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An Assessment of the Effects of Petroleum Exploration on Woodland Caribou (*Rangifer tarandus caribou*) in Northeastern Alberta

BY

Corey James Alexander Bradshaw ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science.

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta
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General	0578
Ancient	0579
Medieval	0581
Modern	0582
Black	0328
African	0331
Asia, Australia and Oceania	0332
Canadian	0334
European	0335
Latin American	0336
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United States	0337
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Plant Pathology	0480
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Biostatistics	0308
Botany	0309
Cell	0379
Ecology	0329
Entomology	0353
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Zoology	0472
Biophysics	
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Nutrition	0570
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Occupational Health and Therapy	0354
Ophthalmology	0381
Pathology	0571
Pharmacology	0419
Pharmacy	0572
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An Assessment of the Effects of Petroleum Exploration on Woodland Caribou (*Rangifer tarandus caribou*) in Northeastern Alberta

DEGREE: **Master of Science**

YEAR THIS DEGREE GRANTED: **FALL 1994**

CBrad

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6 September 1994

WOODLAND CARIBOU DISTURBANCE INDICES

Recent research has shown that woodland caribou react to human-caused disturbance on their winter range in relation to the level and frequency of the disturbance. To predict the degree to which caribou will react to varying disturbances, we have designed a system to quantify various industrial activities in terms of their intensity. This designation is as follows:

Sound of 80 decibels from 100 metres for 1 minute = 1 **bradshaw**

1 **decibradshaw** is sufficient to elicit an attentive response in caribou

1 **kilobradshaw** will cause caribou to walk slowly away from the disturbance

1 **megabradshaw** = 1 **slaght***

1 **decislaght** causes caribou to clear the immediate area

1 **megaslaght** will totally eliminate caribou within a 100-kilometre radius

1 **gigaslaght** will totally remove caribou from northeastern Alberta

Blair Rippin
Head of Wildlife Management
Alberta Department of Environmental Protection
Fish and Wildlife Services
Northeast Region

---

* *Many thanks to Mr. Dan Slaght, Land Use Officer, Alberta Forest Service*

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled AN ASSESSMENT OF THE EFFECTS OF PETROLEUM EXPLORATION ON WOODLAND CARIBOU (*Rangifer tarandus caribou*) IN NORTHEASTERN ALBERTA submitted by COREY JAMES ALEXANDER BRADSHAW in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

S.A. Boutin (Supervisor)

D Hebert

D.M. Hebert

R.J. Hudson

Jan O Murie

J.O. Murie

6 September 1994

I dedicate this thesis to my parents, Philip and Janice, who provided me with a home conducive to learning and achievement. They managed to foster independence in their children while always maintaining a guiding role. Without my father's passion for the outdoors and my mother's pursuit of intellectual prowess, I do not believe I would have developed into who I am today nor been able to achieve all that I have. Thank you.

ABSTRACT

Woodland caribou in northeastern Alberta are relatively sedentary, exist at low densities and are considered "threatened". Increased petroleum exploration and development in this area may contribute to the proposed population decline by increasing energy expenditure during winter. I examined the effects of petroleum exploration on woodland caribou behaviour and modeled the potential energy expenditure resulting from disturbance. Biweekly aerial locations of forty-seven woodland caribou fitted with VHF telemetry collars provided data on movements and habitat use. Telemetry data were combined with digital peatland coverages. Log-ratio analysis of compositions demonstrated that woodland caribou prefer forested fen peatland complexes and concentrate feeding in forested bog islands. I delineated woodland caribou distribution polygons by grouping the preferred habitat types into discrete polygons separated by a relatively intact matrix of upland habitat; these polygons represent 36% of the study area. I measured the effects of simulated petroleum exploration (*i.e.*, loud noise) on caribou behaviour and movement using a Before-After-Control-Impact design. Two-way repeated-measures ANOVA revealed that loud noise caused a significant increase in movement rate of approximately 0.2 m/second during one-hour disturbance. Impact animals moved and average of 2.11 km farther than Controls during, and one hour following, disturbance, and demonstrated significantly greater movement rates than Controls two days following disturbance. This translates into a 16 - 39% increase in daily energy expenditure. Disturbance did not affect the proportion of time allocated to feeding or rapid movement, nor did it influence shifts between habitat types. I developed a simple model to estimate the probable energetic consequences of multiple perturbation encounters and then compared the results to petroleum exploration that occurred in the study area during the past five years. The model demonstrated that on 9 different occasions (*i.e.*, specific areas during specific years), the perturbation encounter rate exceeded 0.0375 encounters/km^2/winter, enough to cause above average weight loss. On one occasion, the encounter rate exceeded 0.1238 encounters/km^2/winter, enough to cause >20% winter weight loss and a possible reduction in female reproductive success. Eight land-use management recommendations are given based on the conclusions of this study.

ACKNOWLEDGEMENTS

I extend many thanks to the members of my supervisory committee, Drs. Stan A. Boutin, Daryll M. Hebert, Robert J. Hudson and Jan O. Murie, who provided excellent scientific direction and insight. It was indeed an honour to be a student of such respected and learned men.

<u>Financial Assistance</u>

The majority of the monies allocated to this project were either directly supplied or raised by the Northeast Region Standing Committee on Woodland Caribou (NERSC), a delegation comprised of industry representatives and government agencies. These include:

- Alberta Energy Co. Ltd.
- Alberta-Pacific Forest Industries Inc.
- Amoco Canada Petroleum Co. Ltd.
- Anderson Exploration Ltd.
- Bow Valley Energy
- Chevron Canada Resources Ltd.
- Home Oil Co. Ltd.
- Husky Oil Operations Ltd.
- Ish Energy Ltd.
- Lakeland Peat Moss Ltd.
- Lakewood Energy Inc.
- Mobil Oil Canada
- Mark Resources Inc.
- Northstar Energy Corp.
- NOVA Corporation of Alberta
- Paramount Resources Ltd.
- Pensionfund Energy Resources Ltd.
- Petrorep (Canada) Ltd.
- Pinnacle Resources Ltd.
- Rio Alto Exploration Ltd.
- Sun Gro Horticulture Canada Ltd.
- Triton Canada Resources Ltd.
- Universal Explorations
- Wascana Energy Inc.

- Alberta Energy
- Alberta Environmental Protection:
    - Fish and Wildlife Services
    - Forest Service
    - Land Use Service
    - Regional Coordination Service
- Energy Resources Conservation Board

Other agencies contributing financial assistance to the NERSC research programme or to me directly included:

- Alberta Recreation, Parks and Wildlife Foundation
- Alberta Environmental Centre
- Association of Canadian Universities for Northern Studies
    - *Beverly and Quamanirjuaq Caribou Management Board*
- Canada-Alberta Partnership Agreement in Forestry
- Canadian Circumpolar Institute
    - *Circumpolar/Boreal Alberta Research Grant*
- Canadian Wildlife Foundation
    - *Orville Erickson Memorial Scholarship Fund*
- Government of the Province of Alberta
- University of Alberta
    - *Department of Zoology*

Logistical Support

Blair Rippin, Head of Wildlife Management, Alberta Fish and Wildlife Services was instrumental in the success of this project. He was always available to assist me with scheduling or provide me with essential equipment. His knowledge of the area and managerial skills made many of the larger logistical obstacles easily surmountable. Blair is committed, helpful and good-natured. Thank you very much, Blair.

Mark Fremmerlid, Cessna 185 pilot with Alberta Central Airways Ltd., made data collection much less an ordeal than I had originally expected. His ability to pinpoint animal locations in the worst weather or densest vegetation never ceased to amaze me. Not only were his piloting and telemetry skills outstanding, but his sense of humour and endless wit made the hundreds of flight hours bearable. Mark is a good friend and I thank him for all his help.

My field assistant, Matthew Evans, was not only willing to work hard, but jumped at the opportunity to lend a hand. His insight and enthusiasm made even the coldest days entertaining. Matt is a good friend and a worthy colleague. Many thanks, Matt, and all the best. I also acknowledge the support, advice and friendship of my colleagues in post-graduate studies at the University of Alberta: Yves Pinsonneault, Hilary Jones, Ainsley Sykes, Rena Vandenbos, Douglas Clark and Dr. Karl Larsen. Many thanks to all of you.

Finally, a word of thanks to my partner and friend, Amy Lightfoot. She endured many unexpected absences and encouraged me every step of the way. Her support and understanding were essential components of this study, and I thank her deeply for all she did.

I required a great deal of support in order to complete the many field components of this study, and I extend my deepest thanks and respect to the following people:

Richard Biel (Field Assistance)
Mark Brown (Field Assistance)
Eric Christensen (Alta.-Pacific Forest Indust., Inc.)
Greg Christensen (Sourcex Seismic)
Brian Cleveland (Canadian Helicopters)
Colin Edey (NOVA Corporation of Alberta)
Ralph Jamieson (Land Use Serv. - Forest Manage.)
Michael Krupa (Alta.-Pacific Forest Indust., Inc.)
Darry Markle (Highland Helicopters)
Jerry Mulder (Forestry Farm Park and Zoo)
Ray Nixdorf (Ministik Wildlife Research Station)
Jack Nolan (Alberta Environmental Centre)
Ken Oszust (Sourcex Seismic)
Len Peleshak (Alberta Environmental Centre)
Brent Pendleton (Forestry Farm Park and Zoo)
Margo Pybus (Alberta Fish and Wildlife Services)
Colin Reed (Canadian Helicopters)
Denis Reindl (Sourcex Seismic)
Olivier Richer (Alta.-Pacific Forest Indust., Inc.)
Perry Robinson (Forestry Farm Park and Zoo)
Joe Smith (Alberta Forest Service)
Daniel Slaght (Alberta Land Use Service)
Orrin Stephen (Field Assistance)
Brenda Stratichuk (Rio Alto Exploration Ltd.)
Stephen Stuckless (Northstar Energy Corporation)
Terry Thompson (U. of Alta. - Dep. of Geography)
Dale Vitt (U. of Alta. - Dep. of Botany)

TABLE OF CONTENTS

CHAPTER ONE - GENERAL INTRODUCTION

CHAPTER TWO - WINTER HABITAT SELECTION AND POPULATION DISTRIBUTION

2.3 Methods

2.4 Results

2.5 Discussion

CHAPTER THREE - RESPONSE TO SIMULATED PERTURBATION

3.3 Results

3.4 Discussion

CHAPTER FOUR - PERTURBATION ENCOUNTER MODEL

4.3 Results, Assumptions and Calculations

CHAPTER FIVE - CONCLUSIONS & IMPLICATIONS

LIST OF TABLES

Table:

LIST OF FIGURES

Figure:

CHAPTER ONE:
GENERAL INTRODUCTION

1.1 Background and Rationale

Edmonds (1991) reported that the North American range of woodland caribou has undergone gradual shrinking since the onset of European settlement, and especially along the southern borders of the boreal forest region. Some have argued that woodland caribou have a poor capacity to adapt to habitat changes and exploitation (Cameron 1983; Cumming 1992) because of their relatively low reproductive rate (Bloomfield 1980). The long-term viability of woodland caribou populations in Alberta came into question in the mid-1970s as a result of public reaction to low numbers (densities in Alberta usually fluctuate around 0.03 caribou/km^2 - Fuller and Keith 1981; Stelfox and Stelfox 1993) as well as suggestions of historical decline (Stelfox 1966; Lynch and Pall 1973; Bloomfield 1980; Edmonds 1986). Contrary to this view, Bradshaw and Hebert (*submitted)* suggest that insufficient evidence exists to conclude that there has been a significant decline in provincial populations over the last century. Nonetheless, regulatory agencies increasingly restricted recreational hunting of woodland caribou in Alberta and eventually discontinued it in 1981 in an attempt to promote population recovery. One possible factor that may be contributing to the apparent decline is human activity in the form of industrial land use (Fuller and Keith 1981; Edmonds 1988; Brown *et al.* 1991; Edmonds 1991). This type of activity may have the potential to effect both individuals and populations by altering the environment in which they exist and by directly influencing the energetic balance of individuals.

In Alberta, provincial policy defines woodland caribou as a threatened species (Anonymous 1985) and the General Wildlife Regulation of the Alberta Wildlife Act designates woodland caribou as an Endangered Animal. In The Committee On the Status of Endangered Wildlife In Canada (COSEWIC) report on woodland caribou, Kelsall (1984) noted that this sub-species is neither threatened nor endangered on a Canada-wide basis, although he declared that some local populations were threatened. COSEWIC lists the western population of woodland caribou as vulnerable. As a result, there is a general perception that the long-term persistence of woodland caribou populations in Alberta is precarious.

Partly due to the concern over woodland caribou numbers, land-use regulations for renewable and non-renewable resource exploration and development were modified throughout the forested region of Alberta (Brown *et al.* 1991). When the regulations were implemented, the petroleum industry generally viewed them as significant physical and economic encumbrances to development while some biologists maintained that they were necessary to ensure caribou survival. A cooperative government-industry committee, the Northeast Region Standing Committee on Woodland Caribou (NERSC), was formed to gain better information on woodland caribou in this region and to improve the relationship between regulators and industry. The committee's mandate was to provide a cooperative forum to discuss and support research on the conservation of woodland caribou in northeastern Alberta while allowing for compatible renewable and non-renewable resource development. Because most industrial activity occurs in the winter, and because winter is often the most biologically stressful time of the year for many northern mammals, my study addresses the particular question of the effects of winter petroleum exploration on woodland caribou behaviour and energetics.

1.2 Adaptations to Winter and Potential Threats of Industrial Disturbances

The potential threat of industrial disturbances to woodland caribou is exacerbated by this animal's physiological adaptations to winter conditions. Caribou reduce their metabolic rate by 25 - 30% and arrest all growth from November through to April or May (Segal 1962; McEwan 1968; McEwan and Whitehead 1970; Dauphiné 1976). Nilssen *et al.* (1984) further suggested that seasonal changes in the resting metabolic rate for reindeer do not reflect changes in basal metabolic rate, but rather changes in food intake. It is also difficult for wild ungulates to meet their maintenance energy and 7% protein requirement in winter, since forage resources generally contain 6 - 8% crude protein (sometimes less) and have low digestibility (Renecker and Hudson 1993). In response to reduced forage quality and abundance, caribou and other northern ungulates reduce winter energy expenditure behaviourally through decreased locomotory activity and anatomically through increased pelage insulation. This agrees with the conclusions of Gaare *et al.* (1975) that reindeer[1] conserve their energy resources in winter by spending a minimal time engaged in high-energy activity.

As well, caribou typically lose between 10 - 15% of their body mass over winter largely through the depletion of fat deposits on the back, inside the gut cavity and in the bone marrow (Steen 1968); this loss may exceed 20% during difficult winters (McEwan 1968; McEwan and Whitehead 1970; Renecker and Hudson 1993). Protein depletion represents only 10% of the total weight lost (Boertje 1985). Unnatural energetic demands during winter could reduce an individual's capacity to recover lost energy in the spring for growth and reproduction (Geist 1971). The added energetic costs associated with the flight response evoked by the temporally and spatially unpredictable occurrences of winter petroleum exploration are potentially dangerous in this regard.

Woodland caribou appear susceptible to industrial disturbances because of their small seasonal movements. They demonstrate no true uni-directional migration, though some females may display a loose fidelity to a particular site during calving year after year (Fuller and Keith 1981). In northeastern Alberta, annual ranges of males may exceed 1200 km^2, whereas those of females are usually less than 600 km^2 (Fuller and Keith 1981). Yet woodland caribou ranges in Alberta appear larger than those of most other woodland caribou populations across Canada. Rock (1992) reported annual ranges of 250 km^2 for woodland caribou in Saskatchewan; Shoesmith and Storey (1977) calculated the mean winter range of a population in Manitoba at 250 km^2, whereas Darby and Pruitt (1984) reported home ranges from 95 - 140 km^2 for another Manitoba population. Mean winter ranges in Ontario for seven different populations were 390 km^2 (Cumming and Beange 1987). Woodland caribou in northeastern Alberta are, however, relatively sedentary when compared to the migratory barren-ground caribou of Alaska and northern Canada that may traverse more than 2000 km annually during spring and fall migrations (Kelsall 1968). Because woodland caribou are relatively sedentary, disturbance from site-specific industrial activity could have a greater impact on this sub-species than on barren-ground caribou.

---

[1] *Reindeer and caribou are members of the same species, Rangifer tarandus.*

1.3 Background in Perturbation Impact Research

Many research projects have attempted to address the questions concerning the potential impacts of human activity on caribou, largely due to increased petroleum exploration and development in northern Canada and Alaska during the last 30 years (Bergerud 1984). Most research projects have followed a mensurative, rather than a manipulative format (Hurlbert 1984; Sinclair 1991) and have addressed many forms of both active and passive disturbance. Studies of caribou behaviour and movements in relation to petroleum exploration *per se* have not been numerous (Urquhart 1973; Slaney 1974; Slaney 1975; Beak 1976; Russell 1977; Horejsi 1979; Penner and Duncan 1983; Penner *et al.* 1983) - most being descriptive, rather than experimental, consultant's reports for petroleum companies. The effects of construction and operation of petroleum infrastructure on caribou have, however, been studied more extensively (Banfield 1974; Jakimchuk *et al.* 1974; McCourt *et al.* 1974; Cameron and Whitten 1979, 1980a 1980b; Cameron et al. 1979; Thompson *et al.* 1980; Wright and Fancy 1980; Banfield *et al.* 1981; Fancy 1983; Whitten and Cameron 1983; Murphy 1988).

Researchers have suggested that caribou can be displaced from previously occupied range when exposed to petroleum exploration and development (Cameron and Whitten 1979, 1980a, 1980b; Cameron et al. 1979; Horejsi 1979; Banfield *et al.* 1981; Whitten and Cameron 1983). In spite of the apparent support for this type of response, most of the previous references were reports lacking detailed statistical analyses and controlled experimental design. In fact, Carruthers *et al.* (1984) dismisses many of the conclusions drawn by some of these reports. However, although this last study was more rigorously designed, the authors' conclusions often contradict the results of their analyses. Shideler (1986) notes that much of the apparent controversy in this issue stems from the broad confidence limits associated with population data gathered from fixed-wing aircraft; these imprecise data were used to conclude whether or not caribou were avoiding development areas. Other unpublished reports (Urquhart 1973; Russell 1977) have claimed that exploration causes minimal displacement of small groups of caribou if landscape topography is negligible. Still other reports (McCourt *et al.* 1974; Wright and Fancy 1980; Penner and Duncan 1983) have stated that minimal or temporary displacement occurs during exploration, development or transportation activities, a view also supported by more convincing experimental studies (Horejsi 1981; Fancy 1983). Other consultant's reports (Slaney 1975; Penner *et al.* 1983; Jakimchuk *et al.* 1974) claimed to find no significant modification in distribution during industrial procedures.

Other forms of disturbance on caribou and reindeer have also been studied. These include perturbation from aircraft (Banfield 1974; Klein 1974; McCourt and Horstman 1974; McCourt *et al.* 1974; Calef *et al.* 1976; Miller and Gunn 1979; Gunn and Miller 1980; Banfield *et al.* 1981; Valkenburg and Davis 1985; Harrington and Veitch 1991; Kitchens 1991; Harrington and Veitch 1992), snowmobiles, vehicles and road systems (Klein 1971; Banfield 1972; Jakimchuk *et al.* 1974; Roby 1978; Banfield *et al.* 1981; Horejsi 1981; Mercer *et al.* 1985; Dau and Cameron 1986; Skogland 1986; Murphy and Curatolo 1987; Tyler 1991), hydroelectric development (Hill 1985; Northcott 1985) and even tourism (Dumont 1993).

Effects of these types of disturbance include displacement from previously occupied range (Cameron and Whitten 1976 & 1978; Bloomfield 1980; Northcott 1985; Dau and Cameron 1986; Skogland 1986), increased movement resulting in increased energy expenditure (Murphy and Curatolo 1987; Murphy 1988; Dumont 1993) and reduction in food intake (Hill 1985; Dumont 1993). Banfield (1972) and Mercer *et al.* (1985) found a general, long-term avoidance of roads and human settlements and Dumont (1993), in a comprehensive study of avoidance behaviour, found that woodland caribou avoid areas of even minimal human activity. He also found increased movement in response to human activity, although Slaney (1975) and Fancy (1983) were unable to demonstrate such effects. Hill (1985) and Dumont (1993) demonstrated that human activity can significantly decrease the proportion of time allocated to energy intake and assimilation (*i.e.*, feeding and resting), although Harrington and Veitch (1991) did not find any such decrease resulting from exposure to low-level fighter jet overflights, nor did Carruthers *et al.* (1984) for caribou near the Trans-Alaskan Pipeline System (TAPS). Murphy and Curatolo (1987) and Murphy (1988) have also demonstrated that physical stress and energy expenditure are exacerbated by a combination of moving disturbances (vehicle traffic) and physical barriers (pipelines).

Other studies have addressed the effects of pipelines and other physical obstructions or barriers that have the potential to deflect caribou from normal migration routes or prevent movement altogether (Miller *et al.* 1971; Banfield 1974; Child 1974; Cameron and Whitten 1976 & 1978; Roby 1978; Klein 1980; Banfield *et al.* 1981; Hanson 1981; Carruthers *et al.* 1984; Murphy and Curatolo 1987). Fancy (1983) found that only 20% of the caribou he observed displayed such responses to barriers, but Klein (1971; 1980) believed reindeer distribution and movement to be limited by roads and highways. Hanson (1981), Whitten and Cameron (1983) and Northcott (1985) believed the effect of physical obstructions to be of significant concern and Miller *et al.* (1971) demonstrated that most caribou were reluctant to deviate from learned travel routes and were easily obstructed by human-made barriers. Bergerud et al. (1984), in a comprehensive and thought-provoking review, suggested that the information available regarding the effects of obstructions and other human disturbances on caribou was uncertain. They suggested that the uncertainty was due to extrapolation from observations on individuals to the population, the variation in the quality of the available information and the use of correlational reasoning rather than hypothesis testing.

Many studies have emphasized the greater degree of sensitivity to human activity by caribou cows and calves (de Vos 1960; Ericson 1972; Bergerud 1974; Roby 1978; Cameron *et al.* 1979; Whitten and Cameron 1983; Dau and Cameron 1986). Calef *et al.* (1976), Miller and Gunn (1979) and Gunn and Miller (1980) found that except during extreme and purposeful harassment, aircraft overflights do not seem to cause a significant separation of cows and young calves. Harrington and Veitch (1992) found, however, a correlation between calf survival and the degree of exposure to fighter jet overflights during the calving and immediate post-calving periods. Although my study focuses on winter perturbation of woodland caribou, and therefore, does not address harassment of calving females, the improvement in petroleum exploration technology may eventually permit exploration to occur during the calving season (May to June). I will discuss this possibility in the management recommendations section of Chapter Five.

The effects of a variety of perturbations on other ungulate species may also provide clues to the potential effects of harassment of caribou. Most of the studies used control groups for comparisons and provided statistical support for their conclusions. Some of these studies include the response of wapiti (*Cervus elaphus canadensis*) to roads and vehicular traffic (Schultz and Bailey 1978) and mining activities (Kuck *et al.* 1985), mule deer (*Odocoileus hemionus*) responses to snowmobiles and persons afoot (Freddy *et al.* 1986) and to all-terrain vehicles (Yarmaloy *et al.* 1988), white-tailed deer (*Odocoileus virginianus*) response to snowmobiles (Huff *et al.* 1972; Bollinger *et al.* 1973; Dorrance et al. 1975; Richens and Lavigne 1978), mountain goat (*Oreamnos americanus*) response to petroleum exploration (Penner 1988) and mining (Johnson 1977), Dall's sheep (*Ovis dalli*) and bighorn sheep (*Ovis canadensis canadensis*) response to industrial development (Reynolds 1974; Morgantini and Mead 1990) or roads (DeForge 1972) and the effects of tourism on chamois (*Rupicapra rupicapra ornata*) (Cederna and Lovari 1985).

Some of the effects determined by the studies cited above include range abandonment and use of sub-optimal habitats following disturbance (DeForge 1972; Huff *et al.* 1972; Johnson 1977; Cederna and Lovari 1985; Kuck *et al.* 1985; Yarmaloy *et al.* 1988). Although Dorrance *et al.* (1975) found minimal response to snowmobile disturbance through range abandonment, Bollinger *et al.* (1973), Reynolds (1974), Richens and Lavigne (1978) and Morgantini and Mead (1990) found none. Under some circumstances, increased vigilance (Penner 1988) or increased movement and energy expenditures (Kuck *et al.* 1988; Freddy *et al.* 1986) were the result of exposure to disturbance. Yarmaloy *et al.* (1988) also found flight (*i.e.*, running from a perceived threat) distances to increase with increased exposure to perturbation.

In spite of the evidence for disturbance effects on caribou and other ungulate species, Bergerud (1974) argued that noise disturbances in the absence of sight or scent usually have little impact on caribou which appear to show little aversion to human activity. Bergerud (1978) argued that caribou adapt well to humans and that no evidence exists to show caribou abandoning ranges because of industrial activity. Instead, he believed that the subtle indirect effect of human activity was the modification of caribou-predator interactions. Bergerud *et al.* (1984), in their extensive review of eight barren-ground caribou populations in North America, re-iterated that there was no evidence to suggest that disturbance activities or habitat alteration affect caribou productivity. They suggested that caribou have a high degree of resilience to human-caused sources of perturbation, and seasonal movement patterns and extent of range occupancy appear to be a function of population size rather than of extrinsic perturbation. They also suggested that caribou and other cervids can withstand periodic severe disturbance without adverse effects on productivity and survival. The question is, then, does continuous, unpredictable harassment have any effect on population demographics. Despite some controversy, the ample evidence of human influence on caribou cited in previous paragraphs suggests that, in certain circumstances, it may. It appears that the degree of response to disturbance depends on a multitude of factors; these may, in fact, be partly responsible for the discrepancies in the studies cited above.

1.4 Studying Disturbance on Woodland Caribou in Alberta

Most studies addressing the effects of industrial perturbation have dealt with barren-ground caribou and reindeer, *R. t. tarandus*. Many of these studies lacked appropriate controls and did not employ a manipulative experimental design, while others provided control groups for comparisons and statistical support for conclusions drawn. The apparent controversy over the degree to which human activities affect caribou seems to be a function of many factors. First, it appears that the specific nature of the disturbance and the degree to which a particular study rigorously investigated its effects on caribou was a major factor in the conclusions advanced. Other factors influencing results include, the frequency of the perturbation (an important consideration for habituation and energy consumption), the size of the study sub-species' home range, the time of year (*e.g.*, whether or not snow is present), the individual's reproductive status (*i.e.*, parous females usually react more to disturbance), age and physical condition (Skogland and Grøvan 1988), and landscape characteristics (*e.g.*, vegetation and topography).

Because the effects of disturbance appear to vary depending on these factors, the present study attempts to resolve concerns about the effects of petroleum exploration on woodland caribou in a forested landscape of negligible topography (*i.e.*, northeastern Alberta). By employing a manipulative methodology and using controls, I hope to elucidate the effects of such perturbations on woodland caribou in this region of Canada. As indicated by Bergerud *et al.* (1984), this type of experimental design allows for proper hypothesis testing and avoids correlational reasoning (*i.e.*, a process which may not necessarily imply causation).

