

HEALTH, NUTRITIONAL CONDITION, AND PRODUCTIVITY OF FEMALE MOOSE
(*ALCES ALCES*) IN NORTHWESTERN ONTARIO

BY

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A THESIS
PRESENTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGY
LAKEHEAD UNIVERSITY
THUNDER BAY, ONTARIO

AUGUST 2003



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ABSTRACT

Creation or maintenance of moose habitat through logging requires an understanding of how particular timber-harvest practices affect nutritional interactions of adult females and their subsequent production of young. I compared ultrasonographic fat measurements of free-ranging adult female moose in northwestern Ontario, Canada, 1998-2001, inhabiting two forest management regimes; a modified clear-cut, following the *Timber Management Guidelines for the Provision of Moose Habitat*, and an unmodified, progressive, and contiguous clear-cut. I also determined pregnancy and in utero twinning by radioimmunoassay of pregnancy-specific protein B (PSPB) and compared the number of expected calves born to the number of calves surviving to winter. As an adjunct to evaluation of reproductive performance, I also examined blood parameters, hair mineral content, and stress hormone metabolite concentration in feces.

For these comparisons to be made, however, reference ranges for blood and hair parameters needed to be established and the effects of handling, individual, temporal, and spatial factors on blood parameter variability measured. Likewise, the radioimmunoassay used to quantify stress hormone metabolites in feces had not been previously used in moose and the affinity of the antibody to the fecal glucocorticoid (GC) metabolites of moose was unknown.

In Chapter 1, *Validation of a generalized fecal glucocorticoid assay for use in moose*, I investigated whether a commercially available multi-species assay (ICN Biomedicals) accurately reflected acute adrenal activation in moose. Recent development of assays for GC metabolites has provided a non-invasive means to assess a variety of human-induced disturbances and environmental conditions on free-ranging animals. Fecal samples are easy to collect year-round and provide an integrated reflection of all GC secretion over a period of time prior to sample collection; however, species-specific differences in steroid metabolism necessitate validation of

the assay used to quantify GC concentration. I pharmacologically challenged 2 captive-raised moose (1 male and 1 female) with adrenocorticotropin hormone (ACTH). A change in fecal GC metabolite levels was detected at 15 and 22 hours after the administration of the ACTH and levels remained elevated for 12 and 50 hours, respectively. Accuracy and parallelism tests demonstrated there was negligible interference from other substances in the feces and that the antibody binds with serially diluted fecal GC metabolite extracts in a dose-dependent manner. I concluded the ICN Biomedicals' antibody could be used to detect a stress response in moose. Further study will be required to define seasonal patterns in adrenal activity, measure response to different types of stress, and evaluate the consequences of chronically elevated stress hormones.

In Chapter 2, *Comparative health status, nutritional condition, and productivity of female moose in northwestern Ontario under two forest management regimes*, the age structure (assessed by tooth wear), body size, and manner in which animals were handled were shown to be similar between landscape treatments. Reference ranges generated for blood chemistry, hematology, and hair mineral content are presented. After controlling for the effects of handling and sampling year, body fat and/or landscape treatment explained little of the variance in these parameters.

In 1999-2000, I collected feces and evaluated stress hormone metabolite concentrations. Values were similar between landscape treatments and comparable to values observed in wild Alaskan moose during mid-winter. Because fecal metabolites represent stress hormone secretion over the previous 1-2 days, the values obtained are unaffected by capture stress making this technique suitable for monitoring adrenal activity in free-ranging moose.

February body fat stores in adult females averaged 8.54% and exhibited little annual variation. Successfully raising a calf to winter modestly affected lipid reserves (8 vs. 9%) and

apparently did not affect subsequent reproductive effort. Nutritional condition and intrauterine fecundity were similar between landscape treatments. Estimates exceeding 165 calves in utero/100 cows were indicative of populations below K carrying capacity. Calf survival to winter (Jan - Feb) was greater in the clear-cut landscape modified by the *Timber Management Guidelines for the Provision of Moose Habitat* than the progressive, contiguous clear-cut (67.3 calves/100 cows vs. 44.2 calves/100 cows) however, which suggested environmental factors affecting calf survival were different between the 2 landscape treatments.

ACKNOWLEDGEMENTS

“Experience keeps a hard school, but a fool will learn in no other.”

Poor Richard

My journey began when Art Rodgers arrived at the Kenai Moose Research Center, Alaska for a visit in spring 1997. How could I have known that his visit would eventually lead to my pursuit of moose in northwestern Ontario? Thanks Art, for your continued support, encouragement, and watching out for my best interests. I would also like to thank committee members Murray Lankester and Azim Mallik for their patience and critical review of my thesis.

The Ontario Ministry of Natural Resources (OMNR), Center for Northern Forest Ecosystem Research (CNFER), provided funding and logistical support throughout my studies. Brad Allison (CNFER) provided timely replies to data requests and collected the fat data in 2001. Thanks to all of the OMNR helicopter pilots for hundreds of hours of safe flying. In particular, Ted Hill, your calm demeanor and willingness to lug the ultrasound back to the ship while we finished-up at the moose made the days more enjoyable. The Alaska Department of Fish and Game (ADF&G) allowed me to take time away from my responsibilities in Alaska to pursue the “professional” degree. Thanks to Tom Stephenson, Kris Hundertmark, Chuck Schwartz, Jeff Hughes, and Wayne Regelin for the opportunity. Tom was responsible for bringing me to the Kenai Moose Research Center; he intimately involved me in moose condition studies and *was* a good friend until he left to California. Amy Stephenson, thanks for always having a spare room available at the house and putting up with discussions of moose rump fat over dinner.

Helicopter Wildlife Management, Northern Mountain Helicopters, and Big Horn Helicopters captured animals in different years. It was challenging immobilizing such large animals as moose by net-gun and physical restraint.

Sean Farley (ADF&G) suggested I measure stress hormones in moose feces. Thanks to Kathleen Hunt and Sam Wasser (University of Washington) for their advice on conducting ACTH challenges.

I am also appreciative of all the friendly people in Thunder Bay who welcomed me into their homes during my stays, took me canoeing on Lake Superior, and introduced me to curling, eh.

Family excursions into the wilderness introduced me to the natural environment and provided me with many useful skills. Thanks Mom and Dad.

Stacy, it is unthinkable what this process would have been like without your willingness to listen, laugh, love, ... and do the dishes.

TABLE OF CONTENTS

Abstract	ii
Acknowledgements	v
List of Figures	viii
List of Tables.....	x
List of Appendices.....	xii
Chapter 1. Validation of a generalized fecal glucocorticoid assay for use in moose	
Introduction	1
Methods	3
Results	7
Discussion	10
Chapter 2. Comparative health status, nutritional condition, and productivity of female moose in northwestern Ontario under two forest management regimes	
Introduction	16
Study Area.....	19
Methods	22
Results	29
Discussion	59
Literature Cited.....	67

LIST OF FIGURES

Fig. 1.1. Fecal glucocorticoid metabolite excretion of a female moose following ACTH (1 IU/kg) injection	9
Fig. 1.2. Fecal glucocorticoid metabolite excretion of a male and female moose following ACTH (1 IU/kg Trial 1 and 3 IU/kg Trial 2) injection	11
Fig. 1.3. Comparison of known and calculated corticosterone levels in serially diluted moose fecal glucocorticoid metabolite extracts.....	12
Fig. 1.4. Comparison of antibody binding in serially diluted corticosterone standards and moose fecal glucocorticoid metabolite extracts.....	13
Fig. 2.1. Map of the study area in northwestern Ontario, Canada, 1998-2001	20
Fig. 2.2. The relationship between age determined from cementum annuli and incisor occlusal surface wear of female moose in northwestern Ontario, Canada, 1995 – 2001	30
Fig. 2.3. Mean (\pm SD) daily snow depth and temperature during winter in northwestern Ontario, Canada, 1998-2001 (Environment Canada, Station no. 6032119, Dryden).....	35
Fig. 2.4. The contribution from individual non-outliers, non-censored outliers, and censored outliers to the total number of outlying values among each of the blood components.....	41
Fig. 2.5. Comparison of blood components that exhibited high outlying values between censored and non-censored individuals.....	42
Fig. 2.6. Comparison of blood components that exhibited low outlying values between censored and non-censored individuals.....	43
Fig. 2.7. Comparison of annual potassium levels in female moose hair between timber-harvest treatments, northwestern Ontario, Canada, January-February 1998-2001.....	46
Fig. 2.8. Comparison of immunoreactive fecal glucocorticoid metabolites in female moose between timber-harvest treatments, northwestern Ontario, Canada, February 1999-2000.....	47
Fig. 2.9. Calf-at-heel status and corresponding ultrasonographic measurements of rump-fat thickness (square-root transformed data) in female moose, northwestern Ontario, Canada, January–February 1998-2001	52
Fig. 2.10. Annual ultrasonographic measurements of rump-fat thickness (square-root transformed data) in female moose, northwestern Ontario, Canada, January–February 1998-2001.....	53

LIST OF FIGURES (CONT.)

- Fig. 2.11. Ultrasonographic measurements of rump-fat thickness (square-root transformed data) in female moose inhabiting 2 timber-harvested landscapes in northwestern Ontario, Canada, January–February 1998-2001 55
- Fig. 2.12. Scatter plot with a fitted line (LOESS smoothed line, tension = 0.950) demonstrating the relationship between Body Condition Score (BCS) and rump-fat thickness (MAXFAT)..... 56

LIST OF TABLES

Table 1.1. Nutritional composition of the aspen-based pelleted moose ration	4
Table 1.2. Trial periods, animal data, and ACTH doses administered to moose in this study	5
Table 1.3. Daily intake and fecal output ($\bar{X} \pm SD$) of moose during ACTH challenge trials.....	8
Table 2.1. Pearson correlation coefficients for morphometric measurements (± 1 cm) of adult female moose in winter, captured in the progressive clear-cut landscape treatment (PCC) northwestern Ontario, Canada, 1995-2001.....	31
Table 2.2. Pearson correlation coefficients for morphometric measurements (± 1 cm) of adult female moose in winter, captured in the modified clear-cut landscape treatment (MCC) northwestern Ontario, Canada, 1995-2001.....	31
Table 2.3. Pearson correlation coefficients for morphometric measurements (± 1 cm) of all adult female moose in winter, captured in northwestern Ontario, Canada, 1995-2001	31
Table 2.4. Pearson correlation coefficients of handling measures for moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, 1999-2001	32
Table 2.5. Multivariate analysis of variance of handling measures of moose as a function of year, treatment, and year by treatment, northwestern Ontario, Canada, 1999-2001	32
Table 2.6. Results from regression analysis of body temperature against other handling measures of moose captured by hand-held net-gun fired from a helicopter, northwestern Ontario, Canada, 1999-2001.....	33
Table 2.7. Comparison of early-winter (November-January) severity indices for moose in northwestern Ontario, Canada, 1997-2001.....	36
Table 2.8. Hematology values of adult female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, January-February 1998-2001. Reference ranges calculated as the interval between the 2.5 and 97.5 percentiles	37
Table 2.9. Serum chemistry values of adult female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, January-February 1998-2001. Reference ranges calculated as the interval between the 2.5 and 97.5 percentiles.....	38
Table 2.10. Factors influencing winter blood hematology values of female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, 1999-2001	39

LIST OF TABLES (CONT.)

Table 2.11. Factors influencing winter blood chemistry values of female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, 1999-2001	39
Table 2.12. Hair mineral concentration of adult female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, January-February 1998-2001. Reference ranges calculated as the interval between the 2.5 and 97.5 percentiles	44
Table 2.13. Multivariate analysis of variance of winter moose hair mineral concentration as a function of year and timber-harvest treatment, northwestern Ontario, Canada, 1998-2001	45
Table 2.14. Comparison of rump-fat thickness (cm), percent total body fat, kilograms total body fat, and calf status between timber harvest treatments in northwestern Ontario, Canada, January-February 1998-2001	49
Table 2.15. Covariance structure model fitting information for the mixed model analysis of repeated rump-fat measures. Smaller values of adjusted Akaike's Information Criterion (AICc) and Schwarz' Bayesian Criterion (BIC) indicate a better fit. The χ^2 -statistic is the null model likelihood ratio test.....	50
Table 2.16. Covariance structure model fitting information for the mixed model analysis of repeated rump-fat measures (following backward stepwise removal of non-significant effects). Smaller values of adjusted Akaike's Information Criterion (AICc) and Schwarz' Bayesian Criterion (BIC) indicate a better fit. The χ^2 -statistic is the null model likelihood ratio test	50
Table 2.17. Effects of covariance structure on <i>F</i> -tests of rump-fat thickness. The row by column intersection is the <i>P</i> -value for the effect associated with the specified covariance structure	51
Table 2.18. Effects of covariance structure on <i>F</i> -tests (following backward stepwise removal of non-significant effects) of rump-fat thickness. The row by column intersection is the <i>P</i> -value for the effect associated with the specified covariance structure.....	51
Table 2.19. In utero pregnancy and twinning determined by pregnancy-specific protein B (PSPB) measured in moose in northwestern Ontario, Canada, January-February 1998-2001	57
Table 2.20. Number of calves at heel observed with radio-collared moose during winter in northwestern Ontario, Canada during 1999-2001	58

LIST OF APPENDICES

APPENDIX I. Hematological parameters and some causes for their deviation from normal	80
APPENDIX II. International System of Units (SI) conversion factors: Hematology.....	81
APPENDIX III. Chemistry parameters and some causes for their deviation from normal	82
APPENDIX IV. International System of Units (SI) conversion factors: Chemistry	83

CHAPTER 1

VALIDATION OF A GENERALIZED FECAL GLUCOCORTICOID ASSAY FOR USE IN MOOSE

INTRODUCTION

Measurement of metabolic activity enhances our understanding of the adaptive responses animals make to challenges from their environment. Physiological responses to stress are mediated by glucocorticoids (GC) (Selye 1950, Ingle 1952, Munck et al. 1984, Buckingham et al. 1997). Stress-induced GC secretion produces marked effects on energy metabolism (Dallman et al. 1989, Rijnberk and Mol 1997) and suppresses immunologic responsiveness through modulation of intracellular mediators (Munck et al. 1984). While a normal stress-response is necessary to maintain homeostasis, prolonged exposure to elevated GCs may suppress growth (Wehrenberg et al. 1990), inhibit sexual maturity (Ramaley 1974), impair normal reproduction (Brann and Mahesh 1991, Rivier and Rivest 1991), and reduce resistance to disease (Goulding and Flower 1997). The primary mammalian GCs are cortisol and corticosterone (Norris 1997). These steroid hormones are released into the systemic circulatory system through activation of the hypothalamic-pituitary-adrenal (HPA) axis. Increases in serum concentrations may be apparent within 10 minutes of the onset of the stimulus (Gwazdauskas et al. 1972). Metabolism occurs in the liver and the resulting conjugated metabolites are excreted in the urine and the bile (Rijnberk and Mol 1997).

In animals not influenced by any extraordinary stress, low basal levels of circulating GCs are the result of episodic pulses of adrenocorticotropin hormone (ACTH) (Krieger 1978, Antoni 1986, Jacobson and Sapolsky 1991). During stress, the mechanisms regulating GC production

are more complex (Aguilera 1994); however, GC levels maintained above basal values are indicative of repeated or persistent stressful stimuli.

Evaluation of endogenous adrenal activity is made difficult by the need for repeated sampling. Restraint or capture is stressful to animals and the overwhelming influence of handling on serum GC concentrations is well documented (Franzmann et al. 1975a, Wesson et al. 1979a, Hastings et al. 1992). More recently, measurements of urinary and fecal GCs and/or their metabolites have been suggested as an alternative approach to detecting stress responses without disturbing study animals (Miller 1988, Miller et al. 1991, Saltz and White 1991a, Saltz and White 1991b, Wasser et al. 1997). Measurements of excreted metabolites provide an integrated reflection of GC production over a period of time prior to sample collection (Rijnberk and Mol 1997, Harper and Austad 2000). Fecal sampling has the additional advantage of being better suited to field application, as feces can be collected year-round (Miller et al. 1991, Brown et al. 1994, Millspaugh et al. 2001).

Interspecific variation in steroid metabolism requires validation of the assay used for quantification of fecal GC metabolites (Wasser et al. 1997). Wasser et al. (2000) demonstrated the ability of a commercially available multi-species corticosterone antibody (¹²⁵I; ICN Biomedicals, Inc., Costa Mesa, CA 92676, USA; Cat. No. 07-120102) to detect increases in fecal GC metabolite concentration after adrenocorticotrophic hormone (ACTH) administration in several animal species, including elk (*Cervus elaphus roosevelti*). The affinity of the antibody to the fecal GC metabolites of moose (*Alces alces*) however, is unknown. A pharmacological challenge with ACTH would establish whether fecal assays accurately reflect acute adrenal activation in moose. In vertebrates, ACTH administration mimics a natural adrenal stress response by causing a rapid rise in circulating GCs (i.e., cortisol and corticosterone), followed by

a return to baseline within a few hours. The same pattern should occur in feces, with the onset of the peak excretion of metabolites delayed by a species-specific lag time. My objective was to demonstrate the affinity of the ICN antibody to moose fecal GC metabolites.

METHODS

MOOSE AND FACILITIES

Because the study objective was to demonstrate the affinity of the ICN antibody to moose fecal GC metabolites (as opposed to determining a mean response by moose to ACTH stimulation) 1 or 2 animals was of sufficient sample size (S. Wasser, University of Washington, Seattle, personal communication). Trials were conducted with two moose (a 9-year-old male and a 9-year-old nonpregnant female) held at the Kenai Moose Research Center (MRC), approximately 60 km northeast of the town of Soldotna, Alaska (60°N, 150°W, elevation 90 m). Animals generally resided within 2.6 km² pens and were fed an aspen-based pelleted ration (Table 1.1) to supplement available natural browse (aspen (*Populus tremuloides*), birch (*Betula papyrifera*), and willow (*Salix* spp.)) during winter (November – April): they fed on natural browse only throughout the remainder of the year. Prior to Trial 1 both animals were restricted to a 4-hectare pen for 2 months and were fed the pelleted ration almost exclusively. In late winter, animals were acclimated to individual outdoor pens (3.1 by 15.2 m) over a 4 day period prior to administration of the ACTH. The following year, the female spent the entire winter in the 2.6 km² pen prior to Trial 2. Trial periods, animal information, and ACTH doses are listed in Table 1.2. Both moose were dam-raised in captivity, but had been used in previous studies and were accustomed to daily human contact and confinement in small handling pens.

