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THE UNIVERSITY OF ALBERTA

Thermoregulation and Maintenance Energy Expenditures of Moose (*Alces alces*) Infested with Winter Ticks (*Dermacentor albipictus*)

by

DWIGHT AFTON WELCH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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DEPARTMENT OF ZOOLOGY

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THERMOREGULATION AND MAINTENANCE ENERGY EXPENDITURES OF MOOSE (*Alces alces*) INFESTED WITH WINTER TICKS (*Dermacentor albipictus*) submitted by DWIGHT AFTON WELCH in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

W.M. Samuel

Supervisor

Date: 26 APRIL 1988

ABSTRACT

Moose (Alces alces) infested with winter ticks (Dermacentor albipictus) suffer a profound, premature loss of winter hair. This parasite has been implicated as an important mortality factor for moose but little information is available on the mechanisms by which it might debilitate or kill moose. This study assesses the influence of tick infestations on the metabolic rates of captive moose. It also examines some of the ways that moose may counteract the negative effect of this parasite.

Infestations of 30,000 ticks on calves resulted in approximately 25% loss of hair and a slight elevation of fasting metabolic rate. Weight changes were unaffected by tick infestation.

Infestations of 50,000 ticks on yearling moose produced a 75% removal of hair but did not appear to elevate the fasting metabolic rate. Both respiration rate and respiratory minute volumes of moose suffering hair-loss were depressed. Presumably this depression resulted in a reduction in respiratory heat loss.

The major conclusions of this study are: 1) winter ticks have little effect on the energy expenditures of captive moose; and 2) moose seem to compensate for the accelerated heat loss by reducing respiratory rate and respiratory minute volume. It is probable, however, that winter ticks are an important mortality factor for moose faced with other stresses.

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CHAPTER I.

INTRODUCTION

Extensive parasite-induced alopecia has been reported for three acarine (ticks and mites) infestations of North American wildlife. Sarcoptic mange, resulting from infestations of Sarcoptes scabei is a common disease of coyotes (Canis latrans)(Pence et al. 1983), wolves (Canis lupis)(Todd et al. 1981), and foxes (Vulpes vulpes)(Prylor 1956, Stone et al. 1974). Psoroptic mange, caused by the mite Psoroptes cervinus, afflicts populations of elk (Cervus elaphus) in Wyoming (Murie 1951, Smith 1984) and Idaho (Colwell and Dunlap 1975) producing extensive alopecia. Alopecia, resulting from infestation by winter ticks (Dermacentor albipictus), is common on moose (Alces alces) (Samuel and Barker 1979, Glines 1983, Glines and Samuel 1984, Drew 1984, McLaughlin and Addison 1986), and to a lesser extent on mule deer (Odocoileus hemionus) and elk (Samuel and Welch unpubl. data).

Each of these maladies is most prevalent during some part of the winter,in Canada and the northern United States. Todd et al. (1981) suggest that the scarcity of mangy coyotes during spring and summer results from heavy overwinter attrition of severely affected individuals. Smith (1984) suggests that a similar seasonal mortality may occur in elk infested with Psoroptes cervinus. Tick-induced alopecia on free-ranging moose occurs later in winter (Glines and Samuel 1984); its chronology is determined by the life cycle of the ticks (Glines 1983, Glines and Samuel 1984, McLaughlin and Addison 1986, Drew and Samuel 1988), rather than by attrition of infested hosts.

The occurrence of acarine-induced alopecias in winter has led researchers to implicate these diseases as important mortality factors for afflicted populations. Both forms of mange have been postulated to cause mortality by denuding affected hosts during the coldest part of winter (Todd et al. 1981, Smith 1984). The loss of insulation may result in hypothermia or exhaustion of energy stores. The occurrence of mange in autumn and early winter, and the propensity for psoroptic mange to afflict weakened individuals (Smith 1984) lend support to this contention. Tick-induced alopecia is purported to inflict a similar energetic drain on moose at a critical time of year (McLaughlin and Addison 1986).

