INFLUENCE OF THE THERMAL ENVIRONMENT
ON FOREST COVER SELECTION AND ACTIVITY OF MOOSE
IN SUMMER

By

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B.Sc., The University of Victoria, 1988

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

in

THE FACULTY OF GRADUATE STUDIES

(Department of Forest Sciences)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

December 1991

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ABSTRACT

I investigated summer thermal cover and the influence of the thermal environment on habitat selection and activity of moose (*Alces alces*). Hemispherical photography was used to estimate the sky view factor (SVF) and effective leaf area index (Le) of coniferous stands as a function of crown closure class (CCC) values from forest cover maps. Moosehorn readings taken at hemispherical photo sites indicated that the CCC scheme correctly ranked stands by canopy closure. The stand attributes of SVF and Le, together with weather data collected in the study area, were entered into a model that simulated the operative temperature (Te) experienced by a moose. 'Hot' conditions existed when Te in the open (Te_{open}) exceeded the upper limit of the upper critical temperature (UCT) range of moose (Te >29.5 °C). 'Cool' conditions existed when Te_{open} was below the lower limit of the UCT range (Te <13 °C). Other research has shown that moose are very prone to thermal stress. During the study, weather conditions were encountered that had the potential to thermally stress moose. Simultaneous Te values declined exponentially with increasing CCC, indicating that a gradient of thermal cover existed across CCCs. At CCCs greater than 4, little additional thermal cover value was realized.

Two hundred and fifty two radio locations were made on four adult cow moose. Because 'hot' and 'cool' weather conditions corresponded to 'light' and 'dark' conditions respectively, the effects of heat and light on habitat selection were indirectly assessed. Moose selected increased cover during 'hot' (thus 'light') conditions ($p < 0.05$). The patterns of habitat selection during 'light' conditions indicated that relative use of CCC = 0 sites increased significantly ($p < 0.05$) as Te_{open} decreased. Shade from willow canopies and convection by water may have allowed or caused moose to use some CCC = 0 sites when

ambient conditions exceeded the UCT. When Te_{open} was 'hot' (thus 'light' conditions), moose located under coniferous cover tended to remain under such cover during subsequent locations. These observations support the conclusion that the thermal environment influenced habitat selection. No correlations between the moose location attributes of distance to an edge/water/road and time of day or Te_{open} were found.

Moose activity/inactivity was inferred from modulating/non-modulating radio signals 326 times. Moose were more active during 'cool' (thus 'dark') conditions ($p < 0.05$). A negative correlation ($r = -0.47$) between the percent of active locations and mean Te_{open} for the hours of 11:00 until 24:00 PDT indicated that moose activity was likely thermally constrained. The mean straight line velocity (MSLV) between successive moose locations did not differ across hours from 11:00 until 24:00 ($p > 0.05$). MSLV was not correlated with Te_{open}; however, a decrease in average MSLV values from 12:00 until 17:00 did correspond to sustained conditions of Te_{open} values above the UCT.

The susceptibility of moose to heat stress, the effectiveness of conifer stands in providing thermal cover, and the relations between habitat selection and the thermal environment suggest that thermal cover is a required, manageable component of cow moose summer range in the study area.

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CHAPTER I: GENERAL INTRODUCTION

At an elementary level, an animal's needs consist of food, water, and cover. Beyond this level, from each need there emanates a complex network of processes and interactions which facilitate fitness-promoting actions.

Knowledge of cover as it applies to large North American ungulates has been deficient. This deficiency stems from cover's extensive and often overlapping functional roles (e.g., security, escape, thermal, etc.) which are difficult to quantify and relate to specific habitat attributes. Of the types of ungulate cover defined by North American managers and researchers, summer thermal cover has received an increasing amount of attention in the literature (e.g., Thomas et al. 1979; Bunnell et al. 1985; Smith and Long 1987; Ritcey et al. 1988; Timmerman and McNicol 1988; Nyberg and Janz 1990). Ideally, managers' concepts of thermal cover are based on research into the physiological needs of animals relative to specific environmental conditions. Having established an apparent need for thermal cover, the ability of different habitats to meet that need can be assessed. For example, habitat units could be ranked according to a scale of thermal cover efficacy. If thermal cover is required, then habitat units to which we ascribe thermal cover value should be utilized predictably by wild animals. Failure to reveal a predictable pattern of habitat use could stem from one of several causes: thermal cover is not used, our definition of thermal cover needs refining, or the metabolic cost of thermoregulation (i.e., by being in a thermally-stressing environment) is outweighed by some benefit (e.g., increased forage consumption).

Extensive research into the physiological effects of heat on domestic ungulates has been used for many years to provide optimal environments for such animals (e.g., Sainsbury 1967; Esmay 1969). By comparison, the amount

of comparable research on wild ungulates is meagre. Renecker and Hudson (1986) found that heart, respiratory, and metabolic rates of moose (*Alces alces* L.) increased exponentially with ambient temperature. Furthermore, during warm summer periods feed intake was reduced and body mass subsequently lost. Their observations suggest that moose should seek thermal cover to mitigate these negative effects. Several authors have investigated relations between moose habitat selection and the thermal environment. However, if need cannot be defined (e.g., by physiological experimentation), observations on habitat use can only imply requirements because they fail to discriminate between requirement and preference (Peek et al. 1982).

Most research on the effects of heat on wild ungulates has been done on free-ranging animals in uncontrolled environments. de Vos (1958) reported that although no correlation between ambient temperature and moose use of aquatic habitats was detectable, moose were more readily observed in the morning and evening than at midday. Schwab (1986) indicated that moose selected summer habitats based on their ability to provide thermal cover; after examining his data, however, I feel his conclusions are untenable. Belovsky (1981), Ackerman (1987) and Renecker (1987) reported that moose habitat choice was correlated with the ambient thermal environment; however, the qualitative nature of thermal cover as these authors described it is of little use to habitat managers attempting to provide summer thermal cover in the habitat mix.

If summer thermal cover is a manageable habitat component required by moose, there is a need to understand and quantify it well enough to manage for it wherever man is altering the landscape or managing for healthy moose populations. Conversely, if summer thermal cover is not a manageable habitat component then time and money allocated to its management are wasted.

PROBLEM AND OBJECTIVES

The conviction that North American ungulates require summer thermal cover, and that this cover can be quantified by forest canopy closure, has been poorly supported by published literature.

This research had two objectives:

1)   to determine the efficacy of forest stands of varying crown closures in providing summer thermal cover,

2)   to determine if adult cow moose select habitats at the level of forest cover polygons based upon polygon-ability to provide thermal cover.

Chapter II addresses the concepts of summer thermal cover and operative temperature as applied to moose.   The relations between ambient thermal environment and animal physiology documented by Renecker and Hudson (1986) and Parker and Robbins (1983) are used to assess the heat-stress-potential of conditions when moose were located.   In Chapter III, patterns of habitat selection and activity of moose are examined in the context of thermal environment.

STUDY SITE

The study site is located at approximately 50° N latitude, 120° W longitude in the Southern Thompson Upland Ecosection of the Southern Interior Ecoprovince (from British Columbia Ministry of Environment 1988).   The biogeoclimatic zone is Montane Spruce (from British Columbia Ministry of Forests 1988).   Elevation ranges between 1400 and 1500 m.   As a result of past fires, most forested sites in this zone are occupied by mature lodgepole pine (*Pinus contorta* Dougl.) (Lloyd et al. 1990).   Veteran and understory trees consist of

Englemann spruce (*Picea englmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The terrain is relatively level and much of the forested area is interspersed with riparian communities. Riparian sites are dominated by sedge (*Carex spp.* L.), willow (*Salix spp.* L.) and glandular bog birch (*Betula glandulosa* Michx.). Forestry represents the major land use practice in this area. Four timber harvesting companies hold cutting rights within the study area. The area is also an important summer cattle range. Moose are present year-round (Keystone Bio-Research 1991), presumably because of a low mean annual snowfall (270 cm; Mitchell and Greene 1981), and the abundance of deciduous browse.

CHAPTER II: QUANTIFYING THE THERMAL ENVIRONMENT

INTRODUCTION

Coniferous or deciduous overstories which shelter an animal from meteorological processes are described as thermal cover (Black et al. 1976). Because thermal cover operates by moderating wind, precipitation and solar radiation, its quantification relies heavily on characterizing the distribution and amount of foliar elements. Norman and Campbell (1989) identify two broad methodologies by which canopy structure is measured: direct and indirect. Direct methods encompass 'destructive sampling' techniques which require that plant organs be clipped and measured. Indirect methods allow inference about canopy structure based on the measurement of canopy-influenced solar radiation and include the use of photometric sensors, hemispherical photography, and moosehorns. Direct techniques tend to be avoided because much effort is required to obtain information from small areas. Conversely, indirect methods can be used to sample large areas quite easily. Perhaps the greatest drawback of indirect techniques is the requirement of a model which describes the interaction between canopy attributes and radiation.

The moosehorn (Robinson 1947; Bonnor 1967) is a simple tool which quantifies tree crown cover within a conical field of view normal to the forest floor. Vales (1986) found that moosehorn estimates of forest overstory were highly predictive of sub-canopy radiation regimes. Hemispherical photography is commonly employed as an indirect means of determining plant cover and canopy radiation regimes (Chen et al. 1991). Having estimated the canopy values of sky view factor (SVF; Reifsnyder 1967; Kelliher 1985) and effective leaf area index (Le; Chen et al. 1991) from hemispherical photos, and given the total global radiation under an open sky, the simultaneous radiation regime beneath a

canopy can be estimated (see Chen et al. 1991). Combining the radiation regime with ambient air temperature, wind speed and physical properties of the biotic and abiotic environment, provides an estimate of the 'equivalent blackbody temperature' or 'operative temperature' (Te; Campbell 1977). Te describes the air temperature of an environment with no wind and no net radiative input or output in which an animal would 'experience' the same thermal environment as it did in its natural habitat. Essentially, it is the net radiative energy increment or decrement to air temperature. Te and its similar variable 'standard operative temperature' (Tes) (Bakken 1980) have been used by other researchers to estimate the thermal environment of wild ungulates (Schwab 1986; Parker and Gillingham 1990).

To assess the thermal cover value of forest cover-types, simultaneous Te values as a function of the crown closure class (CCC) of forest cover polygons were estimated. A simulation model estimated the thermal environment experienced by a moose for a set of conditions which included: weather (air temperature, solar radiation, and wind speed), date, time of day, and CCC. The purpose of these simulations was to expose the nature of the thermal environment under a range of canopy closures, thereby allowing hypotheses concerning moose and thermal cover to be tested (Chapter III). CCC was chosen as the independent variable because of its importance in evaluating and managing wildlife habitat (e.g., Harcombe 1984). If summer thermal cover is found to be important for moose, describing it in terms of CCC will allow managers to utilize a habitat attribute which is commonly described for the province's forests.

The objective was to determine the efficacy of forest stands of varying crown closures in providing summer thermal cover for moose.

METHODS AND MATERIALS

Weather station

A weather station was erected 90/06/17 in a meadow dominated by sedge and glandular bog birch under 1.5 m in height. A Campbell Scientific CR21 data logger recorded hourly averages of readings taken at 60-second intervals from a levelled Li-Cor pyranometer (cosine corrected, model LI200S), Met-One anemometer (model 014A) and temperature/humidity probe (Campbell Scientific model 207). Data were transferred to a cassette recorder and recorded on 60-minute normal bias tapes. The data logger was enclosed in a rain-tight fiberglass case which was covered by a metal radiation shield. This assembly was mounted at a height of 1.5 m on a steel mast. On the same mast, the pyranometer was mounted on the south side at a height of 2.5 m. The anemometer was mounted at a height of 2.9 m. The temperature/humidity probe was placed inside a Stevenson screen on a mast at a height of 2.0 m. The entire station was fenced to exclude cattle and moose. Weekly visits ensured that all components were functioning properly. Data cassettes were read into a personal computer using software supplied by Campbell Scientific. The resulting ASCII files were imported into SYSTAT (Wilkinson 1990).

Hemispherical photography

Using a tripod-mounted Nikon SE camera and a 180° fish-eye lense (8 mm focal length), a minimum of three forest stands corresponding to each of the Ministry of Forests crown closure class codes (CCC) 3 to 8 were sampled. Kodalith Hi-Contrast, black and white, ASA 6 film was used. Photo sites were a minimum of three tree heights (i.e., >30 m in this study) from the nearest different CCC or cover-type. Compass bearings and distances to photo sites were

determined from a 1:15 000 forest cover map. Photos were not taken directly under dead-falls or boughs near the ground. All photos were taken under conditions of no wind. Most photos were taken under an overcast sky. If the sky was not overcast, photos were taken when the sun was behind a cloud to eliminate direct radiation. Light was measured with a Sekonic (model L-398) light meter. The light meter was calibrated with a Li-Cor photometer (model Li 185). To ensure good resolution, photos were taken at a 'shutter priority' speed of 1/2 second. One photo was taken at each of 3, 4, and 5 f-stops above the value indicated by the light meter. Underexposure maximized the contrast between the trees and sky.

Film was processed by UBC Media Services in one batch to ensure constant magnification. Using a Logitech Scanman Plus digital scanner, three sets of photos, each containing three photos were scanned. Each set was judged by J. M. Chen to contain a photo that was overexposed by one f-stop, one that was correct, and one that was underexposed by one f-stop. For the purpose of this study, a correct exposure was one that maximized plant/sky contrast while retaining foliar resolution. Using software developed by Chen et al. (1991), the digital scans were subjected to algorithms which derived estimates of the effective leaf area index (Le)[1], and sky-view factor (SVF) through the integration of gap fractions (Norman and Campbell 1989; Chen et al. 1991). Differences between the SVF and Le values of the underexposed and correctly exposed and the overexposed and correctly exposed were averaged to create two correction factors; one to correct SVF and one to correct Le values of incorrectly exposed photos. From each of the remaining sets of photos, the photo nearest the correct

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[1] 'Effective leaf area index' differs from 'leaf area index'. The former is defined as one half of the total surface area of leaves per unit forest floor area, multiplied by a clumping index (Ω) (for random leaf spatial distribution, $\Omega = 1$; Black et al. 1991). The latter is defined as the projected leaf surface area per unit of ground surface area (Kimmins 1987).

exposure was scanned and subjected to the same computer procedures discussed above. If the 'best' photo of a set was in my opinion underexposed or overexposed (when compared to the 'best' photos identified by J.M. Chen), the Le and SVF correction factors (0.58 and 0.045, respectively) were added or subtracted to obtain corrected Le and SVF values. Ten of 34 photos required correction.

In addition to the photos taken under coniferous stands, seven other sites were sampled. These sites ranged from beneath willow canopies to edge habitats. None had a CCC value defined on the forest cover map. Theoretically, a site with no cover (CCC = 0) has SVF and Le values of 1 and 0, respectively. If the SVF and Le values of these 'other' sites were closer to the theoretical values of a CCC = 0 site than the observed values of CCC = 3 sites, they were assigned to CCC = 1. Since no CCC = 1 sites were mapped in the study area, the purpose of this interpolation was to assess the validity of forcing the regression line through the theoretical point CCC = 0, SVF = 1. Regression equations were fitted to plots of the average SVF and Le values for each CCC against CCC. An additional regression equation was obtained by plotting SVF against Le. Where appropriate, regression lines were forced through the theoretical coordinate pairs (i.e., CCC = 0, SVF = 1; CCC = 0, Le = 0; Le = 0, SVF = 1).

Moosehorn

At each site where hemispherical photos were taken, moosehorn (Bonnor 1967; Bunnell and Vales 1989) estimates of mean crown completeness (MCC) were obtained. Starting directly over the photo site, readings were taken along the cardinal bearings. These readings were a minimum of 3 m apart (to ensure independence of the samples), along a distance such that a minimum of three mature stems were passed within one meter of the observer along each of the

four bearings (T.A. Black pers. commun.). A minimum of ten readings were taken per site. Readings from each site were averaged to determine MCC. MCC values from sites of the same CCC were averaged and correlated with CCC. The data were plotted with the least-square regression line to display the trend of the correlation.