Because woodland caribou in northern Alberta are relatively sedentary, exist at low densities and occupy terrain that is difficult to access, I have chosen to address the effects of industrial disturbances using a behavioural approach and then estimate the energetic consequences of any behavioural modifications resulting from disturbance. By quantifying the response of individuals to a single encounter with simulated industrial activity, I was able to determine the probable energetic consequences of such encounters. I was also able to detect shifts in small-scale habitat use in response to harassment; this aspect is potentially important because woodland caribou tend to select specific habitat complexes (Fuller and Keith 1981). This approach differs from most other harassment studies in that I quantify responses to single encounters and can measure the variance in this response between individuals. Many have shown that caribou may abandon traditional ranges that undergo extensive exploration and development, but few have shown whether these shifts include small-scale changes in habitat use. My approach is more precise because I can measure smaller responses that might be missed at other spatial scales.

I have organized the thesis into three main chapters preceded by this general introduction (Chapter One) and followed by a general conclusion (Chapter Five). Chapter Two addresses habitat use and selection by constructing habitat preference ranks which serve to identify important woodland caribou habitats in the study region. Preference ranks also assist in determining if disturbance promotes shifts to non-preferred habitat types. In Chapter Three I outline the results of a perturbation experiment which measured the effects of simulated noise disturbance on caribou behaviour, movement and habitat use. Chapter Four outlines a model developed to estimate the probability of encounter with noise disturbance generated from typical winter petroleum exploration; I also discuss the probable energetic impact of exposure to winter exploration using the results of Chapter Three. Finally, I combine the results and conclusions of previous chapters in Chapter Five and discuss management recommendations for woodland caribou in northeastern Alberta.

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CHAPTER TWO: WINTER HABITAT SELECTION AND POPULATION DISTRIBUTION

2.1 Introduction

To properly control human activities within the context of wildlife management, land-use regulations must be established from something other than roughly-defined habitat affinities for wildlife species. Woodland caribou are considered to be a sensitive species in regard to land exploitation by the forest harvest and petroleum industries because of their low population densities and restricted distribution (see Chapter One), so determining the habitat types of northeastern Alberta that are used and preferred by caribou is necessary to define specific land-use regulations for these areas. Once the preferred habitats are determined, land-use regulations can be modified to minimize conflict between industry and woodland caribou.

Defining habitat use is the first step in determining the distribution of woodland caribou in northeastern Alberta. Simply noting in which habitat types caribou are more often found roughly outlines their distribution. In addition, representing habitat use in relation to habitat availability designates a habitat type as preferred, randomly used or avoided. This aspect permits a more detailed analysis of each habitat's importance to caribou and outlines hypotheses that could explain differences in preference. Because an animal's proportional use of one habitat type is linked to that of other habitat types (unit-sum constraint) (Aitchison 1986; Aebischer *et al.* 1993), defining the preference of each habitat type relative to all others is important. Ranking habitats from «least preferred» to «most preferred» is essential if the goal is to determine the potential for a disturbance to displace caribou to less-preferred habitat types (see Chapter Three).

The terms often associated with wildlife habitat analysis are sometimes confusing and should be defined. Habitat use is said to be selective (*i.e.*, non-random) if habitat types are used disproportionately to their availability. A habitat is said to be preferred when its use is significantly greater than its availability in the environment (Johnson 1980). Assessing habitat availability is often difficult because an animal may select only a portion of a specific area, even though that area appears to be suitable habitat. This phenomenon may result from intraspecific territoriality, predator avoidance or the avoidance of some perturbation (White and Garrott 1990). For the purposes of this analysis, I have calculated availability using habitat abundance (*i.e.*, the quantity of each habitat in the environment).

Because selection is hierarchal (Johnson 1980) and its determination varies with each level of spatial scale, I determined habitat preference at two different spatial scales by effectively comparing habitat availability to the regional population and to the individual. I also analysed preference using data on feeding activity to determine if this important winter activity occurred within specific habitat types. Unlike first-order selection, which is defined as a species' selection of a geophysical range, second-order selection is the selection of habitats within this range (Johnson 1980). In this case, winter positions of caribou determined by radio telemetry is used to represent a second order of selection for the woodland caribou population of the boreal mixed-wood forest in northeastern Alberta. Third-order selection pertains to habitat preference within an individual's home range. This level of selection reflects the variation in individual habitat preferences as a function of potentially different habitat availability between individuals. Finally, I determined feeding habitat preference by comparing the use of a habitat type for feeding activity versus that habitat's availability within the study area. All levels of selection must also be separated by year to avoid the misleading inferences that can result from pooling data among years, unless no significant difference exists in habitat use between years (Schooley 1994). Ideally, habitat use should also be determined for each individual in the population sample, because different animals may use habitats differently (White and Garrott 1990). Although this is often a difficult task, I was able to determine habitat use per individual.

In this chapter I summarize woodland caribou habitat use and availability of seven distinct peatland habitat types in the study area and discuss preference ranks for second-order, third-order and feeding-habitat selection. The results of the habitat analyses are combined to create criteria for the definition of caribou distribution polygons within and outside of the study area. These polygons represent the distribution of woodland caribou within more or less discrete sub-units of the most preferred habitat types.

2.2 Description of the Study Area

The study area is situated in the northeastern section of the Province of Alberta, Canada (centre: 56°N / 112°W) and encompasses approximately 20 000 km^2 of boreal mixed-wood and peatland vegetation (Figure 2.1).

Elevation varies between 500 and 700 metres above sea level with minimal topographic variation. Lowlands are dominated by black spruce (*Picea mariana*) or black spruce-tamarack (*Larix laricina*) fens and bogs. Ground cover consists mainly of Labrador tea (*Ledum groenlandicum*), peat moss (*Sphagnum spp.*), sedges (*Carex spp.*), bog birch (*Betula glandulosa*) and a variety of lichens (*e.g., Cladina spp.* and *Peltigera spp.*). Along watercourses, willows (*Salix spp.*) are common. Dominant upland vegetation includes quaking aspen (*Populus tremuloides*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*) and some black spruce. Common ground cover species in these more xeric upland sites include alder (*Alnus crispa*), willows, Labrador tea, blueberry (*Vaccinium myrtilloides*) and a variety of lichens.

2.3 Methods

2.3.1. Study Subspecies and Data Collection

All caribou populations in Alberta are woodland caribou, for they all belong to the subspecies, *Rangifer tarandus caribou* (Banfield 1961). It has, however, been accepted that two relatively distinct ecotypes are found in the province: (1) a mountain variety found in the Rocky Mountains of west central Alberta and the foothills near the town of Grande Cache and (2) a woodland or forest-dwelling variety found throughout northern Alberta as well as near Grande Cache (Edmonds and Bloomfield 1984; Edmonds 1986). Figure 2.2 shows the known distribution and abundance of *R. t. caribou* in Alberta and the approximate geographical division between the woodland and mountain varieties. This study applies to the woodland variety.

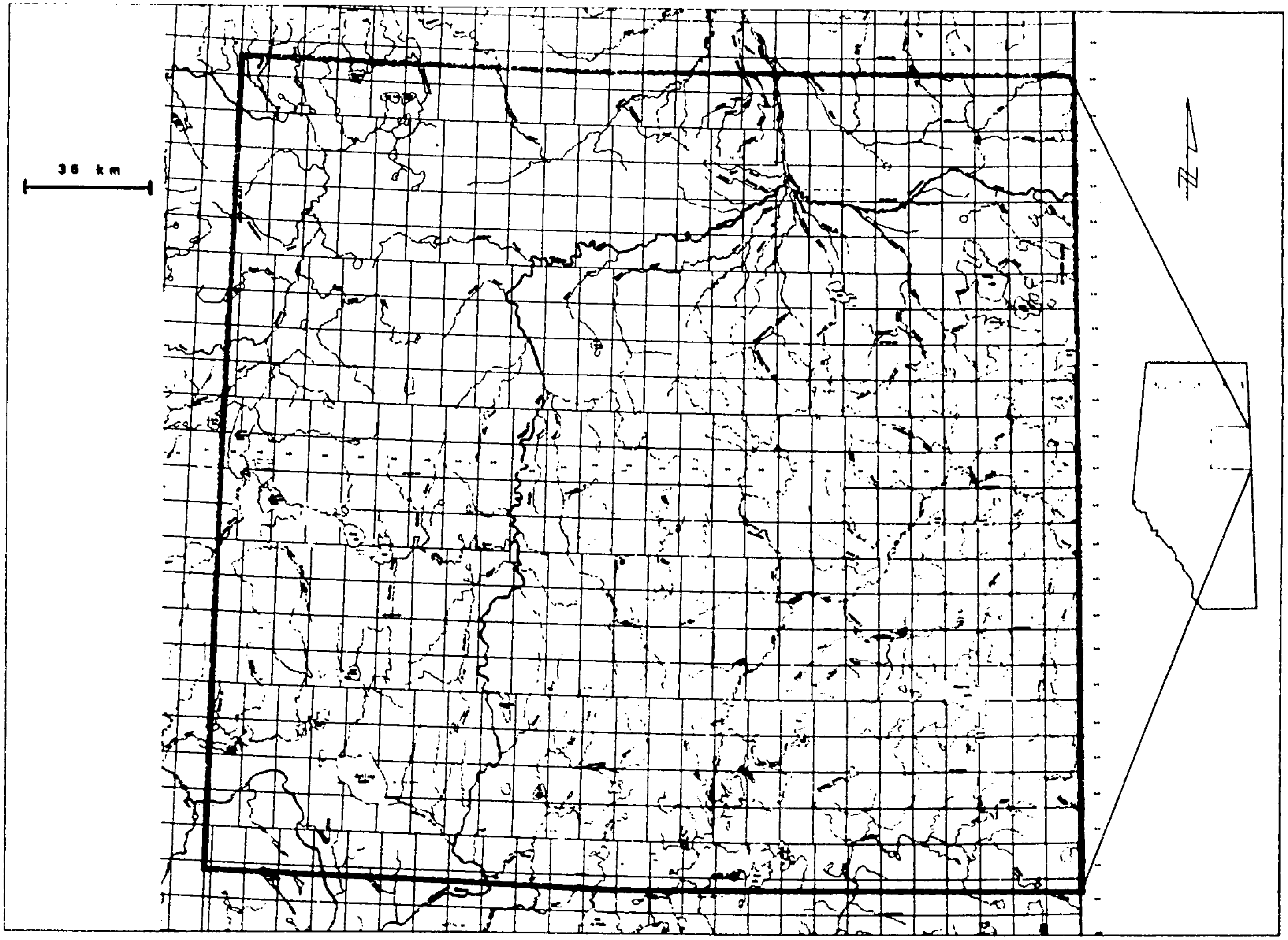

Figure 2.1: Map showing the study area boundary (National Topographic Series Map Sheets 84A, 74D, 83P and 73M), lakes, major and minor watercourses and the Legal Land Description township grid.

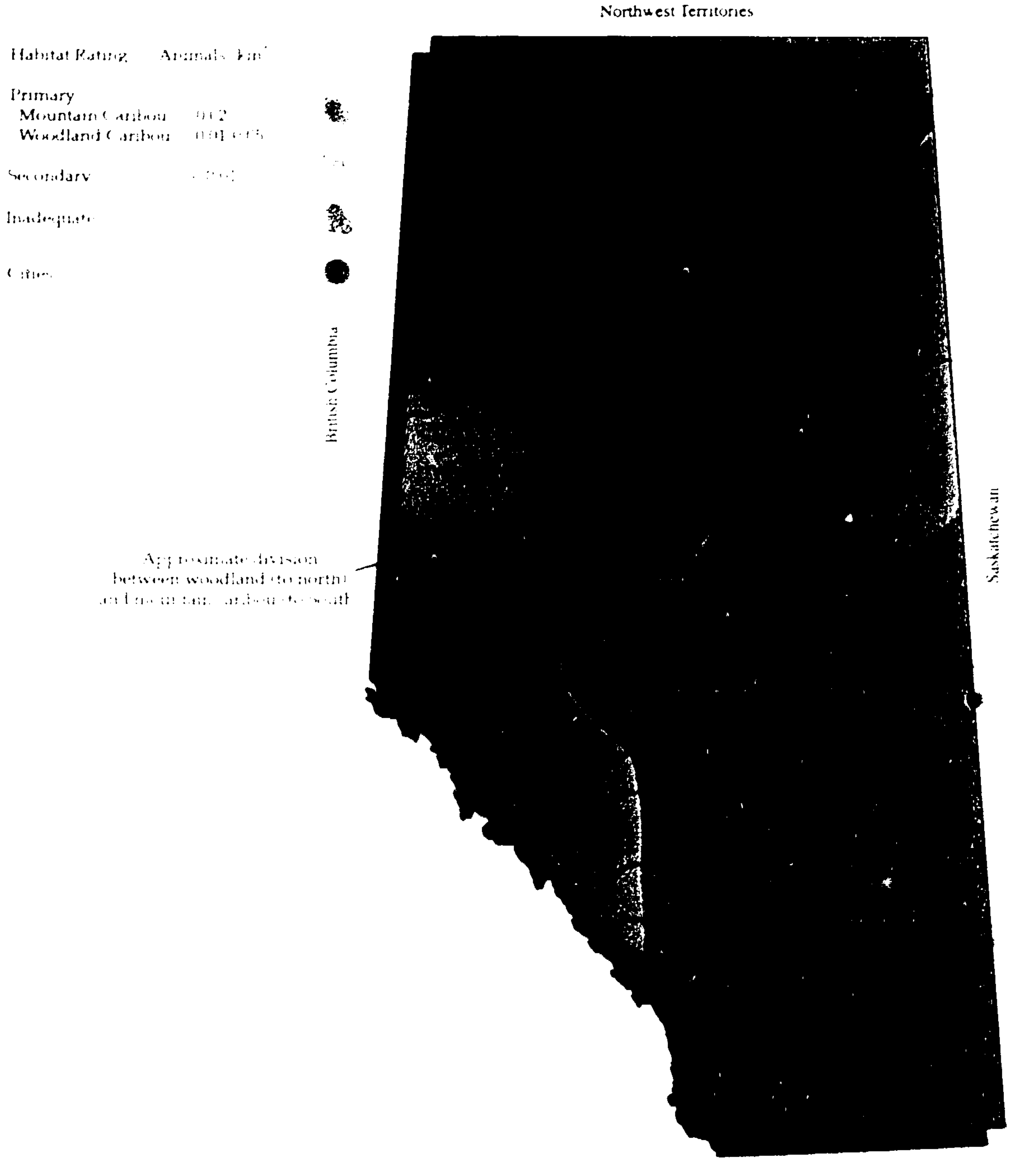

Figure 2.2: The known distribution and approximate population densities of Rangifer tarandus caribou in Alberta (reproduced with permission from Stelfox and Stelfox 1993).

A total of 65 adult woodland caribou were fitted with Very High Frequency (VHF) radio transmitting collars between January 1991 and February 1994 (Table 2.1). Animals were captured[1] using a Bell 206B helicopter and a net-gun[2]. Once the animal was entangled in the net, a ground crew disembarked from the helicopter to process the animal (*i.e.*, measuring body dimensions, extracting blood samples and attaching the transmitting collar). I did not use a set design to locate caribou to be collared in the study area; rather we searched indiscriminately within probable woodland caribou range. When a group of caribou in or near an open area[3] was spotted, the capture crew attempted to isolate the females[4] for collaring, although males were sometimes mistakenly captured. Despite the lack of a sampling design, I believe the number of caribou collared, the total area over which they were collared (*i.e.*, approximately 20 000 km^2) and the subsequent movements made by these caribou ensures a representative sample of woodland caribou in this region of Alberta.

Table 2.1: Collaring schedule for woodland caribou in northeastern Alberta.

NO. FEMALES	NO. MALES	DATES COLLARED
8	2	January 1991
19	5	February 1992
10	1	January 1993
10	1	February 1993
9	0	February 1994
56	9	**Total**

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[1] *Animal treatment procedures were approved by the Canadian Council on Animal Care (CCAC) Animal Welfare Protocol (University of Alberta Biosciences Animal Care Committee No. 587301).*

[2] *The net-gun discharges a 5 x 5 metre mesh net over an animal running from the approaching helicopter.*

[3] *Open areas are required for helicopter manoeuvrability and to avoid entangling the net on vegetation.*

[4] *Females were the target of this study because they provide information on reproduction (the subject of future research in this region) in addition to simple movements and habitat use.*

Animal positions were recorded tri-weekly in the summer[5] and bi-weekly during the rest of the year using a Cessna 185 fixed-wing aircraft equipped with receiver antennae. I estimated individual winter home range sizes by combining the three winter periods[6] from November 1991 to April 1994 (see Results for rationale). I used the Minimum Convex Polygon (MCP) home range estimator as originally described by Mohr (1947) by joining the most outlying location points per individual from the cluster of points collected during the winters. Winter (November - April) ranges were used because industrial activity occurs during this time (see Results section - Chapter 3). Of the 65 caribou collared, I calculated the home range for only 47 due to insufficient data for the most recently collared animals. Ackerman *et al.* (1990) suggested that calculating home ranges using the MCP technique requires a moderate sample size of 20 - 50 location points. As this was not always possible, I included animals with >10 location points in order to maintain a reasonable sample size (*i.e.*, >30), which is the minimum preferred sample size required to represent a population adequately (Aebischer *et al.* 1993).

I defined the habitat composition of the study area using peatland habitat types as described by Vitt *et al.* (1992). Because woodland caribou in northeastern Alberta are commonly observed in the boreal peatland complexes (Fuller and Keith 1981; Bradshaw and Hebert, *submitted),* and often in areas of minimal tree cover, I believe the peatland habitat types of this region better describe the vegetation and drainage characteristics of caribou range than do forest inventory maps. Peatland class description best describes the habitat diversity in lowland areas where caribou are commonly found, but it does not differentiate upland habitats. Instead, this classification combines upland habitats into one category (*i.e.*, habitat G in Table 2.2) where caribou are rarely found in winter (Fuller and Keith 1981).

I determined peatland habitat class distribution with 1:250 000 peatland vegetation inventory maps generated by aerial photography (Vitt *et al.* 1992). Within the study area there are 7 distinct peatland habitat types (Table 2.2), and the approximate

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[5] *Summer caribou positions are recorded for future research and analysis.*

[6] *Although hereafter referred to as three-year home ranges, not all ranges represent three winters combined due to the staggered collaring schedule and animal mortalities.*

peatland coverage in each habitat polygon as calculated by aerial photography (Vitt *et al.* 1992) is also listed in Table 2.2. The distribution of these habitat types in northeastern Alberta is shown in Figure 2.3.

Table 2.2: The peatland habitat types of northeastern Alberta (after Vitt *et al.* 1992).

TYPE	DESCRIPTION	[a]PEATLAND COVERAGE
A	Non-patterned, open peatlands mainly representing minerotrophic fens[b] dominated by *Carex spp.*, *Salix spp.*, *Betula spp.* and Ericaceae.	> 50%
B	Patterned, open minerotrophic fens. Strings and margins with any combination of *Larix laricina*, *Betula spp.* and *Picea mariana*.	> 50%
C	Peatland complexes with >25% forested and >25% open areas, or forested fens with any combination of *L. laricina*, *P. mariana*, *Salix spp.* and *Betula spp.* Peatlands are largely minerotrophic but may have potentially ombrotrophic or oligotrophic areas dominated by *P. mariana*.	> 50%
D	Forested, ombrotrophic bogs[c] or oligotrophic peatlands dominated by *P. mariana*.	85% - 100%
E	As Peatland Habitat A.	15% - 50%
F	As Peatland Habitat C.	15% - 50%
G	Mineral soil (upland areas).	< 15%

[a] *Percentages represent the average coverage of that peatland type within the habitat polygon (e.g., for habitat A, >50% of the ground within each A polygon is non-patterned, open peatland).*

[b] *Peatland complexes affected by mineral soil waters that are relatively enriched in mineral elements (Vitt, in press).*

[c] *The peatland surface is raised above the influence of the surrounding landscape and receives its water and mineral supplies solely from precipitation (Vitt, in press).*

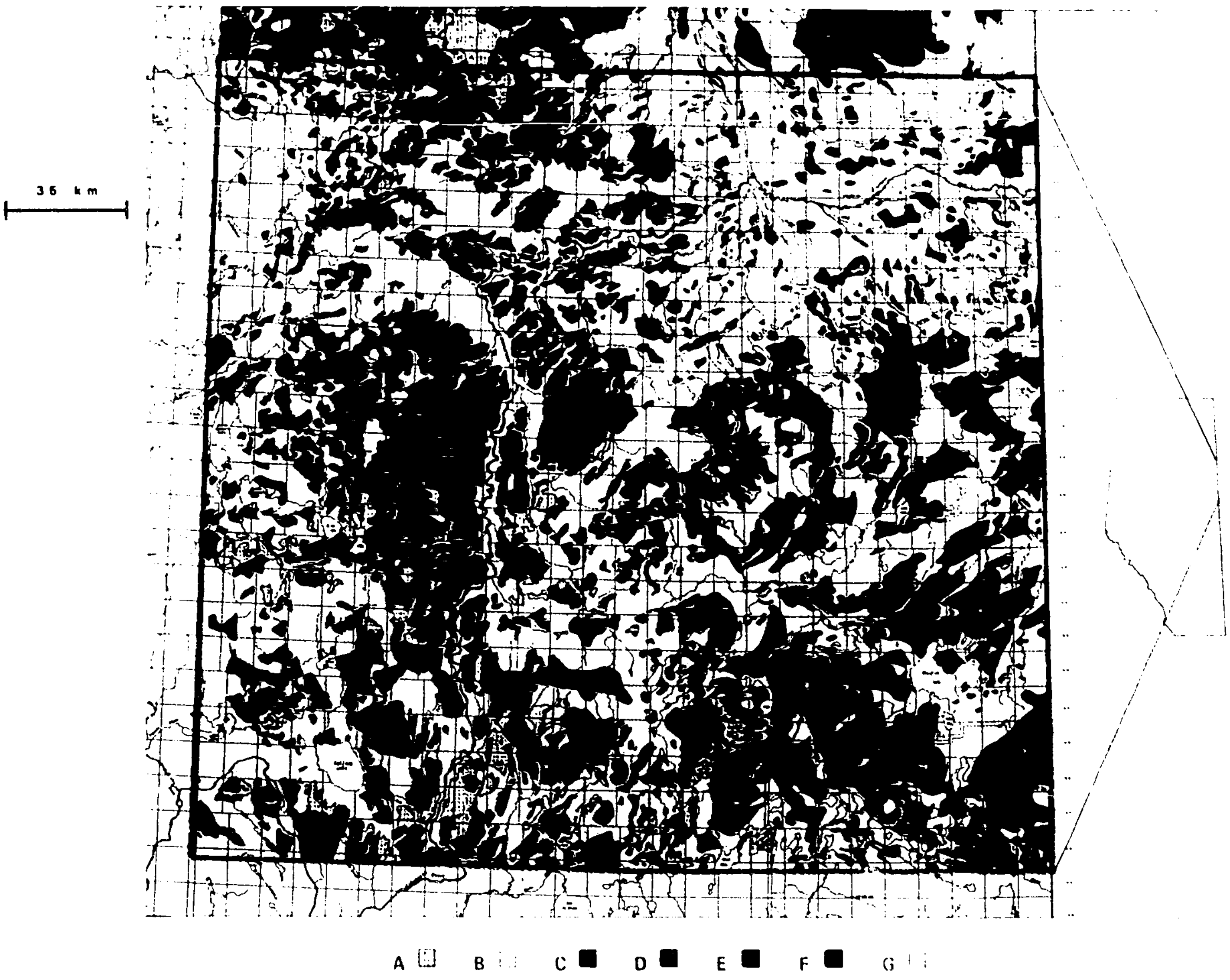


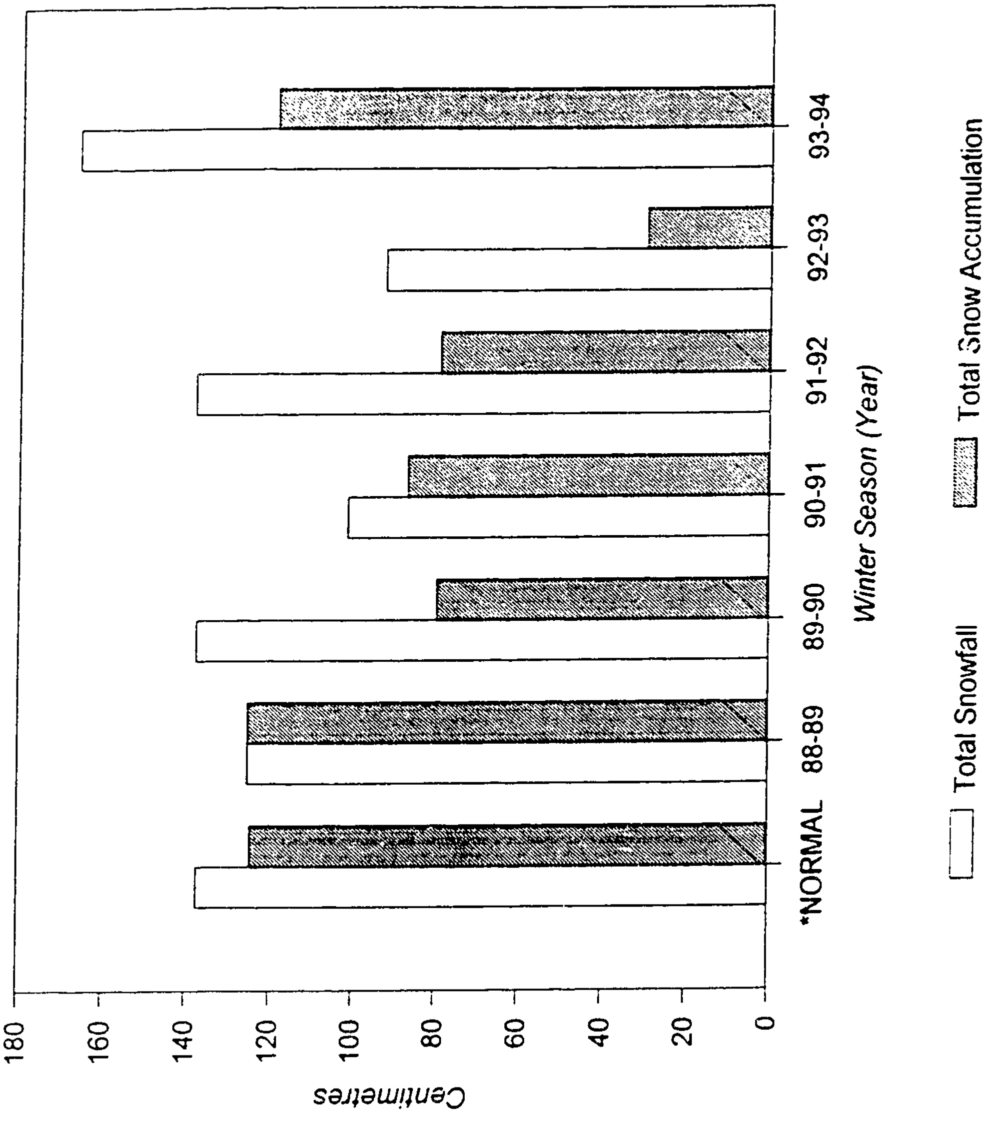
Figure 2.3: Peatland habitat distribution within the study area.

I digitized these maps into a Geographic Information System (GIS) using ARC/INFO® software (Environmental Systems Research Institute, Inc. 1990). To determine second-order selection within the study area, I first identified a study area boundary that reflected the distribution-to-date of all collared caribou locations. The GIS calculated the per cent area of each peatland class in the total study area to establish the proportional availability of each peatland class. For each individual, I expressed the number of animal positions per habitat type as a percentage of the total number of positions recorded during a particular winter season. This provided the observed proportions of habitat use for both second- and third-order selection.

