5.3a,b.

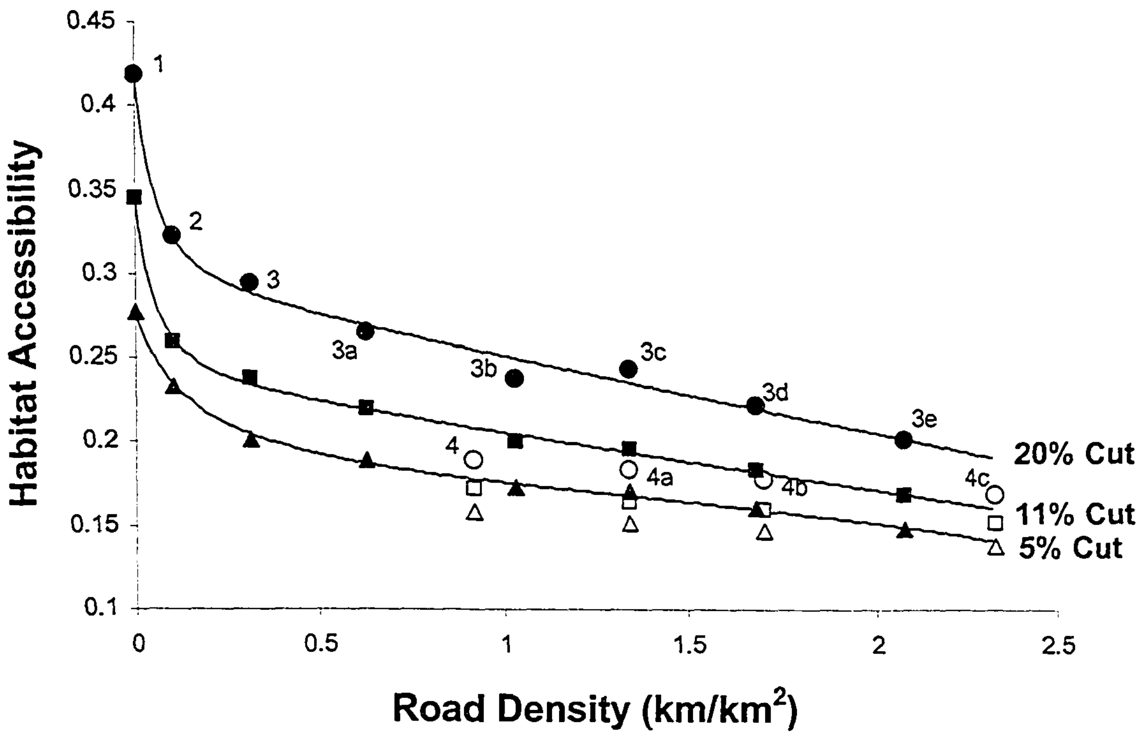


Figure 5.12. Habitat accessibility, indexed by the number of step attempts required to find suitable habitat (see text), given an increasing road density and differing amounts of cutblock habitat. Polynomial curves were fit to the minimal forestry roads scheme (Scenarios 3-3e; filled symbols) but the maximal forestry roads scheme is also shown (open symbols). Scenario labels are provided to aid cross-referencing with Figures 5.3a,b.