Several key differences between mange and tick-induced alopecia may lessen the impact of ticks on survival of moose in tick-enzootic areas. 1)Tick-induced alopecia is rarely extensive on free-ranging moose before March (Glines and Samuel 1984). 2)Moose and winter ticks are sympatric only over the southern, and presumably warmer, portions of moose range. Moose inhabit the forested portions of Canada and Alaska and the northern United States (Figure 1) (Peterson 1955, Kelsall and Telfer 1974, Peek 1974,

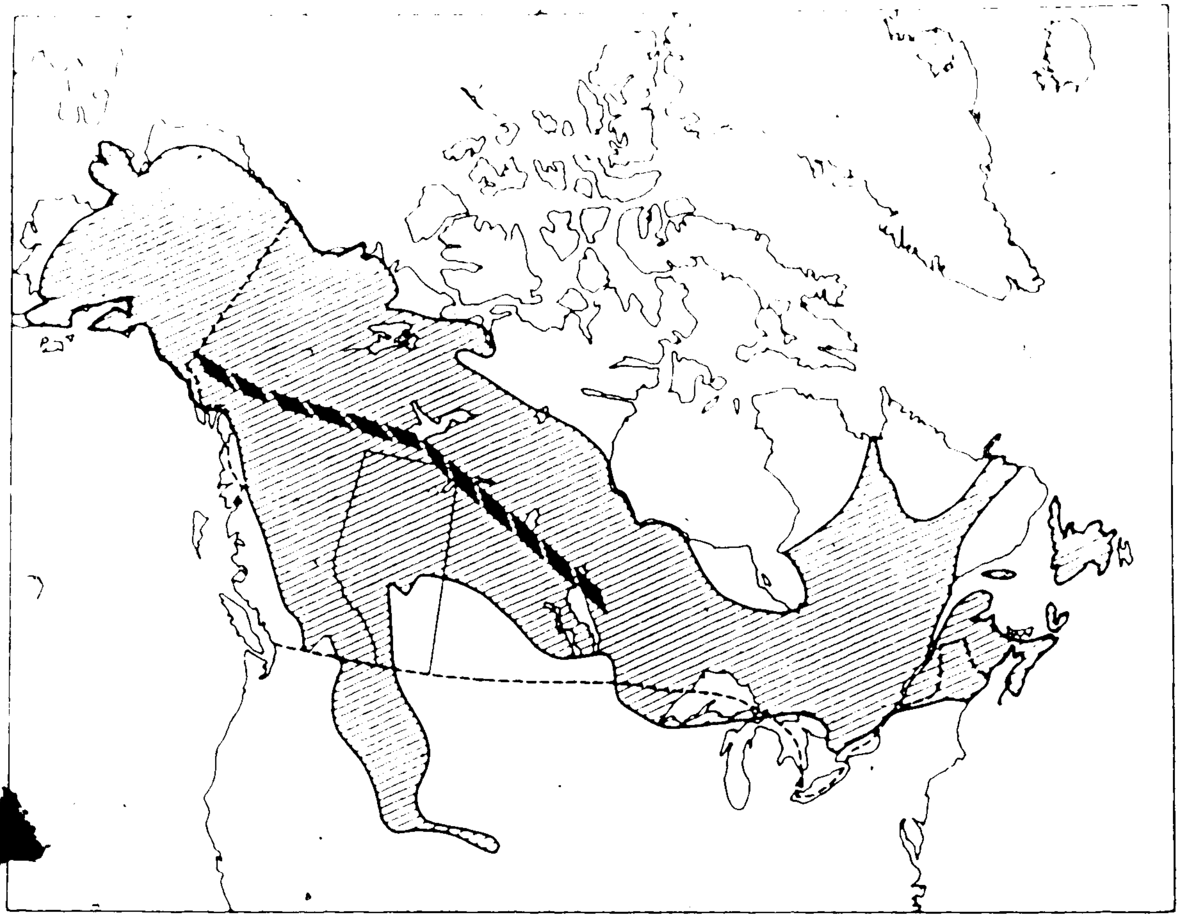

Figure 1. Proposed northern limit of *D. albipictus* in western Canada (▬) and distribution of moose (*Alces alces*) in North America (▨). Moose distribution modified from Coady (1982); tick distribution estimated from Wilkinson (1967) and Samuel (unpubl. data).

Dodds 1974). Although the northern distribution of winter ticks has not been clearly defined, *D. albipictus* has been reported rarely in Yukon or Northwest Territories and never in Alaska (Figure 1) (Wilkinson 1967, Samuel unpubl. data). The timing of the alopecia and geographic distribution of the tick minimize the likelihood of alopectic moose experiencing prolonged periods of extreme cold. 3)Moreover, moose, like most northern ungulates, possess both physiological and behavioral adaptations to lessen heat loss in extreme cold (Whittow 1971); some of these same responses might be employed to offset the effects of uncontrolled heat loss from the skin of afflicted moose. This study is the first attempt to quantify the energetic pathology of tick-induced alopecia on moose.