When few observations are taken on many animals, as was the case for this study (biweekly sampling frequency during winter), pooling data between individuals can be justified (White and Garrott 1990). I first pooled the locations from all individuals per year to determine if any major shifts in habitat use and preference had occurred during the three-year study period. As weather conditions were quite different between years (Figures 2.4 and 2.5), I was concerned that pooling data between years might impart misleading results (Schooley 1994).

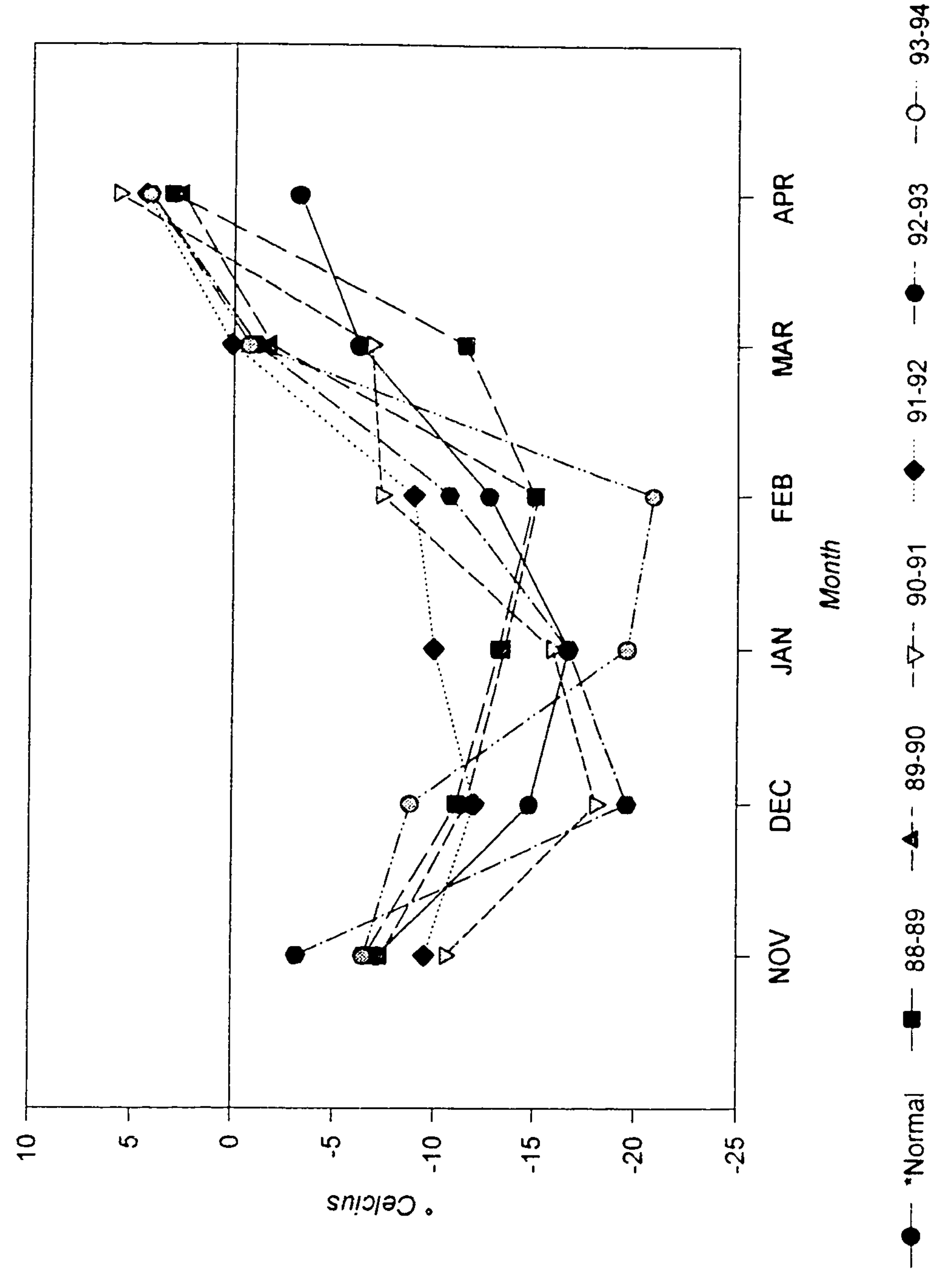
To calculate third-order selection, I determined the per cent area of each peatland class in each animal's MCP home range by overlaying it with the peatland coverage. This gave the expected proportional use of each habitat class per individual if use was random. As in the calculation of second-order selection, I determined caribou use of each peatland class with the radio telemetry data. Note that the difference in second- and third-order selection lies solely in the habitat availability values used in each analysis.

I determined feeding habitat selection using the positions of 94 cratering sites (*i.e.*, where caribou remove snow from the substrate in order to feed on exposed vegetation) during the winter 1993-94 that I located from the air by helicopter (approximately 16 hours flying time). I did not use a set pattern when searching for craters; rather I used an indiscriminate search pattern within the general study area that encompassed all peatland habitat types. A cratering site refers to an area of terrestrial feeding that was composed of 2 to >10 individual craters, each measuring approximately 1 - 2 metres in diameter. I then related these locations to the peatland distribution map to determine



*Mean from 1961-90

Figure 2.4: Total winter snowfall and total month-end snow accumulation (November - April) for the study area (1988-94).



*Mean from 1961-90

Figure 2.5: Mean daily temperatures (November - April) for the study area (1988-94).

in which habitat types feeding occurred. I calculated habitat availability by defining a border around the most outlying cratering sites and by determining the proportion of each habitat type within that polygon. Habitats in which feeding occurred were then compared to habitat availability to determine feeding habitat preference.

2.3.2 Statistical Analyses

I used two methods to analyse habitat use by woodland caribou, the log-ratio analysis of compositions (Aebischer *et al.* 1993) and the Bonferroni analysis described by Neu *et al.* (1974). I performed all analyses using the Microsoft Excel® spreadsheet program. To determine whether habitat use differs significantly from random with the log-ratio analysis of compositions, habitat use and availability proportions must be expressed in relation to another habitat type. The log-ratios of used habitat (y) are expressed as:

$y = \ln (U_{i,n} / U_{c,n})$,

where $U_{i,n}$ = the proportion of habitat *i* used by animal n, and $U_{c,n}$ = the proportion of habitat *c* used by animal *n*. Use and availability log-ratios (d) are calculated using the formula:

$d \equiv y - y_0$,

and $y_0 = \ln (A_{i,n} / A_{c,n})$,

where $A_{i,n}$ = the proportion of habitat *i* available to animal *n*, and $A_{c,n}$ = the proportion of habitat *c* available to animal *n*. I used the peatland habitat C (Table 2.2) as the denominator $A_{c,n}$ because no animals demonstrated zero use proportions for this habitat type. The choice of habitat denominator is, however, largely arbitrary. The residual matrix R_2 is then calculated from the raw sums of squares and cross-products of d (Zar 1984), and matrix R_1 corresponds to the matrix of mean-corrected sums of squares and cross-products calculated from d. From R_1 and R_2, I calculated a chi-squared value (χ_s^2) using the formula:

$$\chi_s^2 = -n \ln \Lambda,$$

where $\Lambda = |R_1| / |R_2|$. When χ_s^2 is greater than $\chi^2_{(\alpha;\, k-1)}$, where k = the number of habitat types, the hypothesis $d \equiv 0$ (habitat use does not differ from random) is rejected.

The log-ratio analysis of compositions also establishes preference ranks for each habitat type and tests for significant differences between them using the formula:

$$d_{i,j} = \ln (X_{Uj} / X_{Ui}) - \ln (X_{Aj} / X_{Ai}),$$

where $d_{i,j}$ = the pairwise difference between habitats *i* and *j*; X_{Ui} and X_{Uj} = use proportions for habitats *i* and *j*; X_{Ai} and X_{Aj} = availability proportions for habitats *i* and *j*. When $d_{i,j}$ is positive, habitat *j* is preferred to habitat *i*; when $d_{i,j}$ is negative, habitat *i* is preferred to habitat *j*. The values $d_{i,j}$ are averaged over *n* individuals and the ratio $d_{i,j}$ mean : standard error gives a *t* value measuring departure from random use. When the ratio is significant at $\alpha = 0.05$, use differs between habitats *i* and *j*. Pairwise differences between all possible habitat comparisons are then displayed in matrix format. This analysis uses the number of animals tracked as the sample size and allows for hypothesis testing between groups and years. This particular analysis does not compare preference of all habitat types to habitat C, rather it compares preference between all habitat types. Log-ratio analysis of compositions also remains powerful in spite of the non-independence of habitat proportions (unit-sum constraint) and the possibility of differential habitat use among individuals (Aebischer *et al.* 1993).

The Bonferroni analysis provided information on habitat use when I could not determine use per individual for the log-ratio analysis of compositions. χ^2 values for each habitat type are calculated using the formula:

$$\chi_i^2 = (U_i - A_i)^2 / A_i,$$

where U_i = the use proportion for habitat *i* and A_i = the availability proportion for habitat *i*. With *k* habitat types, χ_i^2 is compared to χ^2 with $k - 1$ degrees of freedom at $\alpha = 0.05$. To determine preference, avoidance or random use of each habitat type, availability proportions are compared to Bonferroni confidence intervals of use proportions. Bonferroni confidence interval limits are calculated with the formula:

$$U_i \pm z_{\alpha / 2k} \sqrt{[\{U_i (1 - U_i)\} / n]} ,$$

where U_i = use proportion for habitat *i*; $z_{\alpha / 2k}$ = the upper standard normal variate corresponding to a probability tail area of $\alpha / 2k$; k = the number of habitat types; and n = the number of telemetry locations recorded in habitat *i*. When A_i (the availability proportion for habitat *i*) is less than the lower Bonferroni confidence limit for U_i, habitat *i* is said to be preferred. When A_i is greater than the upper Bonferroni confidence limit, habitat *i* is avoided. When A_i lies within the confidence interval, use does not significantly differ from random.

2.3.3 Defining Woodland Caribou Distribution Polygons

Using the results of the habitat preference analyses, I outlined the approximate distribution of woodland caribou within the North-East Region of Alberta. I used the peatland distribution maps (Vitt *et al.* 1992) within map sheets 84H, 74E, 84A, 74D, 83P and 73M (National Topographic System) as the basis for defining distribution boundaries. I will hereafter define the separate distribution areas as woodland caribou distribution polygons.

Of course, it is difficult to precisely define the distribution of wildlife populations based on habitat use and preference analysis due to variable errors in habitat assessment, remote sensing and inventory maps. The researcher must, therefore, rely on a some subjectivity to make decisions in this regard. I first determined the distribution of the preferred habitats within the region. Simply defining the boundaries of these habitats as woodland caribou population patches is illogical because some animals still used areas designated as non-preferred at certain times and in certain areas. Therefore, I defined the more contiguous patches of preferred habitat that would effectively encompass the majority of woodland caribou in this region. A major factor in the definition and selection of these distribution polygons was the minimum area requirement as originally described by MacArthur and Wilson (1967) and Diamond (1975). They suggested that the smaller the island, the smaller the population that inhabits it and the higher the extinction rate or susceptibility to extinction of that population. To avoid the problems often associated with small patches, I attempted to define the boundaries of only the largest, preferred peatland complexes. I did not include small, fragmented areas of preferred peatland habitat types when they were clearly disjunct from larger complexes. Another index used to define islands was the presence of contiguous matrix areas that surrounded the larger preferred peatland complexes. When large areas of matrix separated relatively intact, preferred peatland complexes, the peatland complexes were allocated as separate habitat islands. I also separated these islands when the Athabasca River divided adjacent preferred habitats because caribou movement across this natural barrier is uncommon[7]. I defined secondary woodland caribou polygons as areas between regular distribution polygons containing small, fragmented patches of preferred habitats. I assumed that these areas could be used as movement corridors between larger, more contiguous blocks of preferred habitat. Of course, the delineation of these distribution polygons is somewhat subjective would most likely vary slightly between researchers. I believe, however, that the distribution of preferred peatland complexes is such that any attempt to outline the major areas of woodland caribou distribution using this technique is relatively uncomplicated and accurate.

2.4 Results

2.4.1 Second-order Selection

(a) Annual Variation in Habitat Use

The habitat use frequency distribution from winter 1991-92 to 1993-94 (Figure 2.6) reveals little apparent variation in habitat use between years. I used the Bonferroni

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[7] *I recorded only one instance of a collared caribou crossing the Athabasca River since 1991.*

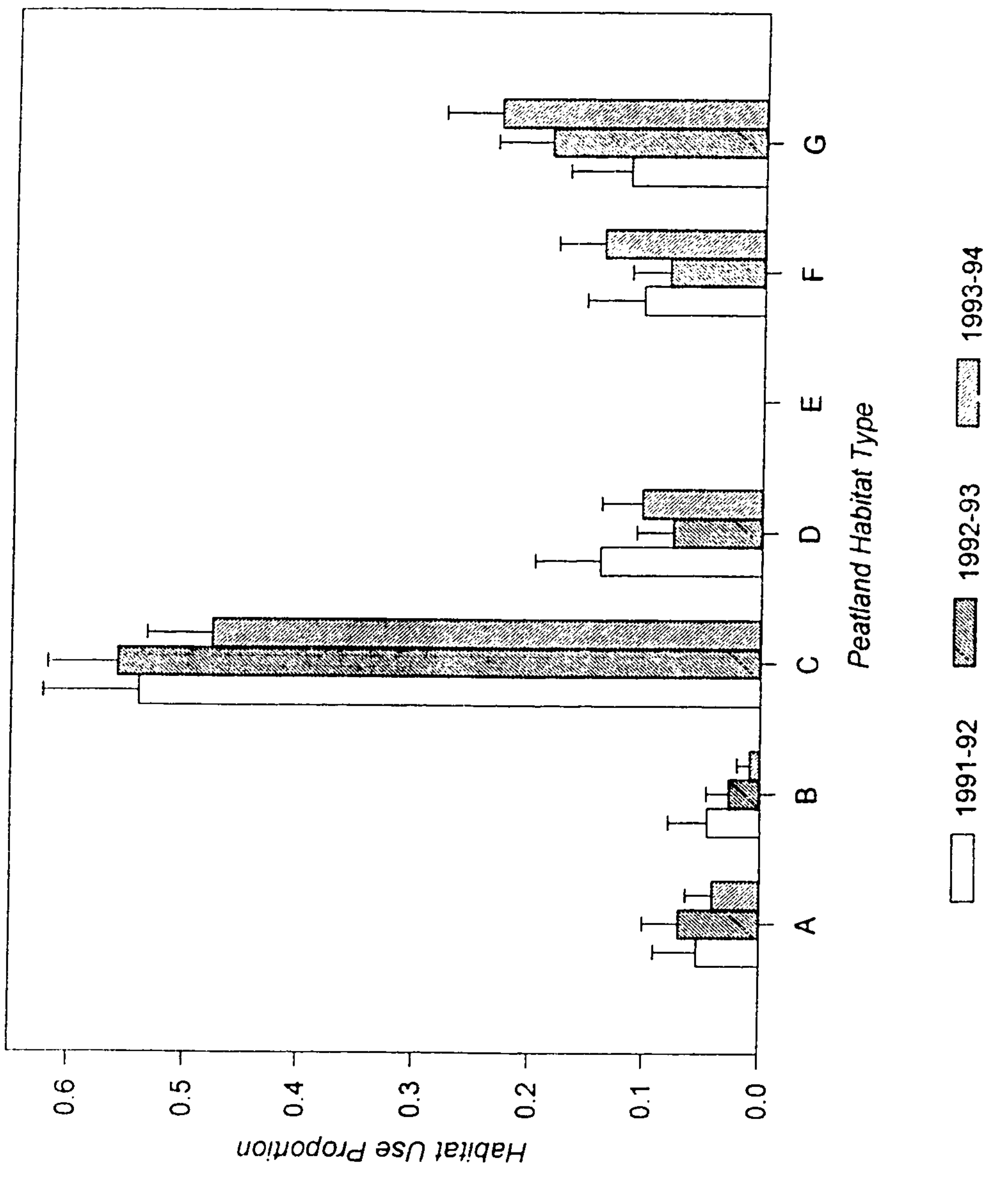


Figure 2.6: Habitat use frequency distribution for woodland caribou in winters 1991-92, 1992-93 and 1993-94 (with 95% Bonferroni confidence intervals).

analysis to determine differential habitat preference between years (Neu *et al.* 1974) (Table 2.3).

Table 2.3: Bonferroni analysis of habitat use for winters 1991-92 to 1993-94. Asterisks indicate conclusion is significant at $\alpha = 0.05$. Conclusions differing between years in boldface.

HABITAT TYPE	[a]MEAN AVAIL	USE 1991-92	CONCL 1991-92	USE 1992-93	CONCL 1992-93	USE 1993-94	CONCL 1993-94
A	0.031	0.054	random	0.070	***prefer**	0.041	random
B	0.013	0.045	*random	0.027	random	0.009	random
C	0.355	0.541	*prefer	0.559	*prefer	0.477	*prefer
D	0.045	0.140	*prefer	0.077	*prefer	0.104	*prefer
E	0.002	0.000	avoid	0.000	avoid	0.000	avoid
F	0.077	0.104	random	0.082	random	0.139	***prefer**
G	0.477	0.117	*avoid	0.186	*avoid	0.230	*avoid

[a] *Represents the mean availability of each habitat type from 1991-92 to 1993-94.*

Differences in pooled second-order preference between years were few: in winter 1992-93 habitat A was preferred, but was used randomly in other years, and in winter 1993-94 habitat F was preferred, but was used randomly in other years. The overall consistency in second-order selection between years despite these two differences, and the relative minor use of habitats A and F suggest that pooling results between years will not produce misleading inferences in habitat selection.

(b) Three-Year Minimum Convex Polygon (MCP) Home Ranges

As I detected no major shifts in habitat use between years, I pooled data between years for each individual. Individual MCP polygons and habitat use were therefore calculated from the cluster of positions taken during the winters from 1991-92 to 1993-94. Apart from one female (NC07) that had a three-year MCP home range of 5 815 km^2 due to extensive movements during winter 1992-93, most radio-collared caribou demonstrated similar use of the region between years. Mean three-year home range area was 613.8 km^2 (s_x = 862.7; n = 47) and ranged from 74.2 km^2 to 5 815.3 km^2. Seven of the 47 animals (14.9%) used in the home range calculations were male. The mean number of location points per individual for which I estimated a home range was 21.5 (s_x = 6.5 ; n = 47).

(c) Analysis by Individual

I transformed the available habitat compositions of the total study area and used habitat compositions (*i.e.*, telemetry locations per individual caribou) to log-ratios y_0 and y and calculated the difference $d \equiv y - y_0$. The residual matrices R_1 and R_2 gave $\Lambda = 0.04909$; habitat use did not differ from random ($\chi^2 = 141.66$; $p < 0.001$; df = 6).

The log-ratio analysis of compositions also gives habitat preference ranking relative to other habitats (Table 2.4).

Table 2.4: Ranking matrix showing mean log-ratios ± standard errors (n = 47) for second-order habitat type comparisons.

HABITATS	A	B	C	D	E	F	G
A	-	0.467 ± 0.635	-3.141 ± 0.511	-0.985 ± 0.709	0.588 ± 0.493	-0.752 ± 0.760	-0.399 ± 0.689
B	-0.467 ± 0.635	-	-3.608 ± 0.451	-1.452 ± 0.703	0.121 ± 0.424	-1.219 ± 0.585	-0.866 ± 0.506
C	2.957 ± 0.566	3.608 ± 0.451	-	2.157 ± 0.527	3.729 ± 0.068	2.389 ± 0.536	2.742 ± 0.462
D	0.985 ± 0.709	1.452 ± 0.703	-2.157 ± 0.527	-	1.573 ± 0.539	0.233 ± 0.817	0.586 ± 0.815
E	-0.588 ± 0.493	-0.121 ± 0.424	-3.729 ± 0.068	-1.573 ± 0.539	-	-1.340 ± 0.511	-0.987 ± 0.429
F	0.752 ± 0.760	1.219 ± 0.585	-2.389 ± 0.536	-0.233 ± 0.817	1.340 ± 0.511	-	0.353 ± 0.649
G	0.399 ± 0.689	0.866 ± 0.506	-2.742 ± 0.462	-0.586 ± 0.815	0.987 ± 0.429	-0.353 ± 0.649	-

Summing the number of positive mean log-ratios per row gives the following habitat ranking, where 0 positive values corresponds to the least-preferred habitat type and k - 1 = 6 positive values corresponds to the most-preferred habitat type (ranks shown above habitat type):

6		5		4		3		2		1		0
C	>	D	>	F	>	G	>	A	>	B	>	E

The log-ratio mean : standard error gives a t value measuring departure from random use and compares use and availability scores between two habitat types. The lines under the habitat ranking indicate that those habitats do not differ significantly from each other at $\alpha = 0.05$.

2.4.2 Third-order Selection

I transformed the available habitat compositions (*i.e.*, MCP home range habitat proportions) and used habitat compositions to log-ratios and the resulting residual matrices R_1 and R_2 gave $\Lambda = 0.05255$; habitat use did not differ from random ($\chi^2 = 138.47$; $p < 0.001$; df = 6). Habitat ranking matrix values are presented in Table 2.5.

Table 2.5: Ranking matrix showing mean log-ratios ± standard errors (n = 47) for third-order habitat type comparisons.

HABITATS	A	B	C	D	E	F	G
A	-	0.678 ± 0.559	-3.057 ± 0.548	0.059 ± 0.708	1.598 ± 0.556	-1.120 ± 0.772	-1.501 ± 0.635
B	-0.678 ± 0.559	-	-3.735 ± 0.415	-0.619 ± 0.661	0.920 ± 0.419	-1.798 ± 0.612	-2.179 ± 0.491
C	2.873 ± 0.602	3.735 ± 0.415	-	3.116 ± 0.534	4.655 ± 0.133	1.937 ± 0.553	1.556 ± 0.392
D	-0.059 ± 0.708	0.619 ± 0.661	-3.116 ± 0.534	-	1.539 ± 0.558	-1.179 ± 0.808	-1.560 ± 0.767
E	-1.598 ± 0.556	-0.920 ± 0.419	-4.655 ± 0.133	-1.539 ± 0.558	-	-2.718 ± 0.521	-3.099 ± 0.393
F	1.120 ± 0.772	1.798 ± 0.612	-1.937 ± 0.553	1.179 ± 0.808	2.718 ± 0.521	-	-0.381 ± 0.667
G	1.501 ± 0.635	2.179 ± 0.491	-1.556 ± 0.392	1.560 ± 0.767	3.099 ± 0.393	0.381 ± 0.667	-

The lines under the habitat ranking indicate that those habitats do not differ significantly from one another at $\alpha = 0.05$:

6 5 4 3 2 1 0
C > G > F > A > D > B > E

2.4.3 Feeding Habitat Selection

I compared the proportional habitat use (*i.e.*, habitats in which I found feeding craters) and habitat availability of 94 cratering sites during 1993-94 to determine feeding habitat preference. Because I could not analyse by individual, I used both the Bonferroni analysis to provide a test for significance (Table 2.6) and the log-ratio analysis of compositions to construct a preference rank (Table 2.7).

Table 2.6: Bonferroni analysis of cratering (feeding) sites (n = 94). Asterisks indicate conclusion is significant at α = 0.05.

HABITAT TYPE	USE	AVAILABILITY	CONCLUSION
A	0.096	0.027	*random
B	0.000	0.015	avoid
C	0.447	0.393	random
D	0.245	0.060	*prefer
E	0.000	0.001	avoid
F	0.106	0.075	random
G	0.106	0.430	*avoid

Table 2.7: Ranking matrix showing log-ratios for cratering habitat type comparisons.

HABITATS	A	B	C	D	E	F	G
A	-	6.308	1.157	-0.130	5.761	0.933	2.680
B	-6.308	-	-5.151	-6.438	-0.547	-5.375	-3.628
C	-1.157	5.151	-	-1.287	4.605	-0.224	1.523
D	0.130	6.438	1.287	-	5.891	1.063	2.810
E	-5.761	0.547	-4.605	-5.891	-	-4.828	-3.081
F	-0.933	5.375	0.224	-1.063	4.828	-	1.747
G	-2.680	3.628	-1.523	-2.810	3.081	-1.747	-

As it was not possible to calculate cratering habitat use per individual, it was impossible to test for significance between habitat-use ranks using the log-ratio analysis of compositions. The number of positive log-ratio values per row gives a habitat ranking similar to the results generated by the Bonferroni analysis:

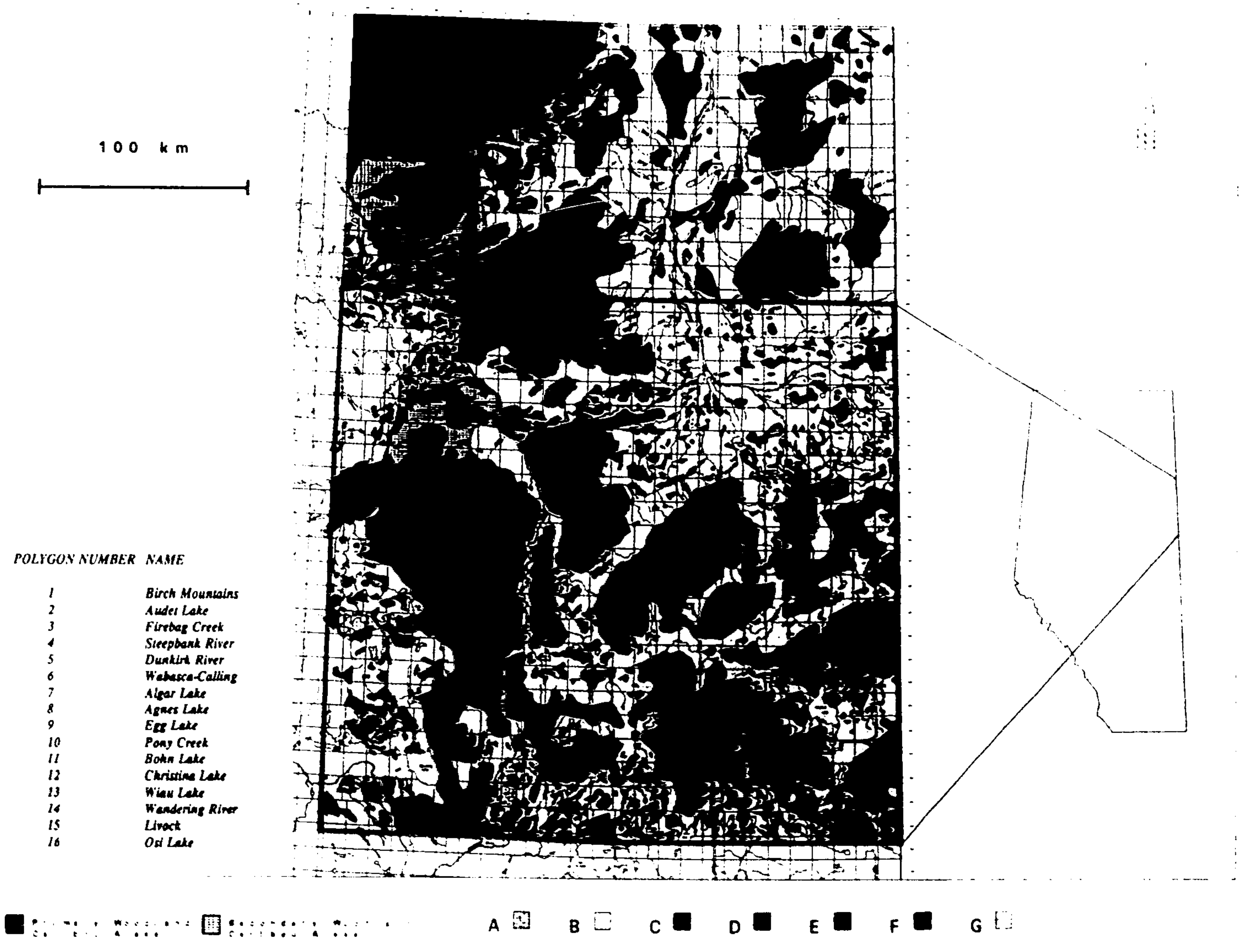
6 5 4 3 2 1 0
D > A > F > C > G > E > B

For feeding sites, habitat D is preferred while habitats G, E and B are avoided.