Equivalent blackbody temperature model

To describe the thermal environment experienced by a moose, a simulation model (Appendix I) based on the 'equivalent blackbody temperature' (Te; Campbell 1977) was developed. Using CCC, hour, day, and the weather data from the field station for that particular time, the thermal environments of forested and open habitats were quantified. The model was not used to determine a moose's energy budget. Because of the assumptions in the model and the problems inherent in extrapolating wind speed from the open to the animal's height in the forest, the model's primary function was to rank environments by Te. Ranking provided an estimate of the relative difference among the Te values of different CCCs. When possible, the effects of altered driving variables on Te were investigated or deduced.

RESULTS AND DISCUSSION

Weather station

Renecker and Hudson (1986) reported that in summer, the upper critical temperature (UCT) (i.e., the ambient temperature above which evaporative heat loss processes of a resting, thermoregulating animal are initiated; Bligh and Johnson 1973) for moose was between 14 and 20 °C. Ackerman (1987) estimated that this same value was between 15 and 17 °C. Renecker and Hudson (1986) found that at air temperatures between 14 and 20 °C, thermal panting was observed and that open-mouthed panting occurred at air temperatures above 20 °C.[1] Many hours during the study period had an average air temperature in excess of 14 °C (Fig. 2.1). Further, the activity and location of moose were often monitored when the air temperature exceeded the alleged UCT (Figs. 2.2 and 2.3). Renecker and Hudson (1986) found that 'radiant heat load' (a measure of the thermal environment incorporating air temperature, wind speed, and solar radiation) did not predict physiological responses of moose to heat better than did air temperature. R.J. Hudson (pers. commun.) expressed surprise at this result, and attributed the inadequacy of radiant heat load as the independent variable to its poor experimental quantification. Because solar radiation and wind speed are important in determining an animal's operative temperature, the large radiation flux densities and low wind speeds recorded in this study (Figs. 2.1, 2.2 and 2.3) should have served to stress moose further.

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[1] An open-mouthed, increased respiratory frequency in response to a thermoregulatory drive to dissipate heat via evaporative cooling is defined by Bligh and Johnson (1973) as 'thermal panting'. The term 'thermal panting' was used by Renecker and Hudson (1986) to describe a closed-mouth increase in respiratory frequency. It is unclear whether 'thermal panting', as Renecker and Hudson described it, acted to dissipate heat or simply reflected an increased metabolic rate.
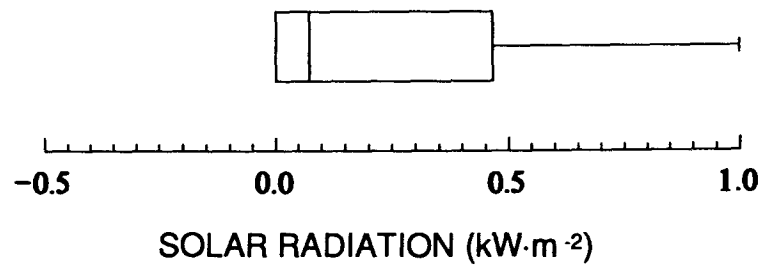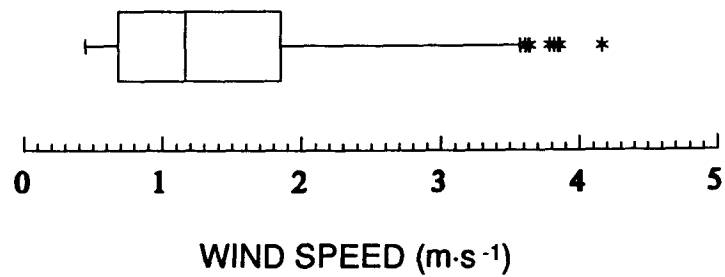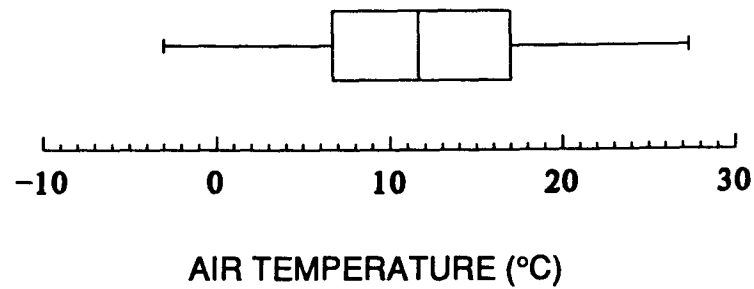
Figure 2.1. Boxplot summaries of hourly means of air temperature, wind speed, and solar radiation for the period of 90/06/17 to 90/09/23. Each plot shows the median and the range of the quartiles. Star points are identified by SYSTAT (Wilkinson 1990) as outliers. Note: complete weather data were not obtained for the period of 90/07/03 to 90/07/07. N = 2247.
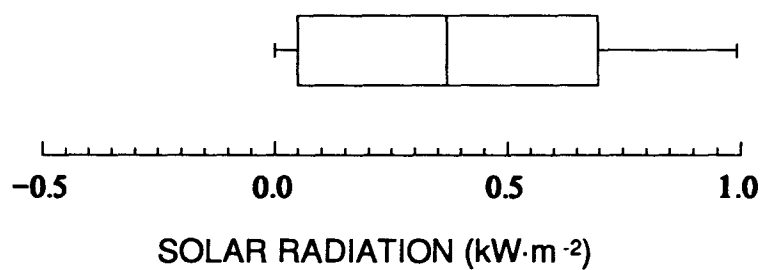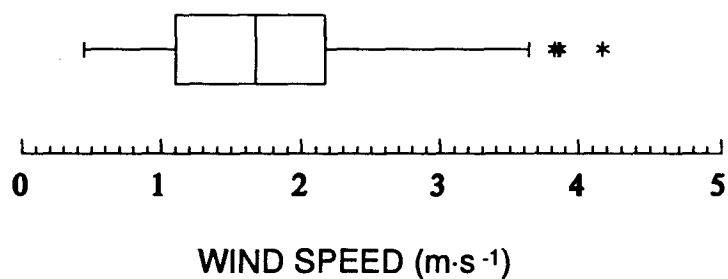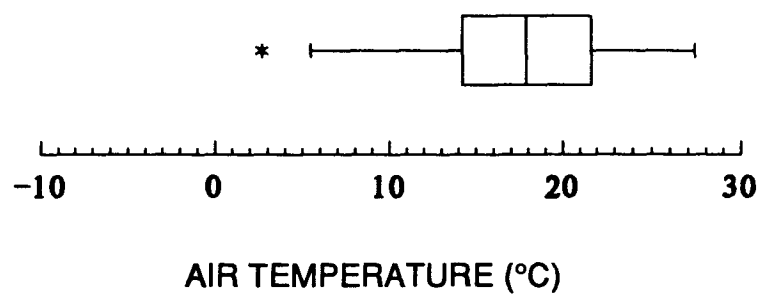
Figure 2.2. Boxplot summaries of hourly means of air temperature, wind speed, and solar radiation for hours when moose activity was determined by telemetry. See Figure 2.1 for boxplot description. N = 326.
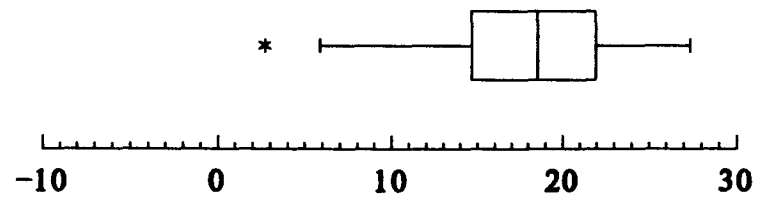
AIR TEMPERATURE (°C)
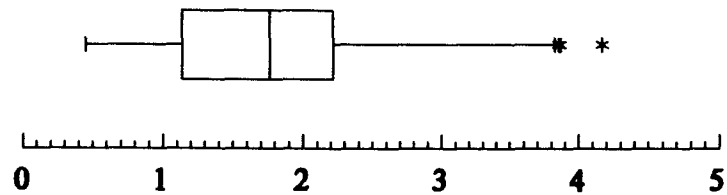
WIND SPEED (m·s⁻¹)
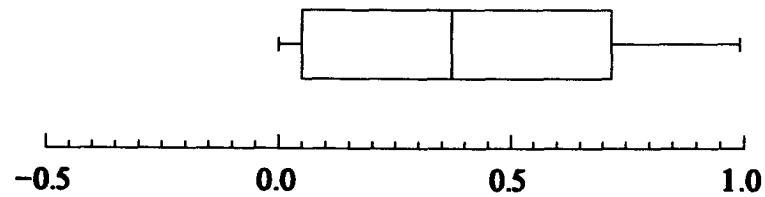
SOLAR RADIATION (kW·m⁻²)

Figure 2.3. Boxplot summaries of hourly means of air temperature, wind speed, and solar radiation for hours when moose locations were determined by telemetry. See Figure 2.1 for boxplot description. N = 252.

Forest canopy

Hemispherical photos and moosehorn estimates were taken at 34 sites (Table 2.1). The lack of a one-to-one relation between mean crown completeness (MCC) and the crown closure limits represented by crown closure class (CCC) was expected (Fig. 2.4). Crown closure, as it appears on the forest cover map, represents the proportion of ground surface covered by a vertical projection of the crown's outermost perimeter (Harcombe 1984; Table 2.2). Because the moosehorn detects not only gaps between crowns, but those within crowns, it is apparent that the two approaches are measuring different but covariant features. The significant correlation ($p < 0.05$, $r^2 = 0.87$) between mean crown completeness (MCC) and crown closure class (CCC) indicated that the CCC values on the forest cover map, if not representative of the actual code limits, correctly ranked the forest cover polygons by crown closure.

The relation between sky view factor (SVF) and CCC was nonlinear (Fig. 2.5). In theory a site of CCC = 0 should have a SVF of 1.0. Although the Ministry of Forests CCC = 0 corresponds to 0-5% crown closure, for the purpose of this study CCC = 0 was assumed to equal 0% crown closure. Forcing the regression line through the point CCC = 0, SVF = 1 appeared justifiable. The natural and forced regressions were significant ($p < 0.05$). Forcing the regression through CCC = 0, SVF = 1 did not change the coefficient of determination ($r^2 = 0.85$). The equation of the forced regression was used to determine CCC-specific SVFs for the simulation model.

Table 2.1. Crown closure class (CCC), sky view factor (SVF), mean crown completeness (MCC) and effective leaf area index (Le) of each site where hemispherical photos were taken. CCC values are from the forest cover map, SVF and Le values from hemispherical photos, MCC from moosehorn readings. Parenthesized CCC values represent estimates based on the relative location of mean SVF for those four locations compared to the mean SVF of CCC = 3 and the theoretical point CCC = 0, SVF = 1 (see Methods and Materials, p. 9).

CCC	SVF	MCC	Le
.	0.157	.	1.30
.	0.351	.	1.36
.	0.365	.	1.91
(1)	0.724	.	0.85
(1)	0.596	.	1.67
(1)	0.698	.	1.15
(1)	0.647	.	1.10
3	0.316	.	1.68
3	0.250	29.9	1.93
3	0.260	.	1.79
4	0.246	37.9	1.87
4	0.110	31.7	3.46
4	0.140	49.7	2.36
5	0.112	41.9	2.98
5	0.186	45.2	2.12
5	0.191	38.5	2.24
5	0.104	63.1	2.62
6	0.113	47.1	3.06
6	0.129	37.2	2.71
6	0.073	46.0	2.54
6	0.170	59.7	2.10
6	0.116	62.0	2.69
6	0.116	.	2.14
7	0.191	53.4	2.30
7	0.061	56.0	3.38
7	0.208	53.2	2.83
7	0.172	40.9	2.15
8	0.097	53.5	3.00
8	0.163	45.0	2.71
8	0.096	53.2	3.58
8	0.117	35.2	2.82
8	0.076	61.0	3.39
8	0.083	61.1	3.19
9	0.112	57.2	3.07
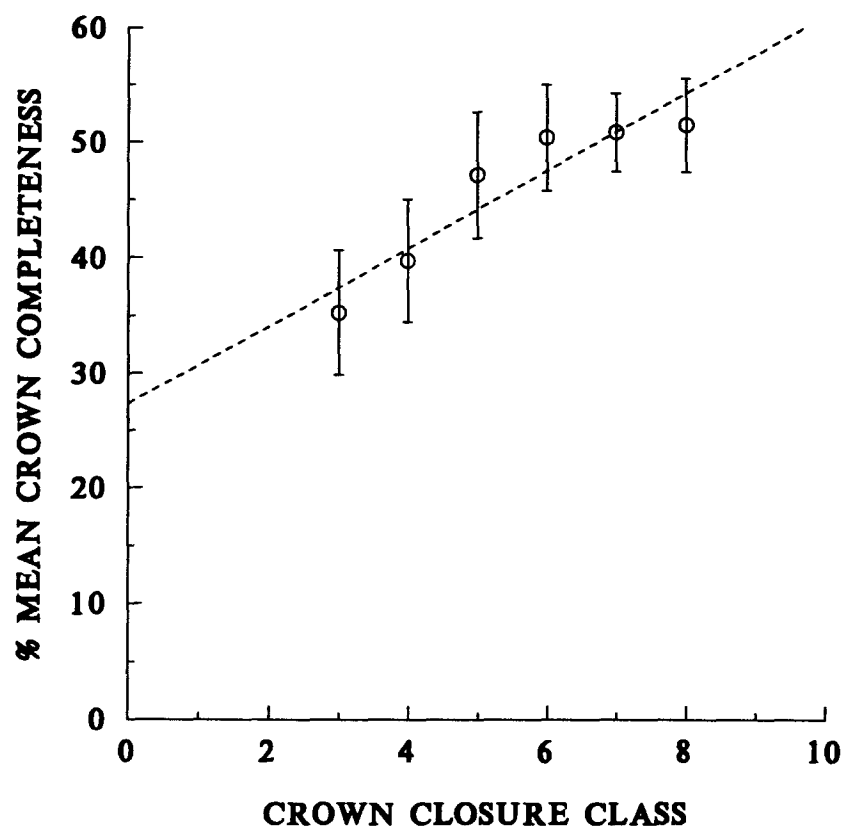
Figure 2.4. Trend of the averages of mean crown completeness for crown closure classes 3 to 8. Error bars denote mean ±1 SE. The dashed line is the line of least squares and is given only to illustrate the trend ($r^2 = 0.87$; $p < 0.05$).

Table 2.2. Crown closure class codes and their corresponding percent limits of coverage. This scheme of cover classes, used by the B.C. Ministry of Forests, does not account for gaps within individual tree crowns.

Crown Closure Class Code	Limits (percentage)
0	0-5
1	6-15
2	16-25
3	26-35
4	36-45
5	46-55
6	56-65
7	66-75
8	76-85
9	86-95
10	96-100
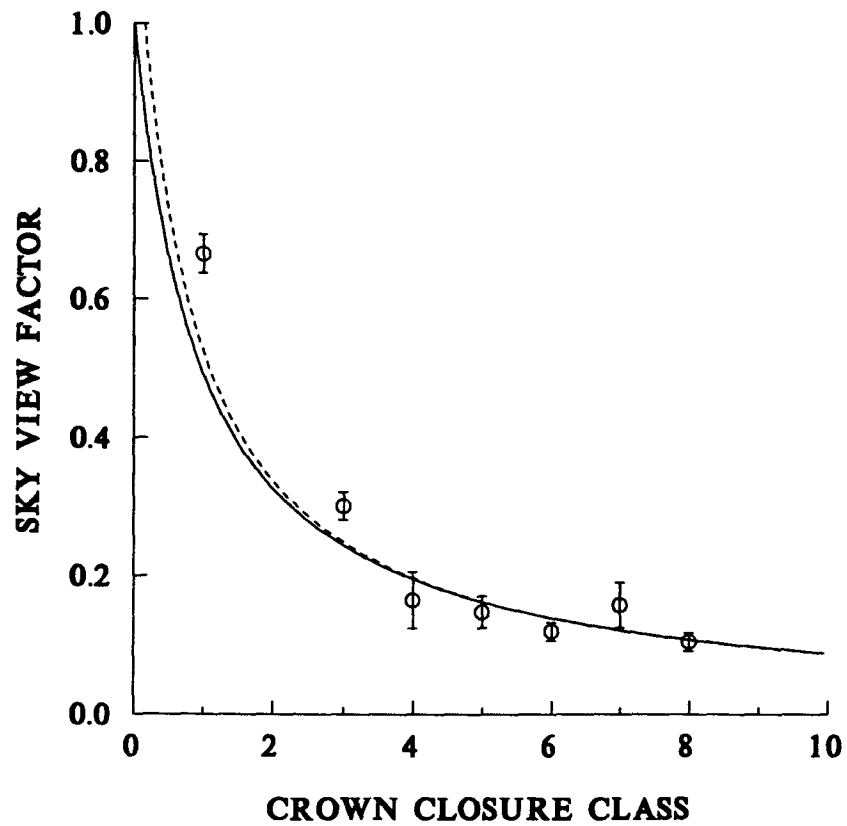
Figure 2.5. Relation between the mean sky view factor (SVF) and crown closure classes 1 to 8. Error bars denote ±1 std. error. The dashed line is the least square regression from a 1/SVF data transformation (Y = 1 / [0.844 + 1.057·X], r^2 = 0.85). The solid line represents the least square regression forced through SVF = 1 from the same transformation (Y = 1 / [1 + 1.03·X], r^2= 0.85).