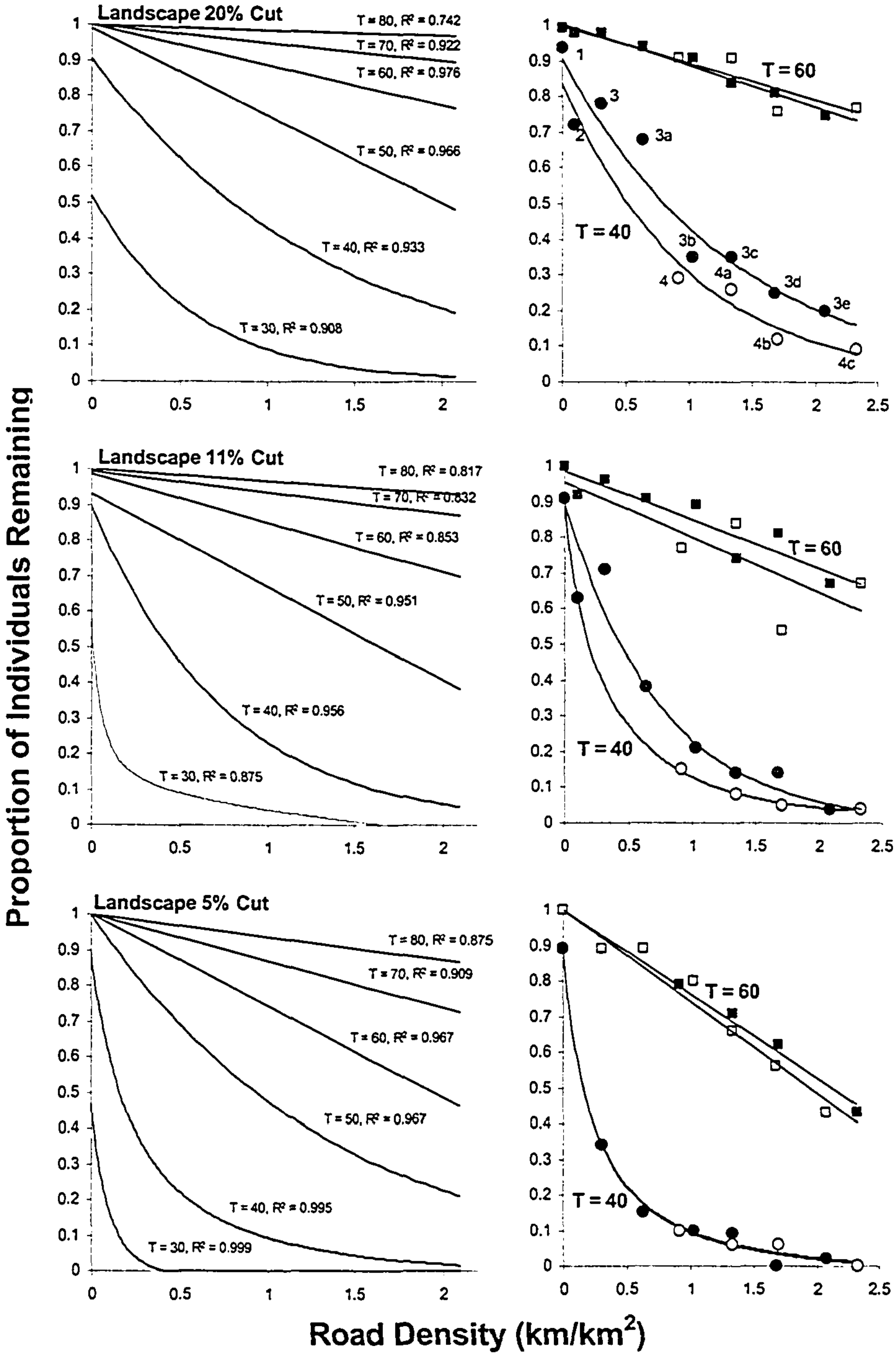


Figure 5.13. Potential rate of emigration from the landscape given an increasing road density and variation in the wapiti tolerance (T) for decreasing habitat accessibility (see text). Results are shown across varying amounts of cutblock habitat. The left panels show the best fit linear or exponential decay model based on R^2 values given a minimal forestry road scenario (Scenarios 3-3e, see text). The right panels show fitted functions for alternative road development schemes, minimal forestry roads (filled symbols) and maximal forestry roads (open symbols), at two levels of T. Scenario labels are provided in the top right panel to aid cross-referencing with Figures 3a,b.

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CHAPTER 6

6.1 SYNTHESIS

The view of the central Rocky Mountains in Alberta from space, and indeed from many vantages on the ground, is one of majestic, snow-capped mountain peaks blanketed by a vibrant wilderness. Yet, research on wildlife inhabiting the region paints a different picture. Wapiti (*Cervus elaphus*), caribou (*Rangifer tarandus*), grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) alike tell a story of change and uncertainty, of a growing menace that affects their daily routines and general well-being. That menace is man in pursuit of all things – trees for his furniture, oil for his car, water for his shower, coal and gas for fuel. The disturbances needed to acquire these things and the footprint left behind have measurable and negative consequences for large mammals. Various compendia detail the negative effects of roads in particular on ecosystem structures and functions (Forman & Alexander 1998; Trombulak & Frissell 2000; Spellerberg 2002; Jaeger *et al.* 2005), but the main effect of roads pertinent to large mammals in Alberta is that roads bring people, in particular people carrying guns, into their world. Much to the chagrin of the wilderness enthusiast, road effects provide a unifying theme to wildlife studies throughout Alberta as throughout the extent of the Rocky Mountain ecosystem and, indeed, throughout the world.

This dissertation was compiled from ongoing research that seeks to develop general relationships and tools to help managers balance the various, and often competing, demands on the forested ecosystems of western Alberta. For this purpose wapiti were a useful species to study in that they are fairly numerous, relatively easy to catch and collar, and they exhibit responses to roads similar to less common and less tractable species like grizzly bears. Moreover, wapiti and other large herbivores (including grizzly bears) stand to profit by the hand of man in the central foothills because cutblocks provide foraging opportunities in a landscape that has otherwise a nearly continuous forest cover. However, Nielsen (2000) highlighted the potential for cutblocks to create "attractive sinks" for grizzly bears in the central Rockies due to the association between cutblocks and roads. I observed the same potential for wapiti even though their responses to cutblocks and roads were made more complicated due to the additional risk of predation by wolves. Wolves affected the movement and habitat use patterns of resident wapiti in my study despite having a negligible effect on their overall survival. Indeed, individuals naive to wolves (translocated wapiti) suffered from a high predation rate but resident wapiti, those experienced with wolves, suffered little. Whether or not wapiti are an important prey item to wolves in the central foothills – they may not be due to the presence of several other, potentially more abundant ungulate species – wolves are clearly important to the daily activities of wapiti. For example, I observed a non-linear pattern in the scale of wapiti movements with respect to cutblock size, which I believe reflected a trade-off between the need of wapiti to use "open" foraging habitats but remaining close to cover to avoid predation. I also observed that the risk of predation from wolves was higher along non-road linear clearings, which are ubiquitous in the central foothills as a result of past exploration for and extraction of gas resources. Wapiti moved more quickly through areas adjacent to linear clearings likely to minimize their mortality risk. These patterns are consistent with observations of wolves and caribou in north-eastern Alberta (James 1999; James & Stuart-Smith 2000) and, taken together, these studies suggest that industrial activities have indirect but important implications for predator-prey dynamics in Alberta.