2.4.4 Characteristics of Woodland Caribou Distribution Polygons

Because of the conclusive results of the habitat preference analysis, I defined a series of distribution polygons represented primarily by habitats C and D as the important woodland caribou sub-population boundaries. These polygons were essentially defined by the natural distribution of the conspicuous peatland complexes within the region.

Figure 2.7 shows the boundaries of the woodland caribou distribution polygons. The natural patterns of the peatland structure in this region yielded 14 independent, primary distribution polygons and 2 secondary polygons that could potentially support movement between neighbouring primary habitat polygons. The polygons defined incorporate 81.55% of the total area represented by habitat C (14 294 km^2 of 17 528 km^2) and 96.88% of the total area represented by habitat D (1 953 km^2 of 2 016 km^2) within map sheets 84H, 74E, 84A, 74D, 83P and 73M. Total area of all six map sheets is 82 225.65 km^2. The areas enclosed by the polygon boundaries are presented in Table 2.8.



POLYGON NUMBER	NAME
1	Birch Mountains
2	Audet Lake
3	Firebag Creek
4	Steepbank River
5	Dunkirk River
6	Wabasca-Calling
7	Algar Lake
8	Agnes Lake
9	Egg Lake
10	Pony Creek
11	Bohn Lake
12	Christina Lake
13	Wiau Lake
14	Wandering River
15	Livock
16	Ori Lake

Figure 2.7: Woodland caribou distribution polygons based on peatland habitat associations.

Table 2.8. Area characteristics of woodland caribou distribution polygons.

POLYGON NO.	NAME	AREA (km^2)	% TOTAL AREA	ZONE TYPE*
1	Birch Mountains	5 146	6.26	1
2	Audet Lake	1 148	1.40	1
3	Firebag Creek	487	0.59	1
4	Steepbank River	1 035	1.26	1
5	Dunkirk River	3 662	4.45	1
6	Wabasca-Calling	6 775	8.24	1
7	Algar Lake	1 876	2.28	1
8	Agnes Lake	451	0.55	1
9	Egg Lake	2 286	2.78	1
10	Pony Creek	507	0.62	1
11	Bohn Lake	1 019	1.24	1
12	Christina Lake	1 228	1.49	1
13	Wiau Lake	2 641	3.21	1
14	Wandering River	1 114	1.35	1
15	Livock	1 438	1.75	2
16	Osi Lake	2 389	2.91	2
	TOTAL	**29 376**	**35.73**	

* Primary Areas = 1; Secondary Areas = 2

Mean primary polygon area is 2 098.3 km^2, or 2.55% of the entire mapped region.

2.5 Discussion

2.5.1 Habitat Selection

For second- and third-order selection, habitat class C (peatland fen complexes with >25% forested and >25% open areas) was the most used and preferred habitat component for woodland caribou in northeastern Alberta. Second-order selection revealed that other habitats were preferred significantly less than habitat C, although they differed insignificantly from one another. Third-order selection also showed significant preference for habitat C, demonstrating that woodland caribou choose localities with approximately the same availability of habitat types as are available across the entire region because only availability proportions varied from second- to third-order analysis. This result confirms that habitat C is important at both the population and individual scales, and its selection is governed possibly by food preferences and availability (Darby and Pruitt 1984). Indeed, other studies of woodland caribou have demonstrated preferential use of similar lowland habitat types during winter (Fuller and Keith 1981; Darby and Pruitt 1984)

Combining three years of telemetry data to calculate winter home range area seems appropriate because woodland caribou often return to the same wintering area year after year (Cumming and Beange 1987; Edmonds 1988). Fuller and Keith (1981) reported mean annual home range areas of 539 km^2 for female woodland caribou in northeastern Alberta, a value similar to the mean home range area of 613.8 km^2 calculated for caribou in this study. It would have been preferable to calculate home range area per winter season if sufficient data had been available because fewer assumptions would have to be made concerning individual habitat availability. Moreover, I would have been better able to discuss differences in habitat preference between years.

Feeding selection revealed a preference for habitat D (forested bogs with 85% - 100% peatland coverage), and use did not differ significantly from random for habitat C at this level. This fact reveals a more subtle component of habitat selection for woodland caribou that would otherwise be missed with second- and third-order habitat selection analysis. Bogs (habitat D) are always acidic and dominated by peat mosses (*i.e., Sphagnum spp.*); they also have fewer nutrients owing to decreased seasonal water flow due to higher elevation above the surrounding landscape (Vitt, *in press*). Decreased water flow in bogs creates a more xeric substrate where trees and dry surfaces without pools of water are common (Glaser and Janssens 1986; Vitt, *in press*). These drier sites provide excellent substrate for lichens of the genus *Cladina*, particularly *C. mitis*, *C. stellaris* and *C. rangiferina* (Vitt et al. 1988). Indeed, in most caribou feeding craters that I examined throughout the study area, I found *Cladina spp.* lichens to be the most common; *Cladina spp.* lichens are a major food item for caribou during the winter season (*e.g.*, Ahti 1964; Ahti and Hepburn 1967; Desmeules and Heyland 1969; Fuller and Keith 1981; Edmonds and Bloomfield 1984). This does not necessarily mean that lichens are a critical food item during winter; rather they are an important food source that may be supplemented by vascular plants of higher nutritional value (Ahti and Hepburn 1967; Kelsall 1968; Klein 1982; Edmonds and Bloomfield 1984; Stelfox and Stelfox 1993).

The Bonferroni analysis between years did not reveal any major shifts in second-order selection during the three-year study period. However, the small difference in preference for habitat F (forested fens with 15 - 50% peatland coverage) may be explained in part by the above average snow conditions of 1993-94. It appeared that caribou were using denser timber stands during the periods of high snow accumulation (late January to early March 1994 - Figure 2.4), and especially when the snow surface was crusted (late February to early March). When travelling on the ground, I noticed that snow crusts were thicker and more solid in open areas than in denser forest stands. Perhaps it was easier for caribou to move and feed in these treed areas where the snow was softer; indeed, observations of woodland caribou moving to denser timber stands under similar snow conditions were reported by Fuller and Keith (1981), Darby and Pruitt (1984) and Edmonds and Bloomfield (1984). The switch from random use to selection for habitat F in winter 1993-94 supports the view of movement to more forested areas. The lower peatland coverage, and hence the higher proportion of xeric mineral soils, suggests greater timber coverage in this habitat type (Vitt, *personal communication*). With greater timber coverage and the corresponding softer snow, locomotion and cratering would be easier. As well, this type of habitat shift may restrict the quantity of potential feeding territory to a smaller proportion of the overall range (Henshaw 1968). The preference of habitat F did not, however, affect the selection of habitats C and D which were consistently preferred in all years.

White and Garrott (1990) believed that much of the selection shown by animals is neutral relative to their fitness, because individual animals often show differences in their preferences. Probably only habitat preferences that are consistent across individuals actually benefit fitness, which may be the case for woodland caribou selecting habitat C. Nonetheless, the demonstration that a habitat type is preferred does not necessarily mean it is critical. Only if its loss affects an animal's fitness can a preferred habitat type be termed as critical (White and Garrott 1990). Although I was unable to test the hypothesis that habitat C or D are critical to woodland caribou, I believe that large areas of these peatland types are crucial to the survival of this species in northeastern Alberta.

2.5.2 Woodland Caribou Distribution Polygons

Woodland caribou in northeastern Alberta are patchily distributed, an observation supported by numerous surveys (Bradshaw and Hebert, *submitted)*. Also, the conclusive results of both second- and third-order selection confirm that these animals restrict the majority of their movements to specific habitat types. The habitat distribution polygons represented primarily by habitats C and D were essentially defined by the natural distribution of the conspicuous peatland complexes within the region. And because most D polygons were nested within a complex of C polygons, defining the distribution polygon boundaries was rather uncomplicated.

The mean primary polygon area (2 098.3 km^2) far exceeds the total area over which male woodland caribou ranged throughout the year (1 196 km^2) described by Fuller and Keith (1981) and the mean three-year winter home range area for the collared animals of this study (613.8 km^2). The three smallest distribution polygons (Agnes Lake, Firebag Creek and Pony Creek) cover areas less than the 613.8 km^2 mean winter home range area, but they were deemed large enough and independent within the mineral soil matrix to potentially support quasi-autonomous sub-populations. Furthermore, their proximity to other, larger polygons suggests a high potential for maintaining continuous sub-populations, based on the theory that population subsistence is a function of proximity to larger, source populations (MacArthur and Wilson 1967). I also compared the existing telemetry location database to determine the percentage of all caribou positions found within the defined distribution polygons. The polygons incorporate 98.52% of all locations (*i.e.*, all seasons) to date (2 404 of 2 440 points from 9 January 1991 to 16 April 1994), suggesting high accuracy in the description of distribution of woodland caribou in the study area.

The notion that woodland caribou populations inhabiting these polygons represent a metapopulation (Levins 1970) stems from my interpretation of Hanski and Gilpin's (1991) definition of metapopulations as: *«...systems of such local populations connected by dispersing individuals»*. Indeed, the relative lack of caribou observations outside of these polygons indirectly suggests they are more or less discrete sub-units or local sub-populations of the regional population. Furthermore, even a sample of 65 marked individuals over three years has provided definite cases of movement between polygons. In 1992, female NC07 moved from the Wabasca-Calling polygon where she was first collared to the Dunkirk River polygon via the Livock secondary area. She returned to Wabasca-Calling later that year. Another female, NC45, moved from the Wabasca-Calling polygon to Agnes Lake polygon with her calf in July 1993 by swimming across the Athabasca River; she has yet to return. Although it is doubtful that true extinction and recolonization have occurred within the habitat polygons defined at this scale, sufficient movement between relatively discrete sub-populations may maintain genetic flow and the viability of the regional population.

The boundaries of these habitat polygons will later serve as management zones where land-use regulations may differ significantly from the surrounding matrix in an attempt to reduce the potential for conflict between woodland caribou and other species with industrial land use (see Management Recommendations - Chapter Five). Secondary areas should be considered possible movement areas and protected from extensive human use. It is, however, important to recognize that although many of the techniques used to define these boundaries were similar to those used in defining multi-species reserve systems, this is not intended as a reserve system. Rather, these areas should serve to identify primary caribou habitat use within northeastern Alberta where industrial land use should be scrutinized to reduce conflict with woodland caribou.

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CHAPTER THREE: RESPONSE TO SIMULATED PERTURBATION

3.1 Introduction

As discussed in Chapter One, caribou demonstrate varied responses to different perturbations under different conditions. Without data on behavioural modification and the corresponding energetic consumption in relation to a specific form of disturbance, it is difficult to extrapolate conclusions from other perturbation studies in dissimilar habitats; neither is it justifiable to generalize the reaction of caribou to disturbance based on a single season or cohort (Roby 1978). The cost of any harassment depends on the distance travelled away from the perturbation source, the cost of excitation before and after locomotion and the food-intake opportunities lost as a consequence (Geist 1978). Harassing stimuli are those which precipitate excitement, such as stimuli that depart from the predicted or familiar physical and social milieu of the animal and those known as stimulus contrast, such as loud or penetrating sudden noises (Geist 1975).

Harassment exists when regulatory systems require energy that would otherwise be available for maintenance, growth and reproduction, such as when environmental contingencies are severe and prolonged (Snyder 1975). When faced with harassment, animals achieve internal organismal stability by sacrificing functions less immediately vital, such as growth, reproduction and resistance to infectious disease and parasitism (Geist 1975; Snyder 1975). Energy expenditure caused by excitation can temporarily double the expenditure for maintenance, and as a rule, excitement increases an animal's metabolism about 25 per cent more than that required for long-term maintenance (Geist 1978).

Exploratory petroleum work (geophysical survey) is a potentially harassing stimulus and perhaps the most threatening stage of petroleum development to woodland caribou. This is because it is often based on a minimum of advance planning, resulting in a spatially and temporally unpredictable series of separate harassment events. The unpredictable nature of exploration usually precludes habituation in large mammals. Furthermore, secret and duplicative exploratory work by several companies can multiply these effects (Klein 1973).

Geist (1971b) suggested that the typical behaviour of a large animal when encountering a harassing stimulus includes several phases. The animal becomes excited if an unpleasant object or any evidence associated with it is sensed, and remains excited even after the object disappears. A previously disturbed animal often avoids the locality where the disturbance was experienced and will generalize a perceived perturbation to all similar objects and localities, either avoiding them or becoming disturbed upon sensing them. Whether woodland caribou respond similarly to petroleum exploration in Alberta's boreal forest is unknown.

In this chapter I describe an experiment designed to determine the degree to which woodland caribou respond to petroleum exploration in northeastern Alberta. The experiment required I simulate noise disturbance produced by petroleum exploration, so I describe the procedures of a typical exploration operation and the noise generated from it. This information was essential in the choice of an effective experimental design and equipment required to best simulate the noise characteristics. I measured several aspects of woodland caribou behaviour in response to this type of disturbance, including changes in movement rate, linear displacement, feeding behaviour and habitat use. The synthesis of the combined results permitted a discussion on the behavioural modifications made in response to a single encounter with simulated petroleum exploration.

The following predictions relate to the behavioural and locomotory reactions expected when woodland caribou are exposed to simulated seismology perturbation. I expect that animals exposed to loud noise increase their daily and hourly rates of movement, linear displacement and rapid movement behaviour, whereas Control animals do not. I also expect exposed animals to decrease the time spent feeding and increase the number of habitat shifts made to non-preferred habitat. Moreover, I predict that many of the measured parameters will differ between years because of differences in mean snow depth.

3.2 Methods

A broad measure of the effects of petroleum exploration noise on woodland caribou movements and behaviour would not have been possible at the population scale because of the vastness of the study area and the associated lack of control. For this reason I designed my experiment to examine changes in behaviour, movement and habitat use in individuals. This approach allows for greater control of experimental conditions and an increased ability to detect subtle responses.

3.2.1 Petroleum (Geophysical) Exploration

To determine the average duration and degree of harassment incurred by petroleum exploration, I first made detailed observations of the exploration process. From 3 - 6 March 1993 and again from 29 - 31 January 1994, I followed five petroleum exploration teams into the field to determine the nature of their operations.

There are four principal phases to any geophysical exploration project in northeastern Alberta. First, a surveying crew marks the areas to be later explored and possibly developed. A second crew consisting mainly of bulldozers and personnel equipped with hand-held chainsaws clear a 5 - 7 metre-wide line (hereafter referred to as a «*seismic line*») through the forest (*i.e.*, removing all trees and other obstacles) following the markers originally laid out by the surveying crew. Within days a drilling rig passes along the cleared seismic line and drills holes approximately 10 metres deep and 30 metres apart the entire length of the line[1]. Approximately 0.25 kg of trinitrotoluene (TNT)[2] are placed in each hole and covered with the excavated mud. Finally, a recording crew strings a line of geophones[3] the length of the cleared and drilled line. The TNT in each hole is sequentially detonated and the resulting

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[1] *Seismic lines may vary in length from <1 km to >40 km.*

[2] *Although the amount of TNT may vary between programmes, I did not vary the noise intensity during treatment of Impact animals..*

[3] *Small, vibration-sensitive instruments fastened to 10-centimetre pegs secured into the ground at regular intervals along a cleared seismic line. Geophones are linked to one another and to a central recording unit.*

reverberations are recorded via the geophones that are linked to a mobile recording unit. After the exploration process is complete, bulldozers «rollback» previously-cleared debris onto the seismic line to impede future access by all-terrain vehicles.

Table 3.1 summarizes the typical characteristics of a seismology programme in lowland areas of minimal topographic relief. Given the rate of progression along a seismic line, I determined that when remaining still I could hear the noises generated from each phase for 0.75 - 1.5 hours. This provided the basis for a 1-hour perturbation exposure period (during perturbation). The noise intensity of a Zon Gun®, a type of propane cannon[4] , used as the source of perturbation varied from 90 - 110 decibels (dB), which was similar to the average noise intensity of each phase of the seismology programme, although the cannon noise was most similar to the blasting phase. I set blast frequency to 1 blast/minute, thus mimicking the intervals of loud noise produced by the exploration procedures.

Table 3.1: Characteristics of a typical seismology programme in peatland areas.

PHASE	SOUND INTENSITY (dB)[a]	DISTANCE AUDIBLE FROM SOURCE (km)	MEAN PROGRESSION RATE (km/hr)
surveying	minimal	minimal	-
clearing & rollback	60 - 70	1.0	0.4
drilling	85 - 95	1.5 - 2.0	0.5
recording	95 - 110	1.5	1.0

[a] Measured with a noise intensity meter.

3.2.2 Measuring Movements of Undisturbed Woodland Caribou

To determine if caribou remain in an area small enough to perform an experiment measuring the short-term movement rates of individuals, it was necessary to determine

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[4] *Propane cannons are often used by farmers to frighten birds from crop fields.*

typical daily movement rates of caribou during winter. To achieve this, I referred to data I had collected during the week of 12 - 18 February 1993. Twice per day I located, using a fixed-wing aircraft (Cessna 185), the positions of 7 caribou previously equipped with radio collars. The aircraft monitored positions at an altitude of approximately 450 - 550 metres above ground level (AGL) which is sufficient to avoid eliciting an excitatory response by the animals (Calef *et al.* 1976; Miller and Gunn 1979; Harrington and Veitch 1992).

The mean daily movement rates and cumulative linear displacement of undisturbed woodland caribou (Figure 3.1) translate to a mean daily linear displacement of 1.56 km (*i.e.*, during 24 hours). Cumulative linear displacements are expressed as the mean displacement from the first position recorded on day 0 to each consecutive day. These data demonstrate that daily movements of caribou are small enough that an individual animal may be approached by someone on the ground and followed reasonably well during a disturbance experiment requiring several hours of monitoring.

3.2.3 Design for Perturbation Experiment

I used an adapted version of more a traditional method of impact analysis, the Before-After-Control Impact (BACI) design (Green 1979). In Green's (1979) method, a sample is taken before and another sample taken after a possible impact, in a disturbed (Impact) and undisturbed (Control) location (Underwood 1994). I adapted this design for two important reasons. First, my design has a temporal replication, as originally suggested in Bernstein and Zalinski (1983) and Stewart-Oaten *et al.* (1986) to avoid the situation where differences may be caused by something other than the human activity in question. Second, a spatial replication for both Impact and Control locations is necessary to separate human-induced effects from natural variation and local trends (Underwood 1994).

I monitored the behaviour and movement of individual caribou during three separate test periods as originally suggested by Miller and Gunn (1979):

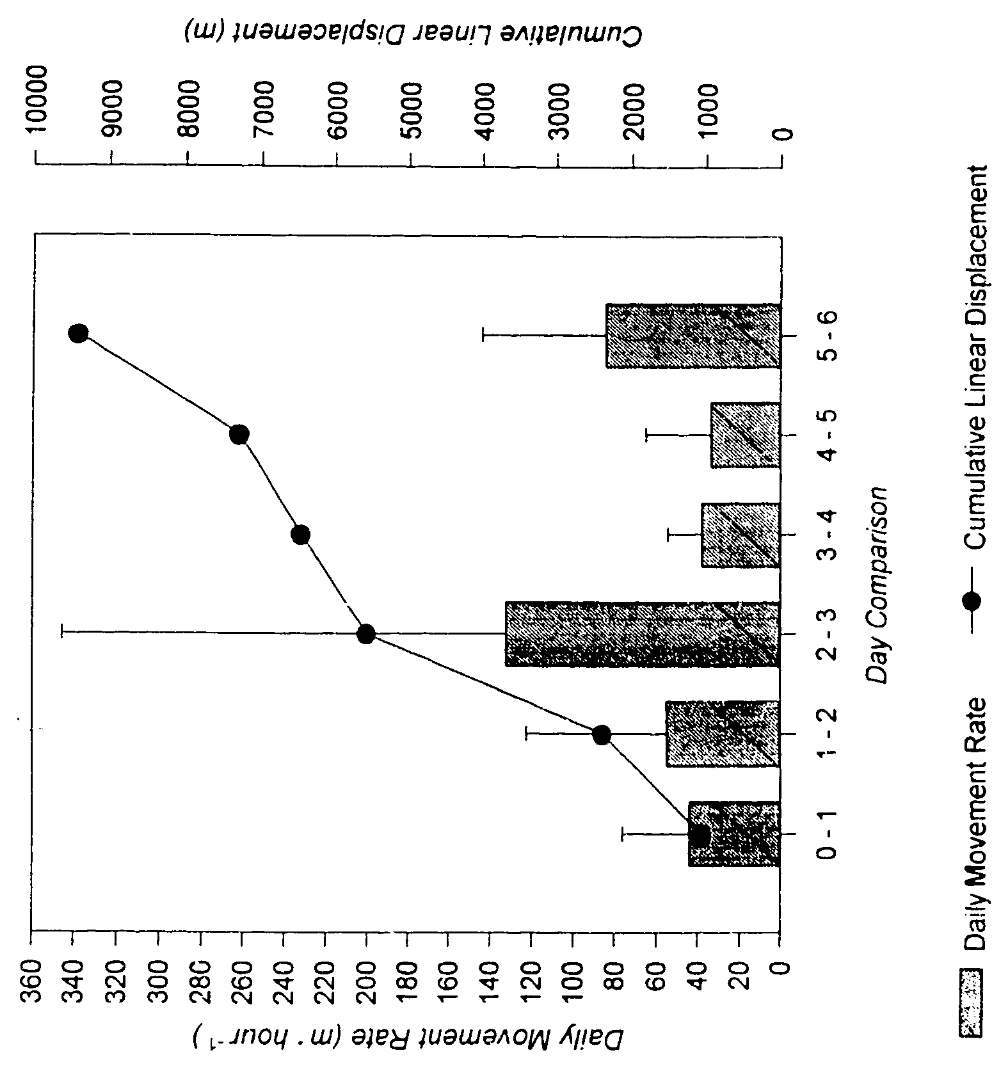

Figure 3.1: Mean daily movement rates (+ standard deviation) and cumulative linear displacement of undisturbed caribou. Day 0 corresponds to the first day of recording (e.g., comparison 0-1 refers to the movement rate from the first afternoon of recording to the afternoon of the second day).

(1) One hour before noise perturbation (pre-perturbation period, or PreP),
(2) One hour during perturbation (during-perturbation period, or DurP) and
(3) One hour following perturbation (post-perturbation period, or PosP).

3.2.4 Experimental Methods

Each animal tested was located from a Cessna 185 at approximately 10-minute intervals during the three-hour experiment. The altitude at which we flew and the vegetation density made it difficult to monitor test animals visually. Therefore, I used an on-board Global Positioning System (GPS) in conjunction with the radio telemetry receiver to obtain latitude/longitude coordinates for each animal position without necessarily seeing the animal. GPS average precision based on 7 different recordings of the same location was 142.8 m (s_x = 69.3 m). To test the accuracy of recorded animal positions using radio telemetry from the aircraft, I randomly placed 10 radio collars around our base camp and recorded latitude/longitude with a mobile GPS unit. The following day I asked the pilot to locate the collars (the pilot had no prior knowledge of the collar positions) and record their position using the on-board GPS unit. The average disagreement between ground and air locations was 151.3 m (s_x = 36.2 m).

In winter 1993 I examined the responses of 5 collared caribou to disturbance using the experimental design described above. In 1993, I treated only 5 Impact animals to determine if the experimental design was feasible. The design was workable so I increased the sample size to 10 (Impact animals) and added 10 Control animals in the 1994 winter experiment. I chose the treatment animals from the pool of collared caribou possessing activity sensors[5] and then randomly assigned either an Impact or Control treatment to each of these animals, thus permitting only one animal to be tested per day[6]. Control animals were treated in the same manner as Impact animals,

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[6] *Because only 12 collars possessed activity sensors in 1994, an additional 8 collared animals were randomly chosen from the entire sample of collared caribou. I randomly chose 5 collared caribou equipped with activity sensors west of the Athabasca River for treatment in 1993.*

[5] *Animal treatment procedures were approved by the Canadian Council on Animal Care (CCAC) Animal Welfare Protocol (University of Alberta Biosciences Animal Care Committee No. 587301).*

except Control animals were not exposed to the noise of the propane cannon.

A Bell 206B helicopter transported one research team member to within an average of approximately 1 kilometre from the caribou to be treated that day. Once on the ground, the team member carried the cannon and propane tank on foot to within a distance of 200 - 300 metres from the animal. Using two-way radios to coordinate timing between the ground person and the monitoring airplane flying above, cannon firing was initiated one hour into the experiment and continued for one hour. After the blasting was complete, the ground person returned to the awaiting helicopter (that was shut down during the entire procedure) and was transported away from the experimental area. The airplane monitoring continued for another hour after blasting ceased. I also recorded daily locations of the test animals for 2 days prior to treatment and for 2 days following treatment (*i.e.*, 4 locations per test animal). I compared daily movements before and after treatment to detect more long-term changes in daily movement rate.

3.2.5 Behavioural Data Collection

Of the 20 radio collared animals monitored (10 Control and 10 Impact) in 1994, 12 collars (6 Control and 6 Impact) were equipped with mercury tip-switch activity sensors that measure changes in animal behaviour (all 5 animals treated in 1993 wore these collars). These sensors provide information as to the position of the animal's head relative to the ground. Beyond a predetermined angle relative to flat ground, the pulse rate of the emitting frequency increases approximately two-fold (Lotek Engineering Inc. 1992). In order to interpret the relationship between pulse rate and specific behaviour, it was necessary to validate my interpretations based on observable, normal behaviours. This proved to be impossible in the field because of the extreme difficulty in observing free-ranging woodland caribou for sufficient time.

I confirmed my behavioural interpretations of the activity data from 15 - 17 June 1993 using captive female woodland caribou at the City of Saskatoon (Saskatchewan) Forestry Farm Park and Zoo. I fitted two adult females with activity sensor-equipped collars and observed them during two days. I was able to remotely distinguish three different behaviours using radio telemetry: feeding (head-down; 100 bpm[7]), low activity (head-up; 63 bpm) and rapid movement (rapidly fluctuating signal). This last behaviour produced a signal resulting from a running or trotting motion that caused the collar to swing to and fro on the neck. I did not use the low-activity data because this signal type was generated from many different behaviours that were indistinguishable without direct observation. Agreement between activity budgets generated from VHF activity sensors and direct observation are typically high for large mammals, ranging from 98% for Dall's sheep (*Ovis dalli*) (Hansen *et al.* 1992) to 94% for wapiti (*Cervus elaphus canadensis*) (Green and Bear 1990).