Table 1.1. Nutritional composition of the aspen-based pelleted moose ration (Don's Alaskan Moose Ration, Alaska Mill and Feed, Anchorage).

Nutrient ^a	
Dry matter (%)	92
Gross energy (kcal/kg)	4450
NDF ^b (%)	35.725
ADF ^b (%)	20.035
Lignin (%)	2.74
Crude protein (%)	10.59
In vitro DMD ^b (%)	70.64
Selenium (ppm)	0.257
Vitamin E (IU/kg)	5.62

^aOriginal ration formulated by Schwartz et al. (1985) with additional Selenium and Vitamin E (Stephenson et al. 2001).

^bNeutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), and Dry Matter Digestibility (DMD) see Van Soest (1994).

Table 1.2. Trial periods, animal data, and ACTH doses administered to moose in this study.

Trial	Date	Animal	Mass (kg)	% Body Fat ^a	ACTH Dose (IU/kg)
1	2-6 May, 2000	Male	550	17	1
1	2-6 May, 2000	Female ^b	485	15	1
2	28-31 March, 2002	Female ^b	465	9	3

^aPercent body fat determined from relationship with ultrasonographic measurements of rump fat thickness developed by Stephenson et al. (1998).

^bThe same female was used in both trials.

FEEDING AND FECAL SAMPLE COLLECTION

Each morning, moose were offered the pelleted ration ad libitum and refusals were collected and weighed (± 0.01 kg). Water and an American Stockman® trace mineralized salt block (IMC Salt Inc., Overland Park, KS 66210, USA) were always available. Feces were collected at regular intervals (~24 hours) prior to ACTH injection and then all feces were collected for the next 3-4 days after injection. Moose either defecated onto a polypropylene woven fabric ground cover (AMOCO Fabrics and Fibers Company, Atlanta, GA 30339, USA) or onto snow. Both substrates allowed urine to pass through which minimized any urine contamination and served to keep the feces clean. To facilitate fecal collection, moose were provided a freshly cut browse stem (aspen, birch, or willow) while the entire defecation was gathered into a plastic, resealable bag. Defecations were labeled with date and time, weighed (± 0.01 kg), and thoroughly mixed. From the mixture, 2 samples (~ 50 g wet matter each) were collected into separate, labeled containers and were stored frozen (-18°C) within 1 hour post-collection until laboratory analysis (within 2-3 months); one sample from each defecation was shipped overnight on dry ice to the University of Washington to be assayed (see below) and the second was dried to constant mass at 55°C in a forced-fan oven to determine dry matter weight.

ACTH ADMINISTRATION AND RADIOIMMUNOASSAY

Moose were temporarily restrained, without anesthesia, on an enclosed livestock scale and received a single dose of ACTH administered intramuscularly in a highly concentrated (200 IU/ml) slow-release gel synthesized by a pharmacist (Hadfield's Pharmacy, Edmonds, WA 98026, USA). The female had been walked onto the scale box at weekly intervals during previous studies, but the bull's weight was only infrequently determined and he was less familiar with the procedure. During Trial 1, the bull became highly agitated and aggressive during the

first attempt to restrain him on the scale. The ACTH dose was successfully administered to the bull 1 hour later. The female was calm during dosing procedures in both trials. All fecal samples were assayed using the ICN corticosterone antibody. Steroids were extracted from 0.2 g dry matter feces by vortexing in methanol (K. Hunt, University of Washington, Seattle, WA 98195-1800, USA). Accuracy and parallelism tests determined whether interference from other substances in the feces occurred and to what extent the antibody binds with serially diluted fecal GC metabolite extracts in a dose-dependent manner (Abraham et al. 1977, Jeffcoate 1981).

The procedures met standards of care and conditions for the use of animals set by the Lakehead University Animal Care Committee (Canadian Council on Animal Care 1984, 1993) and the Alaska Department of Fish and Game.

RESULTS

DRY MATTER INTAKE AND EXCRETION

During both trials, daily dry matter food intake and excretion were stable (Table 1.3). These data provided evidence that animals were acclimatized to the diet and experimental conditions.

ACTH CHALLENGES

Trial 1

The female's fecal GC metabolite levels (11.6 ± 3.4 ng/g) were higher (pooled- $t_{0.05(2)10} = 2.6363$, $P = 0.0249$) than the male's (7.2 ± 2.1 ng/g) prior to ACTH challenge. Furthermore, the female's highest fecal GC metabolite levels were observed prior to administration of the ACTH and there was no indication of a response afterwards (Figure 1.1), hence necessitating a second trial.

Table 1.3. Daily food intake and fecal output ($\bar{X} \pm SD$) of moose during ACTH challenge

trials. All mass values are expressed as dry matter.

Trial	No. of Days	Animal	Daily Intake (kg)	Fecal Mass (kg)	Excretion Rate (excretions/day)	Daily Fecal Mass (kg)
1	5	Male	9.21 \pm 0.40	0.37 \pm 0.11	8.7 \pm 0.58	3.18 \pm 0.03
1	5	Female	6.58 \pm 0.67	0.32 \pm 0.09	7.7 \pm 0.58	2.43 \pm 0.23
2	4	Female	7.49 \pm 1.19	0.33 \pm 0.09	8.3 \pm 2.89	2.71 \pm 1.06

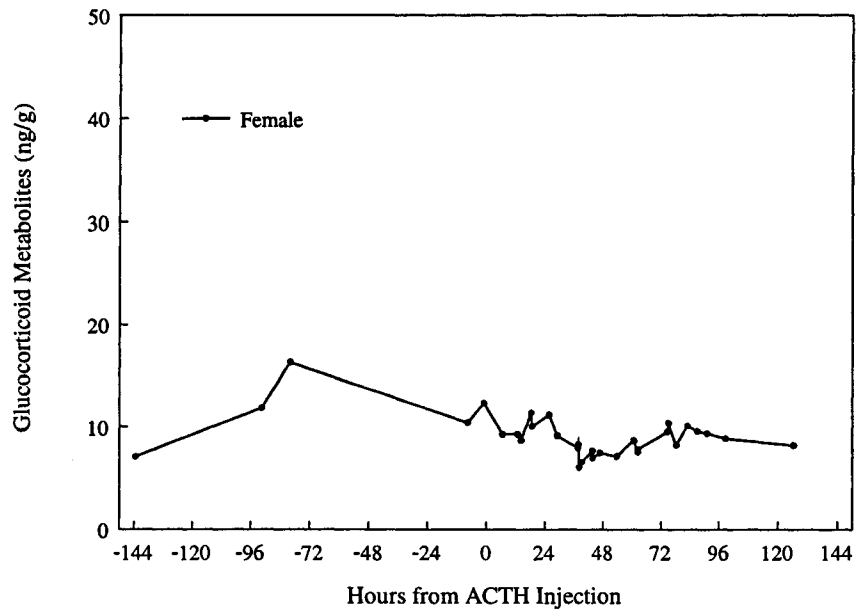


Figure 1.1. Fecal glucocorticoid metabolite excretion of a female moose following ACTH (1 IU/kg) injection.

The male's fecal GC metabolite levels spiked at 19 ng/g dry matter feces between 15 and 22 hours after administration of the ACTH and returned to pre-injection levels within 12 hours (Figure 1.2).

Trial 2

Comparison of the female's basal fecal GC metabolite levels between Trial 1 and Trial 2 were different ($\bar{X} = 11.6$ and $\bar{X} = 27.8$ ng/g, pooled- $t_{0.05(2)9} = -9.5928$, $P < 0.0001$). A change in her fecal GC metabolite levels was detected at about 22 hours after the administration of the ACTH and levels remained elevated for about 50 hours (Figure 1.2).

RADIOIMMUNOASSAY VALIDATION

The accuracy tests had a slope close to 1 and showed negligible interference effects from other substances in the feces (Figure 1.3). The parallelism tests showed that dilutions of moose feces were more-or-less parallel to corticosterone standards (Figure 1.4).

DISCUSSION

My data suggest measurement of fecal GC metabolites with the ICN antibody can be used reliably to detect an acute stress response in moose. Accuracy and parallelism tests demonstrated there was negligible interference from other substances in the feces and that the antibody binds with serially diluted moose fecal GC metabolite extracts in a dose-dependent manner. The 15-22 hour lag time for the appearance of hormone metabolites was consistent with gut passage rate studies in moose on similar diets (Schwartz et al. 1986, Hubbert 1987) and was characteristic of the pattern observed in other ruminants (Wasser et al. 2000, Millspaugh et al. 2002). Without further study, however, interpretation of absolute fecal GC metabolite levels and the rate at which they are excreted should be made cautiously. The excretion pattern of GC metabolites has only recently been studied (Wasser et al. 2000, Millspaugh et al. 2002) and

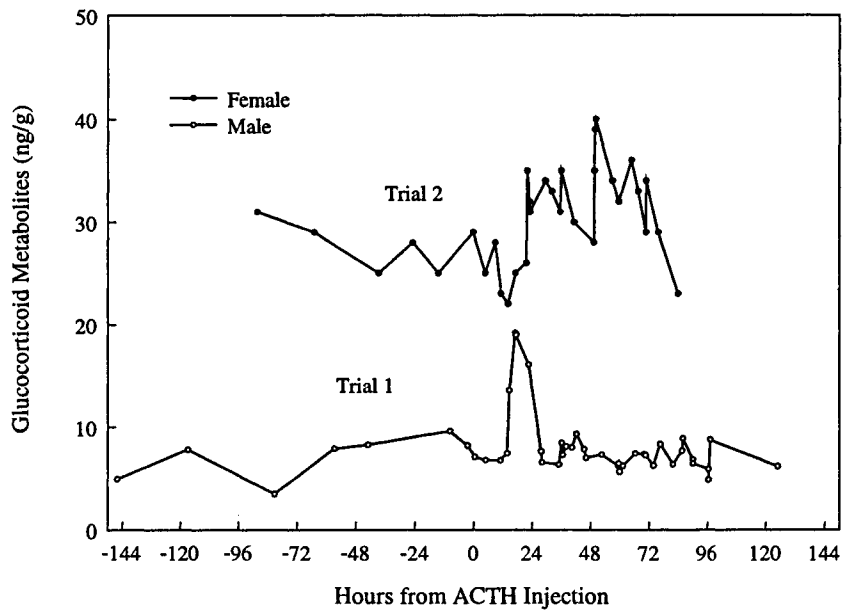


Figure 1.2. Fecal glucocorticoid metabolite excretion of a male and female moose following ACTH (1 IU/kg Trial 1 and 3 IU/kg Trial 2) injection.

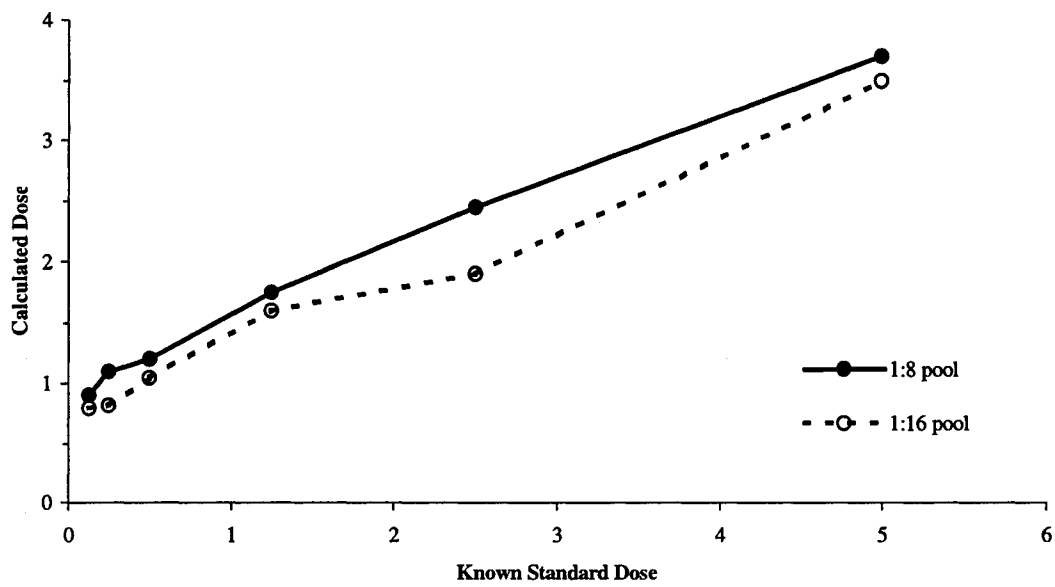


Figure 1.3. Comparison of known and calculated corticosterone levels in serially diluted moose fecal glucocorticoid metabolite extracts.

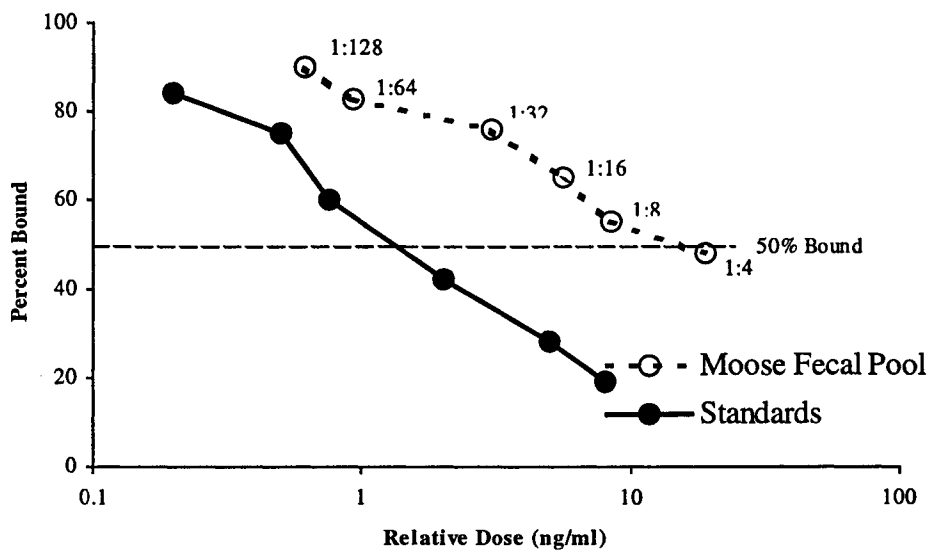


Figure 1.4. Comparison of antibody binding in serially diluted corticosterone standards and moose fecal glucocorticoid metabolite extracts.

factors that affect steroid metabolism (Wiltbank et al. 2000) or gut transit time (Palme et al. 1996) may influence GC metabolite concentration observed in feces. For example, Millspaugh et al. (2002) observed a two-fold difference in fecal GC excretion rate (12 h vs. 24 h) in the same white-tailed deer challenged with ACTH in spring and fall, respectively.

The ACTH dose (1 or 3 IU/kg) administered to moose in this study apparently stimulated sufficient adrenal activation to detect a response in fecal GC metabolite concentration. The peak excretion levels of GC metabolites I observed post-ACTH injection, however, were comparable to the lower range of values observed in wild moose apparently uninfluenced by acute stress (Tomeo 2000, Chapter 2). Control of GC production is complex and a dose dependent response to ACTH has not been established. Results of ACTH doses reported by others to study fecal GC response to stress vary considerably (<1 to 12.5 IU/kg; Wasser et al. 2000, Millspaugh et al. 2002). In a blood study, Bubenik et al. (1994) induced a 4-fold increase (~130-430 nmol/L) in circulating GC levels within 90 minutes after intravenous administration of 40 IU total ACTH in male yearling Alaskan moose (*A. alces gigas*). The 50 h period of elevated metabolite excretion exhibited by the female following 3 IU ACTH/kg injection was considerably longer than the 12 h period in the male following 1 IU ACTH/kg and could have been a result of the greater ACTH dose. It is possible however the male's sharp response in Trial 1 was influenced by the stress he experienced during the dosing procedure, rather than the ACTH itself, as no response was observed in the female. Alternately, the failure to detect a response in the female during Trial 1 could be explained by improper, or incomplete ACTH administration.

Basal values for the female prior to Trial 2 were higher than before Trial 1; following a winter during which her diet was only minimally supplemented with the pelleted ration and she foraged more naturally in the 2.6 km² enclosure. In addition, she weighed 5% less and her body

fat was 40% lower. Perhaps basal GC metabolite levels may be elevated in animals in poorer nutritional condition.

The highest levels of GC metabolites were detected in the feces of the female prior to the administration of ACTH in Trial 1. This suggests she experienced some sort of stressor before the trial began. It is unlikely that moving her into the small pen was disturbing, however, she did experience some distress that affected her intake during the day following confinement. It is possible that the male had been preventing her from eating as much as she wanted at a common feeder over several days prior to the trials. During her first day in the small pen she consumed approximately 7 kg dry matter of feed. The following day she consumed just 3 kg, was lethargic, and did not defecate for several hours. Over the third and fourth day her intake increased to 7 kg dry matter and was stable by the time the ACTH challenge trial began. Animals on restricted rations of a pelleted diet containing large amounts of concentrate may experience subacute forms of bloat or acid indigestion if not gradually introduced to the feed (Van Soest 1994). The resulting imbalance may have been a cause of discomfort and reduced rumen motility stimulating increased GC release.

Because the profile of the HPA axis response may vary considerably according to the nature of the stimulus (Buckingham et al. 1997), more study is required to distinguish between the different types of stress. Important questions to address are how long levels stay elevated and what are the consequences? Furthermore, a temporal approach for animals with known nutrition could demonstrate the effects of body condition on fecal GC metabolite levels.

CHAPTER 2

COMPARATIVE HEALTH STATUS, NUTRITIONAL CONDITION, AND PRODUCTIVITY OF FEMALE MOOSE IN NORTHWESTERN ONTARIO UNDER TWO FOREST MANAGEMENT REGIMES

INTRODUCTION

Understanding how animals are influenced by habitat variation requires examination of the ecological processes at spatial and temporal scales relevant to both the species and the conditions under study. Populations exhibit dynamic behavior across broad spatial scales and require analysis at the landscape level (Holling 1992, Forbes and Theberge 1993, Breininger et al. 1995, Rempel et al. 1997a). Landscape size will differ according to species; occupying some spatial scale intermediate between a species' home range and its regional distribution (Dunning et al. 1992). The composition of habitat types and the spatial arrangement of those habitats describe the landscape pattern (Turner et al. 1989). Animal populations respond to the pattern according to their life history requirements and the resultant environmental factors (either favorable or unfavorable) acting upon them (Morrison et al. 1992).