In systems where wapiti are the primary prey of wolves, such as in Yellowstone or Banff National Park, predation can play a crucial role in limiting wapiti numbers and distribution (Ripple *et al.* 2001; Ripple & Beschta 2004; Hebblewhite *et al.* 2005). Yet, as Hebblewhite *et al.* (2005) observed, human activities can greatly mediate these effects because wolves avoid humans. In the central Rocky Mountain foothills of Alberta wolves are hunted and trapped and, as a result, I observed that wolves avoided areas of high road density. Consequently, I documented a trade-off in mortality risks for wapiti across space – while areas adjacent to roads might provide a refuge from predation it is at the expense of an increased risk of mortality from aboriginal hunters. It is my contention that wapiti are more "wise" to predators than to humans in western Alberta because wolves may be more consistent in their activity patterns and intentions than are the various recreational and industrial human visitors to the area (Lima & Bednekoff 1999). As a consequence, wapiti may choose to occupy areas that carry a higher mortality risk (due to humans) because they fail to appropriately gauge the level of risk (due to their perception of the more pressing need to avoid wolves). This is the prerequisite for an ecological trap (Schlaepfer *et al.* 2002; Kristan 2003) and my observations are consistent with Nielsen (2000) in that cutblocks may form an attractive sink for wapiti in the central foothills due to their association with roads.

At present, the annual survival rate of female wapiti resident in the area (0.91) is within the range of other hunted populations (0.71-1.0; Unsworth *et al.* 1993; Cole *et al.* 1997; Ballard *et al.* 2000; McCorquodale *et al.* 2003) and does not appear to be a factor limiting population growth. However, wapiti mediated their mortality risk by avoiding all areas within ~200 m of a road (see Figure 5.7) and selecting most strongly for foraging areas (cutblocks) that were at least 700 m from the nearest road (see Figure 5.6). As a result, the distribution of wapiti is likely limited by the accessibility of foraging habitat in the central foothills. For this reason, estimates of carrying capacity based solely on the nutritional content of forage may be misleading as to the effective carrying capacity of the region. The perception of "underutilized" habitats, specifically regenerating cutblocks, was a primary consideration in choosing the central foothills as a repository for translocated wapiti. That the success of translocations was undermined by high mortality and emigration rates may indicate that the local population is close to carrying capacity. The creation of cutblocks and pipelines has the potential to greatly affect the distribution and abundance of wapiti in the central foothills. However, the suitability of these habitats for wapiti is compromised by road access and human disturbances – and the road network is rapidly expanding. Given my observations, added to the weight of evidence accumulating from various studies here in Alberta and abroad, it is my contention that access management is a primary concern for wildlife managers in the central foothills of Alberta's Rocky Mountains.

6.2 MANAGEMENT IMPLICATIONS

6.2.1 ACCESS MANAGEMENT

Recognition that the road network cannot grow indefinitely is critical to maintaining any semblance of wilderness in the central Rockies ecosystem. Given the projected trends in the demands for forest and gas resources in Alberta (Timoney & Lee

2001; Brad Stelfox, FOREM Technologies, personal communication), a policy of "no net growth" – where the road network is frozen at a given level through a balance of development and reclamation – may become necessary in the near future to maintain large mammal populations. Pro-active planning and cooperation among industries is needed to minimize the footprint of the growing road network. Given the lack of a comprehensive access management plan in the province, there is a critical need for research that provides guidelines for protecting the integrity of wildlife habitat because defensible data facilitate effective ground-level negotiations when developing access management plans. From my own research, I provide the following recommendations with respect to road development in the central foothills.

Relatively "pristine" foraging habitats, those >700 m from a road, are rare (only 7% of the land base) and highly fragmented (Figure 6.1). These habitats include grasslands, shrublands, wet meadows, patches of deciduous/mixed forest, young burns, reclaimed areas and, in some cases, early seral cutblocks where roads have been reclaimed – each of which provide forage for wapiti, moose, deer, and bears in the central foothills region. New roads and trails should not be allowed to compromise these important and rare habitats. To insure optimal use by wapiti (based on the cutblock selectivity pattern in Figure 5.6), new roads should not approach within 700 m of these core habitats. Neighboring areas, where foraging habitats have been impacted to some degree by roads, could be targeted for access management or road reclamation to increase their value to wapiti and other large herbivores (Figure 6.1).