3.2.6 Determining Shifts in Habitat Use

When an individual increases its movement through an area comprising a mosaic of different habitat types, that individual should cross habitat boundaries more frequently. To test if this occurred, I recorded habitat types from the 1:250 000 peatland coverage map described in Chapter Two (Vitt *et al.* 1992). I characterized each 10-minute position recorded for each treated caribou as one of 7 habitat classes (A to G). When a treated animal changed habitat types over the course of the three-hour perturbation experiment, I recorded this as one change. I also determined if Impact animals were moving to non-preferred habitats. From the conclusions of habitat preferences outlined in Chapter Two, I used habitats C and D (forested-open fens and forested bogs) as the most preferred habitat types, and habitats A, B, E, F and G as non-preferred. Therefore, any shift from habitats C or D to the others constituted a shift from a preferred habitat to a non-preferred one. If shifts to habitats of different quality were random, one would also expect that the number of shifts from less preferred habitats to those preferred would not differ from the number of shifts to non-preferred habitats. Therefore, I defined the movements from habitats A, B, E, F and G to either habitats C or D as shifts to preferred habitat.

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[7] *Beeps per minute.*

3.2.7 Data Treatment and Statistical Analyses

I transformed recorded animal positions from degrees latitude/longitude to Universal Transverse Mercator (UTM) coordinates using transformation software provided by Forestry Canada (Anderson 1993). The UTM map projection gives grid format coordinates (x , y) in metres that are then used to calculate the distance between successive locations. All UTM animal positions were juxtaposed with 1:250 000 digital peatland habitat maps (Vitt *et al.* 1992) with the aid of a Geographic Information System (GIS) using ARC/INFO® software (Environmental Systems Research Institute Inc. 1990) (see Chapter Two). This procedure provided information on the degree of movement between adjacent habitat polygons by both Control and Impact animals.

I analysed each set of parameters (*e.g.*, movement rate, linear displacement, feeding proportions, etc.) for the 1994 experiment using a two-way analysis of variance (ANOVA) with repeated measures. I used the SAS® PROC GLM (General Linear Models) command with the repeated statement (SAS Institute Inc. 1986) to test a model including treatment (*i.e.*, DurP for Impact animals), individual, test period and interactions. All F values were calculated from Type IV sums of squares (SS) to account for the unbalanced design due to treatment. I did not include Impact 1993 animals in this analysis because of the absence of a 1993 Control group. I did, however, perform a second one-way ANOVA with repeated measures using both 1993 and 1994 Impact groups to test for overall differences between years, ignoring specific effects of the treatment (DurP). I determined effects were significant at $\alpha = 0.05$, or tending towards significance at $0.10 > \alpha > 0.05$.

3.3 Results

3.3.1 Caribou Movements - Perturbation Experiment

(a) Movement Rates

I calculated the distance moved between two successive positions and divided this value by the time elapsed between positions (approximately 600 seconds) to obtain movement rate values for each treated animal. Figure 3.2 shows the trajectory of one Impact animal (NC49) during the 1994 perturbation experiment. The mean movement rates per test period (Figure 3.3) demonstrate the temporary effect of loud noise on woodland caribou. Impact animals demonstrated higher movement rates than did Control animals due to perturbation (F = 4.23; p = 0.047; df = 1), although differences due to test period were not significant (F = 0.17; p = 0.841; df = 2). Overall movement rates for 1993 Impact animals were higher than those for 1994 Impact animals (F = 4.74; p = 0.049; df = 1). There was no apparent relationship between the distance the Impact caribou was from the cannon when it was initiated and the animal's subsequent response. When observed, mean group size for both Impact and Control animals was 4 (s_x = 1.8), and there was no apparent relationship between group size and the magnitude of an animal's response to perturbation. Of the groups observed, most responded to the perturbation as a single unit, which agrees with Tyler's (1991) findings for Svalbard reindeer responding to snowmobile harassment. On one occasion when testing an Impact animal, I observed a group of 7 caribou (one of which was the test caribou) split into groups of 5 and 2 in response to perturbation. It is unknown if the groups reunited after the initial separation.

(b) Linear Displacement

I calculated total linear displacement in metres from the first position to the last position recorded for each test period to determine if there was displacement away from the disturbance source (Figure 3.4). Impact animals moved significantly more than did Controls due to perturbation (F = 9.32; p = 0.004; df = 1) and overall displacements were greater in 1993 than 1994 (F = 13.75; p = 0.001; df = 1). The mean distance moved by the Impact animals for the DurP and PosP periods combined

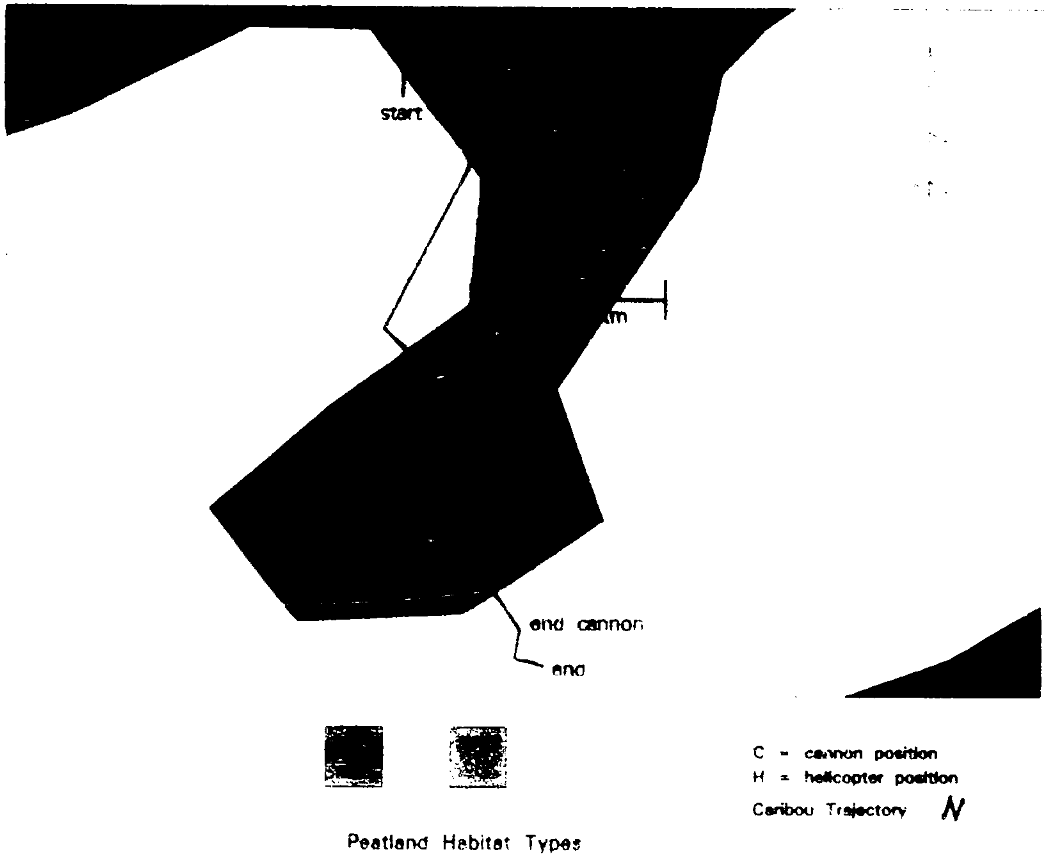

Figure 3.2: Example of an Impact animal's (collar ID# NC49) movement pattern (trajectory) during the 1994 perturbation experiment. «Start» and «end» refer to the first and last locations recorded during the three-hour experiment. «Start cannon» and «end cannon» are placed at the caribou positions when the perturbation began and ended.

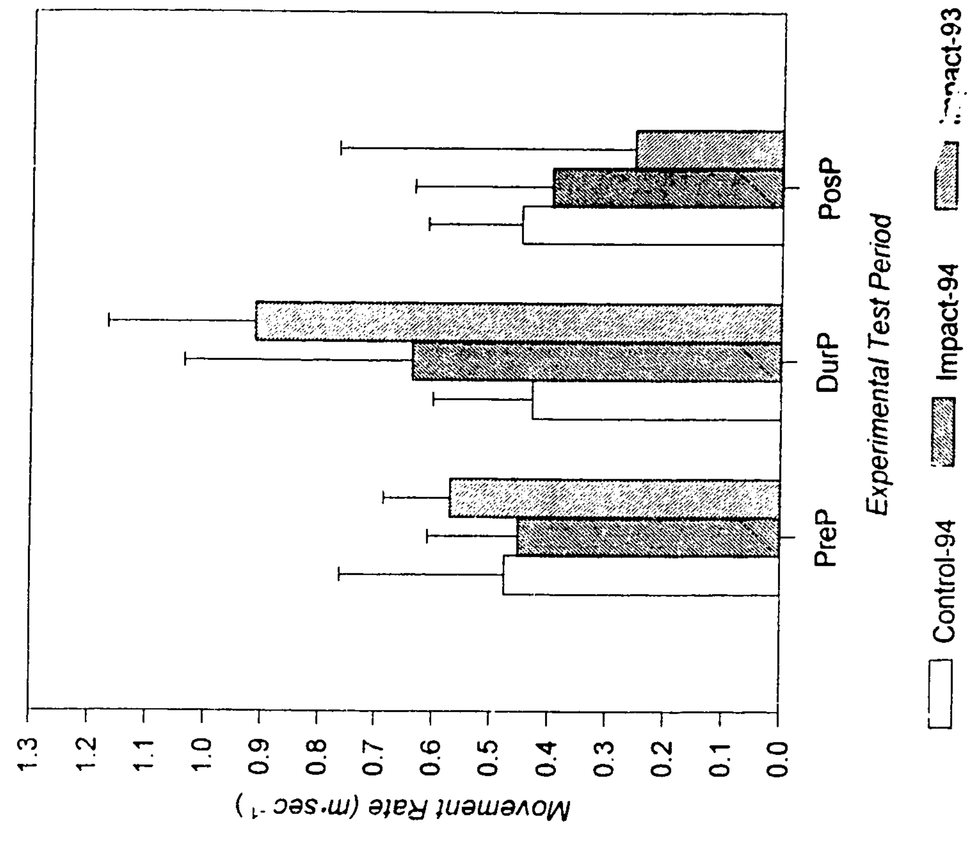

Figure 3.3: Mean movement rates per experimental test period (+ standard deviation).

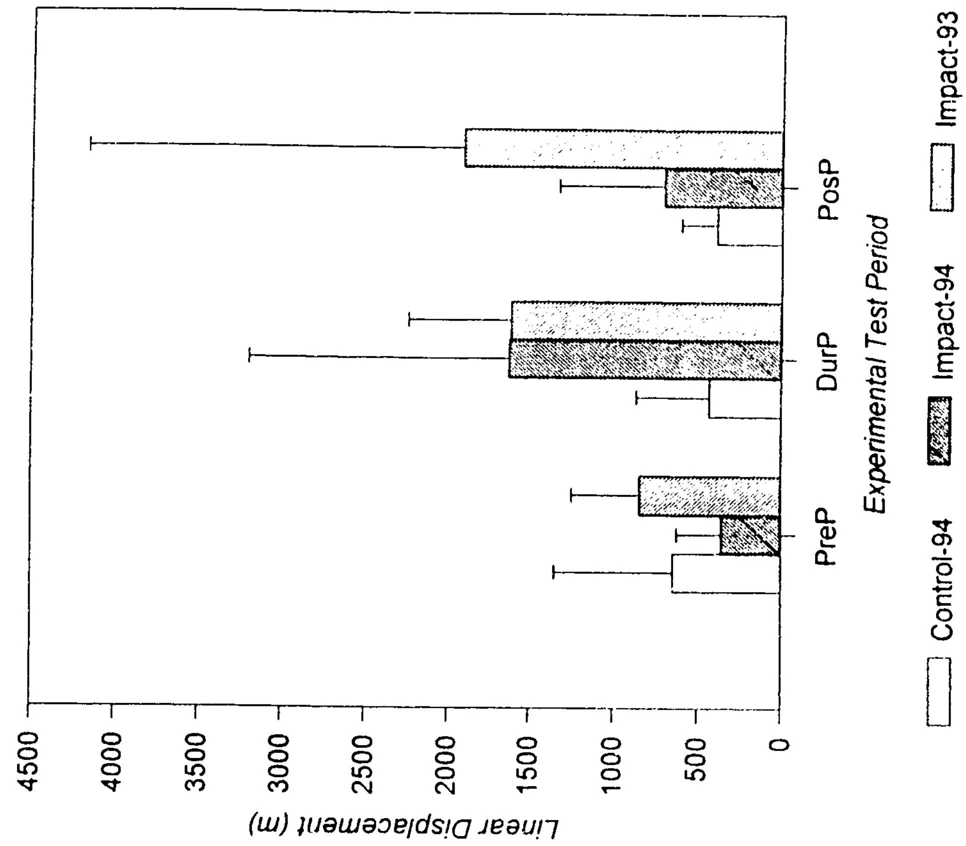

Figure 3.4: Mean linear displacement per experimental test period (+ standard deviation).

was 2.11 km greater than that moved by the Control animals.

3.3.2 Daily Displacement Before and After Perturbation

I compared daily movements 2 days before and 2 days after treatment to detect longer term changes in movement. Figure 3.5 summarizes these daily movement rates averaged over individuals per treatment group. Impact animals again displayed significantly greater daily movement rates than did Control animals (F = 9.05; *p* = 0.009; df = 1). I could not calculate differences between years due to the insufficient sampling frequency of the 1993 Impact group.

3.3.3 Proportion of Time Spent Feeding

I predicted that a response to harassing stimuli involves a reduction in time spent feeding. Head-down signals from the activity sensor were expressed as a percentage of total observation time for which activity signals were recorded. Feeding proportions per 10-minute interval are averaged over individuals (Figure 3.6); the mean differences in feeding proportions due to perturbation (Figure 3.7) were not significant (F = 0.08; *p* = 0.786; df = 1). Impact 1993 animals did, however, feed significantly more during the experiment than did Impact 1994 animals (F = 5.71; *p* = 0.041; df = 1).

3.3.4 Proportion of Time Spent Moving Rapidly

I also predicted that a response to harassing stimuli involves an increase in time spent moving rapidly. Rapidly fluctuating signals from the activity sensor were expressed as a percentage of total observation time for which activity signals were recorded. Rapid movement proportions per 10-minute interval are averaged over individuals (Figure 3.8) and the mean rapid movement proportions (Figure 3.9) due to perturbation were not significantly different (F = 1.67; *p* = 0.211; df = 1). Rapid movement was, however, significantly higher for the 1993 Impact group than the 1994 Impact group

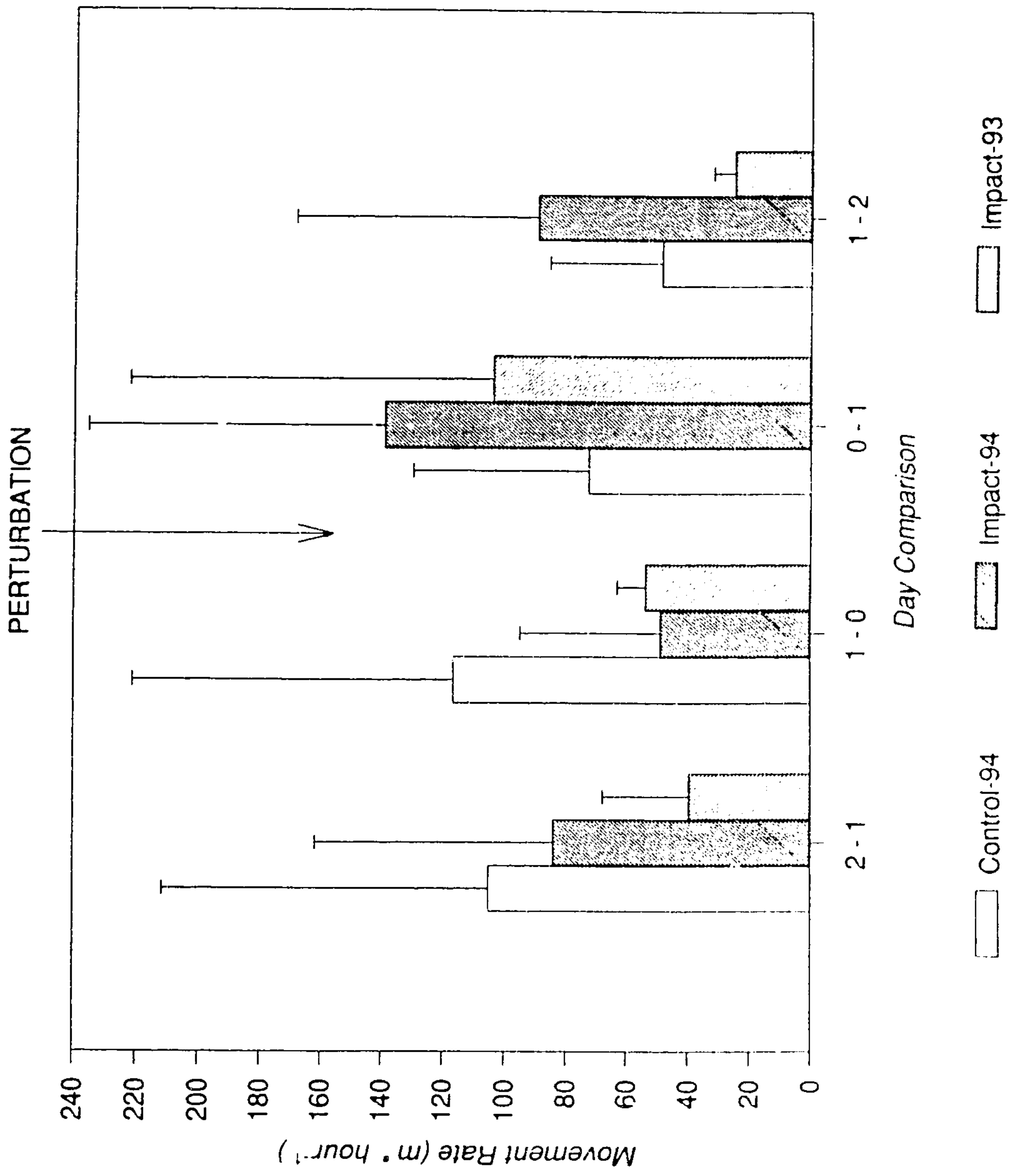

***Figure 3.5:** Mean daily movement rates before and after perturbation (+ standard deviation). Day 0 corresponds to the day of exposure to perturbation (e.g., comparison 0-1 refers to the movement rate from the day of exposure to one day after exposure).*

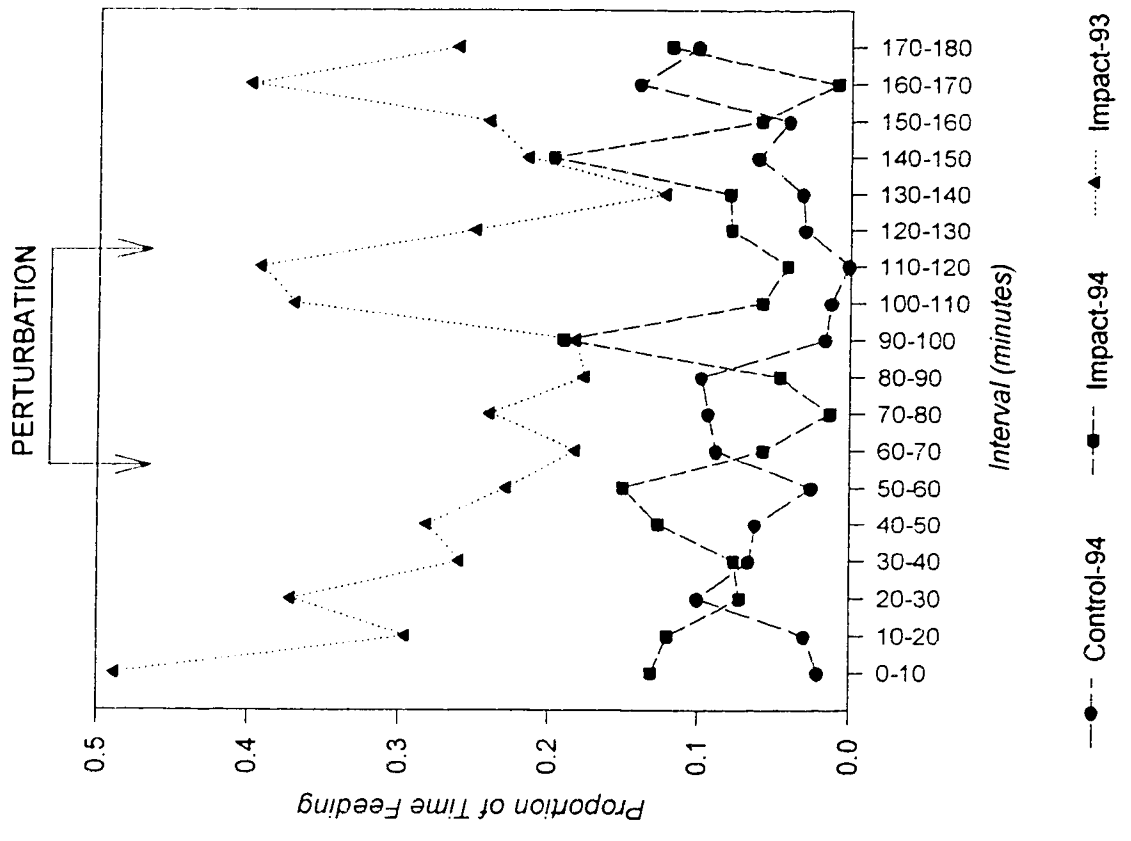

Figure 3.6: Mean 10-minute interval proportions of time spent feeding.

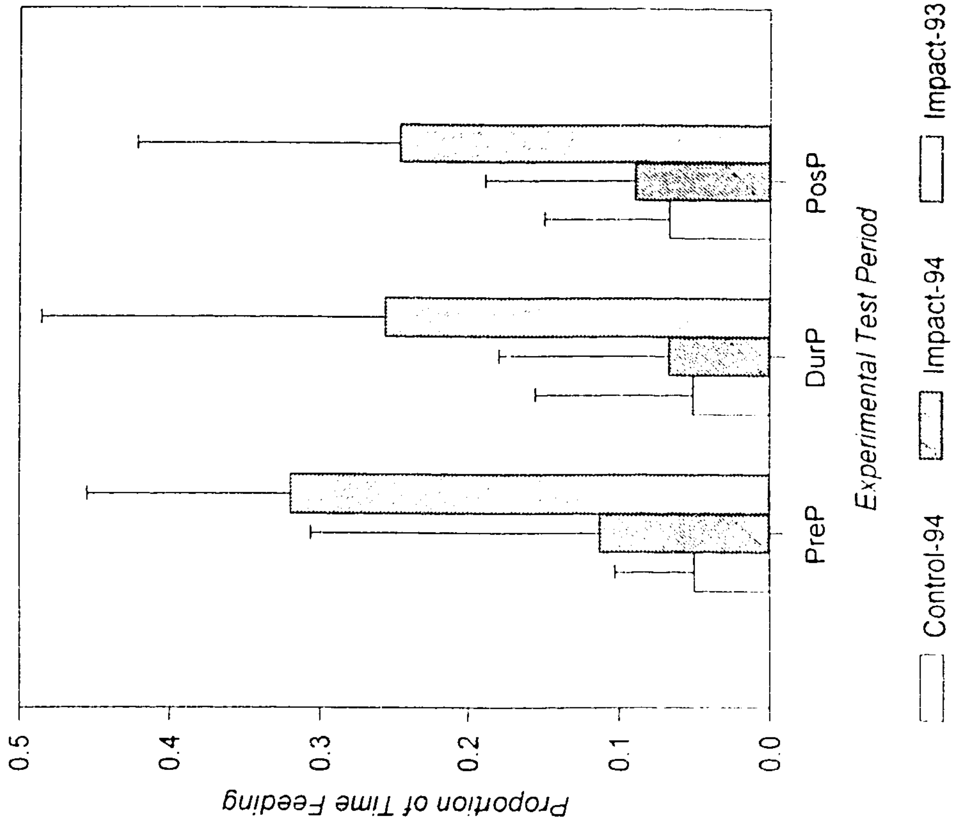

Figure 3.7: Mean feeding proportions per experimental test period (+ standard deviation).

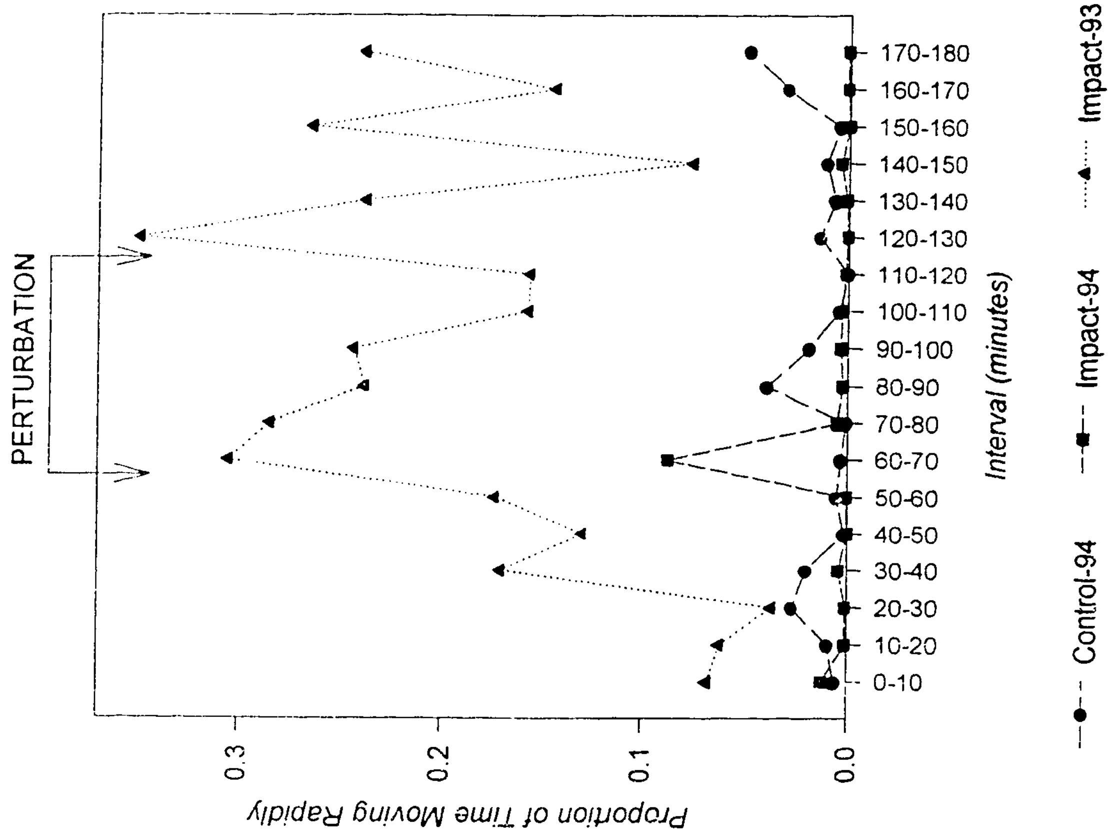

Figure 3.8: Mean 10-minute interval proportions of time spent moving rapidly.