In Figure 2.6, the least square regression line does not correspond to the theoretical relation between Le and CCC adapted from Black et al. (1991):

$$Le = -1/G \cdot \ln(1\text{-}CCC/10) \qquad (1)$$

G represents an angle-dependent extinction coefficient per unit foliage area measured in the direction of the solar beam. For the spherical (random) distribution of leaf inclination angles, $G = 0.5$ (Ross 1981). The discrepancy between the theoretical and observed values of Le versus CCC is likely a product of two things: (1) one of the assumptions of eqn. 1 is that the values of CCC actually represent the range of 0 to 100% crown cover. From Figure 2.4 it is apparent that $CCC = 8$ (according to the moosehorn estimate) had a MCC of less than 55%. Crown cover as employed in eqn. 1 is sensitive to gaps within crowns, therefore MCC as the independent variable should yield a better fit to the theoretical relation; (2) the value of G may not be 0.5, indicating that foliar elements were not randomly distributed, or that the radiation regime was strongly influenced by vertical elements such as tree boles. The potential effects of factors 1 and 2 were supported when a value of $G = 0.25$ yielded a theoretical equation which appeared to agree with the plot of CCC-specific Le and MCC means (Fig. 2.7).

The solar zenith angle (Z) refers to the angle between the sun and a line normal to the earth's surface (cf. solar elevation angle). The function used to determine Le weights that part of the hemispherical photo corresponding to smaller Z values heaviest (Black et al. 1991). Although I did not explore the existence of Z-dependent G values, a small G value (i.e., $G < 0.5$) at low Z (i.e., $Z < 0.6$ radians) is characteristic of a plant structure classified as an erectophile. Erectophiles are plant structures which have a radiation regime strongly influenced by components in the vertical plane (Ross 1981). This explanation is consistent with my cursory observations that the crowns of lodgepole pine
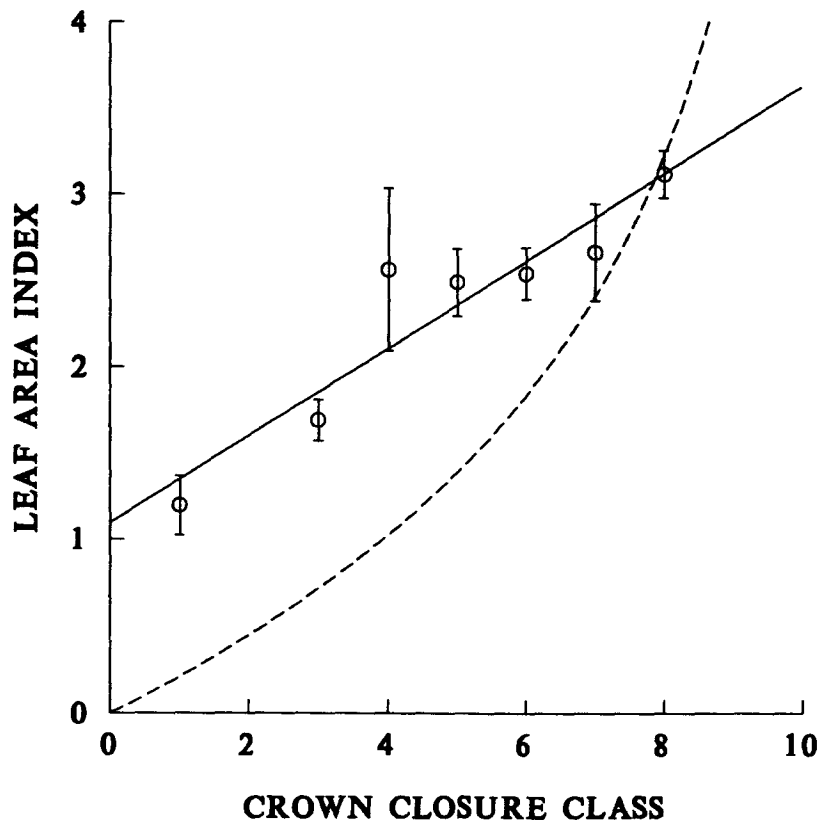
Figure 2.6. Relation between effective leaf area index means and crown closure classes 1 to 8. Error bars represent ±1 std. error. The solid line represents the least square regression. The dashed line represents the theoretical relation between the two variables (see eqn. 1 in text).
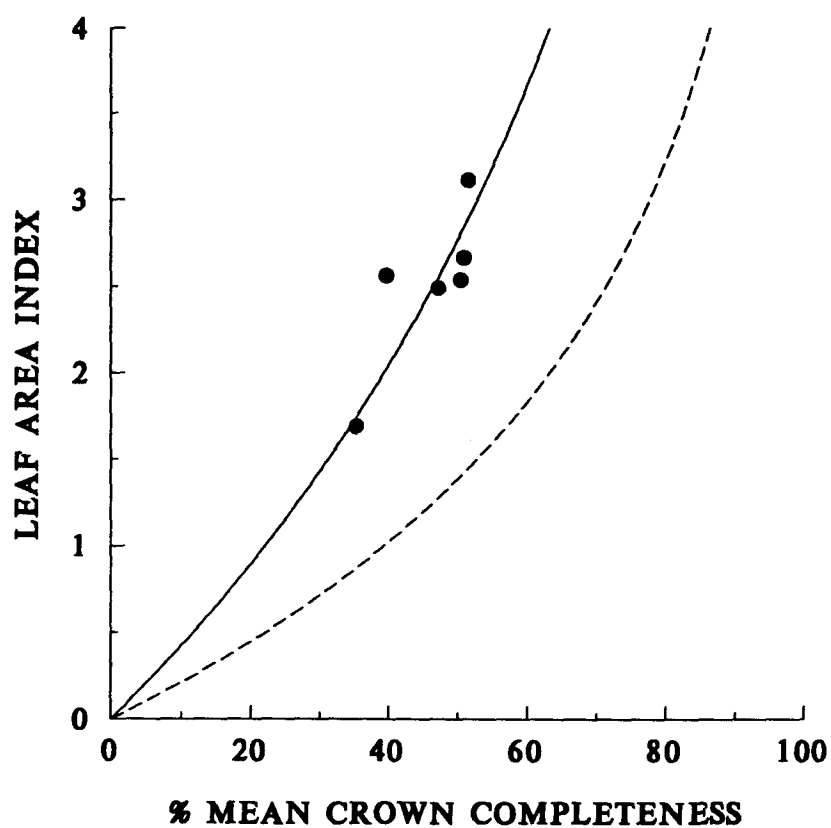
Figure 2.7. Mean leaf area index against mean crown completeness for each of crown closure classes 3 to 8. The dashed line is the theoretical function given by eqn. 1 (assuming a spherical distribution of foliar elements - see text). The solid line corresponds to eqn.1 when foliar elements in the vertical plane predominate (i.e, $G < 0.5$).

tended to be sparser than those of trees such as Douglas-fir (*Pseudotsuga menziesii* (Mirbel.) Franco.). The result was that for the lodgepole pine, boles (thus vertical elements) tended to be more conspicuous.

Owing to the nonconformity of the data to the theoretical function (Fig. 2.6), T.A. Black and J.M. Chen (pers. commun.) recommended that a curve be fitted through a scatterplot of SVF versus Le. In theory, when Le = 0 then SVF = 1. Forcing the curve through this point changed the shape of the relations very little (Fig. 2.8). Using the forced regression, Le was estimated from CCC-specific SVF values.

Thermal cover

Because Te is derived from many variables (Appendix I), thermal cover is very dynamic; that is, it is a product of time, weather, and location. As defined by the simulation model, simultaneous Te values across CCCs decreased exponentially with increasing CCC (Fig. 2.9). From this trend it is apparent that beyond CCC = 4, the marginal increase in thermal cover value is relatively small.

Determining the wind speed under a canopy by extrapolating a known wind speed in the open is difficult. Sub-canopy wind speed is modified by canopy height and structure as well as understory (Bunnell et al. 1985). Further, sub-canopy wind speed is likely influenced by the slope, aspect, and distance to an edge. When moose were located, 75% of the observations occurred when the mean wind speed in the open was less than 2.2 $m \cdot s^{-1}$ (Fig. 2.3). For this reason and the estimation difficulties noted above, no canopy-driven wind attenuation function was incorporated in the model. Instead, two simulations representing extreme conditions were run: (1) a simulation which held wind speed constant across all canopies, and (2) a simulation in which beyond CCC = 0, wind speed was held at 0 $m \cdot s^{-1}$ (Fig. 2.9). Because the equivalent resistance to
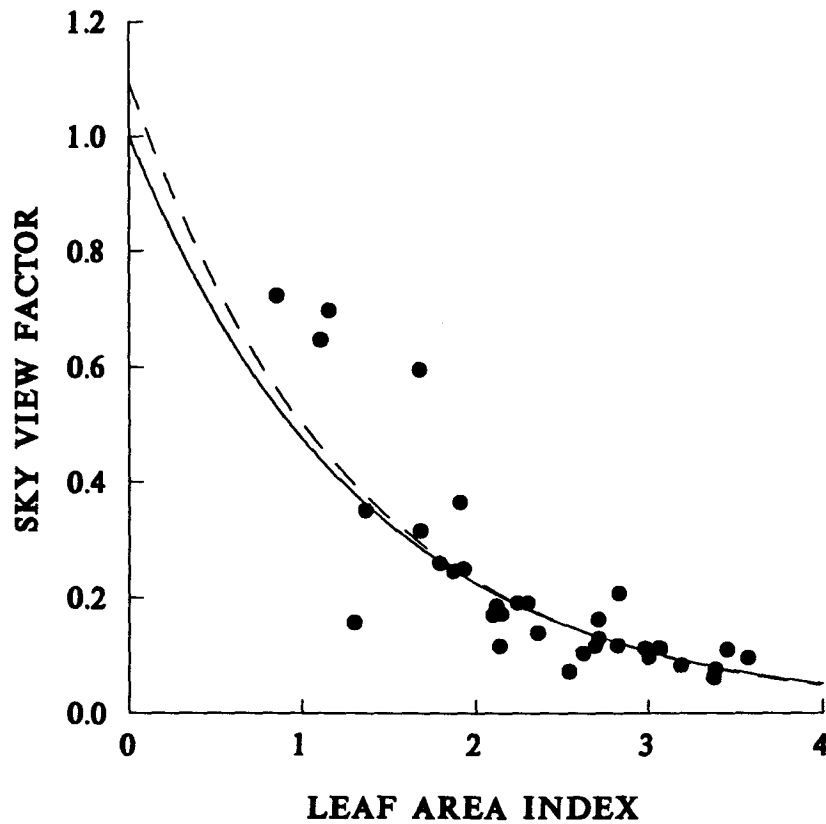
Figure 2.8. The relation between sky view factor (SVF) and effective leaf area index (Le). The dashed line is the least square regression from a log(SVF) transformation (Y = $10^{0.038} \cdot [10^{0.339}]^{-X}$, I^2 = 0.75). The solid line is the least square regression forced through the theoretical point Le = 0, SVF = 1 from the same transformation (Y = $[10^{0.324}]^{-X}$, I^2 = 0.74).
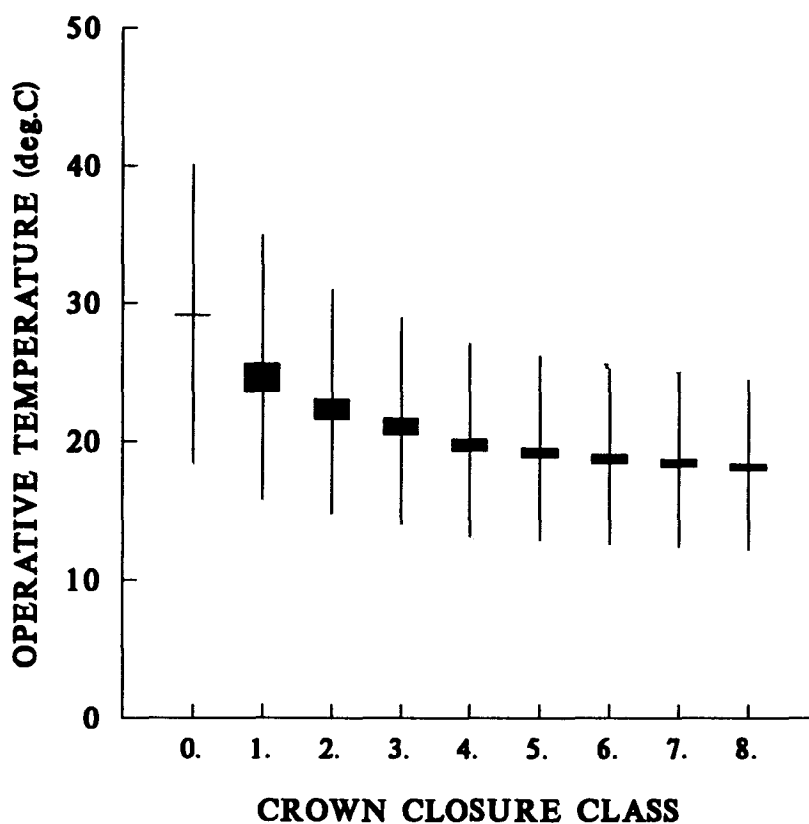
Figure 2.9. Mean operative temperatures by crown closure class (CCC). Weather data (Fig. 2.1) were run through the simulation model (Appendix I) under two conditions: (A) wind speed (as recorded in the open) was held constant across all CCCs, (B) wind speed in CCCs >0 was held constant at 0 m·s⁻¹. The means for simulations A and B are represented by the lower and upper limits of the solid rectangles respectively. Since CCC = 0 was only simulated under condition A, error bars denote ±1 SD. Error bars in the negative y direction denote 1 SD for the simulations of A. Error bars in the positive Y direction denote 1 SD for the simulations of B.

Figure 2.9. Mean operative temperatures by crown closure class (CCC). Weather data (Fig. 2.1) were run through the simulation model (Appendix I) under two conditions: (A) wind speed (as recorded in the open) was held constant across all CCCs, (B) wind speed in CCCs >0 was held constant at 0 $m \cdot s^{-1}$. The means for simulations A and B are represented by the lower and upper limits of the solid rectangles respectively. Since CCC = 0 was only simulated under condition A, error bars denote ±1 SD. Error bars in the negative y direction denote 1 SD for the simulations of A. Error bars in the positive Y direction denote 1 SD for the simulations of B.

heat transfer (r_e) remained constant, the trend in decreasing range of mean Te with increasing CCC resulted primarily from a reduction in the absolute amount of radiation absorbed (R_{abs}) (see Figs. 2.5 and 2.8).

Edgerton and McConnell (1976) showed that during summer months, mean hourly air temperatures in unlogged coniferous forests and in neighbouring clearcuts differed by less than 6 °C. Other research has shown that mean-maximum air temperatures varied little (i.e., less than 3 °C) with stand density (Jemison 1934; Spurr 1957). In their review, Bunnell et al. (1985) stated that "The simplest approach to estimating the influence of forest cover on air temperature is to increase minimum temperatures, and decrease summer maximum temperatures by 2 °C". It appears that the effect of canopy on air temperature is not large. My simulation model assumed that simultaneous air temperatures beneath forest canopies did not vary with CCC, and that these temperatures equalled the hourly means recorded at the weather station. If this assumption was not valid (e.g., simultaneous air temperature increased significantly with decreasing CCC) the net effect would have been a greater rate of decrease in mean Te with increasing CCC on the hottest days. The trend in Figure 2.9 is a result of increased radiation attenuation by canopies of increased CCC. Because Te is determined by adding an animal's net radiative gain to the air temperature (Appendix I), other things being equal, increasingly lower air temperatures yield increasingly lower Te values. Therefore it can be expected that if both radiation and air temperature decreased with increased CCC, Te would decrease more rapidly with increased CCC than if radiative input or air temperature was held constant.