Because compliance from the public may be more tractable if access is never allowed compared to when access is taken away, access controls should be implemented from the outset for any newly created roads. Given the current 2-pass harvest system of timber management, access roads are left in place for a minimum of 16 years until the second pass is completed. Vehicle access should be eliminated during the interim period following the first-pass harvest. For roads requiring reuse either seasonally or after a period of years, vehicular traffic might be effectively eliminated through the use of gates, berms, pulled bridges, or reclaimed sections or road at a fraction of the cost that would be incurred for complete reclamation and redevelopment of roads. Additional access restrictions should be required for well sites developed within wapiti foraging habitats, including cutblocks. In such cases, public access should be blocked and remote control of the well site could be implemented to reduce the amount of visitation required by oil & gas personnel. Critically, assessments of habitat use by wildlife before and after implementing access controls will be needed to evaluate the effectiveness of road management actions for large mammals. Given the high level of off-highway vehicle access in the central foothills, documenting wildlife responses will be necessary to determine whether control of passenger vehicles alone is sufficient to improve habitat effectiveness for wapiti and other large herbivores.

To some degree growth of the road network need not occur at the expense of large mammal populations. However, there is a critical density of roads (1 km/km^2) above which the mortality risk for wapiti increased exponentially in my simulations (see Figure 5.11). Despite extensively searching the entire central foothills during collaring attempts, I did not observe any wapiti occupying a home range where road densities exceeded 1 km/km^2. Although wapiti may occupy such areas, they likely occur at low density. Importantly, even at road densities <1 km/km^2, my model indicated a potentially rapid loss of wapiti either through emigration or mortality as road densities increased. Indeed, the majority of wapiti in my study maintained home ranges where road densities were half that of the critical mortality threshold (Figure 6.2), suggesting that wapiti in this region become increasingly intolerant of roads where densities exceed 0.5 km/km^2. Thus, in addition to developing roads away from foraging habitats, maintaining road densities <0.5 km/km^2 might result in optimal use of areas by wapiti.

6.2.2 IMPROVING WAPITI TRANSLOCATIONS

Using source stock experienced with either wolves or hunters is important to the success of wapiti translocations to the central foothills ecoregion. Given that most of the historic translocations to the central foothills used stock from Banff and Jasper, the Cross Area, and the YaHa Tinda Ranch (immediately south of my study area), managers might expect ~50% of the released animals to have survived through the first year following release. Unfortunately, translocated wapiti in my study established themselves only in areas where wapiti were already locally abundant. Thus, trying to establish wapiti in unoccupied areas via translocation may be infeasible in the central foothills. However, I advocate consideration of soft-releases for future translocations, which may help increase both site fidelity and survival rates (Eastridge & Clark 2001). My approach to soft release in this area is to establish a holding facility at the selected release site (guided by the maps in Figure 3.6), which, in combination with supplemental feeding, would carry animals over until spring. Dispersal was most common during the summer months, and for this reason I do not recommend translocating and releasing animals directly from the truck during spring/summer. Rather, holding animals at the release site for a few months prior to release might quell their desire to return home immediately following release.

My models indicate that a reduction in movement rates alone would increase survival rates.

Containing animals at the release site and providing supplemental feed through the winter months might insure better body condition of wapiti at the time of release compared to mid-winter releases. Declining body condition throughout the winter months likely affected the susceptibility of wapiti to predation by wolves, malnutrition, and accidents, all of which were most prevalent during the winter months following releases. Although wapiti naïve to wolves will still face that novel mortality risk upon release from the enclosures in spring, they may be less vulnerable to predation during the snow-free summer months, especially if they come out of the winter in good body condition. Additional releases of animals from Elk Island Park would provide an excellent test of soft-releases as a method of "head-starting" animals naïve to predators. Little experimental study of the effectiveness of soft versus hard release techniques has occurred (Bright & Morris 1994; Letty *et al.* 2000), thus, I recommend designing future wapiti releases in the central foothills so as to make these necessary comparisons. However, soft-release techniques cannot protect wapiti from hunting mortalities later in the year and selecting release areas with little hunter access or implementing access controls remain an important consideration for translocations of wapiti to the central foothills of Alberta.