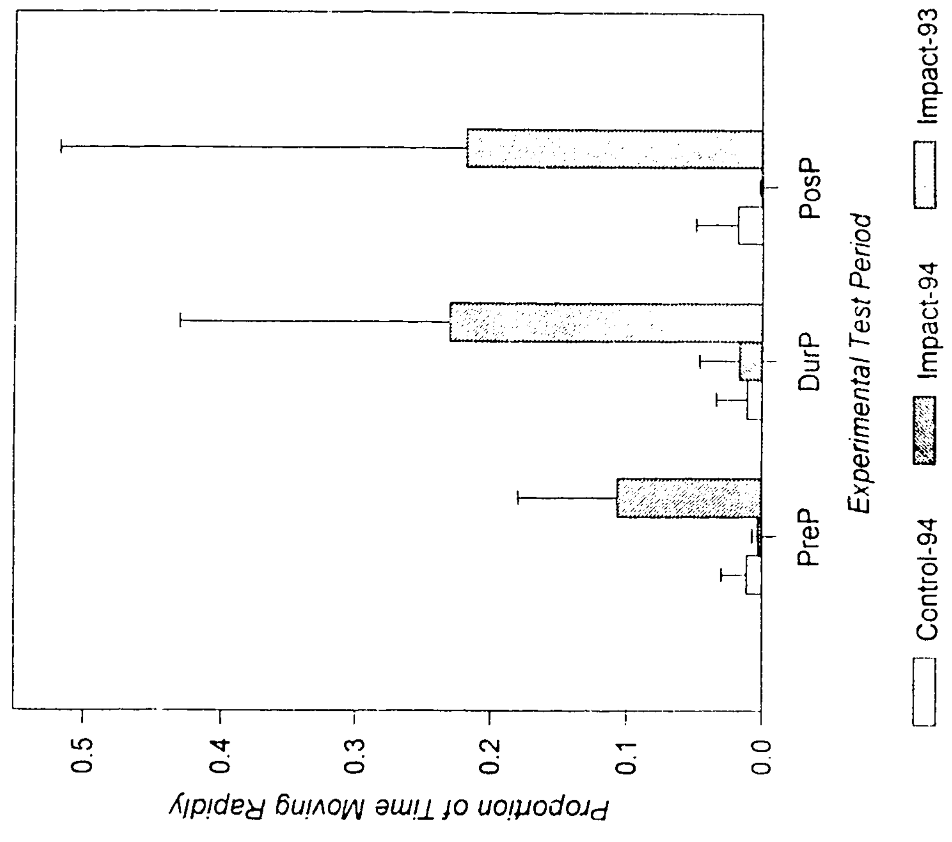

Figure 3.9: Mean rapid movement proportions per experimental test period (+ standard deviation).

(F = 6.50; p = 0.031; df = 1).

3.3.5 Shifts in Habitat Use

(a) Total Habitat Shifts

The mean number of habitat shifts due to perturbation (Figure 3.10) between Impact and Control animals did not significantly differ (F = 0.11; p = 0.747; df = 1), although differences between test periods tended towards significance (F = 2.56; p = 0.091; df = 2). This indicates a tendency to change the number of habitat shifts over time during the course of the experiment. Impact 1993 and Impact 1994 animals did not demonstrate significant differences in mean habitat shifts (F = 0.14; p = 0.717; df = 1).

(b) Shifts to Non-preferred Peatland Habitat Types

I averaged the number of shifts to non-preferred habitats over individuals per test group (Figure 3.11) and found differences due to perturbation were, again, non-significant (F = 2.80; p = 0.103; df = 1), as were differences due to test period (F = 0.47; p = 0.631; df = 2). Control animals did not demonstrate any shifts to non-preferred habitat types. Differences between 1993 and 1994 for Impact animals were not significant (F = 0.56; p = 0.468; df = 1).

(c) Shifts to Preferred Peatland Habitat Types

Mean habitat shifts to preferred peatland types per test period (Figure 3.12) revealed no significant differences due to perturbation (F = 0.08; p = 0.782; df = 1) or between test periods (F = 0.12; p = 0.890; df = 2). Control animals did not demonstrate any shifts to preferred habitat types. Differences between years for Impact animals were not significant (F = 0.78; p = 0.395; df = 1).

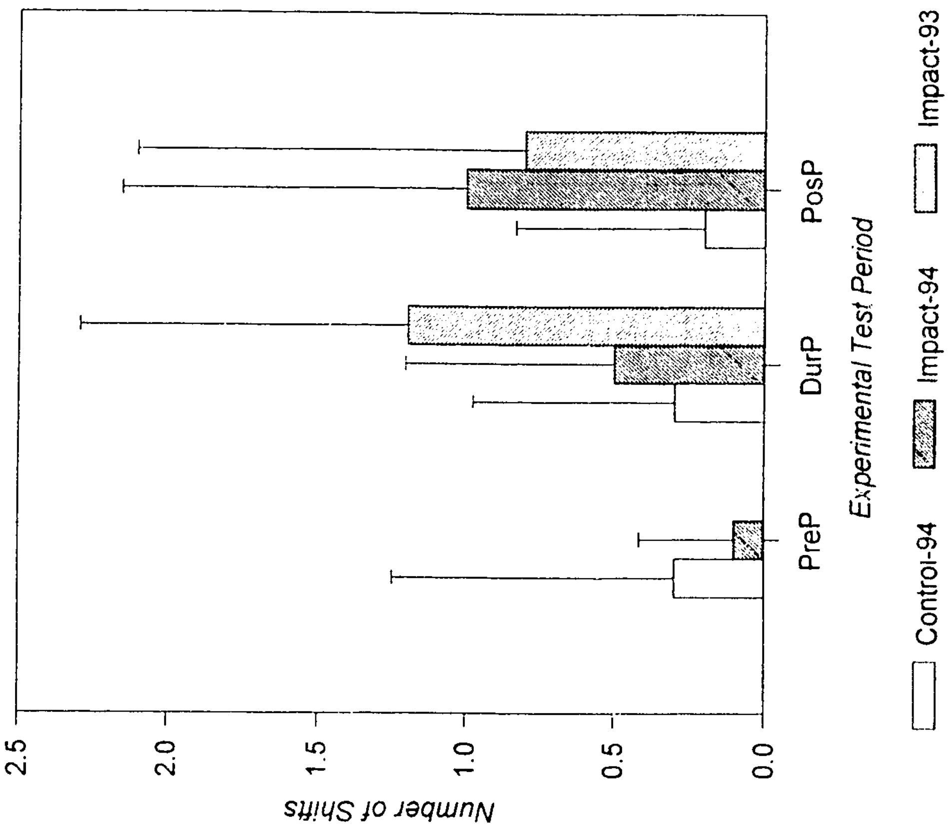

Figure 3.10: Mean number of habitat shifts per experimental test period (+ standard deviation).

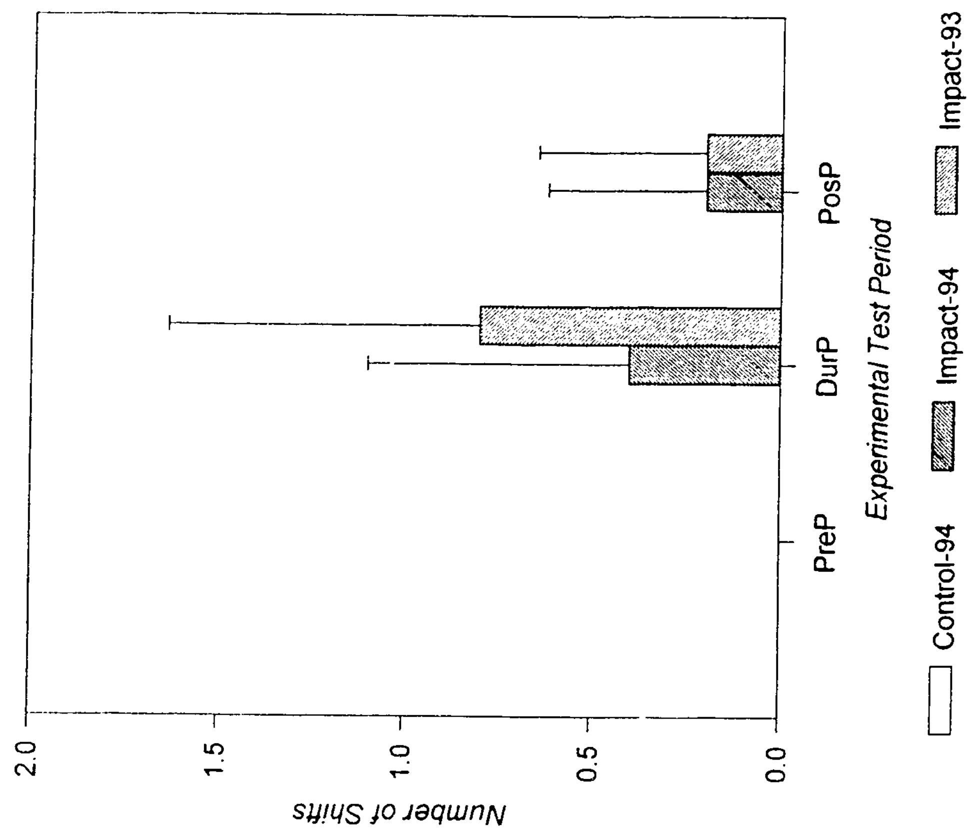

Figure 3.11: Mean number of shifts to non-preferred habitats per experimental test period (+ standard deviation).

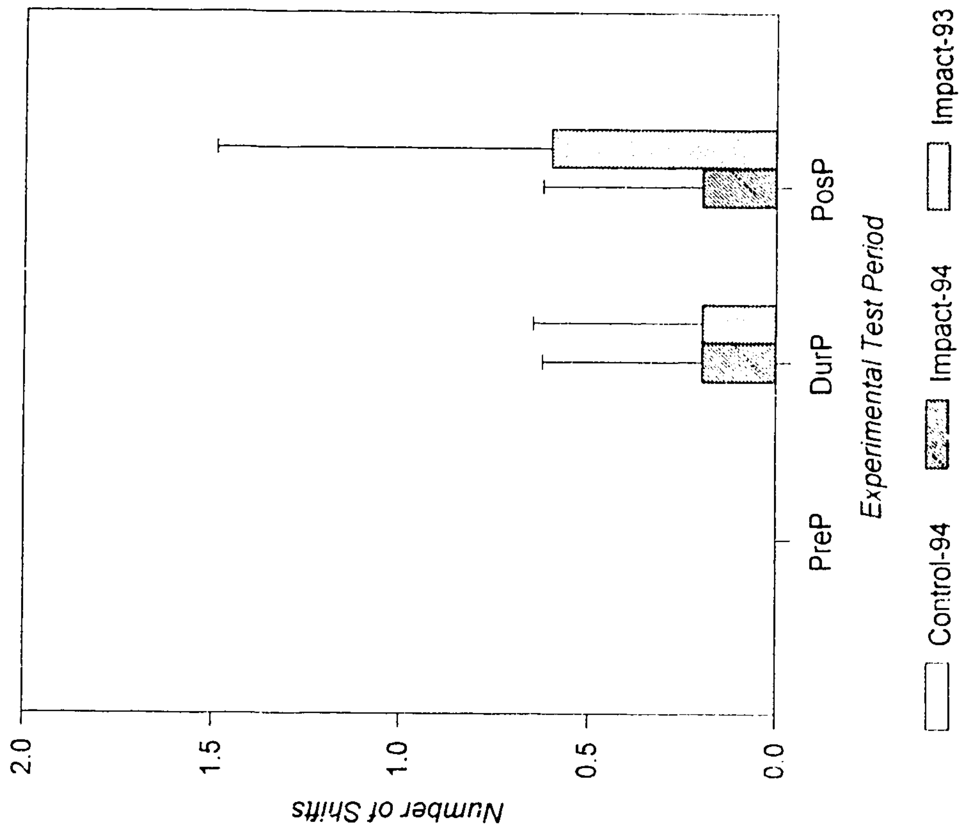

Figure 3.12: Mean number of shifts to preferred habitat per experimental test period (+ standard deviation).

3.4 Discussion

3.4.1 Caribou Movements - Perturbation Experiment

A single encounter with loud noise significantly increased the animal's rate of movement, but this increase occurred only during the period of perturbation (DurP). I also found that overall movement rates were higher in 1993 than in 1994 for Impact animals (ignoring the effects of perturbation). This observation may result from the considerable difference in mean snow depths between winters (Figure 2.4). I tested winter 1993 Impact animals when snow was almost absent in the study area, whereas 1994 Impact and Control animals faced snow depths exceeding 1 m. Although caribou are well-adapted to movement in deep snow (Telfer and Kelsall 1984), depths of 1 metre or greater appeared to impede movement.

Fancy and White (1985) found 0.97 m/sec (3.5 km/hr) to be the energetically-optimal walking speed for caribou, and Fancy and White (1986) found similar rates (0.94 m/sec) for mean walking speeds. For this experiment, the greatest average movement rate recorded (1993 Impact animals - DurP) was 0.91 m/sec in response to perturbation. Even though this value is slightly less than the reported energetically-optimal movement rate, it proved to be an increase from Control movement rates, suggesting an increase in energy expenditure. Deep snow further impedes movement and, consequently, the energetically-optimal walking speed declines (Fancy and White 1985). Indeed, Fancy and White (1987) reported that when caribou experience deep, crusted snow[8], energy expenditure for locomotion can increase by as much as 568%. The mean movement rates recorded for 1994 Impact animals during perturbation were lower than those of the 1993 Impact group, suggesting that caribou compensated for the increased cost of locomotion in deep snow. Daily movement rates between 1993 and 1994 Impact groups do not appear to differ (Figure 3.5).

Geist (1971a) described a reaction to perturbation where a 90 kg caribou is frightened or chased, runs for approximately 10 minutes, walks rapidly for one hour and remains

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[8] *Near the end of February and the first week of March (1994), ambient temperatures increased temporarily above 0°C, causing the surface of the snow to crust when temperatures returned to sub-zero.*

excited for another hour. This entire succession of events requires about 2.80 Megajoules (MJ) above and beyond the average 13.40 MJ daily requirement for the maintenance of body weight (McEwan and Whitehead 1970; Geist 1971a; Moen 1973). Therefore, this added energy cost is almost a 21% increase to the net daily cost of living (Geist 1971a; Klein 1973). The Impact test groups in this study displayed similar behavioural reactions to disturbance, suggesting that even temporary effects can incur a daily net loss of energy.

The lack of observable reaction to perturbation by a few 1994 Impact animals added to the variance and the difference in mean movement rate between years. Gaare *et al.* (1975) found that reindeer in good physical condition were better able to conserve energy by aggregating and standing alert during a perturbation rather than moving and trying to find another foraging location. MacArthur *et al.* (1979) and Chabot (1991) found, however, that even when disturbance fails to induce behavioural responses, it can still elicit important energy expenditures through increased heart rate and oxygen consumption. The deep snows of 1994 may have caused the animals to opt for a strategy of energy conservation by refraining from flight and enduring the stress instead of wasting energy running through deep snow. I observed this behaviour in 3 of the 10 Impact animals treated in 1994, whereas none of the 1993 Impact animals demonstrated this behaviour. I hypothesize that different animals in different physical condition altered their response based on the risk avoidance strategy that best suited their physical condition (Caraco *et al.* 1980). Undernourished animals may have opted to remain in spite of the perturbation to avoid expending further energy on flight through deep snow, whereas healthy caribou may have been willing to incur the energetic costs of flight.

Linear displacement increased as a result of noise perturbation which demonstrates that animals also reacted by avoiding the area of the disturbance. Therefore, in addition to the increase in energy expenditure resulting from increased movement rates, animals were also displaced from their original positions. Moreover, displacement in 1993 was greater than in 1994, thereby agreeing with the hypothesis that deep snow in 1994 impeded movement. Increased displacement resulting from perturbation may also result in increased movement to non-preferred habitat types (see below).

3.4.2 Daily Displacement Before and After Perturbation

Despite daily movement rates varying considerably, a significant effect of perturbation was found. This demonstrates that at least for two days following perturbation, the exposed animal still displayed a reaction to perturbation, although it is unknown for how many days this response typically lasts. I believe, however, that the response to perturbation does not persist for many days following the two post-perturbation days measured in this experiment. Interestingly, these effects at the daily time scale seem to contradict the prediction by Harlow *et al.* (1987) that the effects of a single perturbation encounter are unlikely to extend days past the initial exposure. I did not expect such a response because the effects of perturbation at the hourly time scale persisted only during the exposure test period (DurP).

3.4.3 Proportion of Time Spent Feeding

Caribou behaviour, like that of other ruminants, is characterized by a more or less regular alternation between periods of activity and rest. After a few hours of grazing and slow movement, animals usually lie down to ruminate and rest for a similar period. The winter season is characterized by a 2 - 3 hour grazing period in morning and again in the afternoon, with a regular 2 - 2.5 hour lying period in the middle of the day; on average, grazing takes up from 35 - 50% of a reindeer's time, more in winter than in summer (Gaare *et al.* 1975).

This pattern poses certain problems in the remote detection of feeding behaviour modification in response to perturbation. If Impact animals encountered perturbation during a morning feeding bout, the feeding was likely interrupted. Indeed, on the two occasions that I directly observed the Impact animals before initiating the propane cannon, feeding behaviour on ground vegetation appeared normal. The first blast from the cannon interrupted this feeding as the animals fled from the cannon's position. These direct observations were later verified by the activity sensor data. It is possible that many of the animals showing little or no reduction of feeding in response to perturbation were ruminating at the time of perturbation.

Renecker and Hudson (1993) suggested that insufficient time available for grazing may prevent a wild ruminant from meeting its daily nutrient requirement. Although I relied exclusively on the activity sensor data from each collar to assess feeding behaviour, it was obvious that detecting a significant change in this behaviour would be difficult given the sample size (1993: n = 5; 1994: n = 6) and the chance of disturbing a ruminating animal. Although Figure 3.7 shows a slight trend to a decrease in feeding during the DurP test period, perturbation did not significantly affect the feeding proportion. Nevertheless, my ability to detect changes in feeding proportions between test periods would have increased had I been able to control for feeding versus ruminating animals and had access to more animals equipped with activity sensors.

Figure 3.6 shows that 1993 Impact animals spent more time feeding than did both Control and Impact 1994 animals, and I believe this to be the result of the difference in mean snow depth between winters 1993 and 1994 (Figure 2.4). Animals must spend significantly more time digging to feed as snow depths increase (Vandal and Barrette 1985), but when snow is absent (as in 1993), animals can feed continuously without lifting the head, as I observed for captive woodland caribou at the Saskatoon Forestry Farm Park & Zoo. When deep snow impedes continuous feeding, such as may have happened in 1994, the likelihood of detecting changes in feeding patterns as a consequence of perturbation diminishes.

Gaare *et al.* (1975) also suggested that differences in physical condition dictate the choice of time minimization as a risk avoidance strategy. They found that reindeer in poor physical condition were willing to take more risks by foraging longer distances from predator-safe terrain. Indeed, risk aversion and the variance of foraging bouts depends on the physical condition of the individual - foraging variance and risk exposure increases under energetically stressful circumstances (Caraco *et al.* 1980). An increase in the perceived risk of predation may also cause a shift from a strategy which maximizes foraging efficiency to one where forage efficiency is sacrificed for increased vigilance.

Although I had no direct measure of the nutritional or physical condition of the study animals, the observed differences in feeding proportions between years may not only be a function of snow depth and the associated alteration in feeding behaviour, but the added component of physical condition. Winter 1994 was harsher than winter 1993 (Figures 2.4 & 2.5), and it is possible that the 1994 test animals were in poorer condition. Many Impact 1994 animals may have opted to feed in spite of the perturbation, taking more risks as a function of their poorer health. This modification in behaviour would make the detection of the effects of perturbation less likely.

3.4.4 Proportion of Time Spent Moving Rapidly

Again, low sample size and the variability of rapid movement (*i.e.*, running) made it difficult to detect a perturbation effect on this behaviour. The to and fro movement of the radio collar on the neck of a running animal needed to elicit the rapid fluctuation between head-up and head-down signals may have been hindered by the deep snow of 1994. A constant lope or rapid trot, when not impeded by deep snow, gives a constant fluctuating signal that represents movement requiring high energy consumption. In deep snow, this lope cannot be maintained; the caribou reverts to a hopping or long, striding walk that does not activate signal fluctuation. Indeed, the marked difference in time spent moving rapidly between years (Figure 3.9) supports this conclusion.

Although there was a slight trend to increase rapid movement in response to perturbation, the effect of perturbation was not significant. As with the feeding data, I believe a larger sample size would have aided in detecting any differences. For the two 1994 Impact animals I observed directly, there was an immediate increase in rapid movement (flight) away from the perturbation source. This response was also apparent from the activity sensor data collected remotely from the observation plane. Figure 3.9 shows a non-significant, but visible, trend to increase rapid movement in the DurP test period for 1993 Impact animals, but this response translates into a temporary peak in activity immediately following exposure to perturbation for 1994 Impact animals (Figure 3.8). I suggest that the lack of a more pronounced response may have been a function of snow depth.

Some research has shown that hard running in ungulates can exceed by 20 times the cost of basal metabolism (Brody 1945; Mattfeld 1974). Zhigunov (1961) also showed that reindeer who overexert themselves in cold weather may damage their lungs;

temperatures in northern Alberta often drop below -30°C., and sometimes below -40°C. Another concern is that short bouts of physical activity late in pregnancy may result in spontaneous abortion or reabsorption of the foetus (Zhigunov 1961). Nishikawa and Hafez (1968) found that during the 5th and 10th months of pregnancy (36 - 45% and 81 - 89% of gestation, respectively), horses are endocrinologically susceptible to abortions; they recommended avoiding strenuous physical exercise at this time. Conception in woodland caribou usually occurs from mid- to late September, and with approximately 229-day gestation (7.6 months), calving begins in early to mid-May and continues until early June (Fuller and Keith 1981). Both early and late winter industrial harassment have the potential to cause abortions. If woodland caribou are susceptible to endocrinological foetal abortions, winter perturbations that increase physical exercise have the potential to be hazardous because they cause greater movement and activity.

3.4.5 Changes in Habitat Use

Potentially, the most hazardous and long-term effects of harassment are the avoidance or abandonment of optimal habitats, the reduction in a population's range and, ultimately, the reduction of the population due to loss of access to resources, increased predation or increased net energy cost for existence (Geist 1978). Geist (1978) believed that caribou and wild reindeer can abandon large areas and suffer reductions in population sizes as a result of disturbances. This was a proposed cause for the documented declines of wild reindeer in Norway (Klein 1971). The effects of disturbance are, however, difficult to evaluate for *Rangifer* since significant range shifts tend to occur over decades (Geist 1978).

I did not detect significant increases in movement between habitat patches in response to perturbation, nor was there a difference between 1993 and 1994 Impact animals. There was, however, an effect of time within individuals to alter the number of habitat shifts made during the experiment. Although the total number of habitat shifts did not vary significantly, I predicted that increased movement from preferred to non-preferred habitat types (or vice-versa) may occur upon disturbance. However, I found that perturbation did not significantly increase the frequency of movement to non-preferred habitat types. This was odd because Control animals did not demonstrate any shifts to non-preferred habitats (Figure 3.11), whereas Impact animals in both years demonstrated shifts during and after perturbation. The lack of a significant effect of perturbation may result from the high variance between individuals. Because different habitat types may serve different purposes, disturbance may, in fact, cause what is usually considered a non-preferred habitat to become preferred if it offers escape access or concealment cover. The frequency of movements to preferred habitats did not, however, significantly differ due to perturbation. Tyler (1991) proposed that animals occupying small home range areas are probably capable of instantly selecting the surest route to safest ground. It is possible that the caribou in this experiment were selecting some characteristic of the terrain for escape, although I was unable to measure this with my data.

In conclusion, perturbation did not appear to displace animals to any particular habitat type, such as to non-preferred or poorer quality habitat. As predicted by Russell *et al.* (1993), movement to poorer quality range may result in the intake of lower quality and less digestible forage, which may, in turn, result in a greater net energy loss through a lowered metabolizable energy intake per day. It appears that for the disturbance caused by petroleum exploration, no additional energy loss of this type occurs; the energy lost as a result of perturbation is due solely to the energy expended during displacement and excitement.

3.5 Conclusions

The experimental design I used to determine the degree to which woodland caribou respond to petroleum exploration was practical in detecting the more subtle effects of disturbance. Loud noise disturbance increased the rate of movement and linear distance displaced, but these changes did not continue after the disturbance had ceased. Daily movements increased after disturbance, confirming that a woodland caribou's response to such disturbances persists at a longer time scale. The proportion of time allocated to feeding and moving rapidly, as measured remotely by radio telemetry, did not change in response to disturbance. In agreement with the absence of change in feeding proportions, increased movement resulting from perturbation did not significantly alter movement between different habitat types. Because woodland caribou appear to escape to random habitat types when responding to harassment, they do not experience any net change in range quality and consequently, the quality and intake of forage should remain constant.

In general, the simulated aspects of petroleum exploration have some definite effects on the behaviour of woodland caribou in northeastern Alberta. Although these effects were temporary, the cumulative influence of multiple encounters of this type may have energetic consequences to the individual, and perhaps demographic effects on the population. I address these issues in the following chapter.

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CHAPTER FOUR: PERTURBATION ENCOUNTER MODEL

4.1 Introduction

The current guidelines for geophysical exploration in the Province of Alberta use stringent timing restrictions for operation within woodland caribou ranges. Introduced in 1990, these regulations stipulated that within caribou range (roughly defined by the Alberta Fish and Wildlife Service at that time), geophysical activity was to cease no later than January 15 of the operating winter, due to fears that industrial activity occurring beyond this time was detrimental to caribou survival and reproduction. Since most operations required frozen ground on which to work, the narrow operating window tended to concentrate industrial activity into the latter half of December until January 15. Upon discussion of this land-use management strategy with government authorities, representatives from the petroleum industry and wildlife biologists (including myself) maintained that the January 15 deadline was not based on any substantiated biological information, so the timing restrictions were altered in an attempt to dissipate the impacts associated with geophysical exploration over a longer time. With this modification, all future seismology programmes were to be completed by March 1 of each operating year.

Although the timing restriction guideline policy was uncomplicated to administer, questions were raised as to its overall effectiveness in reducing potential disturbance on woodland caribou. The most important aspect of this type of disturbance is, from an energetic perspective, the amount of disturbance encountered during the winter season and not necessarily the time of disturbance (*i.e.*, greater the number of disturbances, greater the total energy expended by an animal). Of course, there are concerns that the potential effects of disturbance during late pregnancy require land-use managers to implement some timing restrictions, but regulating the number of potential disturbance encounters should be one of the main concerns of an operating guidelines management plan.

Others have shared this view. Gilliam and Lent (1982) summarized the conclusions made by a panel of caribou experts regarding potential impacts stemming from various hypothetical oilfield developments in Alaska. They felt the significance of potential impacts was proportional to both the portion of a caribou herd that was likely to encounter developed areas and the number of times a given animal (especially a female) would encounter the development in a yearly cycle of movements. This idea had earlier support from Wright and Fancy (1980). Calef (1974) and Geist (1978) believed that repeated disturbances can be expected to cause range abandonment, such as occurred in the Fortymile herd of Alaska. Frequent harassment that causes repeated exertion may also impose a burden on the energy and nutrient supply of an animal (Geist 1978).

It is important to be able to predict the frequency at which woodland caribou encounter industrial disturbance during an average winter. This information permits a rough calculation of the average increase in energy consumption that results from harassment and the amount of weight an animal may lose after multiple exposures to harassment. It is doubtful that an exposure to a single perturbation event would prove to be energetically costly on a seasonal scale, but several encounters may lead to a net loss in energy sufficiently greater than the typical losses observed during a normal winter, thereby affecting survival or reproduction (see Chapter One).