Assessment of a species' distribution and demographics can reveal the influence of landscape pattern on populations (Caughley 1977, Van Horne 1983, Hobbs and Hanley 1990), however, an understanding of cause-and-effect mechanisms is needed to determine the processes that control animal responses (Parker et al. 1999, Roloff and Kernohan 1999). The adaptability of ungulates to northern environments is largely influenced by nutritional constraints that affect mass and body composition (Cook et al. 1996, Parker et al. 1999). Acquisition and conservation of energy and protein fluctuate, dependent on environmental limitations and nutrient partitioning

within the animal. Changes in mass and body composition relative to metabolic demands provide a measure of environmental quality (Franzmann 1977, Gerhart et al. 1996).

The inherent capacity of a landscape to sustain ungulate populations is modified by both density dependent (e.g., competition among animals for forage) and independent (e.g., snow depth and temperature) factors. Increased competition for resources is coupled with declines in reproduction and recruitment (McCullough 1979, Clutton-Brock et al. 1987). Deep snow cover reduces the available browse (Schwab et al. 1987) and increases energy expended while traveling to obtain forage (Parker et al. 1984). In addition, temperature may affect feed intake (Renecker and Hudson 1986) and alter daily patterns of habitat utilization (Schwab and Pitt 1991).

Changes in mass and body composition in moose are driven by seasonal differences in forage availability and quality (Schwartz et al. 1987a). As selective browsers, intake in moose is constrained by their ability to locate high quality foods, maximize consumption, and maintain rapid passage rates (Renecker and Schwartz 1998). Early successional deciduous browse species compose the majority of the diet of moose (Houston 1968, Stevens 1970, Regelin et al. 1987, Renecker 1987). Summer leaf diets are efficiently digested by moose, whereas, winter twig diets contain greater amounts of indigestible plant structural components that limit nutrient intake. Consequently, summer is critical for building fat and protein reserves (Van Ballenberghe and Miquelle 1990) that are used during winter when nutritional requirements cannot be met (Schwartz et al. 1987b, Parker et al. 1999).

Because resources allocated to reproduction cannot also be used for growth and/or storing energy, reproductive effort is limited by the nutritional status and body composition of the dam. Reproduction is a series of tissue generating events including ovulation, fertilization, and implantation of the embryo, gestation, parturition, and milk production for the neonatal young

(Swenson 1973). While costs of gestation increase exponentially to nearly 50% above maintenance metabolism during the third trimester when most of the fetal birth mass is accrued, in general, the energy costs of lactation are 2 to 3 times that of gestation (Ofstedal 1985, Robbins 1993). In addition, protein needs increase dramatically towards the end of pregnancy and remain high through the peak of lactation (Orskov 1992). As a result, lactating moose fail to gain weight until lactation is diminished despite high consumption of food (Regelin et al. 1985). Females that have experienced lactation subsequently enter winter in poorer nutritional condition than nonparturient females, or females that gave birth but subsequently lost their calf and did not lactate (Sand 1997, Testa and Adams 1998). The costs of reproduction can be measured in terms of loss of body mass or fat, which may have consequences for future reproduction and survival (Sand 1997, Testa and Adams 1998). Higher costs of reproduction are indicative of factors influencing nutrition of ungulate populations (Adamczewski et al. 1987, Clutton-Brock et al. 1983, Clutton-Brock and Stevenson 1996).

Forest cutting, which has replaced fire as the principal rejuvenating agent of the boreal forest in recent decades, increases forage production for moose (Peek et al. 1976, Crete and Jordan 1982, Thompson and Stewart 1998). Utilization of cutover landscapes by moose, however, is likely affected by the pattern in which it is cut (Peek et al. 1976, Hamilton et al. 1980, Timmermann and McNicol 1988), spatial patterns in forage availability (Risenhoover 1986, Renecker and Hudson 1986), and by the foraging strategy used by moose (Moen et al. 1997). In addition, potential habitat suitability may further be affected by alterations that change predator-prey dynamics (Schwartz and Franzmann 1991), influence levels of parasitism and disease (Lankester and Samuel 1998), or expose animals to increased human disturbance (Millspaugh et

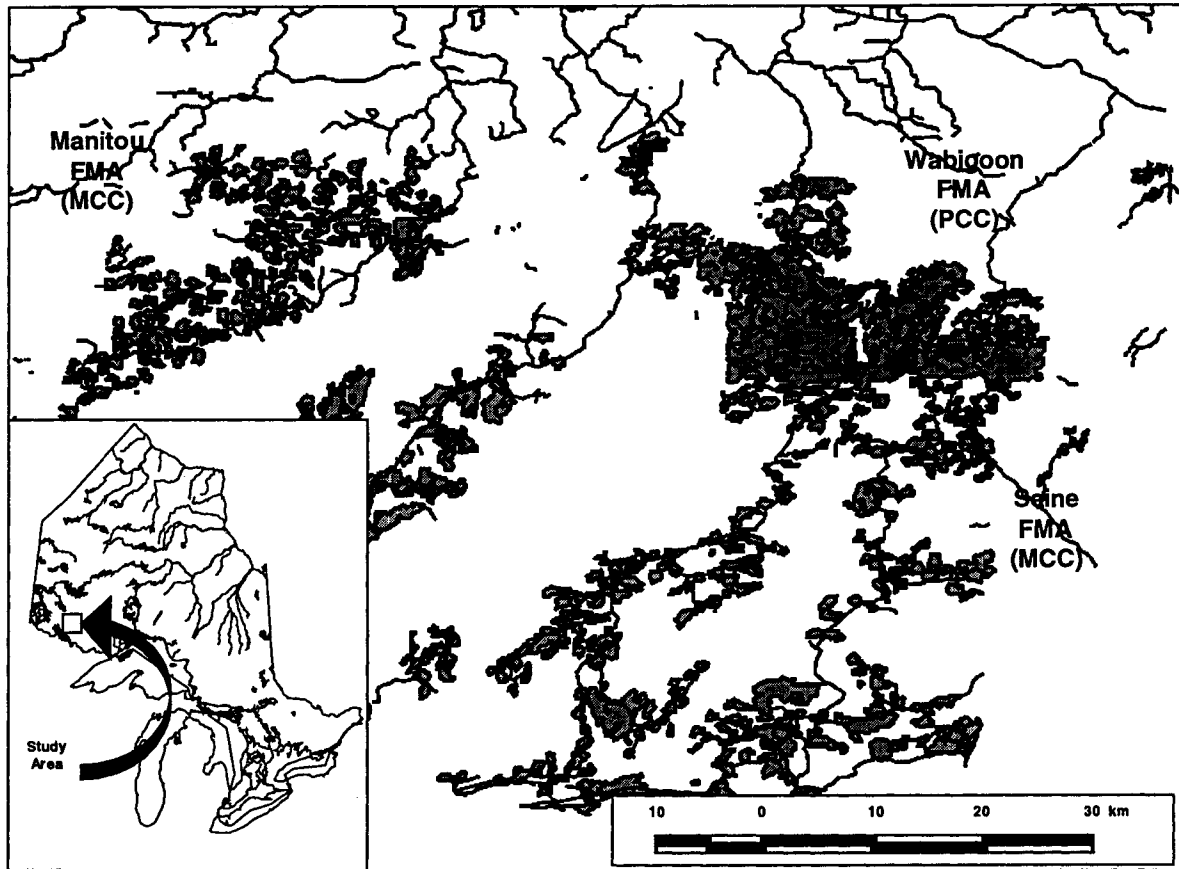
al. 2001) and/or risk of harvest (Rempel et al. 1997a). Accordingly, some timber management practices may produce vegetation patterns more beneficial to moose than others.

My objective was to demonstrate whether landscape-level patterns resulting from two forest management practices had an effect on the health, nutritional condition, and productivity of cow moose inhabiting: 1) a modified clear-cut (MCC), following the *Timber Management Guidelines for the Provision of Moose Habitat* (Moose Habitat Guidelines; OMNR 1988); and 2) an unmodified, progressive and contiguous clear-cut (PCC). The Moose Habitat Guidelines provide moose habitat through timber management planning by protecting or enhancing particular habitat requirements (e.g., 120 m buffers surrounding aquatic feeding sites, 80-130 ha clear-cut block). Timber-harvest occurred over the same period on both of the areas compared, beginning in 1978, and produced two contrasting landscape patterns (Rempel et al. 1997a, Welch et al. 2000). The habitat suitability indices (HSI) for moose (Allen et al. 1987) between the MCC and PCC, however, were similar (0.85 and 0.83 respectively) (Rempel et al. 1997a). During 1977-1992, moose densities increased within PCC but not within MCC, due in part to increased hunter access within MCC (Rempel et al. 1997a).

STUDY AREA

The 5,625 km² study area was located on the Canadian Shield southeast of the town of Dryden in northwestern Ontario, centered at approximately 92°45'W, 49°15'N (Figure 2.1). The rolling topography of the area ranged in elevation from 300 to 550 m above sea level. The forest was transitional between the Quetico Great Lakes - St. Lawrence Forest Region and the English River Boreal Forest Region to the north (Rowe 1972). Post-glaciation soil characteristics (generally less than 1 m deep and coarse in texture) and climate favored the development of eastern white and red pine (*Pinus strobus*, *P. resinosa*) communities, but frequent wildfires and

Figure 2.1. Map of the study area in northwestern Ontario, Canada, 1998-2001. Logging followed *Timber Management Guidelines for the Provision of Moose Habitat (MCC)* in the Manitou and Seine Forest Management Areas (FMA). The Wabigoon FMA was a progressive and contiguous clear-cut (PCC). Shading indicates areas in each FMA where timber harvest has occurred.



logging activities have allowed various boreal species to become established (Rowe 1972). During this study, the forest was characterized by pure and mixed-wood stands of jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), and white and black spruce (*Picea glauca*, *P. mariana*). Balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*), eastern larch (*Larix laricina*), and eastern white (*Pinus strobus*) and red pine (*P. resinosa*) occurred, but were less common (Rodgers et al. 1995). Commonly available browse species used by moose included june berries (*Amelanchier* spp.), mountain ash (*Sorbus americana*), red osier dogwood (*Cornus stolonifera*), trembling aspen, willow (*Salix* spp.), white birch, mountain maple (*Acer spicatum*), beaked hazel (*Corulus cornuta*), balsam fir, pin cherry (*Prunus pensylvanica*), green alder (*Alnus structa* var. *crispa*), and speckled alder (*A. incana* var. *rugosa*) (Rempel et al. 1997b).

Two portions of the study area where moose were collared had been logged following Moose Habitat Guidelines: 1) the MCC landscape within the Manitou Forest Management Area (FMA) was approximately 15 x 40 km (Figure 2.1) and 2) the MCC landscape Seine FMA was approximately 15 x 30 km. The Manitou and Seine FMAs were about 50 km apart. The Manitou FMA was dominated by white and black spruce, while the Seine FMA had a larger jack pine component (Rodgers et al. 1995). A third portion of the study area where moose were collared was logged without following Moose Habitat Guidelines. The PCC landscape within the Wabigoon FMA was approximately 15 x 30 km and was dominated by jack pine (Rodgers et al. 1995).

The study area was located within the Low Boreal Wetland Ecoregion of Canada (National Wetlands Working Group 1988). The land surface area was nearly 50% water,

including numerous narrow streams and rivers less than 10 m wide and ponds and lakes ranging in size from 10 to 100 ha (Rodgers et al. 1995).

Cold winters and relatively dry, warm summers characterized the climate of the study area. Temperatures frequently reached 25°C in summer, -25°C in winter, and fell to as low as -45°C in winter (Environment Canada). Mean annual precipitation is 70 cm (Environment Canada). Snow depth was generally < 70 cm during the study, but often became crusted after a mid-winter thaw in February (A. Rodgers, OMNR, personal observation).

METHODS

MOOSE CAPTURE, HANDLING, AND SAMPLE COLLECTION

NAVSTAR-based GPS collars (LOTEK Engineering Inc. 1993) were maintained on 60 free-ranging adult female moose (35 in the MCC and 25 in the PCC) from January 1995 to February 2001 (Welch et al. 2000). Moose were recaptured during January and February each year and fitted with refurbished collars. This period normally represented the onset of late winter when moose movements began to be restricted by snow. Moose were pursued by helicopter and captured by hand-held net-gun. The duration of the chase (the time from when initial pursuit began until the moose was netted and on the ground) was recorded. Once netted, moose were hobbled, blindfolded, and maintained in semi-sternal recumbency during handling. Body temperature was monitored with a rectal mercury-bulb thermometer and the maximum temperature observed was recorded. Blood was collected by jugular venipuncture using 3.8 cm 18 gauge needles (Monoject®, Sherwood Medical Co., St. Louis, MO, USA) into various blood collection tubes (Sarstedt Monovette®, Germany). The time of blood collection was recorded and samples were protected from freezing. A fecal pellet was obtained directly from the rectum, crushed, and placed into a sterile 100 ml polypropylene container with 10 ml of 85% ethanol

(Ethyl Alcohol Anhydrous, Anachemia, Montreal, QE, Canada) and transported at ambient temperature (-18 to +5°C) for 2 - 8 hours. Hair was collected into resealable plastic bags for determination of mineral status.

I measured the width of the wear on the occlusal surface of the front incisors (± 0.5 mm) to assess age. Tooth wear measurements were compared to those of known age animals determined from cementum annuli (Sergeant and Pimlott 1959). Body condition was evaluated in two ways. A subjective condition score on a scale of 1 -10 (Franzmann 1977) was assigned to each moose. A portable ultrasound (Aloka 210, Corometrics Medical Systems, Inc., Wallingford, CT, USA) with 5MHz linear array transducer was used to measure the maximum thickness (± 0.1 cm) of rump-fat as a predictor of total body fat (Stephenson et al. 1998).

The first time an individual moose was captured, total length along the dorsal body contour from the hairless patch on the nose to the base of the tail, chest girth, hind foot (hoof included), and shoulder height were measured.

Each moose was physically examined for external parasites (i.e., *Dermacentor albipictus*), injuries, and evidence that would suggest the animal was unhealthy. Superficial abrasions were treated with a topical antibacterial and moose with deep or purulent injuries were given a 35 ml intramuscular injection of oxytetracycline. All moose were given a 5 ml intramuscular injection of a solution containing vitamin E and selenium as a preventative measure for capture myopathy (Spraker 1993) prior to release. The procedures met standards of care and conditions for the use of animals set by Ontario Ministry of Natural Resources and the Lakehead University Animal Care Committee (Canadian Council on Animal Care 1984, 1993).

BLOOD, FECAL, AND HAIR ANALYSIS

Typically, up to 22.5 ml of blood was collected for serum, 7.5 ml in ethylenediaminetetraacetic acid (EDTA) tubes for complete blood counts and blood smears, 5 ml in nonenzymatic coagulation citrate tubes for fibrinogen concentration determination, and 1.2 ml in sodium fluoride tubes for glucose concentration determination. Serum and plasma were removed from whole blood by centrifugation within 12 hours and stored at -20°C until assayed. Complete blood counts (CBC) (Coulter MD-2 automated cell counter), hematological profiles (mean corpuscular volume (MCV), mean corpuscular hemoglobin (MCH), mean corpuscular hemoglobin content (MCHC), red cell distribution width (RDW) calculated from direct measurement of hematocrit (Hct), hemoglobin (Hb), and red blood cell count (RBC)), and creation of blood smears were completed within 36 hours by technicians at the Dryden District General Hospital (Dryden, ON, Canada). Differential leukocyte and platelet counts from blood smears and chemistry profiles were completed within 1 month by technicians at the Animal Health Laboratory, University of Guelph (Guelph, ON, Canada). Serum cortisol, progesterone, and thyroxine concentrations were determined by solid-phase, chemiluminescent immunoassay with the Immulite Automated Analyzer (Diagnostic Products Corp., Los Angeles, CA, USA). Fibrinogen concentration was determined by fibrometer method. All other chemistry values were determined using the Hitachi 911 automated system (Boehringer Mannheim, Indianapolis, IN, USA). There was no insert for sodium (Na), potassium (K), or chloride (Cl), but these were run on the Hitachi system by indirect ion selective electrode. Serum insulin-like growth factor (IGF-I) concentration was determined by IGF-1 RIA (Nichols Institute Diagnostics, San Clemente, CA, USA) (R. Nachriener, Michigan State University, East Lansing, MI, USA). Pregnancy and in utero twinning were determined by a moose-specific RIA for pregnancy-

specific protein B in serum (PSPB - Huang et al. 2000) (G. Sasser, BioTracking, Moscow, ID, USA).

Fecal samples were stored at -20°C until processed (within 12 months). Fecal glucocorticoid metabolite (GC) concentrations were determined by solid-phase ¹²⁵I radioimmunoassay (ICN Biomedicals, Inc., Costa Mesa, CA, USA) (K. Hunt, University of Washington, Seattle, WA, USA).

Total nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) concentration in hair samples were determined by an automated combustion method (Gavlak et al. 1994) by technicians at the Soil and Nutrient Laboratory, University of Guelph (Guelph, ON, Canada).

Not all variables were measured for each moose due to limited quantity of sample or other factors.

REPRODUCTIVE SUCCESS

In early December of each year, cows were relocated by telemetry from rotary-wing aircraft and visually observed to determine calf survival. Numbers of calves at heel during recaptures later in January-February were also recorded. The maximum number of calves observed with a cow in either December or January-February was used to determine the number of calves surviving to winter.

WINTER SEVERITY

Winter weather summaries and a winter severity index (WSI) were based on Environment Canada (EC) snow and temperature data collected at the Dryden airport (Station no. 6032119) during the winters of 1998-2001. The mean daily temperature for each month was calculated by summing the average of the hourly temperature (± 0.1 °C) recordings (0500 h

through 2000 h) for each day and dividing by the number of days in the month. The mean daily snow depth for each month was calculated by summing the daily snow-on-ground measurements (± 0.1 cm) for each month and dividing by the number of days in the month.