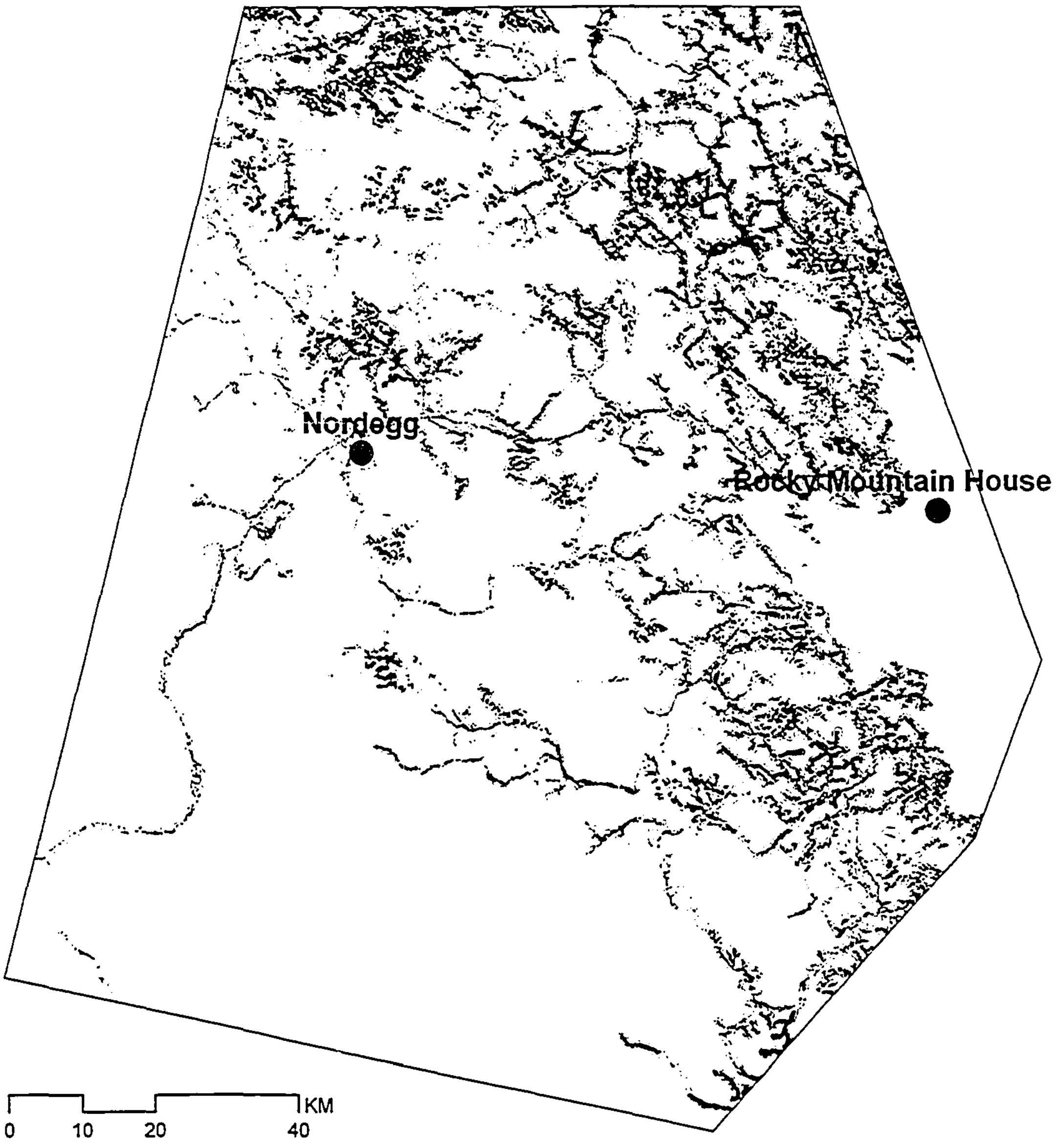

Figure 6.1. Priority foraging habitats (white) for large herbivores in the central Rocky Mountain foothills. Foraging habitats compromised by roads are shown in dark gray (200-700 m from a road) and black (<200 m from a road).