The behaviour of ungulates toward humans and human activity is largely a consequence of our behaviour towards them. When hunted, stalked and repeatedly frightened they will flee, and vigilance may continue long after the perturbation has ceased (Geist 1971b). Animals have the ability to learn, and they demonstrate pronounced alarm responses that allow them to adjust to their environment until it is predictable and not dangerous (Geist 1971b). When some unfamiliar object or stimulus appears, the animal experiences an alarm reaction, and prepares itself physiologically for flight. If the disturbance is common and localized in time and space, the animal soon learns to avoid it. Disturbances likely to be the most detrimental are those that are relatively frequent and unpredictable, such as hunting[1] (Skogland and Grøvan 1988), aircraft harassment (Harrington and Veitch 1992) and tourism (Dumont 1993). If frequent enough, such activities may cause neurosis, loss of weight, loss of appetite, susceptibility to predation, reduced reproductive success or

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[1] *Not including direct mortality.*

even death (Geist 1971b).

Admittedly, many wild ungulate species have successfully habituated, or learned to ignore, human presence and activity (Welles and Welles 1961; Geist 1966; Geist 1967; Holroyd 1967), and certainly the wapiti (*Cervus elaphus canadensis*) and bighorn sheep (*Ovis canadensis canadensis*) of Alberta's national parks show little aversion to the high degree of human activity found there. When exposed to a predictable, frequent event, animals can habituate to the most conspicuous noises and activities. Petroleum exploration is perhaps the most threatening stage of petroleum development because it is based on a minimum of advance planning and is unpredictable in time and space (Klein 1973). In a study measuring stress and habituation in domestic sheep (*Ovis aries*), Harlow *et al.* (1987) demonstrated that serum cortisol[2] did not diminish rapidly over time when the sheep were exposed to an irregular and unpredictable interval of noise stimuli; this indicated that the sheep were not habituating to the stimuli. Likewise, woodland caribou may not habituate to noise stimuli caused by petroleum exploration, as they would to more permanent, sedentary (*i.e.*, predictable) structures such as pipelines and compressor stations.

In this chapter I describe a modelling exercise that calculates (a) the normal winter energetic budget of woodland caribou in northeastern Alberta, (b) the degree to which multiple perturbations can affect winter energy loss and (c) the history and disturbance potential of winter petroleum exploration in northeastern Alberta from 1988 to 1993. Several assumptions are made concerning woodland caribou energy patterns since I was unable to collect energetic data during this study. Most values originate from studies measuring metabolic rates, weight loss and energy consumption rates for a variety of activities and behaviours of barren-ground caribou and reindeer. I also estimated the past potential encounter rates with industrial perturbation in northeastern Alberta. These estimates not only allow for the creation of a simple model by which land use managers can apply a maximum disturbance threshold to caribou range in order to avoid potentially dangerous disturbance intensities, they also permit an estimate of the energetic consequences of past disturbance.

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[2] *Increased concentration of serum cortisol above normal levels is indicative of stress (Bassett and Hinks 1969).*

4.2 Methods

A petroleum company wishing to explore an area of Alberta must first submit preliminary plans and maps for geophysical survey to Alberta Environmental Protection, Forest Management Division. Once the survey is approved and the exploration is completed in the field, the petroleum company submits a final plan with maps for permanent record at the Forest Management Division. Each final plan represents a single exploration programme; this programme is composed of a variable number of seismic lines that are cleared, drilled and recorded within a specific period[3] (see Chapter Three).

I obtained copies of 290 final plans submitted between November 1988 and April 1993 for map sheets 84A, 74D, 83P and 73M (National Topographic System: 55 - 57° N Lat. / 110 - 114° W Long.). I manually digitized all seismic exploration lines that were recorded for geophysical survey in each programme using a Geographic Information System (GIS) with ARC/INFO® software (Environmental Systems Research Institute, Inc. 1990). Attribute data included the start date, completion date and file number of each geophysical survey programme.

To determine the proportion of industrial exploration that occurred within the caribou distribution polygons outlined in Chapter Two, I overlaid the geophysical seismic line coverage with the caribou distribution polygon coverage using the GIS. This information provides the basis for estimating the potential for a woodland caribou to encounter geophysical survey operations.

Finally, I probed the existing scientific literature and referred to the results of my disturbance simulations (Chapter Three) to determine the potential energetic consequences of multiple encounters with perturbations similar to geophysical surveys. I examined the survey data gathered from 1988 to 1993 to determine if any petroleum exploration within the study area could have affected the winter energy balance of local woodland caribou populations. I also estimated the number of encounters that

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[3] *Some programmes incorporated previously-cleared seismic lines, but these represented only a small proportion of the winter geophysical activity.*

would be required to elicit above average to severe weight changes during a winter season.

4.3 Results, Assumptions and Calculations

4.3.1 Estimating Winter Energy Requirements, Weight Loss and the Effects of Perturbation

The following calculations provide rough estimates of winter energy requirements for caribou taken from several publications. The purpose of the following sub-sections is to compare mean winter energy requirements to the probable energy loss resulting from the response to multiple encounters with seismology. I was unable to measure energy expenditure during my disturbance simulations, so estimates of energy loss are based on mean energy costs of various caribou behaviours. This information provides two thresholds that represent (a) the minimum number of perturbation encounters that an animal may experience during winter before net energy loss exceeds the normal maximum and (b) the number of perturbation encounters required to cause weight loss that may reduce female reproductive success.

4.3.1.1 Winter Energy Requirements

To calculate the daily winter energy requirement for a female woodland caribou, I used Boertje's (1985) daily metabolizable energy estimate of 0.637 MJ/kg$^{0.75}$/day (for adult female barren-ground caribou in early winter) and used 132 kg as the average weight of an adult female woodland caribou (Banfield 1961; Rettie, *personal communication*). Therefore, a female woodland caribou requires 24.81 MJ/day. The above value also agrees with the estimate of total daily energy requirement calculated with the Fasting Metabolic Rate (FMR) of 0.403 MJ/kg$^{0.75}$/day for barren-ground caribou (McEwan 1970; Fancy 1986). Adamczewski *et al.* (1993) believed this value to be relatively independent of season and differing diets and environmental conditions. Therefore, using an average female woodland caribou, total daily maintenance energy is 15.69 MJ/day, which represents between 66.5% and 76.9% of total winter daily energy requirement (Adamczewski *et al.* 1993). This gives daily energy requirements for woodland caribou between 20.41 and 23.59 MJ/day. I then combined the above estimates into a range of 20.41 - 24.81 MJ/day. To calculate the total winter energy requirement, the range of daily energy requirements are multiplied by 180 days (November 1 - April 30), which represents the average winter duration in northeastern Alberta. This gives a range of 3673.80 - 4465.80 MJ/winter.

4.3.1.2 Energetic Costs of Perturbation

Boertje (1985) calculated the energy costs of various activities for Alaskan barren-ground caribou. He estimated that it requires 0.00264 MJ/kg/km for walking in moderate snow conditions. Similar walking costs of 0.00205 MJ/kg/km have been estimated for wapiti (Gates and Hudson 1978) and 0.00260 MJ/kg/km for red deer (*Cervus elaphus*) (Brockway and Gessaman 1977). Winter trotting and galloping costs were estimated at 0.035 MJ/kg/hr (Boertje 1985). From my direct observation and activity sensor data described in Chapter Three, the response displayed by many animals exposed to disturbance was immediate rapid movement (*i.e.*, trotting and galloping) for 10 - 15 minutes following the disturbance, followed by rapid walking away from the disturbance source. On average, disturbed animals moved approximately 2.11 km farther during the perturbation and post-perturbation periods than did control animals. Therefore, using Boertje's (1985) estimates, a female woodland caribou exposed to perturbation expends an additional 1.89 MJ for the increased distance travelled and initial rapid-movement response. In deep, crusted snow, the cost of locomotion may increase by as much as 568% (Fancy and White 1987). Thus, a perturbation response in such conditions would cost a female woodland caribou approximately 10.74 MJ (568% of 1.89 MJ) above the daily energy requirement, not including the cost of excitement.

In addition to the simple cost of locomotion, prolonged excitement can itself increase metabolic costs (Webster and Blaxter 1966; MacArthur *et al.* 1979; Chabot 1991), up to 25% more than required for maintenance (Geist 1978). Blaxter (1962) demonstrated that nervousness and increased muscular tension caused a 10% increase in fasting metabolic rates (FMR) of untrained versus trained domestic sheep. Thus, for an average adult female woodland caribou, an additional 2 - 6 MJ may be expended solely due to the excitement caused by a perturbation encounter.

The total energetic cost of a single perturbation encounter is the cost of displacement (1.89 MJ) + the cost of excitement (2 - 6 MJ) = 3.89 - 7.89 MJ. This represents a 16 - 39% increase in the daily energy requirement. Geist (1971a) and Klein (1973) estimated that a single encounter with a perturbation of this type raises the daily energy requirement by approximately 20%, a value that agrees well with my calculations.

4.3.1.3 Winter Weight Loss and the Effects of Perturbation

In this section I estimate the number of perturbation encounters required to cause potential reproductive problems through extensive winter weight loss, and the number of perturbations that would increase normal weight loss above the normal winter maximum. However, it is first necessary to determine normal winter weight loss in the absence of human-caused perturbation. Zhigunov (1961) believed that when female reindeer weight loss exceeds 17% , embryonic absorption may occur, whereas Jacobsen and Skjenneberg (1975) believed over-winter weight loss of 20% in reindeer is common. Cameron *et al.* (1993) suggested that while the possibility of abortion or premature birth resulting from chronic undernutrition cannot be ruled out, such mortality is uncommon. Steen (1968) reported weight loss in overwintering male and female reindeer to range from 10 - 15%, and Dauphiné (1976) found barren-ground caribou calves to lose between 6 - 10% during their first winter. Bergerud (1974) recorded from 8 - 26% winter weight loss for Newfoundland woodland caribou, the 26% weight loss occurring during a winter of excessive snow accumulation (292 cm total end-of-month snow depth). Moreover, of the five winters observed in that particular study, females in the year of excessive snow produced the smallest calves at birth. For the purposes of this modelling exercise then, I assume that woodland caribou typically lose between 10 - 15% of their autumn weight during winter (based on the most commonly cited normal winter weight loss values). I also assume that weight loss exceeding 20% may influence the reproductive success of females, either through embryonic reabsorption or higher neonate mortality. In order for a female to exceed 20% weight loss during winter, she must lose an additional 5 - 10% of her autumn weight. This translates into an additional 6.6 - 13.2 kg lost over winter above normal weight loss.

According to Boertje (1985), winter weight loss of endogenous reserves can be divided into two categories: loss by fat catabolism (90%) and by protein catabolism (10%). Using the energetic values of 39.3 MJ/kg fat (Boertje 1985; Hudson and White 1985) and 5.0 MJ/kg lean tissue[4] (Hudson and White 1985), an additional loss of 6.6 - 13.2 kg per winter resulting from hypothetical disturbance is equivalent to 233.44 - 466.88 MJ (fat) and 3.30 - 6.60 MJ (protein). The combined supplementary energy loss ranges from 236.74 - 473.48 MJ, and when divided by the cost of a single encounter with perturbation (3.89 - 7.89 MJ), it requires between 30 - 122 (mean = 76) encounters to exceed 20% winter weight loss.

Having assumed 15% winter weight loss to be the upper limit during a normal winter, any additional weight loss resulting from industrial harassment puts the animal into an abnormal weight-loss situation. Using the normal weight loss range of 10 - 15% described above, a female will, on average, lose the mean of this range (12.5%). Therefore, in order to exceed 15% winter weight loss, an additional 2.5% must be lost on average. This 2.5% additional weight loss is equivalent to 3.3 kg, or 118.37 MJ. It would therefore require between 15 and 30 (mean = 23) perturbation encounters to induce this loss.

4.3.1.4 Potential Encounter Rate

I have estimated that an encounter rate of 15 - 30 times per winter season is the minimum after which the average caribou begins to lose greater than 15% weight during winter. Likewise when the number of encounters approaches 30 - 122 (20% total winter weight loss), reproductive success of a female may begin to decline. It is necessary to express the number of encounters per unit area in order to estimate the disturbance potential of any region of the study area and to compare disturbance

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[4] *The ratio of water to protein in lean tissues is approximately 4:1.*

potentials between regions. As described in Chapter Two, I calculated that the mean three-year home range of woodland caribou within the study area was 613.8 km^2 . I also showed that this value adequately represented single-winter area use because this sub-species of caribou is relatively sedentary. Despite the obvious problems with home range estimation using the Minimum Convex Polygon technique (Mohr 1947), such as the disproportionate use of the home range polygon, activity centres and extreme values (White and Garrott 1990), I assumed that a woodland caribou demonstrates equal use of all portions of its home range polygon. Therefore, an animal will potentially come into contact with anything occurring within its home range. Using this assumption, the number of encounters divided by the average home range area gives the potential encounter rate where energetics are affected:

(a) Weight loss >15% encounter rate = 0.0244 - 0.0489 encounters/km^2/winter (mean = 0.0375)

(b) Lowered reproductive success (>20% weight loss) encounter rate = 0.0489 - 0.1971 encounters/km^2/winter (mean = 0.1238)

The expression of encounters per unit area permits the estimation of past disturbance potential for the study area. I describe this aspect in the following section.

4.3.2 Geophysical Exploration Attributes

To determine if past seismology (geophysical) exploration has occurred within caribou range to the degree where it may have caused net weight loss in woodland caribou, I intersected the geophysical data coverage with the caribou distribution polygon coverage (Table 4.1). Figure 4.1 represents the total linear distance explored for the entire region and within woodland caribou distribution polygons.

Table 4.1: Details of the geophysical survey programmes completed per winter inside primary and secondary woodland caribou distribution polygons (within map sheets 84A, 74D, 83P and 73M).

WINTER SEASON (Nov. 1 - Apr. 30)	Programmes Completed	Total Distance Explored (km)	[a]Mean Programme Duration (Days)	Mean Seismic Line Length (km)
1988-89	27	772	9.79	7.28
1989-90	44	1454	9.97	7.06
1990-91	46	1337	14.42	5.94
1991-92	17	373	19.17	5.33
1992-93	31	470	12.97	4.85

[a] *Includes all phases of the exploration process.*

4.3.3 Estimating Encounter Potential with Geophysical Exploration

To reasonably predict the potential for woodland caribou to encounter seismology exploration, such as described in Chapter Three, several assumptions must be made. I first assumed that on an average day of exploration, a caribou that is disturbed will only be disturbed once that day. This is because Impact animals moved approximately 2.11 km farther during the DurP and PosP test periods than did Controls, and this distance is similar to the mean rate of progression along seismic lines (including surveying, timber removal, drilling, recording and debris roll-back) between 1988 and 1993 (2.617 km/day). Because disturbed caribou move at a rate similar to the mean seismology progression rate, it is unlikely that an animal will encounter the same seismology programme more than once per day. I also assumed that an animal is equally likely to be disturbed on each operating day of exploration because the duration of a typical programme is such that animals do not habituate to the noise disturbance. Therefore, a caribou within exposure distance of a seismology programme has the potential to be disturbed as many times as the number of days it takes to complete the programme.

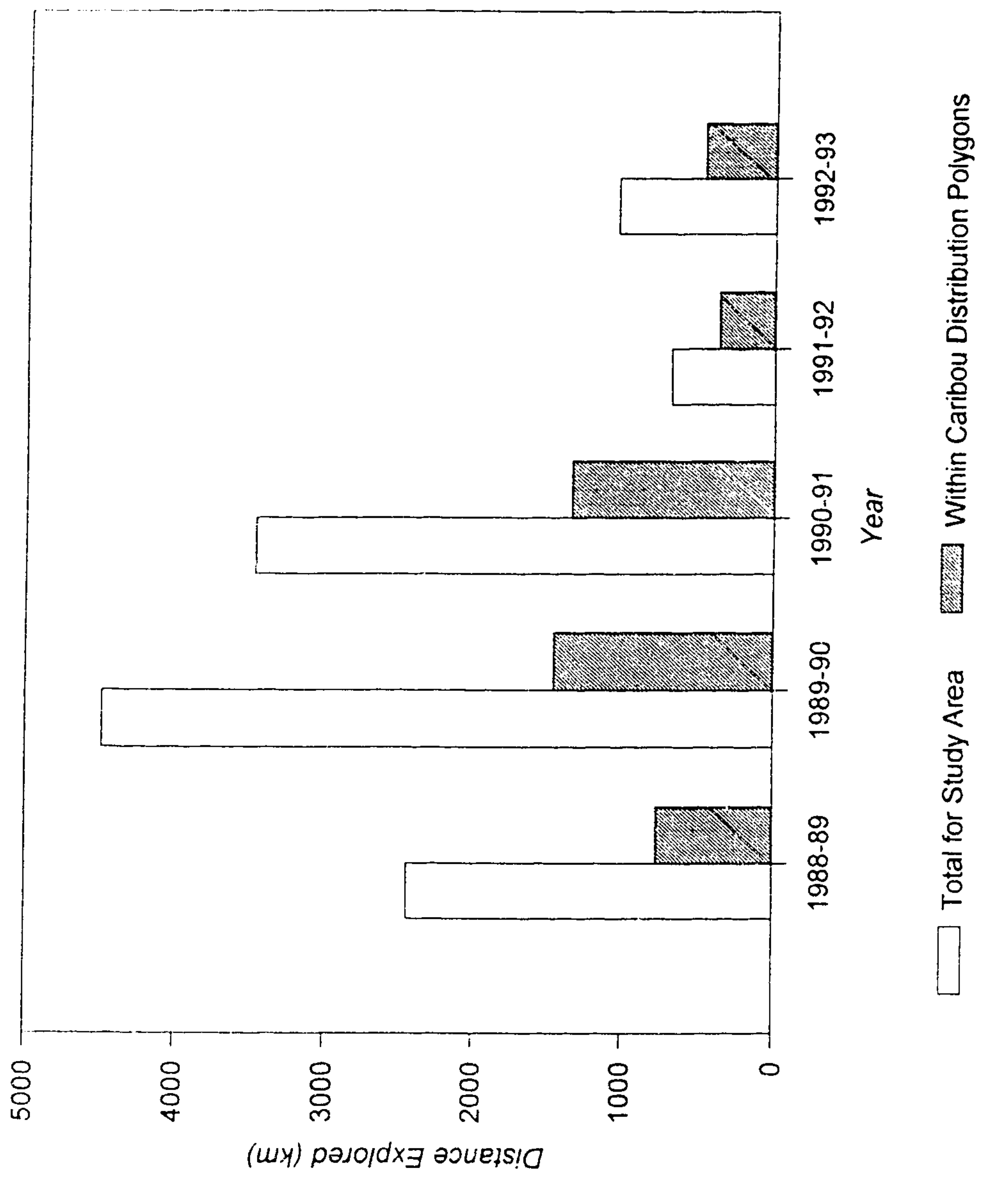

Figure 4.1: Total linear distance explored within the study area and caribou distribution polygons from 1988 to 1993.

The disturbance potential of any one area depends on the rate of exploration that occurs in that area. To simplify the calculation of disturbance potential, I assumed that the distribution polygons defined in Chapter Two represent discrete islands in which an individual animal is likely to remain for the duration of winter. Therefore, the total number of operating days of all exploration programmes combined that occur within a specific caribou distribution polygon represents the disturbance potential, or number of potential perturbation encounters, for that polygon.

The estimate of disturbance potential follows as such: the total linear distance of seismology exploration that occurs within a specific distribution polygon during one winter season (November to April) divided by the average rate of progression of exploration for that season gives the total operating days (*i.e.*, potential disturbance encounters). This value divided by the surface area of the polygon in question gives the potential disturbance encounter rate for that polygon expressed as potential encounters per unit area (Tables 4.2a - 4.2e). All years are expressed separately to stress the variance in geophysical activity between years.

Table 4.2a: Disturbance potential for 11 woodland caribou distribution polygons during winter 1988-89. Mean exploration rate of progression = 4.598 km/day.

POLYGON NAME	POLYGON AREA (km^2)	TOTAL LINEAR EXPLORATION (km)	POTENTIAL ENCOUNTERS (operating days)	DISTURBANCE ENCOUNTER RATE (enc/km^2/winter)
Wabasca-Calling	6775	287.8	62.6	0.0092
Egg Lake	2286	183.3	39.9	0.0174
Pony Creek	507	29.7	6.5	0.0127
Algar Lake	1876	0.3	0.1	0.0000
Agnes Lake	451	0.0	0.0	0.0000
Bohn Lake	1019	92.7	20.2	0.0198
Christina Lake	1228	82.6	18.0	0.0146
Wiau Lake	2641	19.2	4.2	0.0016
Wandering River	1114	28.5	6.2	0.0056
Livock	1438	15.2	3.3	0.0023
Dunkirk River	3662	32.6	7.1	0.0019

Table 4.2b: Disturbance potential for 11 woodland caribou distribution polygons during winter 1989-90. Mean exploration rate of progression = 3.713 km/day.

POLYGON NAME	POLYGON AREA (km^2)	TOTAL LINEAR EXPLORATION (km)	POTENTIAL ENCOUNTERS (operating days)	DISTURBANCE ENCOUNTER RATE (enc/km^2/winter)
Wabasca-Calling	6775	663.7	178.8	0.0264
Egg Lake	2286	302.8	81.6	0.0357
Pony Creek	507	65.2	17.6	0.0346
Algar Lake	1876	0.2	0.1	0.0000
Agnes Lake	451	19.2	5.2	0.0114
Bohn Lake	1019	12.2	3.3	0.0032
Christina Lake	1228	187.9	50.6	0.0412
Wiau Lake	2641	180.8	48.7	0.0184
Wandering River	1114	21.6	5.8	0.0052
Livock	1438	0.0	0.0	0.0000
Dunkirk River	3662	0.0	0.0	0.0000

Table 4.2c: Disturbance potential for 11 woodland caribou distribution polygons during winter 1990-91. Mean exploration rate of progression = 2.282 km/day.

POLYGON NAME	POLYGON AREA (km^2)	TOTAL LINEAR EXPLORATION (km)	POTENTIAL ENCOUNTERS (operating days)	DISTURBANCE ENCOUNTER RATE (enc/km^2/winter)
Wabasca-Calling	6775	514.8	225.6	0.0333
Egg Lake	2286	427.1	187.2	0.0819
Pony Creek	507	76.7	33.3	0.0663
Algar Lake	1876	14.8	6.5	0.0035
Agnes Lake	451	0.0	0.0	0.0000
Bohn Lake	1019	12.2	7.9	0.0078
Christina Lake	1228	48.0	21.0	0.0171
Wiau Lake	2641	153.4	67.2	0.0254
Wandering River	1114	76.0	33.3	0.0299
Livock	1438	7.7	34	0.0024
Dunkirk River	3662	0.2	0.1	0.0000

Table 4.2d: Disturbance potential for 11 woodland caribou distribution polygons during winter 1991-92. Mean exploration rate of progression = 1.237 km/day.

POLYGON NAME	POLYGON AREA (km^2)	TOTAL LINEAR EXPLORATION (km)	POTENTIAL ENCOUNTERS (operating days)	DISTURBANCE ENCOUNTER RATE (enc/km^2/winter)
Wabasca-Calling	6775	93.9	75.9	0.0112
Egg Lake	2286	113.9	92.0	0.0403
Pony Creek	507	67.1	54.3	0.1070
Algar Lake	1876	0.0	0.0	0.0000
Agnes Lake	451	0.0	0.0	0.0000
Bohn Lake	1019	19.0	15.3	0.0150
Christina Lake	1228	11.6	9.3	0.0076
Wiau Lake	2641	48.6	39.3	0.0149
Wandering River	1114	18.9	15.2	0.0137
Livock	1438	0.0	0.0	0.0000
Dunkirk River	3662	0.0	0.0	0.0000

Table 4.2e: Disturbance potential for 11 woodland caribou distribution polygons during winter 1992-93. Mean exploration rate of progression = 1.257 km/day.

POLYGON NAME	POLYGON AREA (km²)	TOTAL LINEAR EXPLORATION (km)	POTENTIAL ENCOUNTERS (operating days)	DISTURBANCE ENCOUNTER RATE (enc/km²/winter)
Wabasca-Calling	6775	140.6	111.9	0.0165
Egg Lake	2286	52.0	41.4	0.0181
Pony Creek	507	92.3	73.4	0.1447
Algar Lake	1876	0.0	0.0	0.0000
Agnes Lake	451	0.0	0.0	0.0000
Bohn Lake	1019	31.2	24.8	0.0244
Christina Lake	1228	19.4	15.4	0.0126
Wiau Lake	2641	74.5	59.2	0.0224
Wandering River	1114	21.5	17.1	0.0154
Livock	1438	0.0	0.0	0.0000
Dunkirk River	3662	39.0	31.0	0.0085

Schematic representation of seismology exploration in each year studied (Figure 4.2) shows some interesting spatial trends. Of particular interest was the clumping of industrial activity in the southern portion of the Wabasca-Calling distribution polygon, and possibly other areas. For most winters, and especially for 1988-89, 1989-90 and 1990-91, almost all programmes occurred within the southern section of the Wabasca-Calling polygon. This area represents approximately 40% of this polygon, or nearly 2700 km^2 , and because this area is sufficient to incorporate an average winter home range area (613.8 km^2), it is more likely that the potential encounter rate was higher in the southern than in the northern section of the polygon. For this reason I also expressed the encounter rate of South Wabasca-Calling for each year using the 2700 km^2 denominator. This gave the following encounter densities (expressed as potential encounters/km^2/winter): 0.0232 (1988-89), 0.0662 (1989-90), 0.0835 (1990-91), 0.0281 (1991-92) and 0.0414 (1992-93).

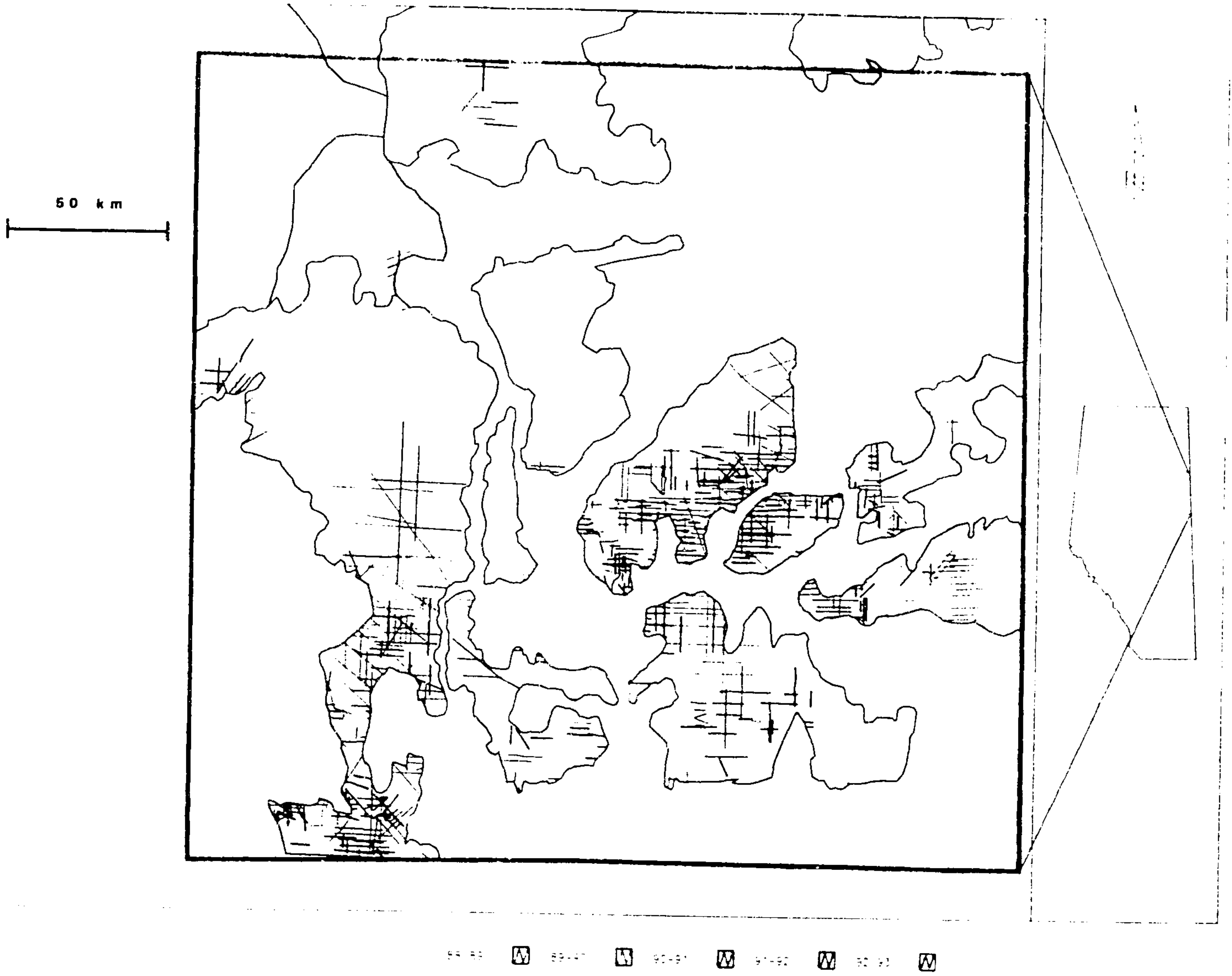

Figure 4.2: Seismic lines explored within woodland caribou distribution polygons from 1988-93.