The WSI was based upon the relative increase in energy expenditure for 1) locomotion in snow (Parker et al. 1984) and 2) temperatures outside the thermal neutral zone (TNZ) of moose (Renecker and Hudson 1986). The relative sinking depth in snow (RELSINK) was based on the relationship between brisket height (BH) and snow depth (SNOWDEPT) as modified by Miquelle et al. (1992):

$$\text{RELSINK} = (\text{SNOWDEPT} \div \text{BH}) \times 100$$

I assumed average brisket height of female moose was 103 cm. The relative increase in energy expenditure to travel through snow (RELINC S) was then calculated as

$$\text{RELINC S} = (0.71 \times \text{RELSINK} \times e^{0.019 \times \text{RELSINK}}) \div 100.$$

A lower critical temperature (TLC) has not been demonstrated for moose, even though heat production estimates have been conducted in temperatures as low as -30 °C (Renecker and Hudson 1986). Moose are susceptible to heat stress in winter, however, when temperatures exceed -5 °C. The relative increase in energy expenditure when temperatures exceeded the TNZ (RELINC T) was calculated as

$$\text{RELINC T} = (((0.925 \times \text{°C}) + 23.54) - 18.78) \div 18.78.$$

A day without snow on the ground and a mean temperature within the TNZ for moose was equal to 1. With snow depth and temperature weighted equivalently, the total daily relative increase in energy expenditure (RELINC TOTAL) was then calculated as

$$\text{RELINC TOTAL} = ((\text{RELINC S} \times 0.5) + 0.5) + ((\text{RELINC T} \times 0.5) + 0.5).$$

The WSI was then the difference between RELINC TOTAL and the actual number of days in winter. I defined winter as November through April and the WSI was calculated as

$$\text{WSI} = \text{RELINC TOTAL} - 181 \text{ (Non-Leap Years)}$$

$$\text{WSI} = \text{RELINC TOTAL} - 182 \text{ (Leap Years).}$$

DATA ANALYSIS

To demonstrate homogeneity among moose sampled between treatments, I compared incisor occlusal surface wear (as an index of age) using a two-tailed t-test with pooled variances, and evaluated moose handling measures using MANOVA techniques. I used Pearson correlation coefficients and MANOVA techniques to determine similarities among morphology parameters for moose sampled from each area. I compared the proportion of females with an offspring at heel between treatments with Fisher's Exact tests and examined annual differences within treatments using a normal approximation of the chi-square test (Zar 1999). Paired-sample t-testing was used to examine the mean difference in fecal GC concentrations between the years 1999 and 2000. Effects of handling, individual, temporal, and spatial factors on variability were modeled in a forward stepwise multiple regression analysis for each blood parameter.

Transformations were used to improve normality when appropriate. All categorical factors were treated as dummy variables, and factors entered into the model in the order of handling effects first (body temperature and elapsed time between capture and sampling), individual effects second (body fat), then area, and year. Alpha-to-enter and alpha-to-remove were set at 0.01 and 0.05, respectively. I analyzed mineral concentrations in hair for statistical differences between area and year for all moose, using MANOVA techniques.

I calculated the reference ranges for blood chemistry, hematology, and mineral concentrations in hair for female moose as the interval between the 2.5 and 97.5 percentiles. By

convention, the reference interval for an analyte with a Gaussian distribution is bound within 2 standard deviations below and above the mean. Many analyte distributions were asymmetrical, however, and an approach other than the conventional method for determining reference intervals was necessary. Two methods discussed by Farver (1997) included 1) the use of transformations, and 2) the use of percentiles. Logarithmic or square root transformation of the analyte values may make the distribution more Gaussian (Zar 1999) allowing for the conventional calculation of the reference interval. These boundaries then can be expressed in terms of the original values by retransformation (Farver 1997). Retransformed values may still be biased (Zar 1999). Alternatively, estimation of the 2.5 and 97.5 percentiles directly, without any distribution assumptions, gives an unbiased estimate of the reference interval. The percentile method, however, is less precise for distributions with long tails (Bland 2000). Expected frequencies of the number of outliers per moose blood panel were calculated from a binomial expansion of $(p + q)^k$, where p is the probability of an outlier (0.05) and q was the probability of no outlier (0.95), and k is the number of blood variables (38) (Fadley 1998). From the binomial model, animals with at least 6 outlying blood values were suspected to have clinical concerns beyond that expected by chance (i.e., the probability of 6 or more outliers per individual < 0.01). Standard MANOVA techniques, t-tests, and regression analyses were performed using SYSTAT[®] 10 software (Copyright[®] 2000 by SPSS Inc.). I analyzed repeated body fat measures with a mixed linear model (PROC MIXED) (SAS[®] System Version 8, Copyright[®] 1999-2000 SAS Institute Inc.) with timber-harvest treatment, year, and calf-at-heel status as factors potentially influencing fatness. Calf-at-heel status was a fixed effect because it represented at least all levels of the factor about which inference was made (0 or 1). The individual moose was a blocking factor within timber-harvest treatment with random effects.

The design was not a connected block-treatment because both treatments were not applied to each moose. I fit the model using all potential factors and then used a backward stepwise removal procedure (α -to-remove = 0.05) to select an appropriate smaller model.

RESULTS

ESTABLISHING HOMOGENEITY OF EXPERIMENTAL UNITS

The lower jaw from 22 study animals that died between 1995 and 2001 were collected. Age, of those animals that died, ranged from 2.5-16.5 years; 50% of these animals were greater than 11.5 years of age. Age determined from cementum annuli of incisor-form teeth was positively correlated with occlusal surface wear (Figure 2.2, tooth wear data were only available for 15 of the 22 jaws collected). Age predicted from this relationship suggests 95% of the animals collared during the study were between 2.5 and 11.5 years old. Comparisons of tooth wear data between the timber-harvest treatments indicated the age structure of the sample populations was similar ($\bar{X}_{MCC} - \bar{X}_{PCC} = -0.3$ mm, pooled- $t_{0.05(2)61} = 1.2385$, $P = 0.2209$).

Absolute body size measurements were similar between timber-harvest treatments ($F_{0.05(2)4/99} = 0.4941$, $P = 0.7400$). Correlation of morphometric measurements was variable for moose within MCC (Table 2.1) and PCC (Table 2.2). Pearson correlation coefficients, among the various measurements after pooling all moose, were generally small (Table 2.3).

Handling measures for moose captured by hand-held net-gun fired from a helicopter are presented in Table 2.4. All four handling measures were different among the 3 years (1999-2001) for which data were available (Table 2.5); however, handling of animals between timber-harvest treatments was similar ($F_{4/122} = 0.4792$, $P = 0.7515$). The effect of increased pursuit and restraint times was an increase in moose body temperature (Table 2.6). Squared semipartial correlations (sr^2) for pursuit and restraint times with body temperature were 0.2217 and 0.0819,

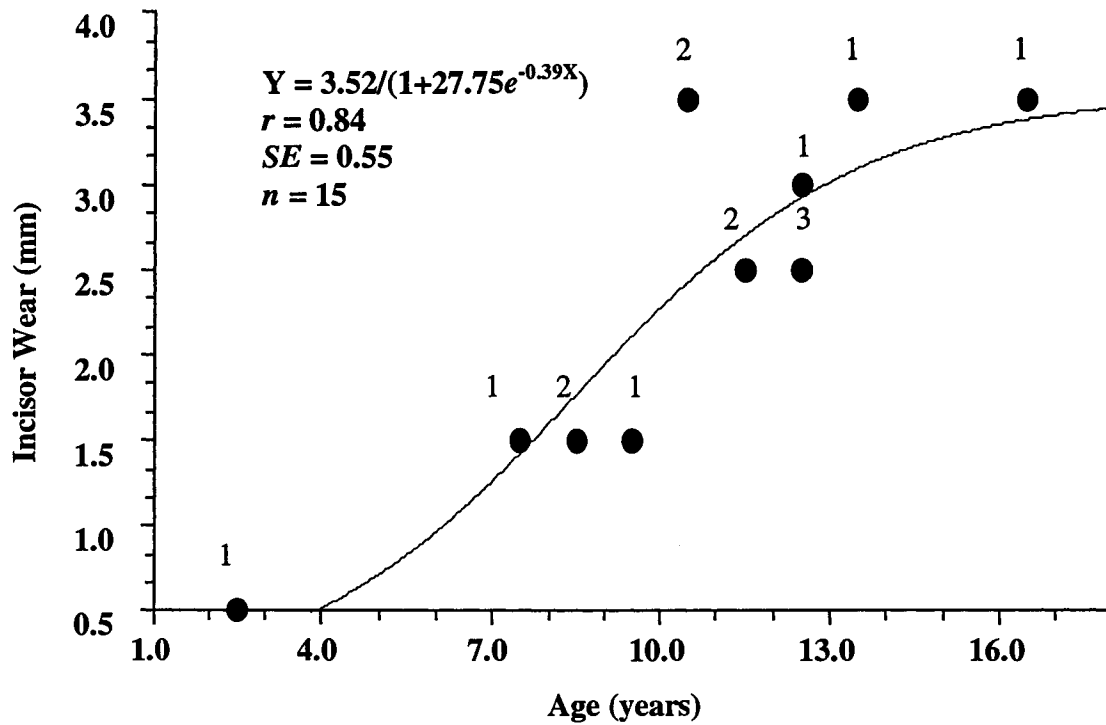


Figure 2.2. The relationship between age determined from cementum annuli and incisor occlusal surface wear of female moose in northwestern Ontario, Canada, 1995 – 2001. The number above each point is the sample size.

Table 2.1. Pearson correlation coefficients for morphometric measurements (± 1 cm) of adult female moose in winter, captured in the progressive clear-cut landscape treatment (PCC) northwestern Ontario, Canada, 1995-2001.

Parameter	Shoulder Height	Chest Girth	Hind Foot Length	Body Length
<i>n</i>	47	47	47	47
Mean (\pm SD)	190.8 \pm 10.6	210.2 \pm 14.6	78.4 \pm 2.3	291.0 \pm 17.7
CV	0.06	0.07	0.03	0.06
Shoulder Height	1.0000			
Chest Girth	0.5366	1.0000		
Hind Foot Length	0.2255	0.4842	1.0000	
Body Length	0.2181	0.4617	0.4559	1.0000

Table 2.2. Pearson correlation coefficients for morphometric measurements (± 1 cm) of adult female moose in winter, captured in the modified clear-cut landscape treatment (MCC) northwestern Ontario, Canada, 1995-2001.

Parameter	Shoulder Height	Chest Girth	Hind Foot Length	Body Length
<i>n</i>	58	58	58	58
Mean (\pm SD)	189.9 \pm 9.4	209.0 \pm 13.3	78.9 \pm 2.7	290.0 \pm 16.3
CV	0.05	0.06	0.03	0.06
Shoulder Height	1.0000			
Chest Girth	0.4093	1.0000		
Hind Foot Length	0.1260	- 0.0706	1.0000	
Body Length	0.1527	0.1891	0.2638	1.0000

Table 2.3. Pearson correlation coefficients for morphometric measurements (± 1 cm) of all adult female moose in winter, captured in northwestern Ontario, Canada, 1995-2001.

Parameter	Shoulder Height	Chest Girth	Hind Foot Length	Body Length
<i>n</i>	105	105	105	105
Mean (\pm SD)	190.3 \pm 10.0	209.5 \pm 13.8	78.7 \pm 2.5	290.4 \pm 16.8
CV	0.05	0.07	0.03	0.06
Shoulder Height	1.0000			
Chest Girth	0.4739	1.0000		
Hind Foot Length	0.1635	0.1643	1.0000	
Body Length	0.1861	0.3236	0.3404	1.0000

Table 2.4. Pearson correlation coefficients^a of handling measures for moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, 1999-2001.

	Pursuit (min.)	Restraint (min.)	Elapsed Time (min.)	Body Temperature (°C)
<i>n</i>	159	159	159	166
Median	5	12	17	39.3
Mean ± SD	6.3 ± 5.4	13.2 ± 5.6	19.6 ± 8.3	39.31 ± 0.83
Range	1 - 28	4 - 42	5 - 48	37.7 - 42.4
Pursuit	1.0000			
Restraint	0.2048	1.0000		
Elapsed Time	0.6430	0.8668	1.0000	
Body Temperature	0.5634	0.3515	0.5897	1.0000

^a Values are the coefficients for the log₁₀ - normal transformed data.

Table 2.5. Multivariate analysis of variance of handling measures of moose as a function of year, treatment, and year by treatment, northwestern, Ontario, Canada, 1999-2001.

Source of Variance	Wilks' Lambda (Λ)	DF	Multivariate <i>F</i>	<i>P</i>
Year	0.6267	8/244	8.0289	<.0001
Treatment	0.9845	4/122	0.4792	0.7515
Treatment by Year	0.8603	8/244	2.3827	0.0173
Univariate Tests	Variable		Univariate <i>F</i>	
Year	Pursuit	2/125	8.5380	0.0003
	Restraint	2/125	29.7298	<.0001
	Elapsed Time	2/125	30.3507	<.0001
	Body Temperature	2/125	9.0906	0.0002
Treatment	Pursuit	1/125	0.0865	0.7692
	Restraint	1/125	0.8483	0.3588
	Elapsed Time	1/125	0.3975	0.5295
	Body Temperature	1/125	0.4172	0.5195
Treatment by Year	Pursuit	2/125	6.1823	0.0028
	Restraint	2/125	1.8288	0.1649
	Elapsed Time	2/125	1.0573	0.3505
	Body Temperature	2/125	2.0854	0.1286

Table 2.6. Results from regression analysis of body temperature against other handling measures of moose captured by hand-held net-gun fired from a helicopter, northwestern Ontario, Canada, 1999-2001.

	Coefficient (β)	SE	<i>t</i>	<i>P</i>
Constant	1.5778	0.0039	406.2131	<.0001
log ₁₀ Pursuit	0.0140	0.0021	6.7774	<.0001
log ₁₀ Restraint	0.0145	0.0035	4.1199	0.0001

Model:
 $\log_{10}(\text{Body Temperature}) = 1.5778 + 0.0140 \cdot \log_{10}(\text{Pursuit}) + 0.0145 \cdot \log_{10}(\text{Restraint}) + \varepsilon$
 $F_{2,128} = 41.2091, P <.0001, R_a^2 = 0.3822, n = 131$

respectively. A large proportion of variance in body temperature was unexplained by my measures.

WINTER SNOW DEPTH AND TEMPERATURE

Snow depth measured at the Dryden airport during winter 1998-2001 was generally less than 40 cm and temperatures were moderate (Figure 2.3). Comparison of early winter severity indices (Table 2.7) suggested metabolic costs prior to capture were higher in 1998 and 2001 than in 1999 and 2000, mainly because of lower snow depths.

HEMATOLOGY AND SERUM CHEMISTRY

Effects of Handling, Individual, Spatial, and Temporal Factors

Reference ranges for hematological parameters and serum chemistries are presented in Tables 2.8 and 2.9, respectively. Handling (time elapsed between initiation of pursuit and sample collection and body temperature) and temporal (year) factors accounted for large portions of the variability in many of the blood parameters, while individual (body fat) and timber-harvest treatment accounted for relatively little of the variation in only a few variables (Tables 2.10 and 2.11). Body fat positively influenced measures of pregnancy hormones (P4 and PSPB) and red blood cell indices (Hb and Hct). Higher values of serum K and AST and lower values of urea were associated with the PCC treatment.

Statistical Outliers

The binomial expansion model yielded 34 (13%) individual outliers (i.e., an excess of 6 blood parameters responsible for the outlier status). Seventeen of these animals had been censored from reference range determination because of abnormalities detected by physical examination at capture (e.g., existing fractures, injuries inflicted by wolves, injuries to the skin and deeper soft tissues on the back of the neck associated with collar attachment). The

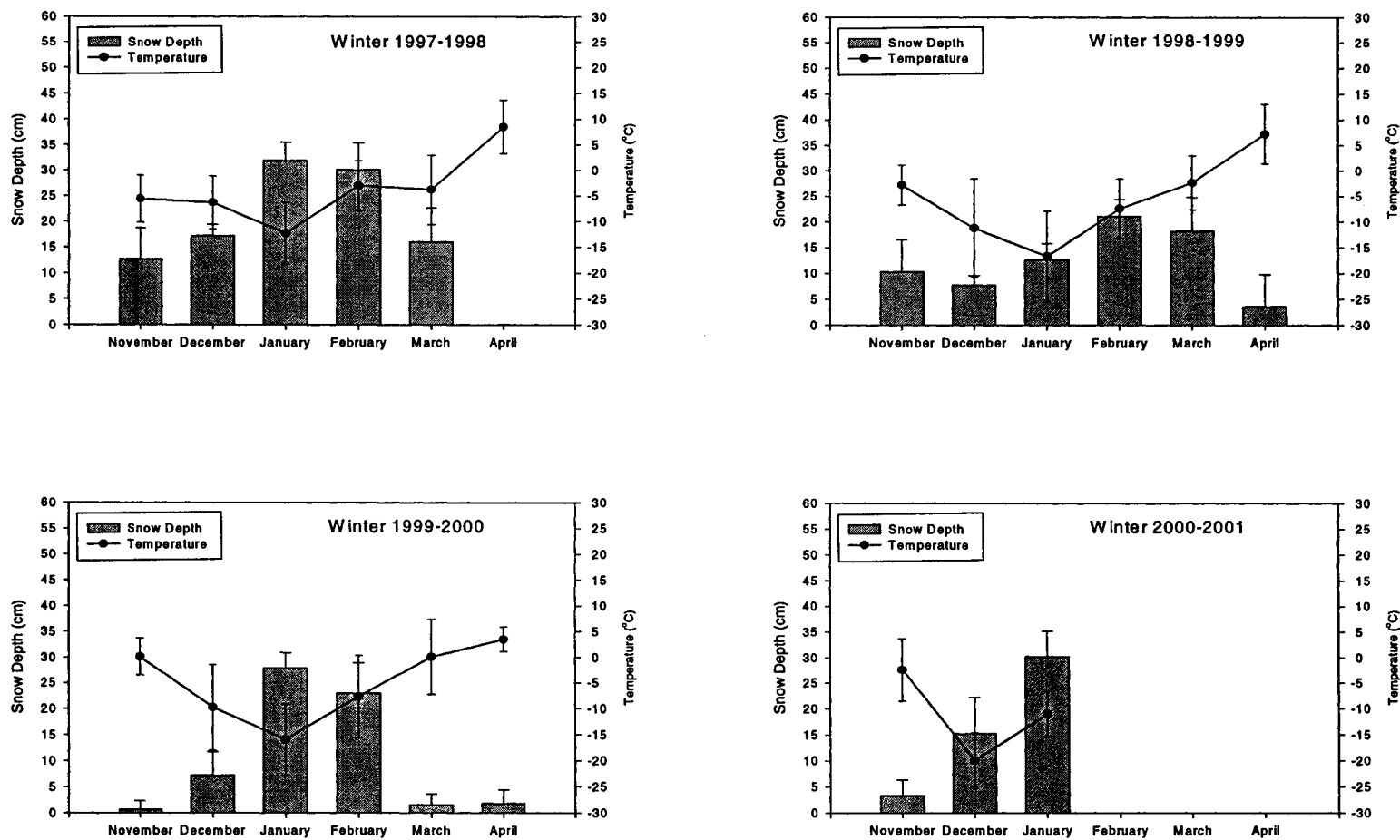


Figure 2.3. Mean (\pm SD) daily snow depth and temperature during winter in northwestern Ontario, Canada, 1998-2001 (Environment Canada, Station no. 6032119, Dryden).