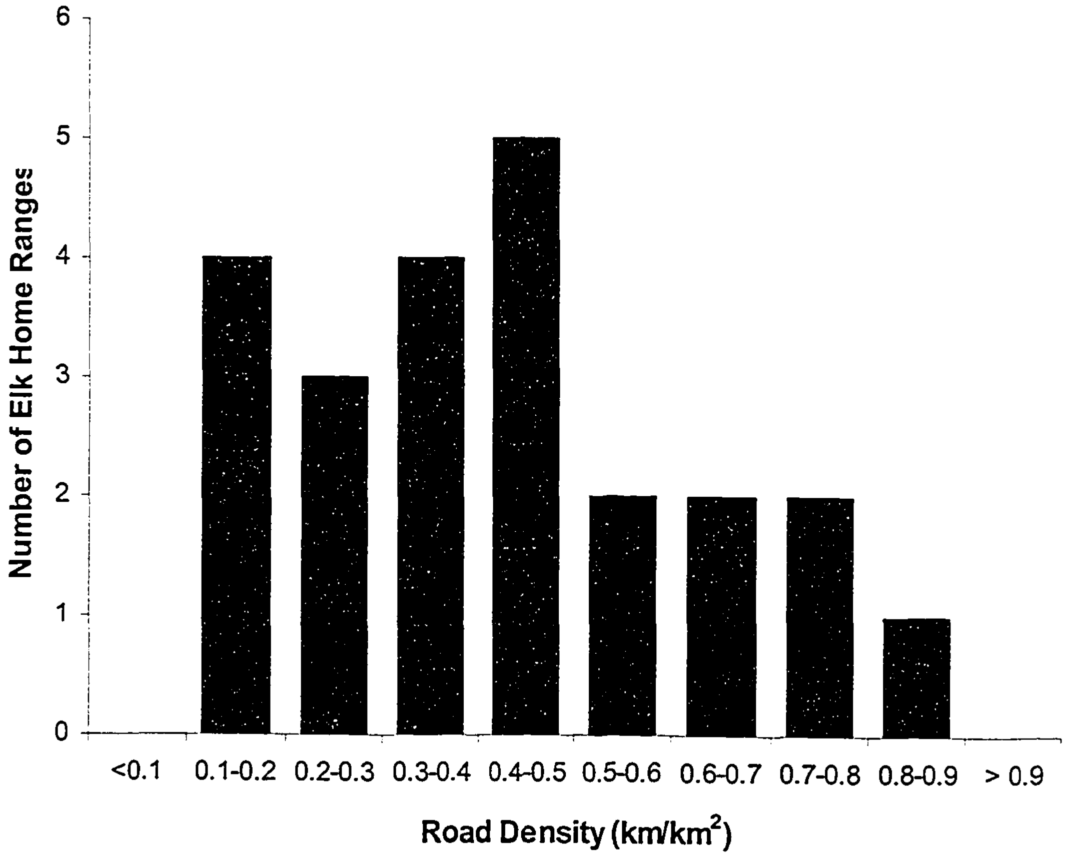

Figure 6.2 Frequency of wapiti home ranges across the range of road densities occupied by wapiti in the central Rocky Mountain foothills of Alberta, Canada.

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Appendix IA. Details of elk releases into the central foothills of Alberta, 2000–2004.

Source Population	Capture	Release	Total N	Demographic Composition						Total Collared	Release Area
				AD_f	YR_f	YOY_f	AD_m	YR_m	YOY_m		
Jasper town site[1]	1/30/00	1/31/00	11	1	7	0	0	0	3	--	Rocky River
Jasper town site	1/30/00	1/31/00	10	9	0	0	0	1	0	5	Mouse Flats
Jasper town site[1]	1/30/00	1/31/00	42	25	5	7	0	0	5	--	Brown Creek
Jasper town site	1/9/00	1/10-11/00	59	31	5	9	0	4	10	5	Mouse Flats
Banff town site	1/25/00	3/16/00	31	11	0	3	2	8	7	6	Trout Creek
Banff town site	12/20/99	1/9-11/00	64	29	14	11	0	0	10	11	Ram Falls
Banff town site	1/5/01	2/28/01	5	5	0	0	0	0	0	5	Sunpine Mainline
Banff town site	1/5/01	2/28/01	5	5	0	0	0	0	0	5	Sunpine Mainline
Banff town site	1/5/01	2/28/01	5	5	0	0	0	0	0	5	Trout Creek
Banff town site	1/5/01	2/28/01	5	5	0	0	0	0	0	5	Trout Creek
Cross Area	12/4/00	12/5/00	7	3	0	2	0	0	2	3	Nordegg River Rd.
Cross Area	12/4/00	12/5/00	4	3	0	1	0	0	0	3	Nordegg River Rd.
Cross Area	12/4/00	12/5/00	4	3	0	0	0	0	1	3	Nordegg River Rd.
Cross Area	12/19/00	12/20/00	16	7	0	1	1	4	3	6	Gypo Creek
Cross Area	12/19/00	12/20/00	8	5	0	2	0	0	1	3	S. Nordegg River
Cross Area	12/19/00	12/20/00	8	3	0	0	2	1	2	3	Colt Creek
Cross Area	1/4/01	1/5/01	9	6	0	2	0	0	1	3	North Ram River
Cross Area	1/4/01	1/5/01	7	5	1	0	0	0	1	3	North Ram River
Cross Area	1/24/01	1/25/01	17	11	0	2	0	1	3	5	Blackstone River
Cross Area	1/24/01	1/25/01	9	3	0	6	0	0	0	3	Jackfish Lake
Cross Area	1/24/01	1/25/01	8	6	0	1	0	0	1	3	Jackfish Lake
Cross Area	12/11/01	12/12/01	15	7	1	3	0	3	1	3	Trout Creek
Cross Area	12/11/01	12/12/01	8	4	0	2	0	1	1	4	Trout Creek
Cross Area	12/11/01	12/12/01	7	3	1	2	1	0	0	4	Trout Creek

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[1] No collar data available, these releases not included in analyses.

Appendix IB. Details of elk releases into the central foothills of Alberta, 2000–2004.

Source Population	Capture	Release	Total N	Demographic Composition						Total Collared	Release Area
				AD_f	YR_f	YOY_f	AD_m	YR_m	YOY_m		
Cross Area	12/11/01	12/12/01	17	10	1	3	0	0	3	5	Elk Creek Flats
Cross Area	1/23/02	1/14/02	15	6	0	5	0	1	3	5	N. Sask. River
Elk Island Park	12/19/01	1/4/02	11	3	0	0	8	0	0	3	Gypo Creek
Elk Island Park	12/19/01	1/4/02	8	2	0	2	0	0	4	2	Nordegg River Rd.
Elk Island Park	12/19/01	1/4/02	5	2	0	0	3	0	0	2	Nordegg River Rd.
Elk Island Park	1/29/02	2/7/02	9	4	0	0	5	0	0	4	Jackfish Lake
Elk Island Park	1/29/02	2/7/02	22	8	0	8	0	0	6	7	Towadina Creek
Elk Island Park	1/5/04	1/26/04	12	3	2	2	3	0	2	2	Cripple Creek
Elk Island Park	1/5/04	1/26/04	12	3	2	1	3	0	3	2	North Ram River
Elk Island Park	1/5/04	1/26/04	12	3	3	1	2	0	3	2	Trout Creek
Elk Island Park	1/5/04	1/26/04	12	4	0	0	5	0	3	1	Nordegg River Rd.
Elk Island Park	1/5/04	1/27/04	12	6	0	1	2	0	3	3	Cutoff Creek
Elk Island Park	1/5/04	1/27/04	11	4	0	3	2	0	2	3	Jackfish Lake
Elk Island Park	1/5/04	1/27/04	9	2	0	1	2	1	3	1	Hummingbird Ck.