If, as discussed above, foliar elements were not randomly distributed (i.e., G ≠ 0.5) but rather approximated an erectophile structure, the primary implication would be that at low values of Z, lodgepole pine canopies would attenuate a

smaller fraction of solar radiation.[1] The effect of decreasing the thermal cover value of increased CCCs would dampen the relation in Figure 2.9.

If either of the assumptions discussed above (i.e., constant air temperature and random foliar distribution) were not met, the relation between Te and CCC (Fig. 2.9) would not be expected to deviate from its present form. Therefore, although the magnitude of the differences between Te values of different CCCs may change modestly, higher CCCs should always provide better thermal cover.

CCC values for forest cover in this study area are given only for coniferous stands. Many of the sites classified as non-productive brush (NPBr) supported climax willow stands. A sample of the larger willow stems revealed heights up to 5 m and ages over 150 years (annuli counts). In some locations, a dense canopy was formed over the ground between tree clumps. One such site (not atypical of the area) yielded a hemispherical photo which had a SVF (0.157) similar to that of a CCC = 6 conifer stand (Table 2.1). Based upon the capacity to intercept solar radiation, it is apparent that willow canopies were capable of providing a level of thermal cover comparable to the denser conifer stands.

Quantifying and comparing the thermal environments of forested sites as a function of CCC appears to be practicable.

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[1] Perhaps it was for this reason that Mitchell and Greene (1981) stated that lodgepole pine canopies make poor thermal cover.

CHAPTER III: COVER SELECTION AND ACTIVITY OF MOOSE

INTRODUCTION

If summer thermal cover is required by a species, we could expect a population deprived of it to exhibit negative symptoms. Such symptoms might manifest themselves directly or indirectly to produce declines in productivity and or survivorship, or habitat abandonment via emigration. Peek et al. (1982) noted that the predicted effects of habitat manipulations are often given in terms of population change. However, they warned that because the population response integrates many factors (e.g., food, predation, weather, and hunter harvest), each must be evaluated prior to naming cover as the causative agent of change. Therefore Peek et al. (1982) suggested that predictions of habitat use (not population change) relative to habitat changes be used to anticipate the effects of cover manipulation.

Methods to evaluate resource preference of wild animals have existed for many years (e.g., Hess and Rainwater 1939). Neu et al. (1974) proposed a technique which permits an animal's observed pattern of resource use to be described as preference, avoidance or used in proportion to availability. Johnson (1980) criticized the classical approach to use-availability studies, and showed that the arbitrary nature of researcher-defined 'availability' and researcher handling of 'doubtful' observations can profoundly affect the conclusions permitted by such studies. Johnson (1980) proposed a technique to evaluate resource preference, and concluded that his technique reduced researcher subjectivity and bias in estimating measures of use and availability. Alldredge and Ratti (1986) compared four techniques for analyzing resource selection, including those of Neu et al. (1974) and Johnson (1980), and found that no one

technique consistently out-performed the others on simulated data. In their study, Type I error was controlled effectively by all techniques, but the occurrence of Type II error "depended on the number of habitats, the number of animals, the number of observations per animal and the magnitude of the differences to be detected".

Assuming that preference can be demonstrated, it may be desirable to assess whether or not a preferred habitat is actually required to maintain population health. Knowledge of which habitat types are required by a species and which are not can be very important to the process of developing an integrated land-use strategy. Conversely, it is not unreasonable that given adequate amounts of required resources but restricted amounts of preferred ones, animals would continue seeking the latter. Catering to a species' physiological needs while ignoring learned or innate behavioural patterns may render any 'bare-essential' management strategy ineffective.

Homeotherms employ many strategies to prevent or reduce heat-stress. Such strategies include the use of cooler microclimates (e.g., thermal cover), and decreasing metabolic heat production via reductions in activity. Several authors have concluded that areas providing summer thermal cover are preferred by elk (*Cervus elaphus* L.) (Young and Robinette 1939; Lyon 1979; Pederson et al. 1980) and moose (Schwab 1986; Ackerman 1987; Renecker 1987). Peek et al. (1982) cite several reports which documented high summer densities of elk in areas with little or no thermal cover. Merrill (1991) concluded that Roosevelt elk (*Cervus elaphus roosevelti* Merriam) inhabiting the blast zone of Mt. St. Helens did not require summer thermal cover. Although the animals in Merrill's study used thermal cover when available, elk which did not use it appeared to cope with increased thermoregulatory costs. F.L. Bunnell (pers. commun.) observed elk in the blast zone of Mt. St. Helens wading into a river on hot days,

presumably to cool off. Merrill (1991) did not report any such behaviour. McCorquodale et al. (1986) believed that because heat and disturbance could restrict forage intake and increase metabolic costs, abundant forage and infrequent disturbance were essential in allowing elk to summer in areas of limited cover.

Kelsall and Telfer (1974) reported that "regions where temperatures exceed 27 °C for lengthy periods, particularly without tall trees to provide shade, or other refugia such as lakes and rivers, do not support moose". To my knowledge, no research has documented a decline in moose population size or productivity attributable to a loss of thermal cover. Indeed, this would be difficult to do because the increases in human access and animal visibility (i.e., loss of security cover) associated with recently logged areas can rapidly increase the legal and/or illegal hunter harvest (Eason 1985; Peek et al. 1987).

Elk have a marked ability to dissipate heat via cutaneous water loss or sweating (Parker and Robbins 1983). Perhaps this is why elk appear capable of tolerating high heat loads without ill-effects (e.g., Parker and Robbins 1983; McCorquodale et al. 1986; Merrill 1991). The extent to which moose sweat to dissipate heat is unclear. Sokolov and Chernova (1987) reported that moose possess sweat glands which actively contribute to thermoregulation. Renecker and Hudson (1986) did not address sweating in moose, but implied that panting was the major cooling mechanism. In areas of harsh winters, decreased summer weight gains may increase winter/spring ungulate mortality (Mautz 1978). Large heat loads impose high thermoregulatory costs on moose which, even in the presence of abundant forage, can reduce summer weight gains (Renecker and Hudson 1986). By deduction, it could be concluded that summer thermal cover is required by moose. Assuming this conclusion is correct, summer thermal cover

needs to be quantified so habitat managers can ensure its existence in managed moose habitats.

The alternate hypotheses tested in this study were that if moose respond to heat load, they would: 1) be located in forest stands providing greater shelter (i.e., higher CCC) at times when heat load was highest, and 2) be least active at times when heat load was highest.

METHODS AND MATERIALS

Moose telemetry

Four adult cow moose collared for the Okanagan Connector Freeway Ungulate Impact Assessment (Keystone Bio-Research 1991) were monitored in this study. All cows had produced calves in years previous to 1990. No calves were sighted with any of the cows in 1990; however, search intensity was lower than in previous summers (Keystone Bio-Research 1991). Because approaching a moose would likely influence its choice of habitat, all telemetry was conducted from roads. Because of logging, highway construction, and recreational activities which occurred during the study, I felt that moose would be habituated to the sound of vehicles. The study period did not overlap with any hunting seasons in the area. Moose were triangulated from the ground using a Lotec receiver, a hand-held Yagi-H antenna, headphones and a Silva Ranger compass. Compass bearings to each signal were taken from a minimum of three sites for each attempted location (e.g., Springer 1979). Information recorded for each location included:

1) animal code,
2) date, time at commencement of location,
   time at completion of location,
3) site-specific compass bearings,
4) modulating/non-modulating signal.

Moose locations were sampled at minimum intervals of one hour. If more than one animal was being monitored on the same day, interlocation intervals often approached 120 minutes. A typical sampling period spanned 13 hours. The interval from 11:00 until 24:00 (PDT) was the most frequent sampling period, however, some hours between 5:00 and 18:00 (PDT) were also sampled. The former period was more frequently sampled in an attempt to discriminate the effects of heat and light on habitat selection and activity. Moose were not fitted with activity collars. According to Van Ballenberghe and Miquelle (1990), a modulating signal was a reliable indicator of collar, therefore moose, movement. If more than one of the location signals was modulating, that location was recorded as 'active'. After moose had moved to other locations within their summer home ranges, I investigated the general area of many telemetered locations to infer the potential value of each site for foraging.

Renecker and Hudson (1986) reported that the upper critical [air] temperature (UCT) for moose in summer was between 14 and 20 °C. A regression of operative temperature in open areas (Te_{open}) against air temperature (Tam) data for hours when moose were located in this study indicated that air temperatures of 14 and 20 °C corresponded to Te_{open} values of 13.0 and 29.5 °C respectively ($Te = 0.03 \cdot Tam^{2.30}$; $I^2 = 0.73$, SE = 1.6, n = 252). I defined hot conditions (Te_{open}:hot) to be when Te_{open} was >29.5 °C, and cool conditions (Te_{open}:cool) to be when Te_{open} was <13.0 °C.[1] Day or 'light' conditions existed when the mean hourly solar flux density (MHSFD) was ≥ 50 $W \cdot m^{-2}$. Night or 'dark' conditions existed when MHSFD was <50 $W \cdot m^{-2}$.

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[1] Renecker and Hudson (1986) conducted their observations under uncontrolled conditions with respect to solar radiation and wind. Had their observations been made in a controlled environment, Te values of 14 and 20 °C would have been used as the thermal limits in this study.

Analysis of telemetry data

Compass bearings were plotted on a 1:15 000 forest cover map. The universal transmercator (UTM) coordinates to the nearest 25 m were recorded for the center of the polygon formed by the intersection of at least three bearings. Habitat features near the estimated location identified by the forest cover map were checked against air photos. If the forest cover map lacked information available from the air photo it was adjusted accordingly.

Telemetry locations were rejected if they met one of two criteria:

1)   three bearings did not intersect,

2)   the polygon bounded by the bearings contained more than one cover-type and had at least one side longer than 300 m.

Other location attributes recorded directly from the forest cover map included:

1)   distance to road - the distance from the center of the bearing polygon (CBP) to the nearest road (roads under this classification were identified as those which were relatively frequently travelled by vehicles),

2)   distance to edge - if a CBP was further than 75 m (half the diameter of telemetry overlays; see below) from a non-forest cover-type, the distance from the CBP to the nearest non-forest cover-type was recorded,

3)   distance to water - the shortest distance from the CBP to any water body that supported riparian or emergent aquatic vegetation was recorded.

Using UTM coordinates, the distance between successive moose locations was divided by the time between those locations to yield a mean straight line velocity (MSLV). Ignoring telemetry error, interlocation distance represented a minimum value, and as such, likely underestimated actual mean velocity.

The average precision of the telemetry system was determined by using a 95% error arc of ±4°. A random sample of 20 moose locations was chosen. The average length of the longest side of each of the error polygons (Springer 1979) was calculated. This averaged length (150 m) was used as the diameter of a circular overlay centered on each pair of UTM coordinates. Analysis of a digitized forest cover map was conducted using TERRASOFT. TERRASOFT was used to quantify the study area by forest crown cover, and obtain information regarding patterns of habitat use by moose from telemetry overlays. Because telemetry overlays often contained more than one cover-type, two types of dependent variables were tested: 1) the area (ha) contained in telemetry overlays by crown closure class (CCC), and 2) the frequency with which each CCC occurred within telemetry overlays (regardless of area). Overall use-availability of forest cover-types was not assessed because I believed that for this type of analysis, the telemetered observations were autocorrelated.

The small surface area to body volume ratio of large animals such as moose results in a reduced rate of heat transfer between animal and environment. The potential effect on cover selection of a delayed response to a hot environment due to thermal inertia was investigated by examining the selection pattern of CCCs across a 13 hour period.

The effect of the thermal environment on subsequent (<120 min. later) habitat selection was tested by examining the patterns of movement between cover-types under Te_{open}:hot and Te_{open}:cool conditions. Habitats were labelled as open (CCC = 0) and cover (CCC >0). When telemetry overlays contained more than one cover-type, that which represented the greater area was used.

Except where noted, statistical testing was done with SYSTAT (Wilkinson 1990). The probability of a Type I error was set at 0.05. If statistical tests yielded

results significant at $\alpha = 0.10$ (but not $\alpha = 0.05$), they are reported as such. The frequency distributions of crown closure class (CCC) for the study area versus habitat within 800 m of a road and Te_{open}:hot versus Te_{open}:cool, were tested with the Kolmogorov-Smirnov (K-S) test of two independent samples. Tests of independent proportions were conducted according to Hicks (1982) (hereafter called Hicks' test). Pearson product-moment correlation coefficients (r) were used. All variables tested for correlations were plotted to check for non-linear relations. Regression values were compared with the paired t-test. The likelihood-ratio χ^2 was used to test for differences in moose activity between Te_{open}:hot and Te_{open}:cool conditions. The K-S test was used to test for a difference between the frequency of velocity intervals for active versus inactive telemetry readings. Tukey's HSD test was used to identify different means when significant ANOVA results were observed. Velocity intervals were selected by an algorithm in SYSTAT (Wilkinson 1990).

RESULTS AND DISCUSSION

Habitat analysis

The results of a GIS evaluation of the proportions of the study area represented by each crown closure class (CCC) did not differ significantly from the results of a similar evaluation of habitats falling within telemetry range of roads (Fig 3.1; K-S test, $p > 0.05$). The similarity between the two distributions in Figure 3.1 indicates that potential moose activity and location sampling was not biased to a habitat mix that was atypical of the study area.

Habitat use

Two hundred and fifty two telemetered moose locations were recorded across a range of ambient light and temperature conditions (Chapter II).
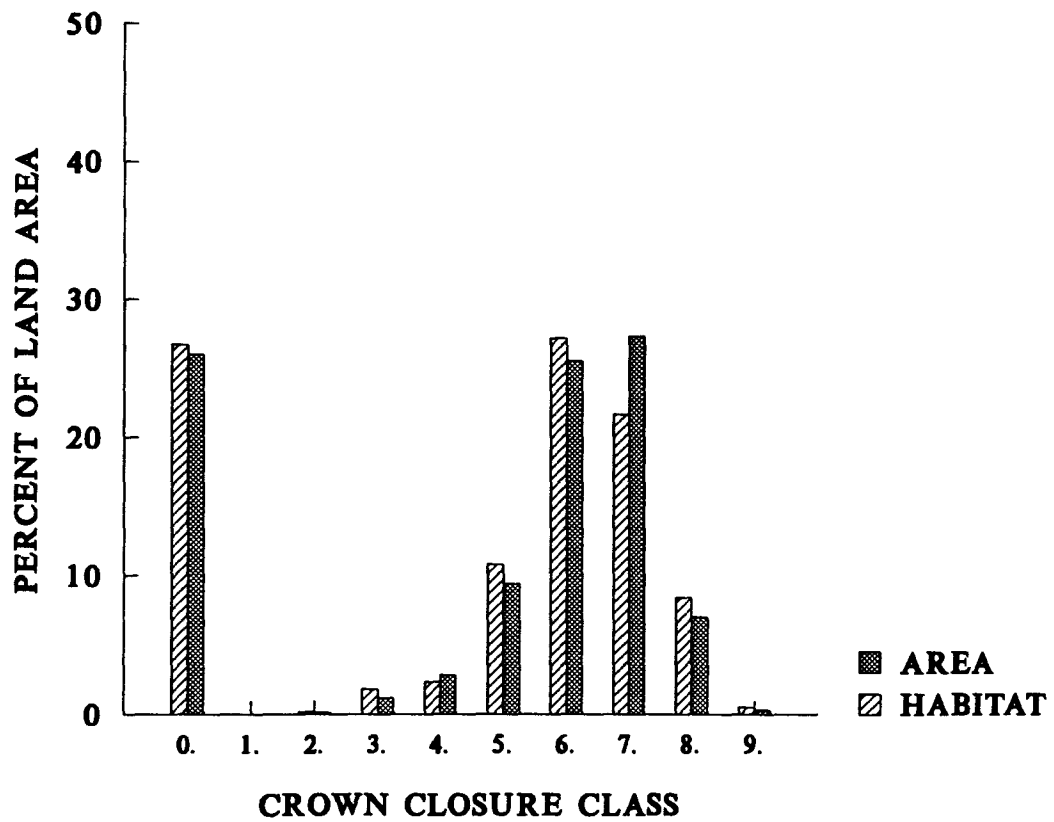
Figure 3.1. Percentages of the entire study area (AREA, 15 970 ha) and habitat within 800 m of a road (HABITAT, 9855 ha) represented by each cover class. For crown closure limits see Chapter II, Table 2.2.