TABLE 2.7. Comparison of early-winter (November-January) severity indices for moose in northwestern Ontario, Canada, 1997-2001.

Winter	Mean Snow Depth (cm)	Winter Severity Index (Snow)	Mean Temperature (°C)	Winter Severity Index (Temp.)	Winter Severity Index (Sum)
1997-1998	20.8	10.4	-8.2	0.7	11.1
1998-1999	10.2	4.1	-10.3	1.2	5.3
1999-2000	12.1	6.0	-8.5	1.8	7.8
2000-2001	16.3	8.4	-11.2	1.7	10.1

Table 2.8. Hematology values of adult female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, January-February 1998-2001. Reference ranges calculated as the interval between the 2.5 and 97.5 percentiles.

	WBC	Seg	Band	Lymph	Mono	Eos	Baso	RBC ^a	Hb	Hct	MCV	MCH	MCHC	RDW	Plt	MPV
<i>n</i>	218	218	218	218	218	218	218	65	218	218	218	218	218	217	217	215
units	x 10 ⁹ /l	x 10 ⁹ /l	x 10 ⁹ /l	x 10 ⁹ /l	x 10 ⁹ /l	x 10 ⁹ /l	x 10 ⁹ /l	x 10 ¹² /l	g/l	l/l	fl	pg	g/l	%	x 10 ⁹ /l	fl
2.5 th	4.05	0.695	0	1.718	0	0	0	6.504	154.4	0.420	63.50	22.85	345.5	15.94	42.2	5.64
97.5 th	16.77	5.720	0.026	10.500	0.752	1.788	0.421	8.408	205.5	0.575	74.55	26.85	369.5	20.96	309.00	9.96
Min	2.3	0.51	0	0.28	0	0	0	4.79	124	0.35	61.9	22.1	343	14.8	7	0
Max	20.4	8.62	0.12	12.96	1.66	3.57	0.98	9.20	211	0.59	75.5	27.3	373	23.0	396	12.0

^a Red blood cell reference range calculated from 1997 samples. The Coulter MD-2 automated cell counter used during 1998-2001 reported values greater than 7.00 as 7.00⁺⁺⁺. The MD-2 did store the actual RBC count internally, however, which was used to calculate the subsequent RBC indices (i.e., Hct, MCV, MCH).

Table 2.9. Serum chemistry values of adult female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, January-February 1998-2001. Reference ranges calculated as the interval between the 2.5 and 97.5 percentiles.

	Fibr	LD	T ₄	Cort	IGF-I	P ₄	PSPB	Ca	P	Mg	Na	K	Cl	TPro	Albu	Glob	A:G
<i>n</i>	192	166	221	221	220	221	207	221	221	221	221	221	221	221	221	221	221
Units	g/l	U/l	nmol/l	nmol/l	nmol/l	nmol/l	ng/ml	nmol/l	nmol/l	nmol/l	mmol/l	mmol/l	mmol/l	g/l	g/l	g/l	-
2.5 th	1.67	174.8	35.1	68.2	1.21	1.01	0	2.293	1.060	0.96	141.6	3.66	85.6	72.6	30.6	28.1	0.611
97.5 th	4.99	448.7	86.5	209.5	19.13	23.35	1683.9	3.099	2.571	1.59	160.5	5.45	104.5	94.5	53.5	55.1	1.779
Min	0.7	110	23	50	0	0	0	2.05	0.81	0.9	135	3.2	81	68	26	24	0.45
Max	7.2	615	100	249	23.6	27.4	2358	3.17	2.71	1.7	169	5.9	106	111	58	75	2.00

	Urea	Crea	Gluc	Chol	T-Bili	C-Bili	U-Bili	AP	GGT	AST	CK	GD	BHBA	NEFA	Osmo	Hapt	Na:K	Ca:P
<i>n</i>	221	221	221	221	221	221	221	221	221	221	221	221	221	221	221	221	221	221
Units	mmol/l	μmol/l	mmol/l	mmol/l	μmol/l	μmol/l	μmol/l	U/l	U/l	U/l	U/l	U/l	mmol/l	mEq/l	mmol/l	g/l	-	-
2.5 th	1.26	117.4	5.61	1.581	0.6	0	0	67.4	5.6	70.6	105.6	0.6	202.7	0.06	279.6	0.041	27.6	1.026
97.5 th	4.05	206.4	11.74	2.919	5.9	1.5	3.5	1539.7	50.5	180.4	1054.6	8.5	449.5	0.45	320.9	1.930	41.5	2.494
Min	0.9	105	2.2	1.42	0	0	0	55	4	65	87	0	186	0	271	0.01	26	0.92
Max	5.0	213	13.3	3.36	7	2	6	1860	154	269	3370	16	576	2.3	340	2.73	46	3.23

Table 2.10. Factors influencing winter blood hematology values of female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, 1999-2001.

Parameter	Source of Variation	DF	R^2	F	P
WBC	Year	1/125	0.0553	7.3213	0.0078
Hb	Body Fat, Year	2/122	0.2436	19.6413	<.0001
Hct	Body Fat, Year	2/122	0.2535	20.7101	<.0001

Table 2.11. Factors influencing winter blood chemistry values of female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, 1999-2001.

Parameter	Source of Variation	DF	R^2	F	P
Fibr	Elapsed Time, Year	2/108	0.3414	27.9870	<.0001
LD	Year	1/80	0.1415	13.1888	0.0005
Cort	Elapsed Time	1/129	0.2469	43.6276	<.0001
IGF-I	Body Temperature	1/127	0.0916	13.9102	0.0003
P_4	Body Fat, Year	2/125	0.2550	21.3936	<.0001
PSPB	Body Fat	1/119	0.1255	18.2280	<.0001
Ca	Elapsed Time, Body Fat, Year	3/124	0.4925	40.1078	<.0001
Mg	Elapsed Time, Year	2/128	0.1597	12.1606	<.0001
Na	Year	2/128	0.3375	32.6027	<.0001
K	Year, Treatment	2/128	0.1275	9.3496	0.0002
Cl	Year	1/129	0.3570	71.6120	<.0001
TPro	Elapsed Time, Body Fat	2/125	0.1036	8.3386	0.0004
Albu	Year	2/128	0.5578	80.7205	<.0001
Glob	Year	2/128	0.3699	37.5782	<.0001
Urea	Treatment	1/129	0.0465	6.2970	0.0133
Crea	Elapsed Time	1/129	0.0959	14.7931	0.0002
Gluc	Body Temperature, Year	2/128	0.2984	27.2258	<.0001
T-Bili	Year	1/129	0.2574	44.7052	<.0001
AST	Treatment	1/129	0.0748	10.4328	0.0016
CK	Elapsed Time	1/129	0.0618	9.5575	0.0024
GD	Year	1/129	0.0572	7.8286	0.0059
BHBA	Year	2/128	0.5286	71.7578	<.0001
Hapt	Year	1/129	0.1775	27.8299	<.0001

contribution from individual non-outliers, non-censored outliers, and censored outliers to the total number of outlying values among each of the blood components is presented in Figure 2.4. Comparison of the values that were responsible for creating outlier status between censored and non-censored individuals suggested differences. There was a trend among the censored animals for high Fibr, Cort, TPro, Glob, Hapt, and Plt and low T4, Albu, A:G, Na, Osmo, and RBC (Figures 2.5 and 2.6). There was no apparent trend among the non-censored individual outliers.

MINERAL STATUS

Reference ranges for hair mineral content are presented in Table 2.12. Annual differences in nitrogen, phosphorus, calcium, and sodium levels accounted for most of the variation (Table 2.13); however, a trend towards significance ($P = 0.0508$) was observed for the timber-harvest treatment effect. Examination of the univariate statistics suggested a difference in mean potassium content ($P = 0.0416$) between treatments. Median potassium levels for moose residing in MCC were approximately 15% higher than PCC in 1998, 1999, and 2001 (Figure 2.7).

STRESS

Fecal GC metabolite concentrations were similar during winter 1999 and 2000 ($\bar{X}_{1999} - \bar{X}_{2000} = 3.72$ ng/g, $SD_{Diff} = 21.75$, paired- $t_{0.05(2)45}$, $P = 0.2520$). After pooling data for both years, comparison between timber-harvest treatments suggested fecal GC metabolite levels were not different ($P = 0.0673$, Figure 2.8).

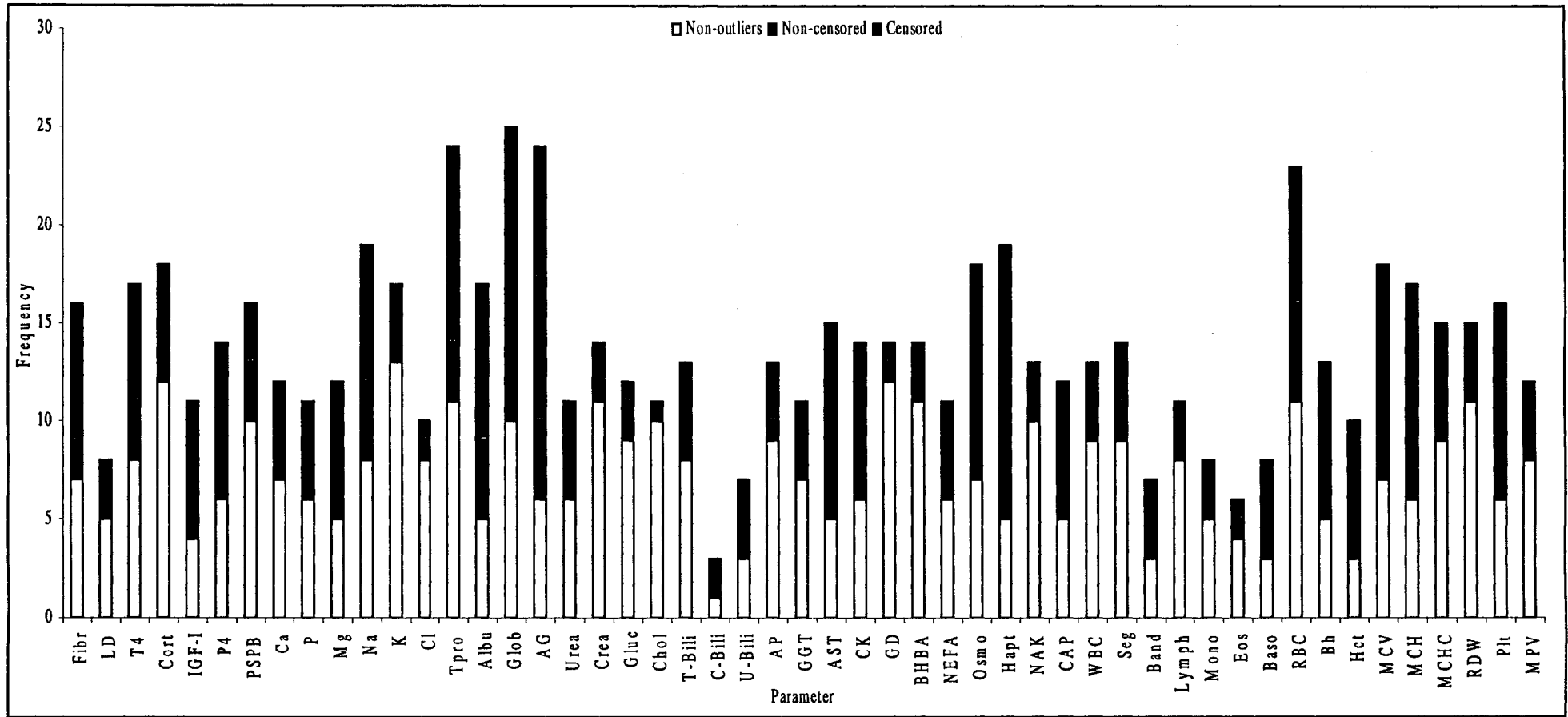


Figure 2.4. The contribution from individual non-outliers, non-censored outliers, and censored outliers to the total number of outlying values among each of the blood components.

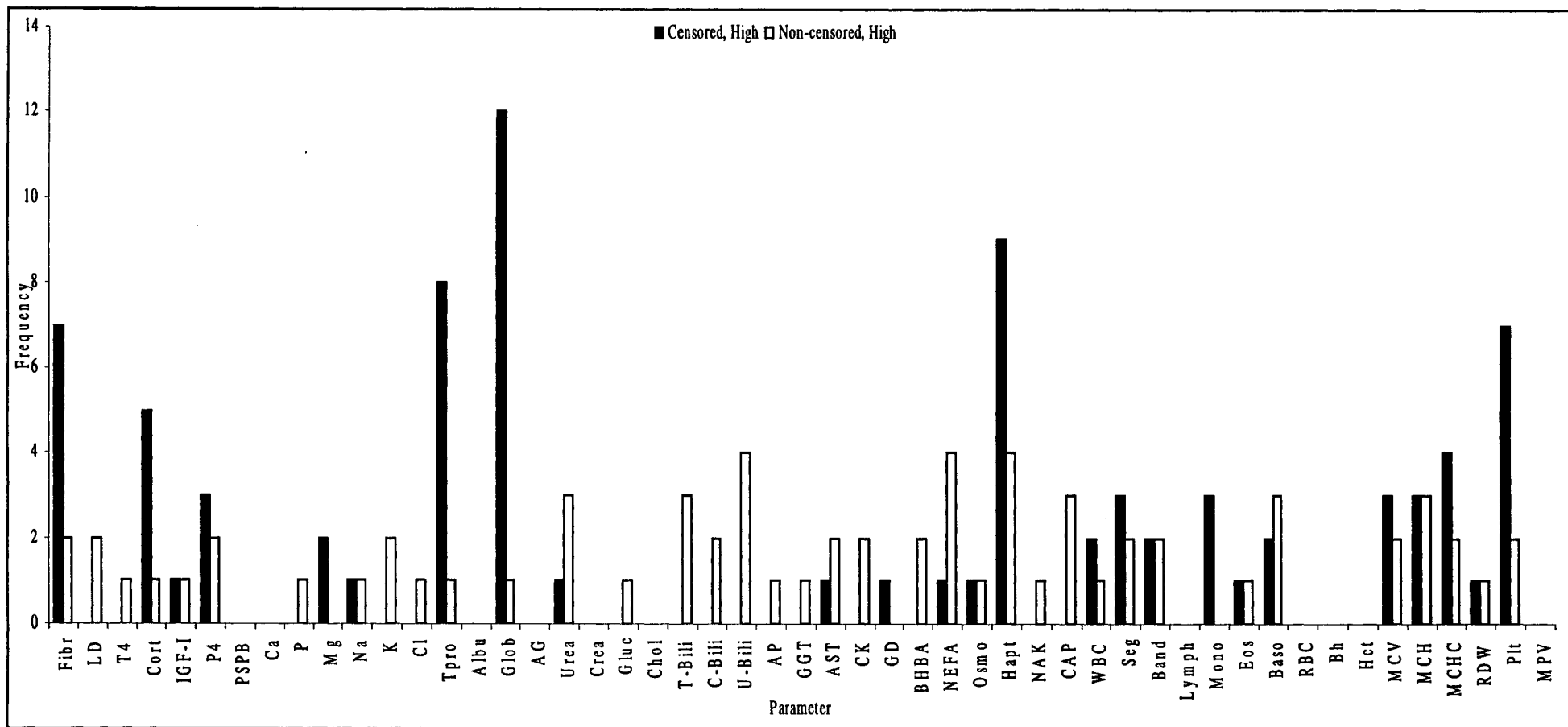


Figure 2.5. Comparison of blood components that exhibited high outlying values between censored and non-censored individuals.

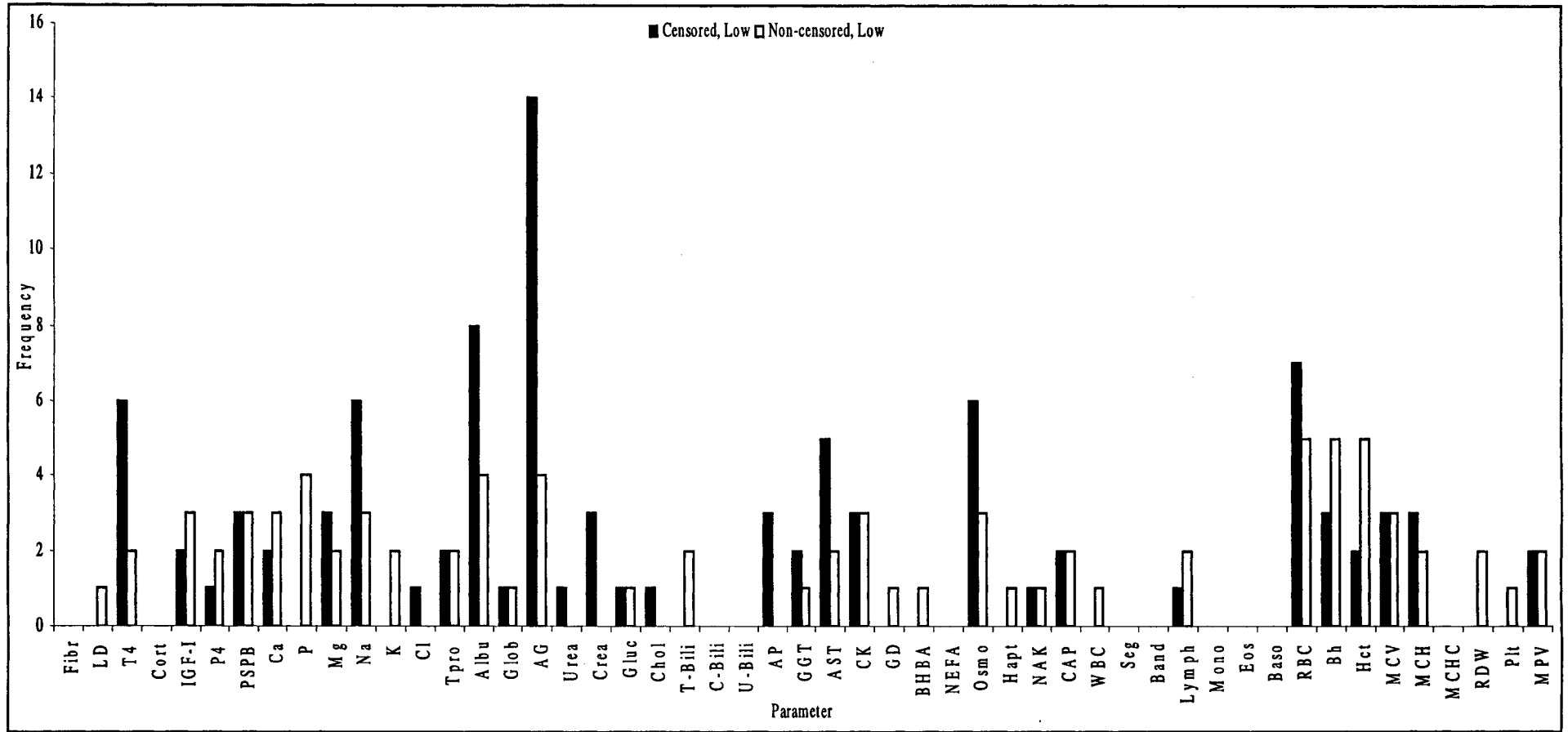


Figure 2.6. Comparison of blood components that exhibited low outlying values between censored and non-censored individuals.