Life cycle and pathology

The life cycle of *D. albipictus* is unique among members of this genus in that all the parasitic life stages occur on a single host individual (Figure 2). In Alberta, engorged female ticks drop from their host in March and April, lay eggs in the leaf litter in late-May and early-June, then die (Drew and Samuel 1986, 1988). Eggs hatch in mid-August and the larvae remain dormant until early September (Drew and Samuel 1985). From late September until snowfall, larvae climb vegetation, aggregate into clumps, and attach to a passing host.

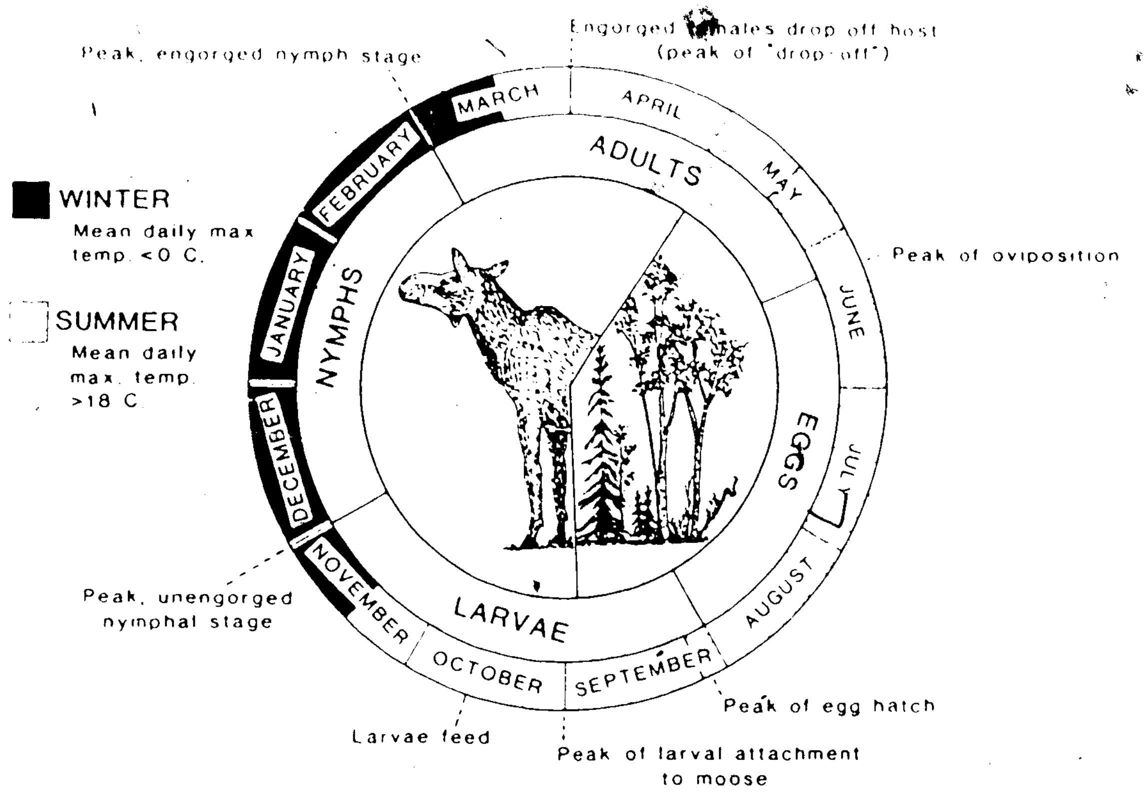

Figure 2. Life cycle of *D. albipictus* on moose in Alberta, Canada. (from Samuel 1987) No copyright involved.

Within two weeks of finding a host, larvae take a blood meal and molt into nymphs (Drew 1984, Drew and Samuel 1988). Upon becoming nymphs, ticks enter a period of relative inactivity that persists until January (Glines 1983, McLaughlin and Addison 1986, Drew and Samuel 1988). Beginning in February, nymphs take a blood meal and molt to adults. During March and April, ticks mate and the females take a large blood meal before dropping from the host (Drew and Samuel 1986, 1988).

Pathology, in the form of alopecia, is most visible on infested moose in late winter, and coincides with the engorgement of nymphs and adults (Glines 1983, McLaughlin and Addison 1986). During the engorgement of these instars, moose are restless and groom intensively (Glines 1983). This grooming often includes fervent scratching with teeth or hooves and deliberate, prolonged rubbing of body parts on trees or, in captivity, on fences. The hair covering areas subjected to such grooming is progressively roughed, broken and, at times, completely destroyed (Glines 1983, McLaughlin and Addison 1986, Samuel et al. 1986). The extent of hair-loss can vary greatly between individual hosts infested with equal numbers of ticks (Glines 1983, McLaughlin and Addison 1986). Variation also occurs between the average extent of hair loss in geographically separated populations and between different years in the same population (Samuel unpubl. data).