The nature of the relation between operative temperature (Te) and air temperature (Tam) for CCC = 0 sites (i.e., Te = $0.03 \cdot Tam^{2.30}$) dictated that for the observed weather data, the upper critical temperature (UCT) for moose in the summer was never exceeded during 'dark' hours. Conversely, only 13% of 'light' hours during the summer were below the UCT (n = 292). Because the opportunity to sample moose locations during 'cool', 'light' conditions was limited, only 3% (n = 4) of locations and 4% (n = 7) of activity samples were taken under such conditions. These small sample sizes precluded direct partitioning of the effects of heat and light on the cover selection and activity of moose.

Both the total area-by-CCC within telemetry overlays and the frequency of CCCs within overlays revealed a significant difference in cover-type selection between Te_{open}:hot and Te_{open}:cool conditions (Figs. 3.2 and 3.3; K-S test, p < 0.05). Total use of CCC = 6 stands was greater during 'hot' (thus 'light') conditions than during 'cool' (thus 'dark') conditions, (Figs. 3.2 and 3.3; Hicks' test, p < 0.05). No difference between total use of CCC = 0 sites as a function of the thermal (thus light) environment was detected (Figs. 3.2 and 3.3; Hicks' test, p > 0.05). The remaining significant difference was that stands of CCC = 7 were used more during 'cool' conditions (Fig. 3.3; Hicks' test, p < 0.05).

All summer forage plants listed by Eastman and Ritcey (1987) and Singleton (1976) for moose in the vicinity of the study area are associated with riparian habitats (thus CCC = 0 in this study). With the exception of edges and a few seepage sites, no forage species were found when telemetered moose locations in conifer stands were investigated on-foot. Increased use of CCC = 6 stands during 'hot' conditions may have reflected use of those areas for the thermal cover they provided. Assuming the warmest scenario of complete wind attenuation(see p. 23), the difference between the two regressions of Te versus Tam for CCC = 0 (Te = $0.03 \cdot Tam^{2.30}$) and CCC = 6
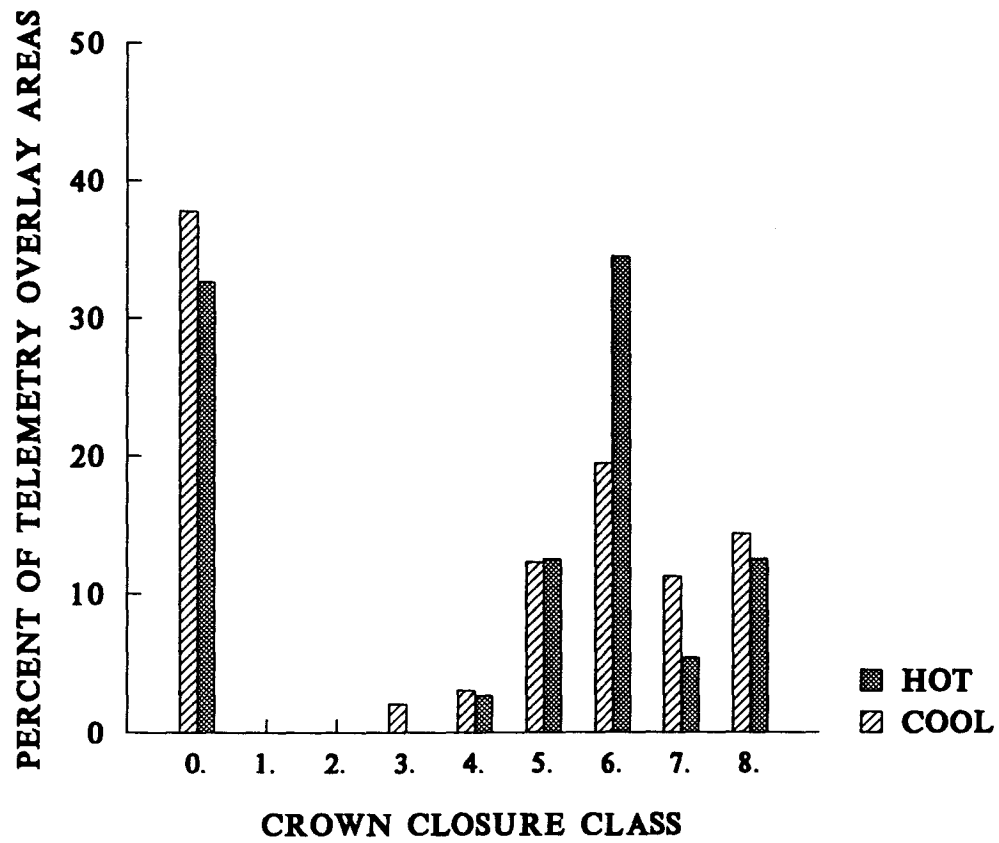
Figure 3.2. Percentage of the total area (ha) contained within telemetry overlays represented by each crown closure class for locations when Te_{open} was hot (light) (n = 124) and cool (dark) (n = 56).
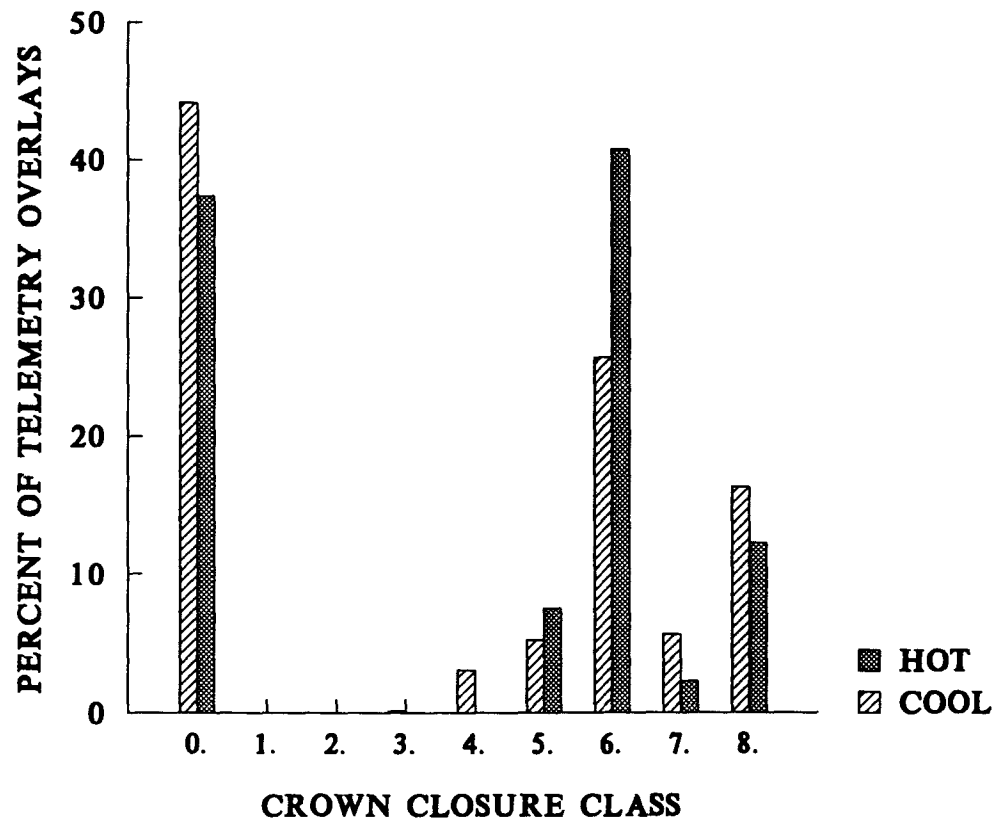
Figure 3.3. Percentage of telemetry overlays containing each crown closure class when hourly Te_{open} values were hot (light) (n = 124) and cool (dark) (n = 56).

(Te = -4.60 + 1.36·Tam, r^2 = 0.91, SE = 2.2 °C) increased exponentially between Tam = 14 and 30 °C (Fig. 3.4). Therefore, as Te_{open} increased above the UCT of moose, the relative value of CCC ≥6 sites as thermal cover also increased. As shown in Chapter II, the marginal increase in thermal cover value for stands greater than CCC = 4 was slight. The relative use of CCC ≥4 (Figs. 3.2 and 3.3) is likely a result of the availability of each cover-type (Fig. 3.1). The regression of Te versus Tam for CCC = 4, (assuming complete wind attenuation; Te = -5.74 + 1.47·Tam, r^2 = 0.88, SE = 2.8 °C), was significantly different than the same regression for CCC = 6 (paired t-test, $p < 0.05$, n = 30). However, for the highest recorded air temperature the largest difference between the two regressions (2.0 °C at 27.5 °C) was within the standard error of each regression.

If CCC = 0 sites provided no thermal cover, the similar use of CCC = 0 and CCC = 6 on Te_{open}:hot days (Figs 3.2 and 3.3) implies that thermal cover was not being selected. As shown in Chapter II, a few sites lacking a CCC designation on the forest cover map (therefore taken as CCC = 0) intercepted an amount of solar radiation comparable to that intercepted by conifer stands of CCC = 6. Cursory observations indicated that habitat polygons designated as CCC = 0 were usually associated with water. The apparent use of water by moose as a heat-sink has been reported (Ackerman 1987; Renecker 1987). Because water's potential to act as a heat-sink and the shade properties of willow trees were not factored into the operative temperature model (Chapter II; Appendix I), it can not be concluded that moose using areas of CCC = 0 were necessarily heat stressed when Te_{open} exceed 29.5 °C. Indeed, the use of some CCC = 0 sites may have served to mitigate the effects of heat stress.
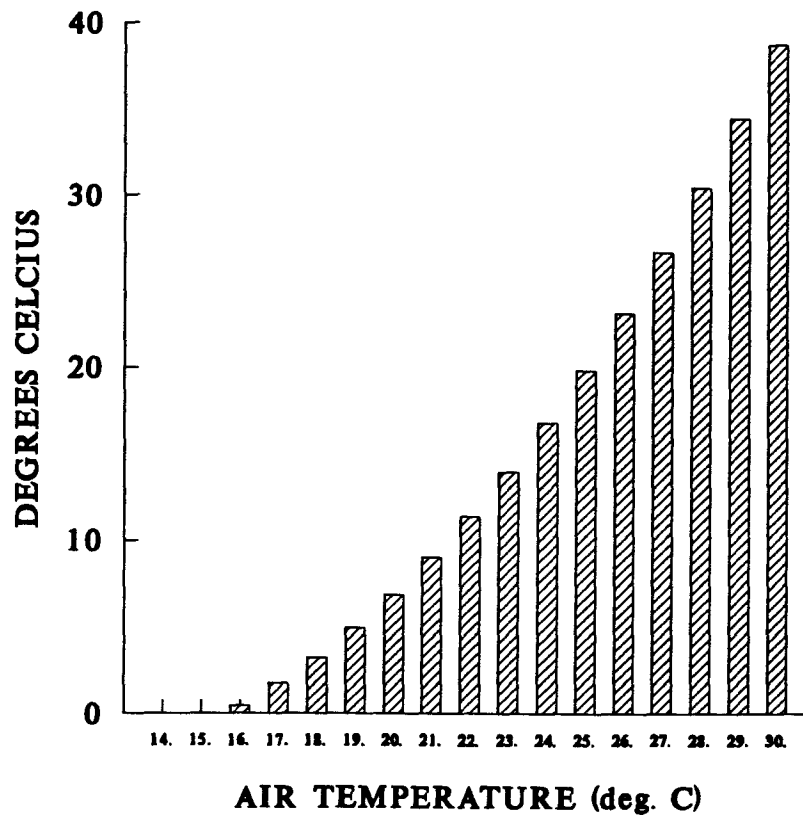
Figure 3.4. Simultaneous differences between the regressions of Te versus air temperature for CCC = 6 and CCC = 0 sites, as a function of air temperature from 14 to 30 °C.

For large animals such as moose, a small ratio of surface area to body volume results in a reduced rate of heat gain (Peters 1983). A slow rate of heat gain could therefore mean that thermal cover is required only after a sustained exposure to hot environments. Alternately, thermal cover might be used before the onset of heat stress as part of an optimization strategy. Figure 3.5 shows how Te_{open} values were distributed for each hour that moose locations were sampled from 11:00 until 24:00. To eliminate the effects of light, the hourly ratios of telemetry overlay areas in CCC = 0 to areas in CCC $\geq$4 were compared from 11:00 until 21:00. A significant increase in the relative use of CCC = 0 sites (p < 0.05; 11:00 until 24:00, r^2 = 0.63; 11:00 until 21:00, r^2 = 0.46) corresponded to a significant decrease in Te_{open} values for the same period (p < 0.05, r^2 = 0.75) (Figs. 3.5 and 3.6). The hour when the largest Te_{open} values were observed (13:00) was the same hour when the ratio of CCC = 0 to CCC $\geq$4 overlay areas was smallest (Figs. 3.5 and 3.6). Since not all sites of CCC = 0 had willow canopies capable of providing thermal cover, use of some forage-rich CCC = 0 sites appeared to be constrained by the thermal environment of such areas. Because an increase in relative use of CCC = 0 sites corresponded to a decrease in Te_{open}, even though 'light' conditions prevailed until 21:00 for most of the summer, thermal constraints explain habitat selection better than a photo-correlated, anti-predator response. Demarchi (1990) also found that use of CCC = 0 sites by moose was least when the potential for thermal stress was greatest.

When individual proportions of cover-pattern-selections were compared between temperature (light) classes, moose on covered sites were most likely to remain under cover when Te_{open} was 'hot' (Fig. 3.7, Hicks' test, p < 0.05). In addition, the least common pattern of cover selection under Te_{open}:hot conditions was 'cover to open'; providing further evidence that habitat selection was thermally constrained.
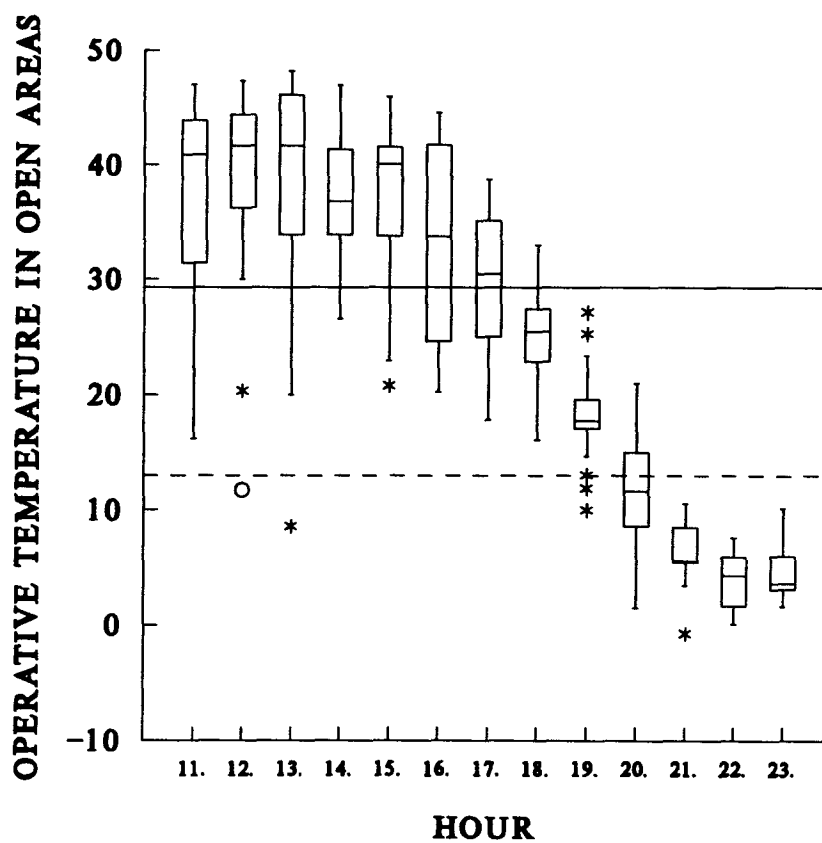
Figure 3.5. Boxplot summary of hourly Te$_{open}$ values when moose were located for the hours of 11:00 until 24:00 (n = 252). Each boxplot shows the median and the range of the quartiles. Star and circle points are identified by SYSTAT (Wilkinson 1990) as outliers. The lines correspond to the UCT (dashed) and the thermal limit for open-mouthed panting (solid) identified by Renecker and Hudson (1986) (see text p. 32).