Table 2.12. Hair mineral concentration of adult female moose captured by hand-held net-gun fired from a helicopter in northwestern Ontario, Canada, January-February 1998-2001.

Reference ranges calculated as the interval between the 2.5 and 97.5 percentiles.

	N%	P%	K%	Ca%	Mg%	Na%
<i>n</i>	218	216	216	216	216	216
2.5 th	15.050	0.00924	0.01879	0.0524	0.01204	0.00219
97.5 th	17.526	0.06363	0.12223	0.1652	0.02519	0.09307
Min	13.70	0.0081	0.0110	0.045	0.0112	0.0010
Max	18.47	0.1210	0.1656	0.205	0.0268	0.1199

Table 2.13. Multivariate analysis of variance of winter moose hair mineral concentration as a function of year and timber-harvest treatment, northwestern Ontario, Canada, 1998-2001.

Source of Variance	Wilks' Lambda (Λ)	DF	Multivariate <i>F</i>	<i>P</i>
Year	0.5479	18/600	7.9017	<.0001
Treatment	0.9430	6/212	2.1341	0.0508
Treatment by Year	0.9032	18/600	1.2223	0.2367
Univariate Tests	Variable		Univariate <i>F</i>	
Year	Nitrogen	3/217	8.0133	<.0001
	Phosphorus	3/217	10.9832	<.0001
	Potassium	3/217	0.8503	0.4678
	Calcium	3/217	14.6326	<.0001
	Magnesium	3/217	1.3010	0.2750
	Sodium	3/217	14.7326	<.0001
Treatment	Nitrogen	1/217	0.2176	0.6414
	Phosphorus	1/217	0.0427	0.8365
	Potassium	1/217	4.2006	0.0416
	Calcium	1/217	0.5654	0.4529
	Magnesium	1/217	2.5481	0.1119
	Sodium	1/217	0.0517	0.8204
Treatment by Year	Nitrogen	3/217	0.7258	0.5376
	Phosphorus	3/217	0.7896	0.5009
	Potassium	3/217	0.6890	0.5597
	Calcium	3/217	3.0086	0.0312
	Magnesium	3/217	0.2112	0.8885
	Sodium	3/217	0.0357	0.9910

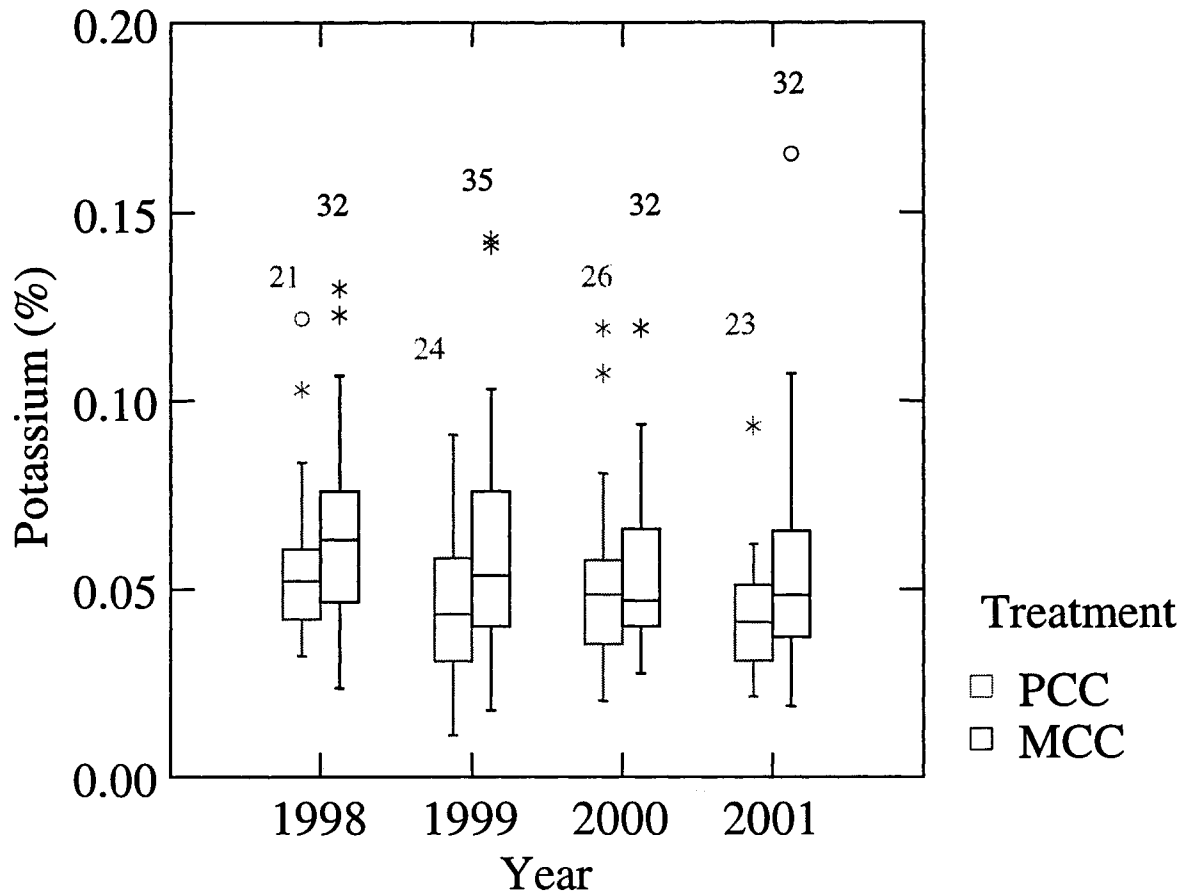


Figure 2.7. Comparison of annual potassium levels in female moose hair between timber-harvest treatments, northwestern Ontario, Canada, January-February 1998-2001. Box plots show the median (center line), upper and lower quartiles (edges of the box), and range (whiskers or special symbols). Outside values are plotted with asterisks (*) and far outside values are plotted with empty circles (°). The number above each box is the sample size. PCC = progressive, contiguous clear-cut, MCC = modified clear-cut.

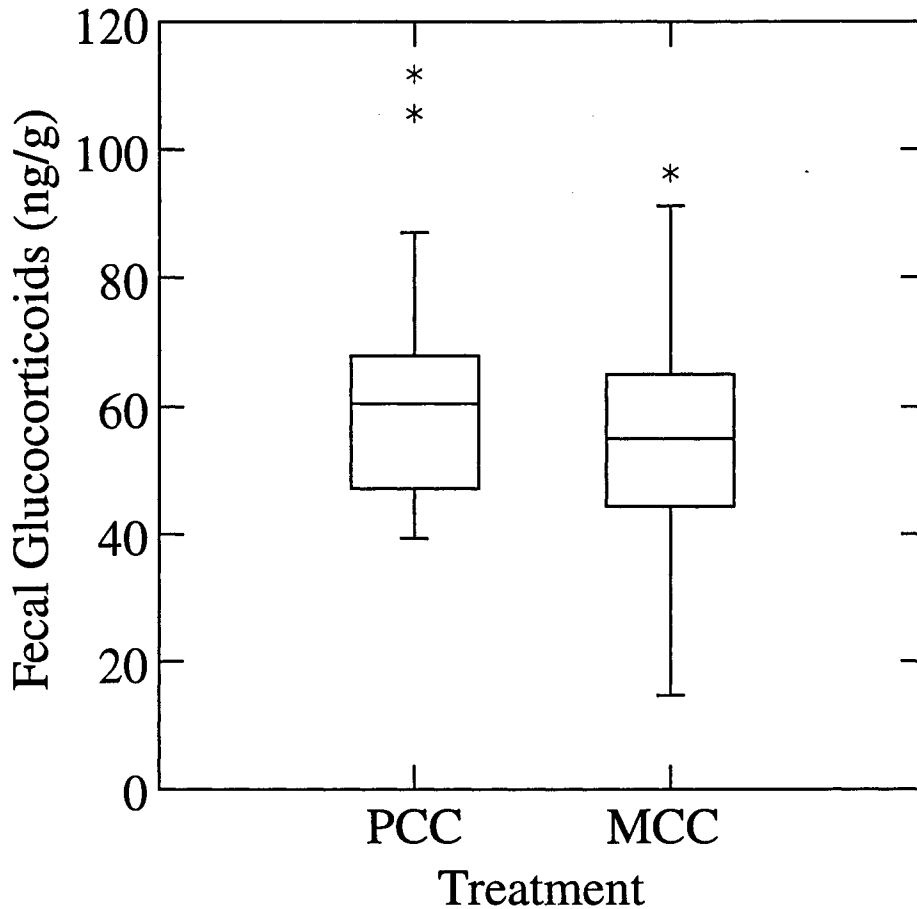


Figure 2.8. Comparison of immunoreactive fecal glucocorticoid metabolites in female moose between timber-harvest treatments^a, northwestern Ontario, Canada, February 1999-2000. Box plots show the median (center line), upper and lower quartiles (edges of the box), and range (whiskers or special symbols). Outside values are plotted with asterisks (*). PCC = progressive, contiguous clear-cut, MCC = modified clear-cut.

^aPooled – $t_{0.05(2),117} = 1.18474$, $P = 0.0673$; $n_{\text{PCC}} = 52$, $\bar{X} = 60.4$, $SD = 15.44$; $n_{\text{MCC}} = 65$, $\bar{X} = 55.0$, $SD = 15.66$.

NUTRITIONAL CONDITION

Body Fat

I obtained 250 measures of rump-fat thickness from 96 individual moose (Table 2.14). Because of telemetry collar malfunctions, deaths, and release of some individuals, fat data were collected from only 26 individuals in all 4 years (1998-2001); 2 or fewer measurements were obtained from 45 moose. Using a general linear model for analysis would require deletion of subjects that had any missing data. Mixed model methodology does not require complete data and can accommodate unbalanced designs, as long as the missing data are random (Littell et al. 1996). Examination of the descriptive statistics for 51 animals (MAXFAT, $n = 180$, $\bar{X} = 1.51$, Median = 1.50, Range = 0.1-4.2) from which I obtained at least 3 rump-fat measures suggested the data were not greatly different from the complete data set of 96 moose; therefore, I used the data from the 51 animal subgroup for further analysis.

The mixed model extends the general linear model by allowing specification of the covariance matrix of the independent random errors (Littell et al. 1996). I assessed the covariance structure of repeated rump-fat measurements within individual moose and present model fitting information in Tables 2.15 and 2.16. I chose a compound symmetric covariance structure for inference in the final model. A generalized least squares fit of a mixed model with compound symmetric error structure is equivalent to ordinary least squares for balanced data (Littell et al. 1996).

Calf-at-heel status in winter was the only statistically significant factor that remained in the model (Tables 2.17 and 2.18). Adult cows accompanied by one or two calves from the previous spring had significantly less rump-fat than those that did not ($P < 0.0001$, Figure 2.9). Differences in mean rump-fat thickness associated with annual (Figure 2.10) and timber-harvest

TABLE 2.14. Comparison of rump-fat thickness (cm)^d, percent total body fat^d, kilograms total body fat^d, and calf status between timber harvest treatments in northwestern Ontario, Canada, January-February 1998-2001.

Treatment	Females with calf				Females without calf				All Females			
	<i>n</i>	Mean	Median	Range	<i>n</i>	Mean	Median	Range	<i>n</i>	Mean	Median	Range
PCC ^a	46	1.07cm	1.00cm	0-3.2cm	59	1.85cm	1.70cm	0.1-4.8cm	106 ^c	1.51cm	1.45cm	0-4.8cm
MCC ^b	88	1.29cm	1.30cm	0-2.9cm	53	1.78cm	1.80cm	0-4.2cm	144 ^c	1.48cm	1.40cm	0-4.2cm
Total	134	1.22cm	1.10cm	0-3.2cm	112	1.81cm	1.80cm	0-4.8cm	250	1.49cm	1.40cm	0-4.8cm
PCC	46	7.81%	7.66%	5.61-12.17%	59	9.40%	9.10%	5.82-15.45%	106	8.70%	8.58%	5.61-15.45%
MCC	88	8.26%	8.28%	5.61-11.56%	53	9.25%	9.30%	5.61-14.22%	144	8.64%	8.48%	5.61-14.22%
Total	134	8.11%	7.87%	5.61-12.17%	112	9.33%	9.30%	5.61-15.45%	250	8.67%	8.48%	5.61-15.45%
PCC	46	23.80kg	23.01kg	12.36-46.44kg	59	32.03kg	30.47kg	13.43-63.48kg	106	28.40kg	27.80kg	12.36-63.48kg
MCC	88	26.14kg	26.21kg	12.36-43.25kg	53	31.27kg	31.53kg	12.36-57.09kg	144	28.11kg	27.27kg	12.36-57.09kg
Total	134	25.34kg	24.08kg	12.36-46.44kg	112	31.66kg	31.53kg	12.36-63.48kg	250	28.23kg	27.27kg	12.36-63.48kg

^a PCC denotes Progressive clear-cut.

^b MCC denotes Modified clear-cut.

^c Cows with undetermined calf status were used in the totals.

^d MAXFAT = Maximum rump-fat thickness, percent ingesta-free body fat = $5.61 + 2.05(\text{MAXFAT})$, kilograms ingesta-free body fat = $12.36 + 10.65(\text{MAXFAT})$ (Stephenson et al. 1998).

Table 2.15. Covariance structure model fitting information for the mixed model analysis of repeated rump-fat measures. Smaller values of adjusted Akaike's Information Criterion (AICc) and Schwarz' Bayesian Criterion (BIC) indicate a better fit. The χ^2 -statistic is the null model likelihood ratio test.

Structure	Description	AICC	BIC	DF	χ^2	P
UN	Unstructured	69.1	86.9	9	23.31	0.0055
CS	Compound Symmetry	59.4	63.2	1	15.62	<.0001
AR(1)	Autoregressive(1)	61.1	64.9	1	13.88	0.0002
ARH(1)	Heterogeneous AR(1)	64.1	73.3	4	17.25	0.0017
ARMA(1,1)	Moving Average AR(1)	60.8	66.4	2	16.33	0.0003
CSH	Heterogeneous CS	62.6	71.9	4	18.72	0.0009
FA(1)	Factor Analytic	64.8	79.3	7	23.05	0.0017
HF	Huynh-Feldt	61.0	70.2	4	20.35	0.0004
FA1(1)	Equal Diagonal FA	60.0	69.2	4	21.37	0.0003

Table 2.16. Covariance structure model fitting information for the mixed model analysis of repeated rump-fat measures (following backward stepwise removal of non-significant effects). Smaller values of adjusted Akaike's Information Criterion (AICc) and Schwarz' Bayesian Criterion (BIC) indicate a better fit. The χ^2 -statistic is the null model likelihood ratio test.

Structure	Description	AICC	BIC	DF	χ^2	P
UN	Unstructured	60.3	78.2	9	22.42	0.0076
CS	Compound Symmetry	50.4	54.2	1	14.97	0.0001
AR(1)	Autoregressive(1)	51.4	55.2	1	13.99	0.0002
ARH(1)	Heterogeneous AR(1)	54.8	64.1	4	16.84	0.0021
ARMA(1,1)	Moving Average AR(1)	51.5	57.2	2	15.93	0.0003
CSH	Heterogeneous CS	53.8	63.1	4	17.89	0.0013
FA(1)	Factor Analytic	55.9	70.5	7	22.30	0.0023
HF	Huynh-Feldt	53.1	62.4	4	18.59	0.0009
FA1(1)	Equal Diagonal FA	52.4	61.7	4	19.29	0.0007

Table 2.17. Effects of covariance structure (Table 2.15) on *F*-tests of rump-fat thickness. The row by column intersection is the *P*-value for the effect associated with the specified covariance structure.

Effect	Covariance Structure									
	VC	UN	CS	AR(1)	ARH(1)	ARMA(1,1)	CSH	FA(1)	HF	FA1(1)
TRT	0.1068	0.1941	0.1598	0.1371	0.1431	0.1598	0.1404	0.1819	0.1618	0.1771
YEAR	0.2067	0.0874	0.1078	0.2028	0.2339	0.1169	0.1265	0.1319	0.1210	0.1202
ATHEEL	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
TRT*YEAR	0.1720	0.1457	0.1244	0.1069	0.0867	0.1181	0.0964	0.1251	0.1179	0.1169
ATHEEL*YEAR	0.6810	0.4321	0.5397	0.5717	0.4838	0.5620	0.4993	0.4116	0.3585	0.2956
TRT*ATHEEL	0.8470	0.8833	0.8121	0.9273	0.9121	0.8327	0.7447	0.8480	0.8789	0.9690
TRT*ATHEEL*YEAR	0.4907	0.3031	0.3998	0.4112	0.4470	0.3766	0.4665	0.3698	0.3856	0.3871

Table 2.18. Effects of covariance structure (Table 2.16) on *F*-tests (following backward stepwise removal of non-significant effects) of rump-fat thickness. The row by column intersection is the *P*-value for the effect associated with the specified covariance structure.