Maintenance metabolism

Physiological maintenance metabolism is the minimum metabolic expenditure of an inactive animal in the absence of heat stress or cold stress (Gessaman 1973). This expenditure is necessary to maintain circulation, respiration, muscle tone and tissue replacement. For young, pregnant or lactating animals, the energetic costs of new tissue generation are essential expenditures that increase maintenance requirements. Maintenance energy requirements vary with age, size, nutritional status and season (Hudson and Christopherson 1985).

Moen (1973) suggests that the presence of parasites or diseases may alter the energetic demands of wild animals. Parasite infections often stimulate humoral and cell-mediated immune responses from their hosts (Allen 1986). The synthesis of antibodies probably consumes some energy. Blood-feeding parasites remove blood and its constituents from the host. This lost tissue must be replaced presumably at some energetic cost. Despite the potential influences of parasites on the maintenance requirements of their hosts, few studies of this interaction have been undertaken.

Thermoregulation

Heat loss and heat dissipation from endotherms are identical processes, the transference of heat from the organism to the environment. They differ only in the desirability of that transfer to the organism. At relatively cold temperatures, the transfer of heat energy to the environment is called heat loss whereas the same process at higher temperatures is called heat dissipation.

Mammals possess many mechanisms by which to regulate the rate of heat flow to the environment. These mechanisms can be divided into two general classes: passive heat transfer, those processes that require little additional energy expenditure to alter the rate of heat flow; and active heat transfer, those processes that move heat at some additional energetic cost. Although heat transfer processes probably lie along a continuum of energetic cost rather than falling into discrete classes, active and passive regulation are treated here as separate classes for simplicity.

Passive regulation of heat transfer requires minimal expenditure of energy. It is accomplished by adjusting the orientation of the pelage, the circulation of heat-laden blood, the rate of water evaporation, and the aspect of body surfaces with respect to incoming radiation.

Fur insulation is a notable component in the adaptation of mammals to climate (Scholander 1955). Resistance to heat flow is achieved by establishing a temperature gradient in the air trapped within the fur (Scholander et al. 1950). Therefore, thermal resistance increases as fur depth increases (Stevens 1972, Jacobsen 1980, Gebrehmedin 1987). Some heat is conducted to the outer surface of the hair and thereafter lost by radiation or convection (Stevens 1972, Moen 1984). Insulative value of hair decreases slightly as the density of the hair increases (Gebrehmedin 1987). More dense hair, although a slightly poorer insulator than sparse hair, has a greater resistance to disturbance by wind or rain and is less subject to compression by the weight of a bedded animal (Jacobsen 1980).

Thermal properties of pelage of white-tailed deer (Jacobsen 1980) and of reindeer (Hart 1956) differ between body regions and between seasons. Summer hair is short and sparse while winter hair is longer and dense. Pelage on the legs is shorter than on other body regions and varies little seasonally (Jacobsen 1980). Greatest fur depth, and greatest seasonal variability in depth, occur in the coat covering the trunk (Jacobsen 1980). Although few estimates of any thermal characteristics of moose hair coats have been published, similar regional and seasonal variations probably exist.

Piloerection allows mammals to vary the effective depth of their hair coat, thereby altering its insulative value. White-tailed deer, by piloerection alone, can double the depth of their pelage and, at -20°C in still air, can afford a heat savings of nearly twice the basal heat production (Stevens 1972). Piloerection is probably a graded response, allowing a range of pelage depths between some upper and lower limits. In captive cervids, this response is usually noted at around the lower critical temperature (Parker and Robbins 1984). Conversely, heat transfer through the hair coat can be enhanced by reducing the angle of individual hairs, thereby reducing the depth of the hair coat and of the layer of insulating air.

External disruption to the hair coat can markedly impair its ability to impede heat flow. Wind causes eddies within the fur, effectively reducing the depth of trapped air and increasing convective heat loss (Gebrehmedin 1987, Moen 1984, Stevens 1972). Wetting pelage reduces its thermal resistance to about one-half its dry value by accelerating transfer processes within the coat and by disrupting the physical structure of the coat (Lentz and Hart 1960, Webb and King 1984).

No data have been published on the effects of parasite-induced grooming or the resulting hair disruption and destruction on the flow of heat through affected fur. It is reasonable to assume that any parasite-induced grooming could sufficiently disrupt the structure of the pelage to reduce its insulative value. The loss of hair depth that occurs as hair shafts are broken or lost completely must decrease the pelage's ability to regulate heat flow.