Appendix II. General description of landscapes within 10-km radius of release locations in the central foothills of Alberta, Canada, 2000-2004.

Release Area	UTM East	UTM North	Percent Forested[1]	Ratio Cut: Meadow[2]	Linear Feature Density (km/km^2)	Road Density (km/km^2)	SD in Elevation	Mean Wolf RSF
Blackstone River	547230	5855340	77.39	1.50	0.51	0.42	44.51	0.5250
Colt Creek	565801	5829134	73.01	2.46	2.49	2.03	80.08	0.5278
Cripple Creek	563997	5783865	75.42	1.87	1.30	1.06	183.53	0.4204
Cutoff Creek	5984436	5758697	86.05	0.06	0.30	0.25	87.45	0.4825
Elk Creek Flats	579671	5772312	83.43	0.36	0.58	0.49	90.35	0.4567
Gypo Creek	576370	5808267	75.83	1.25	0.79	0.65	197.17	0.3436
Hummingbird Creek	570516	5770033	64.11	0.07	0.20	0.16	151.96	0.3016
Jackfish Lake	592968	5831306	67.27	6.70	0.78	0.64	46.55	0.5412
Sunpine Mainline	601032	5787743	82.74	7.02	1.33	1.32	137.75	0.4186
Mouse Flats	539068	5807795	89.58	0.27	0.12	0.10	156.15	0.4678
Nordegg River Road	567409	5846305	82.10	8.48	0.89	0.74	30.76	0.5114
North Ram River	581013	5791817	92.06	0.51	0.23	0.19	112.32	0.3836
N. Saskatchewan River	576370	5808267	75.83	1.25	0.79	0.65	197.17	0.3436
Ram Falls	587468	5775272	85.37	0.46	0.29	0.23	94.45	0.4621
South Nordegg River	565801	5829134	73.89	5.75	2.00	1.65	96.35	0.5284
Towadina Creek	593248	5791810	86.33	1.44	1.35	1.10	131.96	0.3840
Trout Creek	587991	5808658	75.13	2.32	1.89	1.57	83.78	0.4684

[1] Obtained from the satellite image classification after releases conducted, original cover evaluation using the Alberta Vegetation Inventory identified all sites as having less than 85% forest cover.

[2] Percent of area cut / percent of area that is natural meadow.

Appendix III. Summary of the fate of radio-collared elk by source population. Percentages were calculated as the number of individuals corresponding to each fate (N) out of the total number of collared individuals from that source population (47, 60, 32, and 91 for MP, CCA, EINP, and residents, respectively).

	Mountain Park		Cross Area		Elk Island		Resident	
Fate	N	(%)	N	(%)	N	(%)	N	(%)
Censored								
Immediate collar failure							1	(1.1)
Improper collar attachment							4	(4.4)
Severe signal interference			2	(3.3)	1	(3.1)	1	(1.1)
Recovered GPS collar	2	(4.3)	4	(6.7)			29	(31.9)
Settled outside study area					1	(3.1)		
Lost contact (unknown cause)	3	(6.4)	2	(3.4)	2	(6.3)	7	(7.7)
Stopped monitoring	8	(17.0)	14	(23.3)	6	(18.8)	32	(35.2)
Mortality								
Potential Capture Myopathy					3	(9.4)	3	(3.3)
Predation by wolf (*Canis lupus*)	9	(19.1)	11	(18.3)	8	(25.0)	2	(2.2)
Predation by cougar (*Felis concolor*)			2	(3.3)	1	(3.1)		
Predation by grizzly bear (*Ursus arctos*)	1	(2.1)						
Predation by black bear (*U. americanus*)			1	(1.7)	1	(3.1)		
Hunter–killed or Poached	19	(40.4)	10	(16.7)	2	(6.3)	6	(6.7)
Vehicle collision	1	(2.1)	2	(3.3)	1	(3.1)		
Malnutrition suspected	1	(2.1)	1	(1.7)	2	(6.3)	2	(2.2)
Accidental			2	(3.3)	2	(6.3)		
Unknown	3	(6.4)	8	(13.3)	2	(6.3)	4	(4.4)
Dispersed (>20 km from release site)	9	(19.1)	24	(40.0)	7	(21.9)	--	

Appendix IV. Model selection for covariates affecting elk survival during the first-year post-release into the central foothills of the Rocky Mountains in Alberta, Canada from 2000-2004. The model log-likelihood (LL) and number of estimated parameters (*K*) is shown for each model-building step. The difference in Akaike's Information Criterion (adjusted for small-sample sizes; ΔAIC_c) is shown in comparison to the final, most parsimonious model and calculated for an effective sample size equivalent to the number of failures ($n = 71$). Covariate interactions with risk type (wolves, hunting, other) or strata (population source) are indicated by "x".