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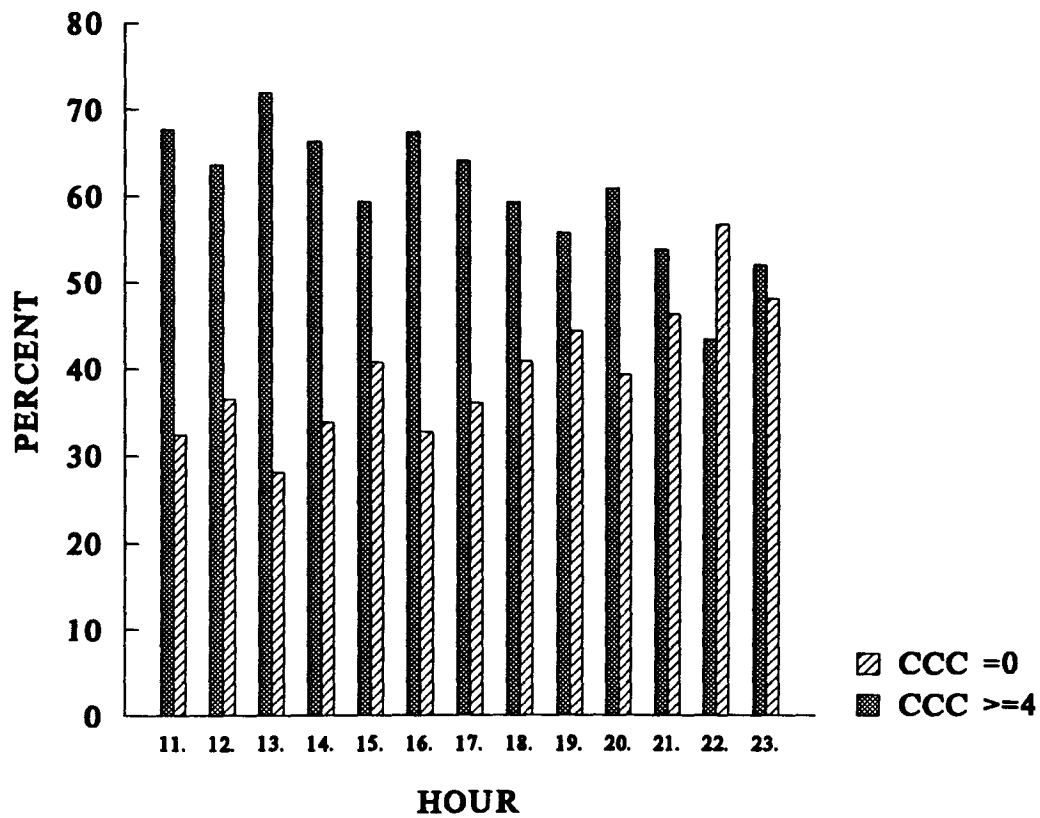
Figure 3.6. Percentage of telemetry overlay areas in CCC = 0 and CCC ≥ 4 for the period from 11:00 until 24:00 (n = 243 locations). The relation between the ratio of CCC = 0 to CCC ≥ 4 overlay areas and hour is significant ($r^2 = 0.63$, $p < 0.05$).
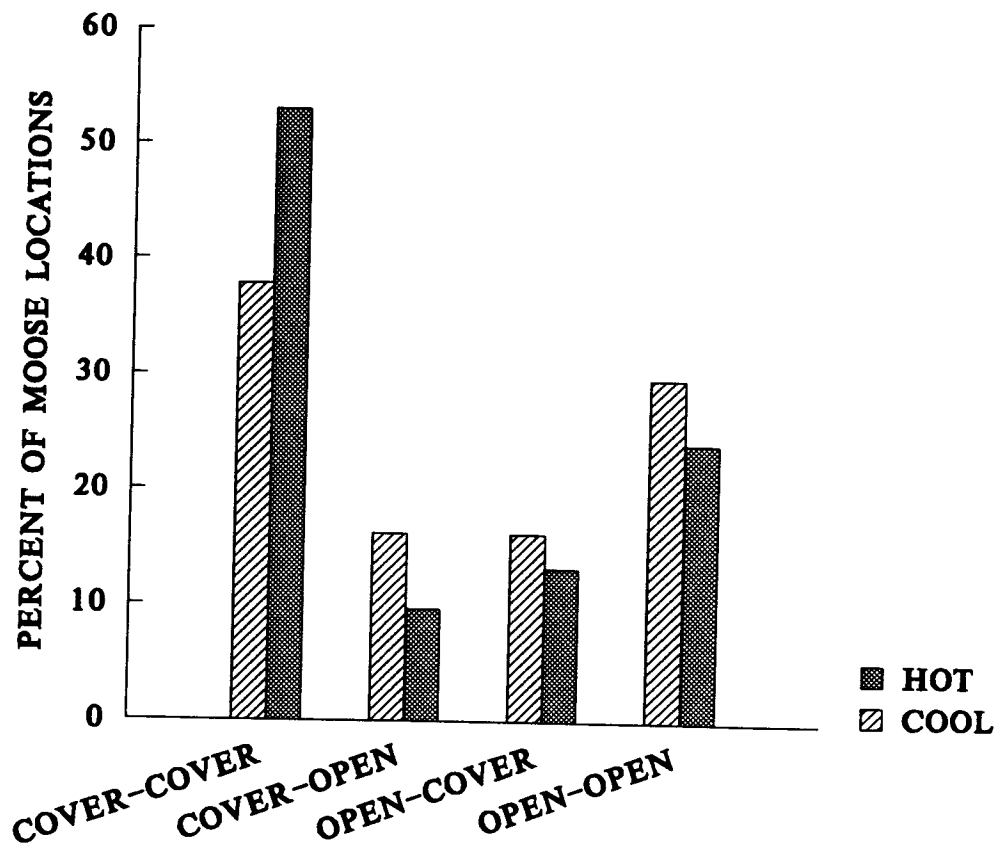
Figure 3.7. Percentage of successive radio locations (i.e., < 120 minutes apart) represented by cover type at time = t and cover type at time = t + 1 when Te_{open} was hot (n = 83) and Te_{open} was cool (n = 37).

No appreciable correlations (all r >-0.20 and <0.20) were found between moose location distance to a road/habitat edge/water body and Te_{open} or time of day. These observations are consistent with Demarchi's (1990) results which showed that these location variables were independent of three time intervals between 15:00 and 03:00. Interpreting these results in the context of other researcher's findings would be difficult. The geographical variation in number, type and human-usage of roads, the degree of habitat interspersion, and physiographic nature of habitats is certainly great across moose range (e.g., Kelsall and Telfer 1974; Eastman and Ritcey 1987). Putman (1988) concluded that the diel patterns of cervid activity are very plastic. If disturbance caused by humans denied moose access to preferred or required resources near roads, moose might shift their use of such areas to times when the disturbance was minimal (e.g., night). Because vehicular traffic in the study area did not appear excessive to me, and roads were not associated with particular geographic and therefore habitat features as they are in some areas (e.g., forage-rich valley bottoms), the lack of change in 'distance to road' across hours was expected. The high degree to which cover-types and riparian areas were interspersed in the study area (GIS analysis) may explain the findings that moose distances to an edge or water were not correlated with Te_{open} or hour of day.

Moose activity

Moose activity was sampled 326 times over a range of ambient light and temperature conditions (Chapter II). Relative moose activity was greater under Te_{open}:cool (thus 'dark') conditions (x^2, p < 0.05, Fig. 3.8). Cervid activity patterns can be temporally modified to avoid predators and other disturbances (Putman 1988). If predator activity is correlated with light conditions and moose attempt to avoid predators (e.g., to protect calves), temporal differences in moose
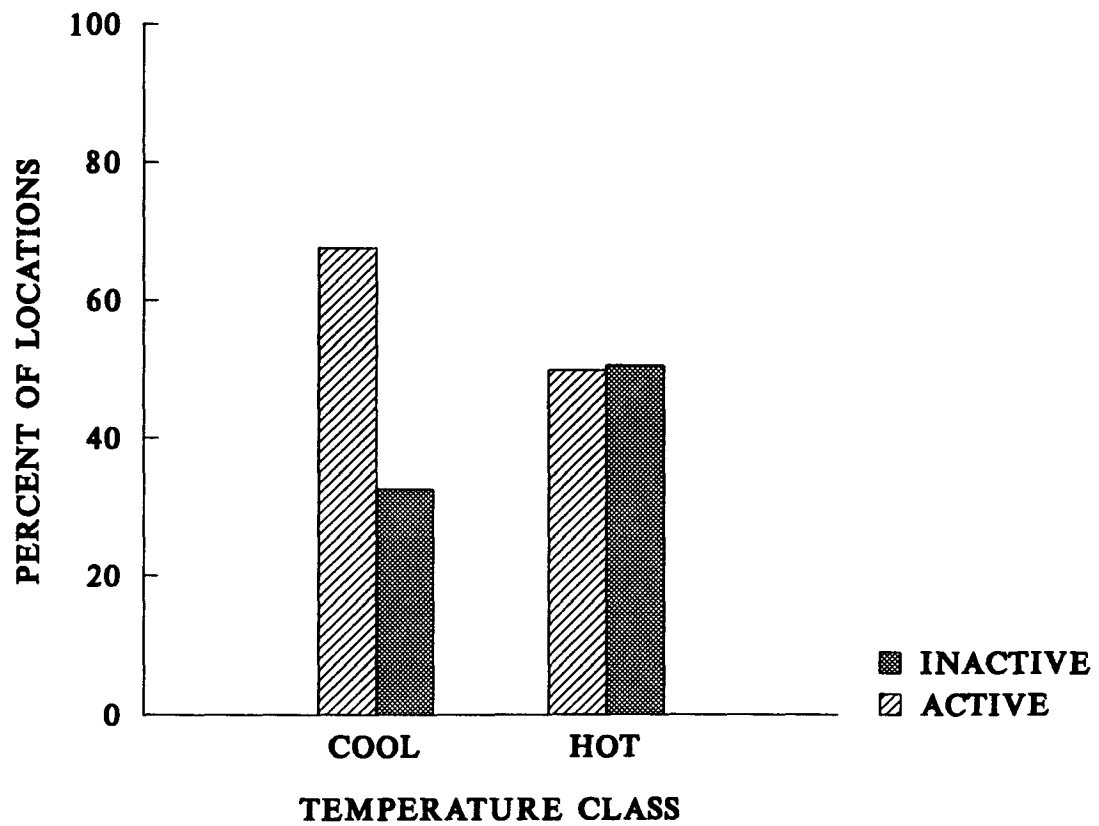
Figure 3.8. Percentage of active and inactive radio locations under Te_{open}:hot (light) (n = 155) and Te_{open}:cool (dark) (n = 77) conditions.

behaviour may reflect a predator-avoidance response. The estimated mortality rate for adult cow moose in the vicinity of the study area is extremely low (3.2%), while for calves it is quite high (49%) (Keystone Bio-Research 1991). Although predation on moose calves in the study area has not been researched, potential predators occurring there include: black bear (*Ursus americanus* Pallas) and cougar (*Felis concolor* L.). Amstrup and Beecham (1976) reported that in summer, black bear activity peaks were crepuscular and diurnal. Van Dyke et al. (1986) reported that cougars were most active at night. Assuming the risks of predation by black bear and cougar were equal, the temporal segregation of these predators might mean that moose habitat selection or activity was not constrained by predators.

Using radio telemetry, Risenhoover (1986) concluded that variations in activity levels of moose were attributable to linear travel. Distance travelled or activity levels of moose in summer have been reported to be greatest at night (Phillips et al. 1973; Joyal and Scherrer 1978), at night and early in the morning (Van Ballenberghe and Miquelle 1990), and at dawn and just after and at dusk and just after (Belovsky and Jordan 1978). Van Ballenberghe and Miquelle (1990) noted that shorter activity bouts 'appeared' to be associated with warmer temperatures at midday, however, their data were not tested. de Vos (1958) noted that although moose were not as readily observed at midday compared to morning and evening, they 'seemed' to be observed more on hot compared to cool afternoons. Despite this trend, de Vos was unable to demonstrate a correlation between air temperature and moose observability. Joyal and Scherrer (1978) reported that moose 'seemed' more active on clear [thus, likely warmer] summer days but that no significant differences between the movements on clear, cloudy or rainy days were detected. Sample sizes were not reported in any of the above papers which subjectively commented on changes in moose

activity on warmer days. Ackerman (1987) found that as black globe temperature increased, forage-bout duration decreased significantly and bedded duration increased significantly. In both instances, the reported r^2 value was less than 0.40. I believe that because the data presented by Ackerman in those analyses represented weekly averages of both independent and dependant variables, his results are inconclusive.

Published evidence conclusively demonstrating a strong effect of heat on the activity levels of moose is lacking. In this study, mean interlocation straight-line velocity (MSLV) was not correlated with Te_{open} ($r = -0.06$, $n = 205$) or hour ($r = 0.03$, $n = 205$); from Figure 3.9, however, a trend of decreasing velocity existed from 12:00 until 17:00. The curved line in Figure 3.9 demonstrates how Te_{open} changed across those hours when velocity was estimated. The trend in decreasing velocity as the duration of exposure to Te_{open} >29.5 °C increased supports the hypothesis that moose decrease travel distance (thereby potentially decreasing activity) with increasing ambient heat load. An ANOVA conducted on the mean velocities from 12:00 until 18:00 indicated a significant difference between means at $\alpha = 0.10$. Testing the means revealed that the significant result was due to the difference between values at 12:00 and 16:00.