Effect	Covariance Structure									
	VC	UN	CS	AR(1)	ARH(1)	ARMA(1,1)	CSH	FA(1)	HF	FA1(1)
ATHEEL	0.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

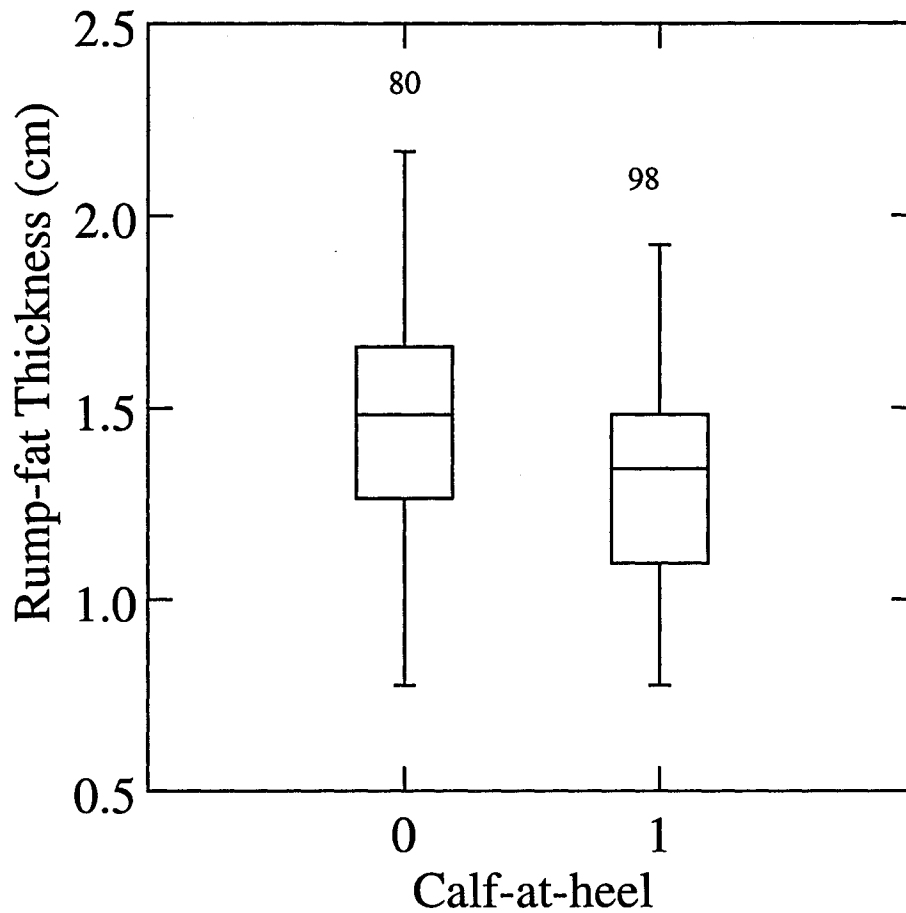


Figure 2.9. Calf-at-heel status and corresponding ultrasonographic measurements of rump-fat thickness (square-root transformed data) in female moose, northwestern Ontario, Canada, January–February 1998-2001^a. Box plots show the median (center line), upper and lower quartiles (edges of the box), and range (whiskers). The number above each box is the sample size.

^aEffect: ATHEEL $F_{1/163} = 26.67$, $P = <0.0001$.

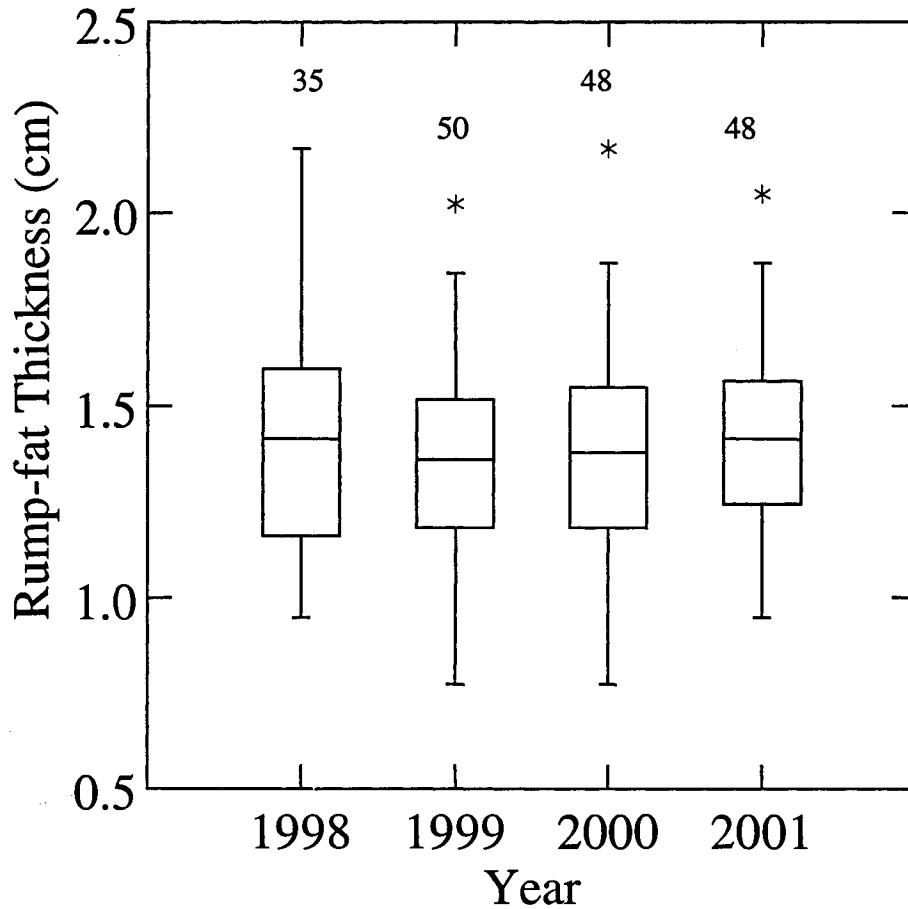


Figure 2.10. Annual ultrasonographic measurements of rump-fat thickness (square-root transformed data) in female moose, northwestern Ontario, Canada, January–February 1998–2001. Box plots show the median (center line), upper and lower quartiles (edges of the box), and range (whiskers or special symbols). Outside values are plotted with asterisks (*). The number above each box is the sample size.

treatment (Figure 2.11) were not significant. In contrast to annual and treatment effects, successfully raising a calf to winter negatively affected fat stores by 20% (least squares means estimate (\pm SE) for MAXFAT, $\bar{X}_{\text{ATHEEL}=0} = 1.73 \text{ cm} \pm 0.03$, DF = 97.3; $\bar{X}_{\text{ATHEEL}=1} = 1.17 \text{ cm} \pm 0.03$, DF = 79.9).

Body Condition Scores

Body Condition Score (BCS) was positively related to rump-fat thickness, but the relationship appeared to be curvilinear (Figure 2.12). In addition, most of the scores given to moose utilized only a small range of the available scale. Only 10 of 249 scores were less than 6 (MAXFAT Mean = 0.48 cm, SD = 0.48, Range = 0 – 1.5) and 5 moose were given a BCS greater than 8 (MAXFAT Mean = 3.42 cm, SD = 0.74, Range = 2.6 – 4.2). The remaining 234 scores were between 6 and 8 (MAXFAT Mean = 1.49 cm, SD = 0.80, Range = 0 – 4.8). These data suggest BCS was relatively insensitive to the differences in nutritional condition I observed. BCS were similar between timber-harvest treatments ($F_{1/231} = 0.0052$, $P = 0.9428$). Comparable to rump-fat thickness, BCS was negatively affected by calf-at-heel status ($F_{1/231} = 12.9259$, $P = 0.0004$).

REPRODUCTION

Pregnancy-specific protein B (PSPB) concentration in blood suggested pregnancy (95%CI = 88.4-96.3%) and twinning (95%CI = 65.4-78.7%) rates of adult females in my sample were high (Table 2.19). Contingency table analysis stratified by year, further suggested pregnancy ($\chi^2 = 0.5433$, Mantel-Haenszel $P = 0.4611$) and in utero twinning rates ($\chi^2 = 1.5010$, Mantel-Haenszel $P = 0.2205$) were similar between treatments. The proportion of cows observed with at least one calf at heel the following winter (Table 2.20) was similar each year

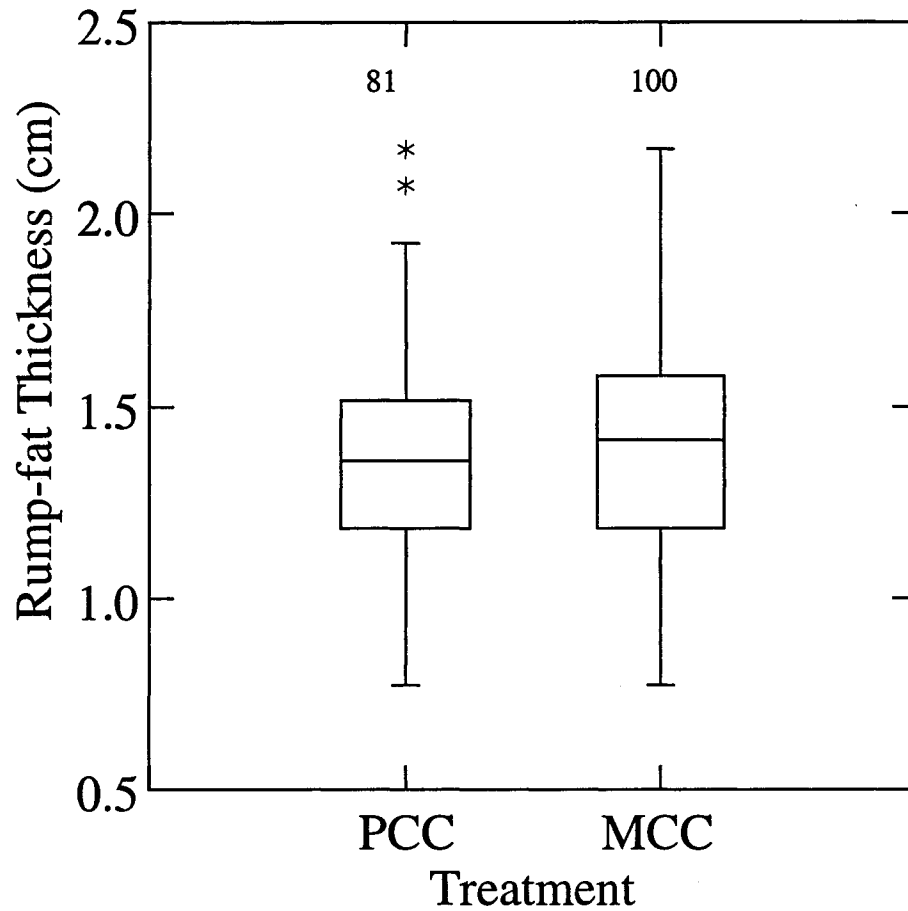


Figure 2.11. Ultrasonographic measurements of rump-fat thickness (square-root transformed data) in female moose inhabiting 2 timber-harvested landscapes in northwestern Ontario, Canada, January–February 1998-2001^a. Box plots show the median (center line), upper and lower quartiles (edges of the box), and range (whiskers or special symbols). Outside values are plotted with asterisks (*). The number above each box is the sample size. PCC = progressive, contiguous clear-cut, MCC = modified clear-cut.

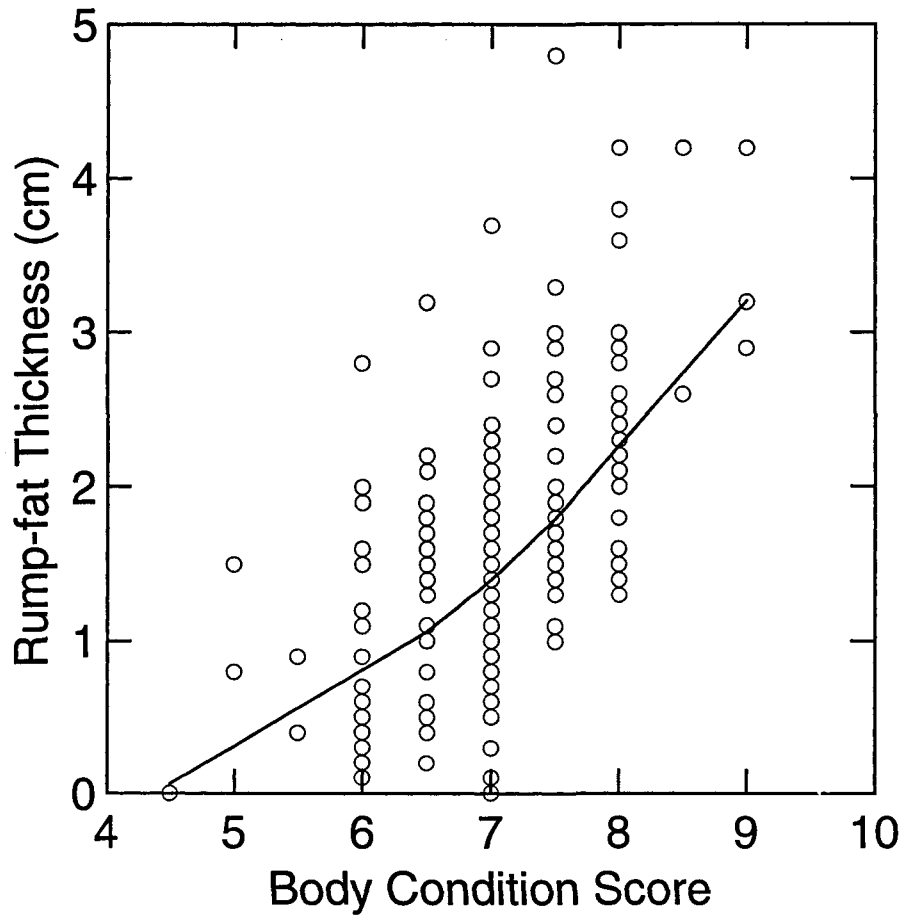


Figure 2.12. Scatter plot with a fitted line (LOESS smoothed line, tension = 0.950) demonstrating the relationship between Body Condition Score (BCS) and rump-fat thickness (MAXFAT) (all moose measured and scored 1998-2001, $n = 249$).

TABLE 2.19. In utero pregnancy and twinning determined by pregnancy-specific protein B (PSPB) measured in moose in northwestern Ontario, Canada, January-February 1998-2001.

Year	Parameter	Progressive clear-cut	Modified clear-cut
1998	Pregnant	27	34
	Single	7	6
	Twins	20	28
	<i>n</i>	31	38
	in utero Calves:100 Cows	151.6	163.2
1999	Pregnant	27	31
	Single	7	8
	Twins	20	23
	<i>n</i>	27	31
	in utero Calves:100 Cows	174.1	174.2
2000	Pregnant	21	26
	Single	7	4
	Twins	14	22
	<i>n</i>	22	31
	in utero Calves:100 Cows	159.1	154.8
2001	Pregnant	23	32
	Single	7	3
	Twins	16	29
	<i>n</i>	23	34
	in utero Calves:100 Cows	169.6	179.4
Total	Pregnant	98	123
	Single	28	21
	Twins	70	102
	<i>n</i>	103	134
	in utero Calves:100 Cows	163.1	167.9

TABLE 2.20. Number of calves at heel observed with radio-collared moose during winter in northwestern Ontario, Canada during 1999-2001.

Winter	Parameter	Progressive clear-cut	Modified clear-cut
1998-1999	Alone	21	13
	Single	7	18
	Twins	1	2
	<i>n</i>	29	33
	Calves at heel:100 Cows	31.0	66.7
1999-2000	Alone	17	13
	Single	8	17
	Twins	0	4
	<i>n</i>	25	34
	Calves at heel:100 Cows	32.0	73.5
2000-2001	Alone	6	13
	Single	17	21
	Twins	0	0
	<i>n</i>	23	34
	Calves at heel:100 Cows	73.9	61.8
Total	Alone	44	39
	Single	32	56
	Twins	1	6
	<i>n</i>	77	101
	Calves at heel:100 Cows	44.2	67.3

within MCC ($\chi^2_{0.05,(2)2} = 0.0126$, $0.990 < P < 0.995$), but the proportions were different within PCC ($\chi^2_{0.05,(2)2} = 13.023$, $0.001 < P < 0.005$). Overall, the proportion of cows observed with at least one calf at heel in winter was greater in MCC than PCC (0.65 versus 0.47, $\chi^2_{0.05,(2)1} = 6.027$, Fisher's Exact test $P = 0.016$).

DISCUSSION

HEALTH

Alterations from normal hemostasis occur during stress and the significance of these changes on diagnostic interpretation of moose physiological characteristics is not completely understood. Evaluating the effects of physical-restraint capture techniques on blood parameters was particularly important in my case because moose are more commonly sampled following chemical immobilization (Schmitt and Dalton 1987). Results from my analysis of animal handling measures revealed significant annual differences that could be attributed to different capture personnel in different years. Furthermore, I demonstrated that handling measures (i.e., elapsed time and body temperature) affected several blood parameters. Many other studies that have examined the effects of different restraining techniques have clearly demonstrated that without standardization of collection methods, blood values are more indicative of the state of stress at the time of sampling than actual physiological condition of individuals (Seal et al. 1972; Wesson et al. 1979a,b; Karns and Crichton 1978; Mautz et al. 1980). Capturing free-ranging moose over large areas by hand-held net-gun fired from a helicopter does not easily facilitate consistency. The animal's reactions to the helicopter, environmental conditions (e.g., closed vs. open habitat, snow conditions, ambient temperature), and capture crew experience influence capture efficiency, which ultimately affects animal welfare. Interpretation of diagnostic tests without careful examination of the sampling technique must be regarded cautiously.

None of the blood variables I examined adequately explained variation in ultrasonographically measured rump-fat depth of cow moose. Many blood components have previously been evaluated for their usefulness in determining past nutrition in deer species. Serum proteins (Franzmann and LeResche 1978, Messier et al. 1987, DelGuidice et al. 1992, Brown et al. 1995), non-protein nitrogen (urea N; Seal et al. 1972, 1978; DelCalesta et al. 1975; DelGuidice et al. 1987, 1990, 1992; Brown et al. 1995), cholesterol (Seal et al. 1978; DelGuidice et al. 1987, 1990; Messier et al. 1987), non-esterified fatty acids (NEFA; DelCalesta et al. 1975, Seal et al. 1978, Card et al. 1985, Brown et al. 1995), thyroid hormones (thyroxine (T₄) and triiodothyronine (T₃); Seal et al. 1972, 1978; DelGuidice et al. 1987, 1990, 1994; Brown et al. 1995; Cook et al. 2001), and erythrocyte evaluation (RBC, Hb, PCV; Franzmann and LeResche 1978, Seal et al. 1978, DelGuidice et al. 1992) have been consistently associated with nutrition or body condition in both observational and experimental studies. Individually, the relationships have lacked the sensitivity (large variance in response) and the specificity (response attributed to protein, energy, or protein*energy interaction) necessary to quantify consequential differences in nutrition or condition of individuals. For example, serum urea N (SUN) is reduced by low protein intake and consequently has been one of the most widely used indices of nutritional quality (Harder and Kirkpatrick 1996). Studies in white-tailed deer (*Odocoileus virginianus*; DelGuidice et al. 1994) and reindeer (*Rangifer tarrandus tarrandus*; Säkkinen et al. 2001) have demonstrated, however, that SUN levels remain unchanged in animals fed low protein diets containing sufficient energy, even though animals may lose up to 25% of their initial mass. Relationships between blood values and the amount of fat in an animal's body also exhibit poor predictive capability (Messier et al. 1987 – fat content = $-4.81 + 0.147(\text{total serum protein})$, $R^2 = 0.36$; Keech et al. 1998 – rump-fat depth = $0.28 + 1.68(\text{creatinine}) - 0.03(\text{AST})$, $R^2 = 0.34$), or

are affected by seasonal interactions (Cook 2000 – no relationship between body fat (%) and T_4 in September, body fat (%) = $-6.229 + 2.997(T_4)$, $R^2 = 0.72$ in December, body fat (%) = $-7.151 + 2.693(T_4)$, $R^2 = 0.65$ in March).