In total (*i.e.*, including the estimates for South Wabasca-Calling), there were 9 occasions[5] where the potential encounter rate exceeded the mean 15% weight loss encounter rate of 0.0375 encounters/km^2/winter (23 encounters). There were 5 occasions where the potential encounter rate exceeded the lower 20% weight loss threshold of 0.0489 encounters/km^2/winter (30 encounters). There was also 1 occasion (Pony Creek polygon in 1992-93) when the potential encounter rate actually exceeded the mean 20% weight loss encounter rate of 0.1238 encounters/km^2/winter (76 encounters), which was the highest potential encounter rate during the five years studied. This is largely due to the slow industrial progression rate for that year and the small surface area of this particular distribution polygon.

4.4 Discussion

Determining the potential for human-caused disturbance to influence the energy budget of large herbivores depends on a number of factors, such as the validity of energetic values from the literature. Lacking direct measurement of energetic values from the animals in this study, several assumptions concerning the energetic impact of disturbance were made. The available literature concerning caribou energetics is extensive, and different methods consistently calculate similar energetic values, so my estimates of daily energy requirements appear valid. Establishing the mean energetic cost of an average perturbation encounter in terms of the costs of locomotion and excitement was, however, difficult given the multitude of factors that may influence this value. Fancy and White (1987) found that the net cost of locomotion for barren-ground caribou was the lowest of any terrestrial species studied, suggesting that selection for locomotor efficiency has occurred in species undertaking long migrations. Although woodland caribou do not demonstrate any long-distance migrations, it is likely that they have retained high locomotor efficiency. However, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) who have shorter legs and are more sedentary than barren-ground caribou (Nilssen *et al.* 1984), have a net cost of locomotion that is 24% higher than that predicted by Fancy and White's (1987) equations.

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[5] *In a particular distribution polygon during a particular year.*

Because I limited my calculations to average snow-depth and temperature conditions, years of particularly adverse winter conditions may alter the results of the model. It is possible that during winters of high snow accumulation and incidences of surface crusting, the cost of displacement due to perturbation may actually triple (Fancy and White 1987). High snow accumulation can also induce considerable weight loss through lowered foraging opportunities. Hobbs (1989) modeled the effects of severe winter weather on mule deer energetics and found that severe conditions had greater impact on energy intake than energy expenditure. Others (Swift *et al.* 1980 and Fancy 1986) agree that the processes controlling energy intake rather than energy expenditure are generally more influential in determining cervid energy balance. Russell's (1976) simulations demonstrated that although boreal ranges are more favourable than tundra ranges in terms of winter energy balance, greater energy expenditures were predicted for barren-ground caribou in boreal ranges that are associated with deeper snow than tundra ranges. It is possible that when high snow accumulation impedes locomotion and feeding, winter weight loss may exceed 20%. During such winters, the energetic effects of multiple perturbation encounters may effectively contribute to increased calf and adult mortality rates for that year. Moreover, weather effects on physical condition may persist into subsequent years, even when those years are relatively mild (Hobbs 1989). From a management perspective, flexibility in applying limits to exploration within caribou range should be maintained during harsh winter conditions.

As suggested by Wright and Fancy (1980) and Gilliam and Lent (1982), the significance of perturbations is proportional to both the portion of a caribou herd that is likely to encounter the area of perturbation and the frequency at which an individual animal encounters the perturbation in a specific period of time. I assessed the disturbance potential of petroleum exploration in northeastern Alberta by limiting my calculations of disturbance intensity to the areas of woodland caribou distribution (see Chapter Two). Assuming equal animal densities throughout these areas is most likely invalid, but the areas do represent the major concentrations of woodland caribou in this region. It is also important to note that within these areas, caribou travel in small groups consisting of usually <10 individuals. When a group encounters a disturbance, all individuals in that group are likely to respond similarly (Tyler 1991); therefore, the portion of the population that is affected by petroleum exploration is greater than if individuals were solitary. On the other hand, the grouping of individuals has the added effect of reducing the encounter rate with disturbance; an even or random distribution of animals would increase the probability of encounter.

Assessing the frequency of disturbance encounters required the assumption that a relationship exists between the amount of linear exploration and the rate of progression along exploration lines. Using these estimates I was able to predict the number of operating days where interactions between caribou and industry could occur. Of course, the design of exploration programmes can influence the potential for multiple encounters per day. When large programmes require different phases to operate simultaneously over large areas, the probability of multiple encounters increases. When a programme is designed to concentrate activity in one area before moving to the next, encounter rates with woodland caribou should be reduced. The assumption of one potential encounter per operating day is a conservative estimate of seismology exploration's disturbance potential.

Weight loss exceeding the norm of 10 - 15% per winter may have numerous effects on the population. Indeed, the effects of maternal undernutrition and weight loss during winter may have far more serious consequences on the developing foetus, and later, on the development and survivorship of the calf than on the survival of the female. Dauphiné (1976) suggested a relationship between physical condition and reproductive performance in female caribou, and Cameron *et al.* (1993) found that perinatal calf survival varied directly with female weights, suggesting that forage intake of females in late pregnancy is positively correlated with birth weight of their calf (Varo and Varo 1971; Bergerud 1975; Espmark 1980; Rognmo *et al.* 1983; Skogland 1984; Eloranta and Nieminen 1986; Adamczewski *et al.* 1987). Likewise, Haukioja and Salovaara (1978) and Rognmo *et al.* (1983) reported that small calves are more likely to perish during the early post-partum months than larger ones.

Cameron *et al.* (1993) also found that maternal undernutrition late in gestation may delay the date of parturition, a view supported also by Bergerud (1975), Espmark (1980) and Skogland (1983). The consequences of delayed parturition can be serious (Cameron *et al.* 1993), including reduced time for calves to ingest high-quality summer forage and consequently, less opportunity for growth before winter (Baskin 1979; Bergerud 1975; Skogland 1983, 1985) and a higher likelihood of calf mortality due to predation and undernutrition (Dauphiné and McClure 1974; Bergerud 1975; Couturier *et al.* 1990; Whitten *et al.* 1992).

Other studies have either modelled or attempted to calculate the effects of disturbance on ungulate energetics. Hobbs (1989) found that daily disturbance increased simulated mortality in mule deer does and fawns during a severe winter, and the extreme case of two disturbances per day, each causing the animals to move 500 m, almost doubled mortality of does. Mortality was, however, insensitive to disturbance during a mild winter. Skogland and Grøvan (1988) measured weight loss in reindeer herds exposed to varying degrees of disturbance from hunters. They found that herds experiencing greater encounter rates lost significantly more weight over winter compared to herds with lower disturbance. Boertje (1985) predicted that energy costs of physiological stress from insects and predators had only a minor influence on the energy requirements of caribou and reindeer; he did not, however, model energy expenditures from human harassment. Russell (1976) predicted significant increases in heat production during insect harassment for barren-ground caribou, and Cuyler and Øritsland (1993) calculated that disturbances that increase activity in Svalbard reindeer reduce the energy conserved by lying[6], thereby increasing the animal's energy needs and reducing winter survival when food resources are scarce. It is likely, then, that disturbance can have significant energetic consequences for northern ungulates when considering the delicate balance that exists between energy expenditure and forage availability in variable winter conditions.

4.5 Limitations of the Model

True validation of a model is impossible because critical proof cannot be obtained (Hudson and White 1985), although corroboration of the results may be acquired by a sensitivity analysis (*i.e.*, to determine how precisely model parameters are known) or by comparison to empirical data. Because I was unable to corroborate the results generated from this simple model with empirical data, my model is subject to more

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[6] *By lying 45% of the time Svalbard reindeer may conserve the equivalent of approximately 15 days' energy requirement over winter (Cuyler and Øritsland 1993).*

limitations than a model that has. Apart from a controlled experiment designed to measure a caribou's weight loss during winter after exposure to several different disturbance frequencies, there is no way of testing the conclusions generated by my model. On the other hand, a discussion of the models' advantages and limitations helps to describe the general usefulness of the results.

All models are influenced by the variance associated with each parameter used in the generation of results, and the greater the number of parameters, greater is the variance associated with the output values. For this reason, I incorporated only five variables to estimate the energetic consequences of exposure to disturbance: the range of normal winter weight loss for caribou, the per cent weight loss that may cause female reproductive success to decline, the cost of an encounter with petroleum exploration and the translation of this additional cost to the amount of fat and protein catabolized. I had originally considered incorporating additional variables into the model such as maximum daily forage intake rates, the net cost of eating, the digestibility of forage, etc., but these variables could not be measured or estimated adequately for woodland caribou in Alberta. Some may argue that I have not effectively modeled the complexity of weight loss in ungulates with this simplistic model, which may be a correct conclusion. On the other hand, the addition of imprecise variables would have rendered my results more and more inconclusive. Therefore, given the lack of empirical data with which a more complex model could have been constructed, I feel these simple calculations are a good first step in estimating the potential energetic consequences of petroleum exploration on woodland caribou in northeastern Alberta. Models are not right or wrong, simply more or less useful in interpreting current data and assisting in future research or management decisions (Hudson and White 1985).

Assumptions required to construct even the simplest models may reduce the conclusiveness of the results. A major assumption in the calculation of additional winter weight loss due to disturbance is that woodland caribou cannot compensate for this loss by increasing forage intake. If, however, after a certain number of encounters with disturbance the net energy lost is replaced by an increase in forage intake, the net cost of disturbance may have been overestimated. Indeed, Robbins *et al.* (1981) suggested that ungulates recovering from nutritional stress may have higher levels of forage consumption. The regulation of forage intake in wild herbivores is controlled internally by digestion efficiency, rate of passage of digesta through the digestive system, energy balance, body composition and endocrinological status, and externally by season and forage quality (Arnold 1985; Hudson and White 1985). Moreover, the requirement of rumination is a major determinant of foraging time and therefore, the maximum intake of forage (Robbins 1983), suggesting that compensatory feeding may only function to a to a certain limit. Despite the variability associated with forage intake and the fact that compensation of abnormal weight loss may be achieved to some degree through increased intake rates, Luick (1977) and Holleman *et al.* (1979) performed experiments where reindeer fed lichens *ad libitum* lost weight during winter. Because these animals apparently were unable to increase their intake in order to offset the loss of weight, there seems to be a maximum forage intake rate. Moreover, because above average weight loss during winter (*e.g.*, >20%) has been suggested or demonstrated to reduce the reproductive success of female caribou (Zhigunov 1961; Rognmo *et al.* 1983; Cameron *et al.* 1993), compensatory feeding at this degree of weight loss does not appear to function.

Another assumption used for this model was that woodland caribou do not habituate to the disturbance resulting from petroleum exploration (for reasons described in the introduction of this chapter). If this assumption is incorrect, the magnitude of a caribou's reaction to loud noise should decrease with each successive encounter. This phenomenon would therefore cause the model to underestimate the encounter threshold, and would permit greater intensities of petroleum exploration within caribou range. This is because the energy expended during an encounter would be less than that of the previous encounter, until the response to disturbance eventually became negligible. However, even if habituation occurs to some degree, there is little evidence to suggest that disturbance-experienced caribou would ignore the presence of loud noise. Indeed, I found that many of the Impact animals tested within areas traditionally prone to high intensities of petroleum exploration demonstrated average escape responses and displayed little sign of habituation.

Another assumption was that caribou were unlikely to encounter the same geophysical programme more than once per day, based on the distance moved by a disturbed animal and the mean progression rate of exploration. If this assumption is incorrect, and a caribou can encounter the same programme more than once per day, the total winter energy loss calculated for a given region may be underestimated. On the other hand, I also assumed that an individual caribou is equally likely to be disturbed on each operating day of exploration. If this assumption is incorrect, a caribou disturbed repeatedly by the same programme may habituate to some degree or learn to avoid the area of exploration. In this case, the total winter energy loss calculated for a given region may be overestimated.

Two additional assumptions that require discussion include the degree that caribou were excited by the disturbance and the reaction of caribou at different distances from the source of disturbance. I assumed that in addition to the simple cost of displacement, excitement causes energy expenditure to increase by 10 - 25% by elevating the metabolic rate (Geist 1978). I was unable to measure or directly calculate this cost, so the total cost of a single perturbation is not explicit. However, I provided a wide range for the cost of a perturbation to account for the high variance associated with this value. Another concern is the evaluation of how caribou might respond to a far-off disturbance, such as one several kilometres from the animal's position. The animals in this situation may walk slowly away from the source of the noise, or they may choose to ignore it. If this occurs, only the caribou within the immediate vicinity of an exploration programme may be affected by the disturbance, and only these animals would lose weight due to disturbance. As mentioned in Chapter Three, there was no apparent relationship between the distance the Impact caribou was from the source of disturbance when it was initiated and the animal's subsequent response. In fact, one Impact caribou responded to the disturbance source that was over 800 m from its position, and then the animal proceeded to move several kilometres from the disturbance.

Two other important considerations in this simple model include the relevance of the 15% weight-loss threshold and the proportion of the population actually experiencing abnormal weight loss. The 15% weight-loss threshold simply estimated the number of encounters required to induce weight loss beyond this level **on average**. In other words, this threshold indicates that 50% of the population exposed to the same amount of disturbance would exceed 15% weight loss. Is 50% biologically relevant? Some may argue that such a high proportion of the exposed population experiencing abnormal weight loss is unacceptable from a conservation perspective, whereas nonconservationists may feel that the average is an acceptable compromise between economy and ecology. The other consideration concerning the actual proportion of the entire woodland caribou population experiencing abnormal weight loss is important in order to effectively estimate these effects on the entire population. If only a small proportion of the population is experiencing the weight loss described by the model, then the reduction in reproductive success of these animals may be compensated by the reproduction of the more numerous, non-exposed animals. On the contrary, if most of the population experiences these levels of disturbance, the combined effects may actually reduce population increment or exacerbate decline. One method of estimating this proportion is to define zones of relatively high exploration intensity and multiply those areas by the caribou density in those zones. This would give the number of caribou experiencing high exploration intensities, and when compared to the regional population, would give the proportion of the population likely experiencing abnormal weight loss. Unfortunately, there are not yet any precise estimates of woodland caribou density for this region.

In conclusion, I have outlined the advantages and limitations of a simple model that calculates the energetic consequences of multiple encounters with petroleum exploration. As with any model, certain assumptions were required to construct this model - some of which may be more or less biologically tenable. Despite the obvious limitations, this model is the first attempt at estimating the biological consequences of petroleum exploration in northeastern Alberta, and it provides important information for future research and land-use management.

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CHAPTER FIVE: CONCLUSIONS & IMPLICATIONS

5.1 Assessment of Approach and Methods

Until recently, the limited research on woodland caribou in northeastern Alberta has been largely descriptive (Fuller and Keith 1981), and did not permit a reliable estimate of the potential impacts of industrial exploration and development on caribou. The renewed interest in developing northern Alberta, especially in terms of petroleum development and timber harvest, and its potentially detrimental effects on woodland caribou has been addressed in this research project.

Major gains in knowledge of habitat selection were possible through an extensive radio telemetry programme that identified key caribou ranges and provided information for future research of woodland caribou population structure and function. Furthermore, applying the results of the habitat analysis to other areas of Alberta is a cost-effective and efficient method of assessing caribou distribution outside of the study area.

I used a manipulative method for assessing the effect of loud noise on behaviour and movement - observing individual response to single perturbation events. This technique was also required because other research addressing this aspect of wildlife management was almost always done in open tundra, thereby permitting a visual assessment of an animal's behavioural modification to human exploration and development. Visual assessment was nearly impossible in the dense boreal forest of northeastern Alberta. Moreover, many disturbance studies revealed major response trends from a herd or even population perspective (Cameron *et al.* 1979; Whitten and Cameron 1983; Mercer *et al.* 1985; Northcott 1985; Dau and Cameron 1986) . My approach permitted a relatively precise measurement of even small movements and behavioural changes in individuals, even when the animals were not always in sight. The difficulty in testing many individuals and the problems associated with the activity sensors were, however, disappointing. Perhaps instead of measuring behavioural modification using remote sensing, other indirect methods of measuring feeding modification through ground tracking would be more productive.

The reductionist approach (*i.e.*, monitoring individuals) also has limitations in extrapolation to population-scale effects (Bergerud *et al.* 1984). An ideal technique would be to expose individuals continuously to a varying number of perturbation bouts during winter in order to assess the effects of different exposure regimes on individual energy balance and mortality and natality rates. Measurement of body mass in early and late winter would have provided some key information on normal winter weight changes and those resulting from disturbance. In retrospect, I believe this last component should have been added to the experimental procedure and it should be included in future research. Without the corroboration of empirical data, predictions of weight change and the cumulative effects of multiple perturbation encounters can only be modeled using values from previous research. Nonetheless, I believe my estimates of multiple perturbation effects and the threshold encounter densities deemed to cause minor to excessive weight loss provided a reasonable means to assess perturbation effects. Future research should, however, corroborate these predictions.

Geographic Information Systems (GIS) provide an excellent tool for summarizing and processing large amounts of spatial data. Although the task of mapping all geophysical exploration programmes within the study area during a five-year period was tedious, the GIS permitted spatial analyses that summarized the total disturbance potential for any portion of the study region. Without this powerful tool, I would have found it difficult to assess the amount of disturbance that had recently occurred in caribou range, and I would not have been confident in developing management guidelines to control excessive exploration. I recommend that future research in this area should concentrate on the development of a more sophisticated model that incorporates average caribou movement rates, hierarchal habitat selection values, improved home range determination and area-specific exploration intensities. Generating random movement models and simulated exploration regimes would better model the disturbance potential for specific areas of the region. I believe, however, that my predictions on minimum disturbance thresholds are reasonable estimates.

The direct and indirect costs of perturbation encounters under varying weather conditions could also be the focus of a more complicated computer model. A model of stochastic inclement weather and the effects of cumulative perturbations would better define management options on a yearly basis. This technique would allow for a better understanding of the long-term effects of industrial exploration and development on woodland caribou populations. Based on the predictions generated from the simple model described in Chapter Four, wildlife managers should be able to reduce abnormal energy loss in woodland caribou by controlling the amount of industrial exploration planned for northeastern Alberta.

5.2 Conclusions

Chapter One outlined the concerns of a speculated woodland caribou population decline in northeastern Alberta and the hypothesized effects of industrial harassment thought to be contributing to the decline. Woodland caribou in this region are relatively sedentary, exist at low densities and occupy terrain that is difficult to access. A literature review of disturbance research highlighted an apparent controversy over the degree to which human activities affect caribou. An caribou's reaction depends on how sedentary it is, its age, physical condition and reproductive status, the type and frequency of perturbation, the time of year and landscape characteristics.

Chapter Two addressed winter habitat selection and constructed peatland habitat preference ranks in lowland areas. I found that woodland caribou prefer forested fen peatland complexes and concentrate feeding in forested bog islands; these preferences did not vary greatly during the three-year study period. Using the results of the habitat analyses, I determined woodland caribou distribution by grouping the preferred habitat types into discrete distribution polygons. These polygons incorporate the majority of the woodland caribou population in northeastern Alberta.

In Chapter Three I outlined the results of a perturbation experiment that measured the effects of simulated noise disturbance on caribou behaviour and movement. Simulated petroleum exploration noise caused temporary increases in movement rates during perturbation, longer-term increases in daily movement rates after perturbation and increases in linear displacement. Disturbance did not change the proportion of time allocated to feeding or rapid movement, nor did it significantly affect shifts to different habitat types. Most parameters measured were significantly different between 1993 and 1994 - most likely the consequence of the higher snowfall and snow accumulation in 1994.

Chapter Four outlined a model developed to estimate the probability of encounter with noise disturbance generated from typical winter petroleum exploration. I also discussed the probable energetic impact of exposure to winter exploration combined with the results of Chapter Three. A simple model that estimated the probable energetic consequences of multiple perturbation encounters was compared to petroleum exploration during the past five years. I found that several woodland caribou distribution polygons within northeastern Alberta experienced sufficient exploration to have caused significant weight loss in the caribou found there. Because the amount of petroleum exploration differs between years, it is essential that land-use planning focus on methods of reducing the number of exploration programmes in different areas of high industrial use. Only by subscribing to this method of land-use management will an effective strategy be developed to achieve biological integrity and economic prosperity.

5.3 Management Recommendations

During the 27 months that I have devoted to this project I have developed some opinions on how land-use guidelines should be defined for woodland caribou in northeastern Alberta, based both on the conclusions of this study and on personal conjecture. I offer them as a guide to modify existing land-use regulations.

(1) Based on the findings presented in Chapter Four, I recommend that management regulations enforce 23 potential perturbation encounters during winter as the maximum disturbance threshold. Beyond this value, mean winter weight loss exceeds that which occurs in the absence of disturbance. The exposure rate within any one woodland caribou distribution polygon should not exceed 0.0375 encounters/km^2/winter (*i.e.*, 23 encounters expressed as a function of mean winter home range area).

Using this value as the maximum encounter threshold, future management can determine at which point geophysical exploration should be discontinued during mid- to late winter. I suggest that managers use the following formula to assess the disturbance potential for a given area:

Exposure Rate (encounters/km^2/winter) = (**DISTEXPL** ÷ **PROGRATE**) ÷ **POLYAREA**,

where **DISTEXPL** = the cumulative distance (km) to be explored within a specific woodland caribou distribution polygon (as defined in Chapter Two); **PROGRATE** = the mean progression rate (km/day) of geophysical exploration programmes (2.6174 km/day - 1988 to 1993); and **POLYAREA** = the surface area (km^2) of the woodland caribou distribution polygon in which the exploration occurs, or the area of a portion of the polygon in which most exploration is planned (see recommendation 3). When the exposure rate exceeds 0.0375 encounters/km^2/winter, further exploration should be discontinued in that area. Although this represents a minimum exposure rate before abnormal weight loss occurs, other industrial activities may contribute to localized disturbance potentials (see recommendation 2).

(2) Land use in northeastern Alberta includes other industrial activities in addition to geophysical exploration. These include pipeline construction, compressor station construction, timber harvest, peat harvest and other similar activities. Because these procedures likely contribute to the disturbance potential, I believe the 0.0375 encounters/km^2/winter to be an effective index of maximum industrial exposure. If industrial activity other than geophysical exploration becomes excessive, this threshold may have to be decreased. Management authorities should eventually discover means of incorporating these additional activities into the calculation of a safe disturbance exposure threshold.

(3) Because exploration activity may be concentrated to one area of a woodland caribou distribution polygon, the area that incorporates the majority of this activity should be used as the denominator in the calculation of the potential encounter rate for that year (see Chapter Four). Although some subjectivity is required to delineate these areas, it better reflects the actual disturbance potential for specific areas of caribou range.

(4) Timing restrictions during late pregnancy, calving and post-calving should be maintained. Although most petroleum exploration occurs when the ground is frozen (*i.e.*, November - April), improvements in technology soon may permit exploration to continue into late spring and summer. I suggest that all potentially harassing exploration and development be stopped from April 1 to July 31 each year to allow female caribou to rear their calves in the absence of potentially harmful disturbance. As suggested in Chapter One, female caribou and calves are normally the most susceptible to disturbance regimes during this critical time of their annual life cycle.

(5) I suggest that extensive geophysical programmes should avoid situations where different phases of the exploration process operate simultaneously over large areas. This has the effect of increasing the probability of multiple encounters for caribou in the general area of the exploration. When a programme is designed to concentrate activity in one area before moving to the next, encounter rates with woodland caribou should be reduced.

(6) Some attempt should be made to reduce the number of independent seismic lines created within woodland caribou range. Excessive fragmentation resulting from localized, intense geophysical exploration may influence the relationship between predators and caribou. Although this aspect of caribou biology is to be addressed in the near future by the North-East Region Standing Committee on Woodland Caribou (NERSC), land-use managers should incorporate this aspect into existing regulations.

Fragmentation resulting from geophysical exploration has been recorded in the Weldwood of Canada Ltd. (Hinton Division) Forest Management Agreement (F.M.A.) area from 1954 to 1993 (Weldwood of Canada 1994). This F.M.A. lies to the immediate west of Jasper National Park and incorporates 10 121 km^2 of the Rocky Mountain foothills region. The F.M.A. was granted to Weldwood of Canada by the Province of Alberta in 1954 and incorporated 7 800 km^2 until 1988. The total area removed by seismic lines from 1954 to 1993 was approximately 12 290 ha, or a mean removal rate of 315 ha/yr. An additional 13 456 ha was removed by petroleum dispositions (well-site clearing, pipeline rights of way, *etc.*) during the same period. Therefore, the total forested area removed in the F.M.A. from petroleum exploration and development between 1954 - 1993 was 25 746 ha, or 3.17% of the total area[1].

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[1] *Total area of the F.M.A. was calculated as a weighted average of the 1954 - 1987 area and the 1988 - 1993 area based on years in effect.*

This is equivalent to 660 ha removed per year, or 0.081% of the total area per year.

Given the extent of forest cover removal and the linear form of the cut-over polygons (*e.g.*, seismic lines), I suggest that research be done to examine the potential effects of fragmentation on caribou and other wildlife species. The creation of edge habitat (*i.e.*, the junction of two different landscape elements) often alters the species composition of the neighbouring habitats and may affect interactions between species (Yahner 1988). Indeed, the effects of excessive fragmentation may upset the balance of predator-prey interactions more to the detriment of caribou than excessive perturbation.

(7) An effort should be made to restrict as much as possible all access into woodland caribou distribution areas to prevent increased hunting and poaching. Existing road access should be controlled within caribou range and an attempt made to reduce the number of new access roads constructed each year. This potential source of mortality seems important in light of the traditionally isolated habitats that woodland caribou normally occupy.

(8) Secondary caribou areas (see Chapter Two) should be protected from extensive fragmentation and the development of large, impenetrable barriers that could impede movement between primary caribou distribution polygons. Although these areas do not likely shelter large numbers of woodland caribou, sufficient preferred habitat types exist to facilitate movement between adjacent caribou distribution polygons. Excessive development in these secondary areas could prevent this movement and reduce the long-term viability of the regional population.

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