The percentage of active locations (Fig. 3.10) appeared to mimic the pattern of mean hourly velocities (Fig. 3.9), but when the frequency distributions of active and inactive locations versus velocity interval (Fig. 3.11) were compared, no significant difference was detected (K-S test, $p > 0.05$). Because MSLV does not account for activities such as foraging in a small (e.g., <2 ha) patch, the similarity between the two activity distributions in Figure 3.11 was not unexpected.
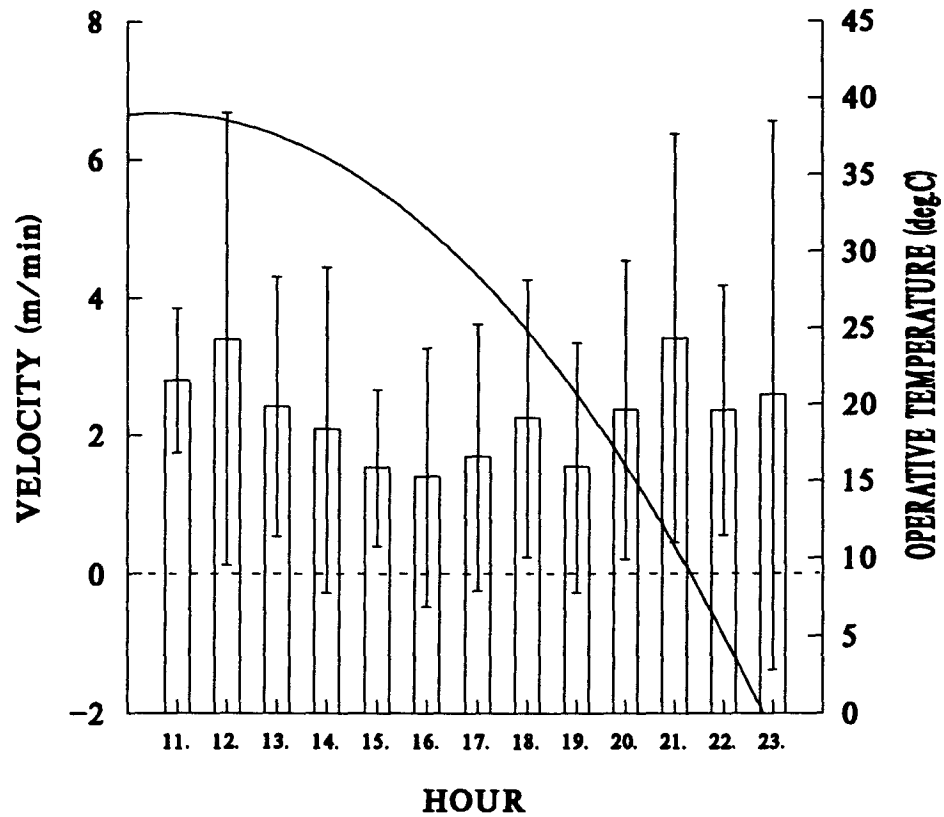
Figure 3.9. Average 'mean straight line velocity' between successive moose locations from 11:00 until 24:00. Error bars denote ±1 standard deviation (n = 209). The curved line represents the least square regression of operative temperature in open areas against hour for times when moose were located (n = 242; r^2 = 0.75; p < 0.05).
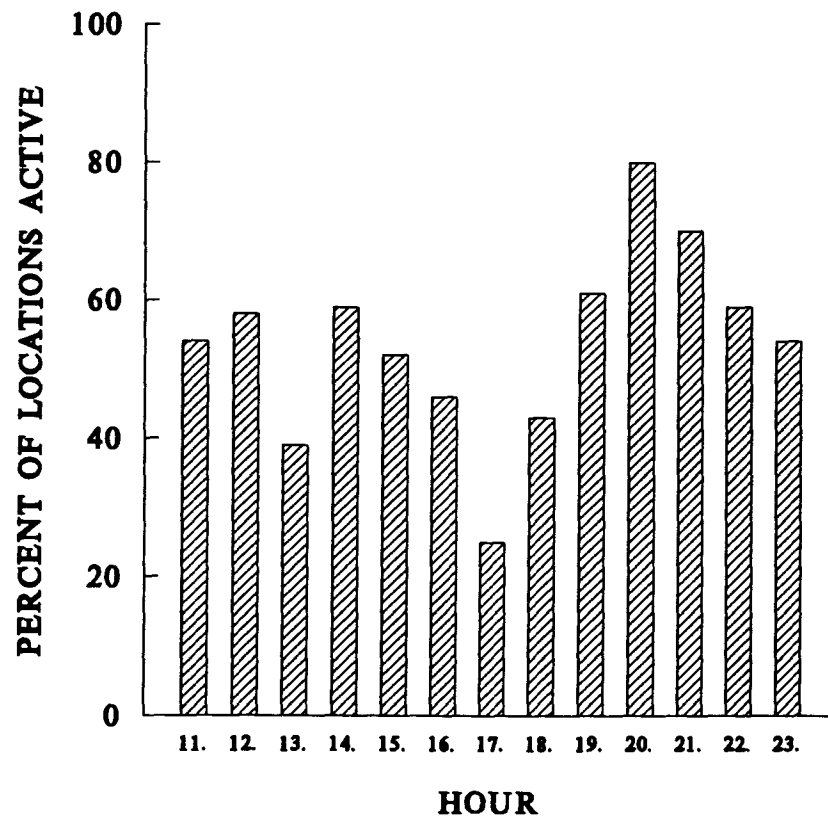
Figure 3.10. Percentage of 'active' moose locations as determined by radio telemetry, for the hours of 11:00 until 24:00. (n = 301).
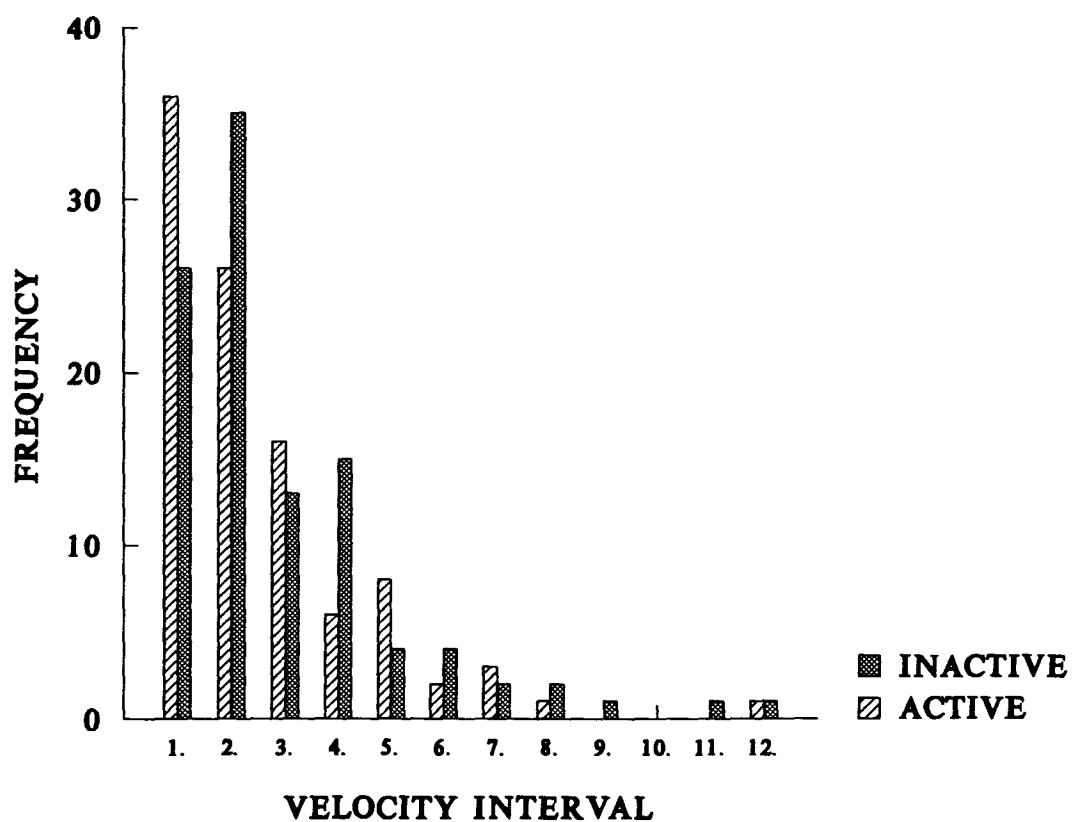
Figure 3.11. Frequency distribution of active and inactive radio locations for 12 straight-line velocity intervals. Each velocity interval corresponds to a range of 1 m·min⁻¹ (e.g., velocity interval 1 = 0.00 to 0.99 m·min⁻¹, 2 = 1.00 to 1.99 m·min⁻¹, etc.).

The effect of the thermal environment on moose activity was analyzed in the context of Te_{open}. Therefore, use of stands providing thermal cover may have allowed for increased activity when activity was thermally constrained on $CCC = 0$ sites. However, without knowledge of habitat-specific activities (e.g., foraging, bedding, travel) any explanation of observed differences between the activity levels of hot/cool conditions would be highly speculative; potentially arguing for or against thermal constraints on activity. A negative correlation between percent of locations active and mean hourly Te_{open} ($r = -0.47$, $n = 13$) indicated a trend of decreasing activity with increasing Te_{open}. This observation also favours the view that moose were responding to heat and not predators, because for most of the summer, 'light' conditions existed until 21:00.

The susceptibility of moose to thermal stress in the summer (Renecker and Hudson 1986), the influence of forested sites on the thermal environment (Chapter II), and the patterns of cover selection found in this study indicate that summer thermal cover for moose exists as a manageable habitat component.

CHAPTER IV: SUMMARY AND CONCLUSIONS

Four adult cow moose with radio collars were monitored on the southern Thompson Plateau during the summer of 1990. The opportunity to sample moose activity and habitat selection at times when moose could have been thermally stressed was realized. The relation between mean crown completeness (MCC) and crown closure class (CCC) indicated that CCC values from the forest cover map correctly ranked stands by crown cover. The exponential decline in Te across CCCs showed that a definite gradient of thermal cover existed. The strong effect of forest canopy on solar radiation attenuation indicated that greater than CCC = 4 (corresponding to MCC >40%), little thermal cover value was gained. The effect of wind on the operative temperature (Te) of habitats appeared to be minimal under the observed weather conditions. Neither the effects of uneven air temperatures across CCCs nor a nonrandom distribution of foliar elements are believed capable of changing the thermal cover regime across CCCs such that hypothesis testing for the existence of thermally-correlated moose habitat selection would be hampered.

With respect to forest crown closure, the relative abundance of habitats within telemetry range of roads was the same as that of the entire study area. This finding implied that the opportunity to sample moose locations in the various crown closure classes (CCC) was not determined by vehicle access. 'Hot' conditions were defined as those which exceeded the upper critical temperature (UCT) of moose in summer. 'Cool' conditions were below UCT. Because the opportunity to sample under 'cool', 'light' conditions was restricted, it was not possible to directly partition the effects of heat and light on moose habitat selection and activity. These effects were indirectly assessed by examining changes in cover selection and activity patterns across a 13 hour period.

Cow moose selected different habitats between 'hot' and 'cool' (thus 'light' and 'dark') conditions. CCC = 6 was the most frequently selected coniferous cover. Use of CCC = 6 stands was greatest when Te_{open} exceeded UCT. When compared to CCC = 0 sites (assuming no water or deciduous canopy cover), the thermal cover value of CCC = 6 sites increased exponentially with air temperature. Overall use of CCC = 0 sites was not restricted when ambient conditions exceeded UCT. Because of the water and shade from willow trees associated with some CCC = 0 sites, the ability of such sites to mitigate heat-stress could not be discounted. Prolonged periods of hot conditions in the open (Te_{open}:hot) appeared to affect cover selection. As Te_{open} declined, relative use of CCC = 0 sites during 'light' hours increased. By seeking thermal cover when the rate of heat build-up on CCC = 0 sites was greatest and not after they became thermally stressed, moose may have been able to increase total daily use of open (foraging) habitats. Belovsky (1981) reported that observed use of [summer thermal] cover by moose agreed with the predictions of an 'optimization' model. One of the constraints in Belovsky's model was an upper limit to body temperature. Putman (1988) identified predators and weather as factors which can influence habitat use by cervids at an intra-seasonal level. Because the pattern of habitat use from 11:00 until 21:00 changed despite continued 'light' conditions, and assuming the diel risk of predation was constant, habitat selection by moose appeared to be thermally constrained. The cover of successive moose locations was influenced by the Te and cover of previous locations when patterns of cover selection between 'hot' and 'cool' conditions were analyzed separately. When Te_{open} was 'hot', moose under coniferous cover tended to remain under such cover. The least common pattern under Te_{open}:hot conditions was 'cover to open'.

Likely because of habitat interspersion in the study area, the moose location attributes of distance to an edge and distance to water were not correlated with time of day or Te in the open (Te_{open}). The lack of a correlation between location distance to a road and time of day may have been a result of moose habituation to vehicles.

Moose activity was greater under 'cool' (thus 'dark') than 'hot' (thus 'light') conditions. The mean straight line velocity (MSLV) between successive moose locations did not differ from 11:00 until 24:00. MSLV was not correlated with Te_{open}. A decrease in MSLV from 12:00 until 17:00 corresponded to a sustained period of exposure to Te_{open} >UCT. This observation implies that moose may have reduced movement with increased exposure to hot environments. Activity did not increase with increased MSLV, but did increase as mean hourly Te_{open} values decreased from 11:00 until 24:00. In addition to selecting thermal cover, reduced activity at high Te_{open} values could eliminate the need to thermoregulate, or minimize the metabolic costs of thermoregulation.

Research on moose physiology suggests that moose require summer thermal cover regardless of forage abundance (i.e., Renecker 1987). The results of this study indicate that moose select summer thermal cover and that this cover can be quantified. The primary management implication is that for moose in this area, managing summer thermal cover at the level of forest cover polygons appears warranted. It is my opinion that if security cover needs are met and riparian sites are adequately fringed with coniferous stands of CCC ≥4, the thermal cover requirement of moose on summer range will be met.

LITERATURE CITED

Ackerman, T.N. 1987. Moose response to summer heat on Isle Royale. M.S. Thesis. Michigan Technological Univ., Houghton, MI. 53 pp.

Alldredge, J.R. and J.T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 50:157-165.

Amstrup, S.C. and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. J. Wildl. Manage. 40:340-348.

Bakken, G.S. 1980. The use of standard operative temperature in the study of the thermal energetics of birds. Physiol. Zool. 53:108-119.

Belovsky, G.E. 1981. Optimal activity times and habitat choice of moose. Oecologia (48):22-30.

Belovsky, G.E. and P.A. Jordan. 1978. The time-energy budget of a moose. Theor. Pop. Biol. 14:76-104.

Black, H., R. Scherzinger, and J.W. Thomas. 1976. Relationships of Rocky Mountain elk and Rocky Mountain mule deer habitat to timber management in the Blue Mountains of Oregon and Washington. p. 11-31 In: S.R. Heib (ed.), Proceedings of the elk-logging-roads symposium. Idaho. 142 pp.

Black, T.A., J.M. Chen, X. Lee, and R.M. Sagar. 1991. Characteristics of shortwave and longwave irradiances under a Douglas-fir forest stand. Can. J. For. Res. 21:1020-1028.

Bligh, J. and K.G. Johnson. 1973. Glossary of terms for thermal physiology. J. Appl. Physiol. 35:941-961.

Bonnor, G.M. 1967. Estimation of ground canopy density from ground measurements. J. For. 65:544-547.

British Columbia Ministry of Environment. 1988. Ecoregions of British Columbia, map.

British Columbia Ministry of Forests. 1988. Biogeoclimatic Zones of British Columbia, map.

Bunnell, F.L. and D.J. Vales. 1989. Comparison of methods for estimating forest overstory cover: differences among techniques. Can. J. For. Res. 20:101-107.

Bunnell, F.L., K.L. Parker, L.L. Kremsater and F.W. Hovey. 1985. Thermoregulation and thermal cover of deer and elk on Vancouver Island: problem analysis. Research, B.C. Ministry of Environment and Parks and B.C. Ministry of Forests and Lands. IWIFR-28. Victoria, B.C. 137 pp.

Campbell, G.S. 1977. An Introduction to Environmental Biophysics. Springer, New York. 159 pp.

Chen, J.M., T.A. Black and R.S. Adams. 1991. Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. Agric. For. Meteorol. 56:129-143.

de Vos, A. 1958. Summer observations on moose behaviour in Ontario. J. Mamm. 39:128-139.

Demarchi, M.W. 1990. Daily summer movements of moose in the southern interior of British Columbia. Unpublished. B.C. Ministry of Transportation and Highways report. 36 pp.

Eason, G. 1985. Overharvest and recovery of moose in a recently logged area. Alces 21:55-75.

Eastman, D.S. and R. Ritcey. 1987. Moose habitat relationships and management in British Columbia. Swedish Wildl. Res. Suppl. 1:101-117.

Edgerton, P.J. and B.R. McConnell. 1976. Diurnal temperature regimes of logged and unlogged mixed conifer stands on elk summer range. USDA For. Res. Note. PNW-277. 6 pp.

Erbs, D.G., S.A. Klein, and J.A. Duffie. 1982. Estimation of the diffuse radiation fraction for hourly, daily and monthly-average global radiation. Solar Energy, 28:293-302.

Esmay, M.L. 1969. Principles of Animal Environment. AVI Publishing Inc., CT. 325 pp.

Gates, D.M. 1980. Biophysical Ecology. Springer-Verlag, New York. 611 pp.

Geiger, R. 1965. The Climate Near the Ground. Harvard Univ. Press, Massachusetts. 611 pp.

Harcombe, A.P. 1984. Wildlife habitat handbooks for British Columbia: problem analysis. British Columbia Ministry of Environment, Kamloops. 236 pp.

Hess, A.D. and J.H. Rainwater. 1939. A method for measuring the food preference of trout. Copeia 3:154-157.

Hicks C.R. 1982. Fundamental Concepts in the Design of Experiments. Holt, Rinehart and Winston. 425 pp.

Jemison, G.M. 1934. The significance of the effect of stand density upon the weather beneath the canopy. J. For. 32:446-451.

Johnson D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Joyal R. and B. Scherrer. 1978. Summer movements and feeding by moose in western Quebec. Can. Field-Nat. 92:252-258.

Kelliher, F.M. 1985. Salal understory removal effects on the soil water regime and tree transpiration rates in a Douglas-fir forest. Ph.D. thesis. University of British Columbia. 123 pp.

Kelsall J. and E. Telfer. 1974 Biogeography of moose with particular reference to western North America. Nat. Can. 101:117-130.