Still, comparisons of blood profile data may be a useful procedure to assess the general health of animals (Fadely 1998, Trumble and Castellini 2002). Blood profile evaluation requires quantification of the natural variability in blood components and determination of reference ranges (Jain 1993, Gascoyne et al. 1994). Examination of the values that result in outlier status may reveal environmental or disease factors acting at the population level. In this study, the trend observed in abnormal hemograms of compromised (i.e., censored) individuals was consistent with their injuries. Fibrinogen, Glob, and Hapt are acute phase proteins and are elevated in infections and inflammatory conditions (Jain 1993). Hypoalbuminemia may be a result of decreased synthesis or increased catabolism (Kaneko 1997a) and is associated with chronic infection and inflammation (Jain 1993). The presence of markedly elevated serum protein concentration is the probable cause of an accompanying hyponatremia (low serum sodium) because electrolytes are dissolved only in the aqueous phase (Carlson 1997). Secretion of thyroid hormones from the thyroid gland is regulated by thyroid stimulating hormone (TSH) and is inhibited by glucocorticoids (Kaneko 1997b). Endotoxins produced in wound sepsis activate biosynthesis of platelets (Dodds 1997). Anemia from reduced erythropoiesis is caused by chronic inflammation (Duncan et al. 1994). The lack of a trend among the non-censored individual outliers suggests no common cause for their aberrant status.

In contrast to other body tissues that are in a state of dynamic flux, hair is formed in a relatively short time and becomes isolated from the body's continuing metabolic activities (Hopps 1977). Mineral concentrations in hair have been correlated with deficiencies associated

with nutritional disease (Flynn et al. 1977). The significance of the difference in moose hair potassium content that I observed between PCC and MCC is difficult to establish. The potassium requirement of ruminants is about 0.6 – 0.8% of the diet (NRC 1984). Signs of abnormal potassium balance (including weakness, paralysis, or hyperexcitability due largely to changes in membrane potential (Brobst 1997)) were not observed in my study. Very little is known about the mineral requirements of moose (Schwartz and Renecker 1998), but potassium intake should normally be adequate because both terrestrial and aquatic plants are replete in potassium (Wilde 1962), at least during the growing period. Winter forages may have lower available potassium (Robbins 1993), but the large hindgut in concentrate selectors, such as moose, probably functions to conserve and absorb essential minerals (Holand and Staaland 1995).

Hair mineral levels reflect element accumulation over a period of time prior to collection, and therefore, are suggestive of differences in potassium balance during late summer/fall hair growth. Franzmann et al. (1975b) demonstrated variation in 4 macro-mineral elements of moose hair, including potassium, associated with seasonal changes in nutrition. Mean (\pm SD) potassium levels in hair taken from Kenai Peninsula moose were lowest in May ($0.0258\% \pm 0.0074$) and highest in October ($0.2090\% \pm 0.0762$). The large range of potassium levels I observed in February ($0.0110 - 0.1656\%$) was not drastically different, but reference values for moose hair elements have not been determined previously. Anke (1965) reported hair potassium levels related to body stores required for normal development in domestic cattle as 0.0300% . This would suggest that most of the animals I sampled were likely meeting minimum requirements. The consistent differences in hair potassium levels between PCC and MCC likely point to a divergence in diet composition, or, lower potassium levels in similar forage species. Peek et al.

(1976) reported differences in potassium content of the winter twigs of aspen, beaked hazel, and willow associated with conifer plantations in northern Minnesota. Mineral concentrations may also decline with increased intensity of moose browsing (Danell and Bergstrom 1989).

Another major consideration in the understanding of habitat alteration on ungulate population health is the effect of physiological stress. Measurements of GC metabolites in feces were similar between landscape treatments and provided an integrated reflection of all GC secretion over the previous 1-2 days (Chapter 1). In addition, the ranges in fecal GC metabolite concentration I observed were similar to values obtained from moose in rural central Alaska, USA during March ($n = 211$, 25 – 116 ng/g feces, Tomeo 2000). In contrast, fecal samples collected within Alaska's largest urban area (Anchorage, ~260,000 residents in 2000), exhibited a range of values twice as great ($n = 62$, 54 – 221 ng/g feces). Anthropogenic factors (e.g., harassment from domestic dogs, interactions with motorized vehicles, fragmentation of suitable moose habitat) likely contributed to the high stress levels observed in the Anchorage moose population (Tomeo 2000). Interestingly, moose in the Anchorage area may also be at K carrying capacity (KCC) as evidenced by damage to preferred browse species and an observed twinning rate of 5-7 twins:100 cows (personal communication, R. Sinnott, Alaska Dept. of Fish and Game). Further studies are needed to demonstrate the response of fecal GC to a variety of already well-known physiological stressors (i.e., poor nutrition, reproduction, high temperature, deep snow), as well as the lesser-understood neurogenic varieties (e.g., interactions with predators, conspecific aggressions).

NUTRITIONAL CONDITION

Measurement of animal condition over an extended period may indicate the optimal level of nutrition obtainable on a landscape and may demonstrate the degree to which body condition

is sensitive to variation in landscape pattern. Obtaining repeated measures of individual body condition from large free-ranging ungulates, however, has been limited by a lack of practical and reliable techniques for monitoring body fat and mass. More recently, Stephenson et al. (1998) developed predictive equations of total body fat and body mass from ultrasonographic fat measurements for application in live animals. The ultrasound technique provides a direct measure of body condition, which can be monitored relative to nutrition, reproductive success (gestation and lactation), and energy expenditure (Stephenson et al. 1998).

Ultrasonographic fat measurements were similar between landscape treatments. February body fat stores in northwestern Ontario females averaged 8.54% ingesta-free body fat (IFBFAT) and fluctuated no more than 0.4% annually. For comparison, female moose in Alaska's boreal forest regions average 7-10% IFBFAT in March (T. Stephenson, California Department of Fish and Game, personal communication). Significant annual differences (-3.9% IFBFAT) in moose body fat stores have been reported when the number of days that snow levels were greater than 53 cm (moose "knee height") increased from 0 – 17 (Stephenson 1996). If moose in this study attained similar fatness each fall, then these data suggest that the climatic conditions moose experienced during early winter did not affect the rate at which body fat stores were used.

Although significant, calf-at-heel status only modestly affected adult female lipid reserves in February (8 vs. 9% IFBFAT). Testa and Adams (1998) observed a greater difference (9 vs. 15% IFBFAT) between female Alaskan moose with and without a calf present in November. Females in this Alaskan population also exhibited low twinning rates (12%) and experienced reproductive pauses in years following successful calf rearing. A decline in pregnancy (98 vs. 77%) and twinning (31 vs. 10%) rate was observed in a separate Alaskan moose population when mean March body fat estimates declined between years from 9 to 8%

(Keech et al. 2000). In this study, I did not obtain estimates of calf survival before December of each year. I determined that > 89% of the collared females were pregnant each year, however, and it is likely that many of the cows without a calf present in December experienced some duration of lactation. Thus, I may have underestimated lactation costs. My data suggests, however, that there were not any negative effects on subsequent reproductive effort for those females that successfully raised a calf.

PRODUCTIVITY

The reproductive potential for moose is determined by the age of first reproduction, litter size, length of reproductive cycle, and reproductive life (Schwartz 1998). The adult pregnancy rate of North American moose is 84.2% and is consistent (CV 6.8%) over a wide variety of habitats and winter conditions (Boer 1992). Fecundity is more variable and is a sensitive indicator of habitat quality (Franzmann and Schwartz 1985). Boer (1992) reviewed 12 North American moose studies and reported average intrauterine fecundity rates for populations below, near, and above KCC as 124.1, 106.1, and 88.0 calves/100 adult females, respectively. The constant pregnancy rates and high annual in utero twinning I observed are indicative of populations below KCC. The suggestion that neither MCC or PCC moose are nutritionally limited is consistent with previous work that indicates forage production for moose in boreal forest regions is greatest 10-30 years following disturbance (Eastman 1974, Kelsall et al. 1977, Doer 1983).

Although fecundity was similar between landscape treatments, the number of calves surviving to winter was greater in MCC than PCC. Some reproductive losses of moose occur during late gestation (Testa and Adams 1998, Stephenson et al. 2001), but the vast majority generally occurs as neonatal losses within the first few months after birth (Gasaway et al. 1977,

Ballard et al. 1981, Franzmann and Schwartz 1986, Testa 1998, Keech et al. 2000). We observed wolves (*Canis lupus*) and attributed deaths of radio-collared adult moose to wolves in both MCC and PCC. Black bear (*Ursus americanus*) were also common during summer. In addition, hunters in Ontario regularly harvest calves, but higher calf harvest in PCC does not agree with Rempel et al. (1997a) whose research suggested the PCC moose population increased because of limited hunter access (i.e., lower road density than MCC).

CONCLUSIONS

Consistent with the similarity of habitat suitability indices for moose between the MCC and PCC landscapes (Allen et al. 1987, Rempel et al. 1997a), differing landscape-level patterns resulting from forest management practices in each had little effect on the health, nutritional condition, or reproductive effort of cow moose. However, calf survival to winter was greater in the MCC landscape that incorporated the *Timber Management Guidelines for the Provision of Moose Habitat* (OMNR 1988) than the progressive, contiguous clear-cut, suggesting environmental factors affecting calf survival were different between the 2 landscapes. These results highlight the need to use a combination of techniques to evaluate the capacity of habitats to support animals.

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APPENDIX I. Hematological parameters and some causes for their deviation from normal (Duncan et al. 1994, Kaneko et al. 1997).

Abbreviation	Parameter	Change
RBC	Red blood cell count	Increase: excitement, dehydration, Decrease: anemia
Hb	Hemoglobin concentration	Increase: excitement, dehydration, Decrease: anemia
Hct	Hematocrit	Increase: excitement, dehydration, Decrease: anemia
MCV	Mean corpuscular volume	Increase: reticulocytosis, Decrease: iron deficiency
MCH	Mean corpuscular hemoglobin	Decrease: iron deficiency, reticulocytosis
MCHC	Mean corpuscular hemoglobin concentration	Decrease: iron deficiency, reticulocytosis
RDW	Red cell distribution width	Increase: anemia, reticulocytosis
Plt	Platelet count	Increase: excitement, endotoxins, Decrease: splenic congestion
MPV	Mean platelet volume	Increase: responsive thrombopoiesis, Decrease: platelet destruction diseases
WBC	White blood cell count	Increase/Decrease: caused by change in the number of any leukocyte
Seg	Segmented neutrophils	Increase: excitement, parturition, corticosteroids, infection, inflammation, hemorrhage, toxins, malignancy, Decrease: increased tissue demand, reduced production
Band	Band neutrophils	Increase: diminished storage reserve of mature (segmented) neutrophils
Lymph	Lymphocytes	Increase: excitement, infection, Decrease: corticosteroids, acute systemic infection
Mono	Monocytes	Increase: disease, bacteremia
Eos	Eosinophils	Increase: parasitism, hypersensitivity
Baso	Basophils	Increase: hypothyroidism, endocrine disease

APPENDIX II. International System of Units (SI) conversion factors: Hematology (Duncan et al. 1994, Kaneko et al. 1997).

Abbreviation	Parameter	Conventional Unit	x Conversion Factor	SI Unit
RBC	Red blood cell count	$\times 10^6/\mu\text{l}$	1	$\times 10^{12}/\text{l}$
Hb	Hemoglobin concentration	g/dl	10	g/l
Hct	Hematocrit	%	0.01	l/l
MCV	Mean corpuscular volume	fl	same	fl
MCH	Mean corpuscular hemoglobin	pg	same	pg
RDW	Red cell distribution width	%	same	%
MCHC	Mean corpuscular hemoglobin concentration	%(g/dl)	10	g/l
Plt	Platelet count	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
MPV	Mean platelet volume	fl	same	fl
WBC	White blood cell count	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
Seg	Segmented neutrophils	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
Band	Band neutrophils	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
Lymph	Lymphocytes	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
Mono	Monocytes	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
Eos	Eosinophils	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$
Baso	Basophils	$\times 10^3/\mu\text{l}$	1	$\times 10^9/\text{l}$

APPENDIX III. Chemistry parameters and some causes for their deviation from normal
(Duncan et al. 1994, Kaneko et al. 1997).

Abbreviation	Parameter	Change
Albu	Albumin	Increase: dehydration, Decrease: disease, malnutrition, blood loss
A:G	Albumin:Globulin ratio	Decrease: selective loss of albumin or increased globulins
AP	Alkaline phosphatase	Increase: acute or chronic hepatic disease, bile-duct obstruction
AST	Aspartate amino transferase	Increase: soft tissue damage, liver, kidney, or pancreas injury
C-Bili	Bilirubin, conjugated	Increase: hepatic disease, bile-duct obstruction
T-Bili	Bilirubin, total	Increase: internal hemorrhage, hepatic disease, sepsis, starvation
U-Bili	Bilirubin, unconjugated	Increase: hepatic disease, cholestatic disorders
Ca	Calcium	Increase: acidosis, excessive bone resorption, parathyroid disease, renal disease, Decrease: alkalosis, malnutrition, malabsorption, hypoalbuminemia, renal disease
Ca:P	Calcium:Phosphorus ratio	
Cl	Chloride	Increase: dehydration, acidosis, Decrease: alkalosis
Chol	Cholesterol	Increase: postprandial, disease, Decrease: malnutrition
Cort	Cortisol	Increase: stress, malnutrition
CK	Creatine kinase	Increase: soft tissue damage
Crea	Creatinine	Increase/Decrease: relative to muscle mass, renal disease
Fibr	Fibrinogen	Increase: acute inflammatory disease
Glob	Globulin	Increase: acute inflammatory disease, disease, abnormal hepatic function
Gluc	Glucose	Decrease: hepatic insufficiency, renal disease, malnutrition
GD	Glutamic dehydrogenase	Increase: hepatic necrosis, bile-duct obstruction
Hapt	Haptoglobin	Increase: acute inflammatory disease
IGF-I	Insulin-like growth factor I	Decrease: malnutrition, hypothyroidism, sepsis, corticosteroids
LD	Lactate dehydrogenase	Increase: soft tissue damage
Mg	Magnesium	Decrease: dietary deficiency, malnutrition
NEFA	Non-esterified fatty acids	Increase: diminished caloric intake, pancreas disease
Osmo	Osmolality	Correlated with serum Na except when serum water content deviates widely from normal, or when abnormally high levels of foreign low-molecular-weight substances are present in the blood
P	Phosphorus	Increase: renal disease, parathyroid disease, Decrease: dietary deficiency, parathyroid disease
K	Potassium	Decrease: diarrhea, excessive renal loss, dietary deficiency
PSPB	Pregnancy-specific protein B	
P ₄	Progesterone	
Na	Sodium	Increase: dehydration, Decrease: disease, diarrhea, blood loss, adrenal insufficiency, sequestration of fluid (e.g., peritonitis)
Na:K	Sodium:Potassium ratio	
T ₄	Thyroxine, total	Decrease: disease, malnutrition
TPro	Total serum protein	Decrease: nitrogen loss
Urea	Urea	Increase: tissue protein catabolism, Decrease: diminished protein intake, hepatic insufficiency
BHBA	β-Hydroxybuterate	Increase: diminished caloric intake
GGT	γ-Glutamyl transferase	Increase: cholestatic disorders

APPENDIX IV. International System of Units (SI) conversion factors: Chemistry (Duncan et al. 1994, Kaneko et al. 1997).

Abbreviation	Parameter	Conventional Unit	x Conversion Factor	SI Unit
Albu	Albumin	g/dl	10	g/l
AP	Alkaline phosphatase	U/l	same	U/l
AST	Aspartate amino transferase	U/l	same	U/l
C-Bili	Bilirubin, conjugated	mg/dl	17.10	μmol/l
T-Bili	Bilirubin, total	mg/dl	17.10	μmol/l
U-Bili	Bilirubin, unconjugated	mg/dl	17.10	μmol/l
Ca	Calcium	mg/dl	0.2495	nmol/l
Cl	Chloride	mEq/l	1	mmol/l
Chol	Cholesterol	mg/dl	0.02586	mmol/l
Cort	Cortisol	μg/dl	27.59	nmol/l
CK	Creatine kinase	U/l	same	U/l
Crea	Creatinine	mg/dl	88.40	μmol/l
Fibr	Fibrinogen	mg/dl	0.01	g/l
Glob	Globulin	g/dl	10	g/l
Gluc	Glucose	mg/dl	0.05551	mmol/l
GD	Glutamic dehydrogenase	U/l	same	U/l
Hapt	Haptoglobin	mg/dl	0.01	g/l
LD	Lactate dehydrogenase	U/l	same	U/l
Mg	Magnesium	mg/dl	0.4114	nmol/l
NEFA	Non-esterified fatty acids	mEq/l	same	mEq/l
P	Phosphorus	mg/dl	0.3229	nmol/l
K	Potassium	mEq/l	1	mmol/l
P₄	Progesterone	ng/ml	3.18	nmol/l
Na	Sodium	mEq/l	1	mmol/l
T₄	Thyroxine, total	μg/dl	12.87	nmol/l
TPro	Total serum protein	g/dl	10	g/l
Urea	Urea	mg/dl	0.1665	mmol/l
BHBA	β-Hydroxybuterate	mg/dl	0.096	mmol/l
GGT	γ-Glutamyl transferase	U/l	same	U/l