Model	Description	LL	*K*	ΔAIC_c
FORAGE ENCOUNTER MODEL: F + (F x Risk)	Running average of total forage (herb + browse) biomass (F) interacted with risk type (Risk)	–305.38	9	30.88
WOLF ENCOUNTER MODEL: WA + (WA x Source)	Relative probability of wolf occurrence at elk location (W) weighted by annual wolf harvest index (A) interacted with population source (Source)	–308.84	10	40.80
HUNTER ENCOUNTER MODEL: R + (R x Risk) + L+ (L x Risk)	Mean proximity of road between previous and current location (R) and the proximity of linear clearing at the current location (L), both interacted with risk type (Risk)	–306.25	12	41.62
FULL MODEL: FORAGE + WOLF + HUNTER + Potential confounding variables	Potential confounding variables included March–May snowfall, June–July rainfall, resident elk density, release group size, and rate of elk movement over interval of risk (from previous to current location) interacted with risk type or population source where appropriate	–280.32	24	23.20
REDUCED MODEL	Removed non-contributing terms for parsimony	–284.62	18	13.80
SEASONAL MODEL: REDUCED MODEL + T + (T x Risk)	Included variable for time period (T) and interactions with risk type (Risk) to meet proportional hazards assumption	–278.85	20	8.26
FINAL MODEL (see Table 4)	Removed non-contributing terms for parsimony	–276.22	19	0.00

Appendix V. Model selection for covariates affecting elk survival during the second and subsequent years post-release into the central Rocky Mountain foothills of Alberta, Canada from 2000-2004. The model log-likelihood (LL) and number of estimated parameters (K) is shown for each model-building step. The difference in Akaike's Information Criterion (adjusted for small-sample sizes; ΔAIC_c) is shown in comparison to the final, most parsimonious model and calculated for an effective sample size equivalent to the number of failures ($n = 21$). Covariate interactions with strata (population source) are indicated by "x".

Model	Description	LL	K	ΔAIC_c
FORAGE ENCOUNTER MODEL: B + (B × Source)	Browse biomass at current location (B) interacted with population source (Source)	–54.85	7	32.98
WOLF ENCOUNTER MODEL: W + (W × Source)	Relative probability of wolf occurrence at elk location (W) interacted with population source (Source)	–55.01	7	33.58
HUNTER ENCOUNTER MODEL: R + (R × Source)	Running average of proximity of road (R) interacted with population source (Source)	–50.26	7	24.08
FULL MODEL: FORAGE + WOLF + HUNTER + Potential confounding variables	Potential confounding variables included March – May snowfall, June – July rainfall, resident elk density, release group size, and movement rate interacted with risk type or population source where appropriate	–32.25	20	27.06
REDUCED MODEL	Removed non-contributing terms for parsimony	–35.08	11	5.72
SEASONAL MODEL: REDUCED + T	Included variable for time period required to meet proportional hazards assumption	–31.09	12	0.74
FINAL MODEL (see Table 7)	Removed non-contributing terms for parsimony	–33.72	10	0.00

Appendix VI. Model selection for covariates affecting the retention of elk within 30-km of their release location or mortality during the first year following translocation to the central Rocky Mountain foothills of Alberta, Canada from 2000-2004. The model log-likelihood (LL) and number of estimated parameters (*K*) is shown for each model-building step. The difference in Akaike's Information Criterion (adjusted for small-sample sizes; ΔAIC_c) is shown in comparison to the final, most parsimonious model and calculated for an effective sample size equivalent to the number of failures ($n = 81$). Covariate interactions with failure type (mortality or dispersal) and strata (population source) are indicated by "×".

Model	Description	LL	*K*	ΔAIC_c
FORAGE ENCOUNTER MODEL: H + (H × Risk)	Running average of herbaceous biomass (H) interacted with risk type (Risk)	−255.13	6	25.52
WOLF ENCOUNTER MODEL: W + (W × Risk)	Relative probability of wolf occurrence at elk location (W) interacted with population risk type (Risk)	−385.77	6	286.80
HUNTER ENCOUNTER MODEL: RV + (RV × Risk) + L + (L × Risk)	Road visibility index at elk location (RV) and proximity of linear clearing (L) interacted with risk type (Risk)	−383.80	8	288.86
GEOPHYSICAL BARRIERS MODEL: O + (O × Risk) + (O × Strata) + NF + (NF × Risk) + V + (V × Risk)	Proximity of terrain obstacles (O), total amount of non-forested habitat (NF), and the proximity of a large river (V) interacted with type of risk (Risk) or population source (Strata)	−314.25	11	158.76
FULL MODEL: FORAGE + WOLF + HUNTER + GEOPHYSICAL BARRIERS + Potential confounding variables	Potential confounding variables included March – May snowfall, June – July rainfall, resident elk density, release group size and movement rate interacted with risk type or population source where appropriate	−227.66	33	51.58
REDUCED MODEL (see Table 9)		-231.87	13	0.00