Keystone Bio-Research. 1991. Environmental assessment of the Okanagan Connector Freeway. Unpublished. British Columbia Ministry of Transportation and Highways and British Columbia Ministry of Environment report. 220 pp.

Kimmins, J.P. 1987. Forest Ecology. Macmillian Publishing Co., New York, NY. 529 pp.

Lloyd, D., K. Angrove, G. Hope and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. B.C. Ministry of Forests, Land Management Handbook No. 23. 398 pp.

Lyon, L.J. 1979. Influences of logging and weather on elk distribution in western Montana. USDA For. Serv. Res. Paper INT-236. 11 pp.

Mautz, W.W. 1978. Nutrition and carrying capacity. p. 321-348. In: J.L. Schmidt and D.L Gilbert (eds.) Big Game of North America: Ecology and Management. Stackpole Books, PN. 494 pp.

McCorquodale, S.M., K.J. Radeke, and R.D. Taber. 1986. Elk habitat use patterns in the shrub-steppe of Washington. J. Wildl. Manage. 50:664-669.

Merrill, E.H. 1991. Thermal constraints on use of cover types and activity time of elk. Behav. Sci. 29:251-267.

Mitchell, R. and R. Greene. 1981 Identification and interpretation of ecosystems of the Western Kamloops Forest Region. First Approximation. B.C. Ministry of Forests, Land Management Handbook No. 2.

Monteith, J.L. 1973. Principles of Environmental Physics. American Elsevier, New York, NY. 209 pp.

Neu, C.W., C.R. Byers, J.M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. Agric. Meteorol. 8:25-38.

Norman, J.M. and G.S. Campbell. 1989. Canopy structure. p. 300-325 In: R.W. Pearcy, J. Ehlinger, H.A. Mooney and P.W. Rundel (eds.), Plant Physiological Ecology: Field Methods and Instrumentation.

Nyberg, J.B. and D.W. Janz (tech. eds.). 1990. Deer and elk habitats in coastal forests of Southern B.C. B.C. Ministry of Forests. 310 pp.

Paldridge, G.W. and C.M.R. Platt. 1976. Radiative Processes in Meteorology and Climatology. Elsevier Scientific Publishing Co., New York. 318 pp.

Parker, K.L. 1987. Body-surface measurements of mule deer and elk. J. Wildl. Manage. 51:630-633.

Parker K.L. and C.T. Robbins. 1983. Thermoregulation in mule deer and elk. Can. J. Zool. 62:1409-1422.

Parker, K.L. and M.P. Gillingham. 1990. Estimates of critical environments for mule deer. J. Range Manage. 43:73-81.

Pederson, R.J., A.W. Adams and J.M. Skovlin. 1980. Elk habitat in an unlogged and logged forest environment. Oregon Dept. of Fish and Wildl., Wildl. Res. Rep. No. 9. 121 pp.

Peek, J.M, D.J. Pierce, D.C. Graham and D.L. Davis. 1987. Moose habitat use and implications for forest management in northcentral Idaho. Swedish Wildl. Res. Suppl. 1:195-199.

Peek, J.M., M.D. Scott, L.J. Nelson, D.J. Pierce and L.L. Irwin. 1982. Role of cover in habitat management for big game in northwestern United States. Trans. N. Amer. Wildl. Conf. 47:363-373.

Peters, R.H. 1983. The Ecological Implications of Body Size. Cambridge Univ. Press, New York. 329 pp.

Phillips, R.L., W.E. Berg and D.B. Siniff. 1973. Moose movement patterns and range use in Northwestern Minnesota. J. Wildl. Manage. 37:266-278.

Putman, R. 1988. The Natural History of Deer. Comstock Publishing Associates, New York. 191 pp.

Reifsnyder, W.E. 1967. Radiation geometry in the measurement and interpretation of the radiation balance. Agric. Meteorol. 4:255-265.

Renecker, L.A. 1987. Bioenergetics and behaviour of moose (*Alces alces*) in the aspen-dominated boreal forest. Ph.D. Thesis, University of Alberta. 265 pp.

Renecker L.A. and R.J. Hudson 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Can. J. Zool. 64:322-327.

Risenhoover, K.L. 1986. Winter activity patterns of moose in interior Alaska. J. Wildl. Manage. 50:727-734.

Ritcey, R., D. Lowe, A. Harestad, R.W. Campbell and A.P. Harcombe. 1988. Species habitat relationship models for mammals. Vol 5 In: A.P. Harcombe (tech. ed.), Wildlife habitat handbooks for the Southern Interior Ecoprovince. British Columbia Ministry of Environment and B.C. Ministry of Forests, Victoria. 252 pp.

Robinson, M.W. 1947. An instrument to measure forest crown cover. For. Chron. 23:222-225.

Ross, J. 1981. The Radiation Regime and Architecture of Plant Stands. Dr. W. Junk Publishers, London. 391 pp.

Sainsbury, D. 1967. Animal Health and Housing. Williams and Wilkins Co. Baltimore. 329 pp.

Schwab, F.E. 1986. Moose habitat selection in relation to forest cutting practices in northcentral B.C. Ph.D. Thesis. Univ. of British Columbia, Vancouver. 176 pp.

Singleton, J.M. 1976. Food habits of wild ungulates in British Columbia: Bibliography and plant synopsis. B.C. Fish and Wildife Branch. 51 pp.

Smith, F.W. and J.N. Long. 1987. Elk hiding and thermal cover guidelines in the context of lodgepole pine stand density. West. J. Appl. For. 2:6-10.

Sokolov, V.E. and O.F. Chernova. 1987. Morphology of the skin of moose (*Alces alces*). Swed. Wildl. Res. Suppl. 1:367-375.

Springer, J.T. 1979. Some sources of bias and sampling error in radio triangulation. J. Wildl. Manage. 43:926-935.

Spurr, S.H. 1957. Local climate in the Harvard Forest. Ecology 38:37-46.

Swinbank, W.C. 1963. Longwave radiation from clear skies. Quart. J. Roy. Met. Soc. 89:339-348.

Thomas, J.W., J. Black, Jr., R.J Scherzinger and R.J Pedersen. 1979. Deer and elk. p.104-127 In: J.W. Thomas (ed.), Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington. USDA For. Serv., Agr. Handbook 533. WA. 512 pp.

Timmerman, H.R. and J.G. McNicol. 1988. Moose habitat needs. For. Chron. 64:238-245.

Vales, D.J. 1986. Functional relationships between salal understory and forest overstory. Research, British Columbia Ministry of Environment and Parks and B.C. Ministry of Forests and Lands. IWIFR-32, Victoria. 121 pp.

Van Ballenberghe, V. and D.G. Miquelle. 1990. Activity of moose during spring and summer in interior Alaska. J. Wildl. Manage. 54:391-396.

Van Dyke, F.G., R.H. Brocke, H.G. Shaw, B.B. Ackerman, T.P. Hemcker and F.G. Lindzey. 1986. Reactions of mountain lions to logging and human activity. J. Wildl. Manage. 50:95-102.

Wilkinson, L. 1990. SYSTAT: the system for statistics. Systat Inc. Evanston, IL. 677 pp.

Young, V.A. and W.L. Robinette. 1939. A study of the range habits of elk on the Selway Game Preserve. Univ. of Idaho Bull. No. 16, Moscow. 47 pp.

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APPENDIX I
OPERATIVE TEMPERATURE SIMULATION MODEL

Simulation model inputs from canopy data:

Sky view factor (SVF):
$$SVF = 1/((1.03 \cdot CCC)+1)$$
where:

        CCC = crown closure class from the forest cover map

Effective leaf area index (Le):
$$Le = \log_{10}(SVF)/-0.324$$

Calculation of diffuse (S_d) and direct (S_b) components of total global radiation (S_t):

Convert total global flux density (W·m^{-2}) to total hourly flux (MJ·m^{-2}) ($S_t = S_t \cdot 0.0036$)

I_o = total hourly extraterrestrial radiation of a horizontal surface (Erbs et al. 1982)
$$= (24/(2\pi)) \cdot 1.360 \cdot 3.6 \cdot (\cos(lat)\cos(\delta)(\sin(0.26179)-$$
$$\sin(0))+(2\pi/360) \cdot 15 \cdot \sin(lat)\sin(\delta))$$
where:

        lat = latitude in radians

        δ = solar declination
$$= 0.006918-0.399912 \cdot \cos(\phi)+0.070257 \cdot \sin(\phi)-0.006758 \cdot \cos(2\phi)+$$
$$0.000907 \cdot \sin(2\phi)-0.002697 \cdot \cos(3\phi)+ 0.00148 \cdot \sin(3\phi)$$

        where:

            $\phi = 2\pi Ju/365$

            where:

                Ju = Julian day

determine ratio (K_t) of global flux (S_t) to extraterrestrial flux on a horizontal surface (I_o):

$K_t = S_t/I_o$ (Erbs et al. 1982)

if $K_t \leq 0.22$ then $S_d = (1-0.09 \cdot K_t) \cdot S_t$

if $K_t > 0.22$ and ≤ 0.8 then $S_d = (0.9511 - 0.1604 \cdot K_t + 4.388 \cdot K_t^2 - 16.638 \cdot K_t^3 + 12.336 \cdot K_t^4) \cdot S_t$

if $K_t > 0.8$ then $S_d = 0.165 \cdot S_t$

convert S_d back to hourly flux density (W·m^{-2}) ($S_d = S_d/0.0036$)

convert S_t back to hourly flux density (W·m^{-2}) ($S_t = S_t/0.0036$)

determine direct radiation (S_b):

$S_b = S_t - S_d$

determine direct radiation beneath canopy (S_{bu}):

$S_{bu} = S_b \cdot e^{(-G \cdot Le/cos(\theta))}$ (Nilson 1971, Black et al. 1991)

where:

    e = base of the natural logarithm

    G = angle-dependant extinction coefficient per unit foliage area measured in the direction of the solar beam (0.5 for randomly distributed foliar elements; Ross 1981)

    θ = solar incident angle with respect to the normal to the slope (= the solar zenith angle (Z given below) when slope=0)

determine diffuse radiation beneath the canopy (S_{du}):

$S_{du} = S_d \cdot e^{(-G \cdot Le)}$ (Black et al. 1991)

Calculation of Operative Temperature (Te) (Campbell 1977):

$Te = Tam + (r_e \cdot (R_{abs} - \varepsilon_s \sigma Ta^4))/\rho c_p$

where:

    Te = operative temperature (°C)

    Tam = air temperature (°C)

    Ta = air temperature (°K)

    r_e = parallel equivalent resistance to convective and radiative heat transfer (s·m^{-1})

    R_{abs} = radiation absorbed by animal surface (W·m^{-2})

    σ = Stefan-Boltzman constant (5.67·10^{-8} W·m^{-2}·°K^{-4})

    ρc_p = density of air (ρ) · specific heat (c_p) (1200 J·m^{-3}·°K^{-1}; Campbell 1977)

Thermal resistance between animal's outer surface and environment (r_e):

$1/r_e = 1/R_{ha} + 1/R_r$

where:

R_r = resistance to longwave radiation transfer

$= \rho c_p/(4\varepsilon_s \sigma Ta^3)$

where:

ε_s = emissivity of animal surface (1.0 for caribou; Monteith 1973)

R_{ha} = conditional resistance to convection:

if $Gr \cdot Re^2 < 1$ then $R_{ha} = 307 \cdot (d/U)^{0.5}$ (forced convection dominant; Campbell 1977)

if $Gr \cdot Re^2 \geq 1$ then $R_{ha} = 840 \cdot (d/(T_{sk}-Tam))^{0.25}$ (free convection dominant; Campbell 1977)

where:

d = characteristic dimension (1.02 for a 350kg moose; adapted from Parker 1987)

U = windspeed (m·s^{-1})

Re = Reynolds number

$= (U \cdot d) \cdot \upsilon^{-1}$

Gr = Grashof number

$= agd^3 \cdot (T_{sk}-T_{am}) \cdot \upsilon^2$

where:

a = coeffecient of thermal expansion of fluid (1/273 for air; Campbell 1977)

g = accelleration due to gravity (9.8m·s^{-2})

T_{sk} = Temperature of skin (0C)

$= (34.688 \cdot e^{(0.0033 \cdot Tam)}$ (Renecker and Hudson 1986)

υ = kinematic viscosity of air

$= 1.151 \cdot 10^{-5}$ m·s^{-1} at standard temperature and pressure

Calculate longwave radiation under the canopy:

sky-longwave radiation beneath canopy (L_s):

$$L_s = SVF \cdot L_{sky}$$

where:

L_{sky} = sky longwave radiation

= $(R \cdot c\varepsilon_a + (1-Rc))\sigma Ta^4$ (Swinbank 1963)

where:

ε_a = sky emissivity (=0.674+0.007·(Ta); Gates 1980)

Rc = ratio of observed 'total global solar radiation' to potential clear sky global radiation

= S_t / S_{go}

where:

S_t = global irradiance measured by the pyranometer ($W \cdot m^{-2}$)

S_{go} = clear sky global irradiance

= $S_0 \cos(Z)(0.271+0.706 \cdot \tau^{(1/\cos(Z))})$ (Gates 1980)

where:

S_0 = solar constant (1360 $W \cdot m^{-2}$)

τ = atmospheric transmissivity (0.78 in this study)

Z = solar zenith angle

= $\cos^{-1}(\sin(\delta)\sin(lat)+\cos(\delta)\cos(lat) \cos(TLA-13) \cdot 2 \cdot \pi/360)$

where:

TLA = local apparent time

= Td+LONGEQ+EQ (Paldridge and Platt 1976)

where:

Td = 24 hour time of day

LONGEQ = standard longitude correction (0 in this study)

EQ = equation of time

= $0.000075+0.001868 \cdot \cos(\phi)-0.032077 \cdot \sin(\phi)-0.014615 \cdot \cos(2\phi)-0.040849 \cdot \sin(2\phi)$

longwave radiation from plant canopy $(1\text{-SVF}) \cdot L_p$

where:

L_p = conditional function of Le

if Le >2 then $L_p = \varepsilon_{ca} \sigma T_{ca}{}^4$
where:

ε_{ca} = emissivity of canopy (0.97; Black et al. 1991)
T_{ca} = temperature of canopy (assumed to equal T_a: Tan et al.
1978)

if Le ≤ 2 then $L_p = ((\varepsilon_{ca} \sigma T_{ca}{}^4) + ((1 - \varepsilon_{ca}) \cdot ((\varepsilon_{gr} \sigma T_{gr}{}^4) + ((1 - \varepsilon_{gr}) \cdot (\text{SVF} \cdot L_{sky}))))) / (1 - ((1 - \varepsilon_{ca}) \cdot (1 - \varepsilon_{gr}) \cdot (1 - \text{SVF})))$

where:

ε_{gr} = emissivity of the ground
= 0.97 (Parker unpubl. cited in Parker and Gillingham
1990)
T_{gr} = temperature of the ground (approximated by Ta; Black
et al. 1991)

longwave radiation from the ground (L_g):

$L_g = \varepsilon_{gr} \sigma T_{gr}{}^4$

Calculate radiation absorbed by animal (R_{abs}):

$R_{abs} = \text{SW} + (.5 \cdot L_g) + (.5 \cdot L_s) + (.5 \cdot (1 - \text{SVF}) \cdot L_p)$
where:

coefficients of 0.5 denote proportion of animal's surface area exposed to
each type of longwave radiation

SW = amount of shortwave radiation absorbed
= $a_s (\text{Ap}/A \cdot S_{bu} / \cos(\theta) + 0.5 \cdot S_{du} + 0.5 \cdot \text{SWGR}$
where:

coefficients of 0.5 denote proportion of animal's surface area
exposed to each type of shortwave radiation
a_s = absorptivity to shortwave radiation (0.75; taken as the mean of the
seasonal values for mule deer (0.7, 0.8) given by W.P.
Porter in Parker and Gillingham 1990)
Ap/A = ratio area on a surface perpendicular to the solar beam to total
surface area for a shape simulating an ungulate (0.3;
Campbell 1977)

$S_{bu}/\cos(\theta)$ = amount of direct radiation beneath the canopy on a surface
perpendicular to the beam (W·m^{-2})

SWGR = short wave radiation reflected from the ground
 = Albedo·Stu (Albedo=0.2; upper limit given for woodland by
 Geiger 1965)