Variations in the flow of heated blood to portions of the skin surface allow mammals to regulate the rate of heat loss from those regions. Reduction of blood flow to the skin results in a drop in skin temperature. This reduction of skin temperature lessens the thermal gradient between surface and environment, thereby reducing heat flow (Jacobsen 1980). Further heat savings can result from employing counter current heat exchange to rewarm blood returning from the skin to the body core (Thauer 1965).

Excess heat, generated during physical exertion or in warm surroundings, may be dissipated across the skin surface. To achieve this, large quantities of heat-laden blood are circulated immediately below the skin surface. Placing body surfaces in contact with a cool substrate can further enhance heat dissipation (Jacobsen 1980), as can exposing the radiating surfaces to cooler radiant environments (Wathen et al. 1971).

Appendages of numerous animals are especially competent sites of heat dissipation or conservation. The appendages often lack substantial insulation, possess abundant and variable vascularization (Wathen et al. 1971, Hales 1983), and high surface:volume ratios. The ears of jackrabbits (Lepus californicus) (Wathen et al. 1971), and grey kangaroos (Macropus spp.) (Kelly and Wallis 1985) serve as heat dissipaters in warm climates. The tails of mice (Gordon 1983), rats (Rand et al. 1965), muskrats (Ondatra zibethica) (Johansen 1962), beaver (Castor canadensis) (Steen and Steen 1965), rat-kangaroos (Potorous tridactylus) (Hudson and Dawson 1975), coypu (Myocastor coypus) and tamar-wallaby (Macropus eugenii) (Krattenmacher and Rubsamen 1987) also serve as labile avenues of heat exchange. The legs of white-tailed deer (Jacobsen 1980), and reindeer (Rangifer tarandus)(Segal 1980) possess a similar ability to modify the rate of heat loss.

Blood flow to, and heat loss from, skin on the torso may be similarly controllable. Skin temperatures well below core temperature have been reported on the torsos of moose (Renecker and Hudson 1986), white-tailed deer (Stevens 1972), mule deer and elk (Parker and Robbins 1984) subjected to cold environments. This ability to establish a thermal gradient within the skin, and possibly into the underlying tissue, increases the effective depth of normal pelage and may offer some degree of insulation in the absence of hair.

Evaporative heat loss occurs as water is vaporized from the skin or respiratory surfaces. This process dissipates 2.26 kJ with each gram of water evaporated. Evaporative losses occur at two sites; respiratory evaporation occurs along the surfaces of the nose, mouth, trachea and lungs, whereas cutaneous evaporation occurs over all or part of the skin.

Cutaneous evaporation or sweating is an increasingly important avenue of heat loss as body size increases (Taylor and Rowntree 1974, Parker and Robbins 1985). Cutaneous evaporation by elk in summer coat could potentially dissipate heat at a rate of 209% of metabolic heat production while mule deer may shed only 17% of metabolic heat production by that means under similar conditions

(Parker and Robbins 1984). The rate of cutaneous evaporation can be impeded by thick pelage (MacLean 1963). However, discharge of cutaneous water may enhance heat transfer through pelage as does external wetting.

Cutaneous water loss varies seasonally. Cutaneous evaporation by mule deer and elk in summer increases with increasing ambient temperature but is negligible in winter even at similar skin temperature (Parker and Robbins 1984).

Respiratory evaporative heat loss can be minimized by reducing the temperature of expired air (Jackson and Schmidt-Neilson 1964). Cooling of expired air results in condensation of moisture from respiratory air onto the mucosa of the upper respiratory tract (Blix et al. 1983). This condensation returns to the nasal tissue 2.26 kJ of heat for each gram of condensed water. This cooling is accomplished by protracting exhalation (Hammel et al. 1962) and by a counter current vascular arrangement in the upper respiratory track (Blix et al. 1983, Johansen et al. 1985).

Respiratory evaporation can be maximized during exertion or in hot surroundings by allowing respired air to leave the body at about body temperature. The saturation of air as it passes through the respiratory system results in the dissipation of heat energy. Expired air temperatures approaching body temperature have been reported from reindeer (Hammel et al. 1962, Blix et al. 1982), mule deer and elk (Parker and Robbins 1984) and numerous African ungulates (see review of Parker and

Robbins 1985). Because passive forms of heat transfer are energetically inexpensive, animals employ them whenever possible to maintain a desirable rate of heat transfer to the environment. Over some range of environmental conditions, passive regulatory adjustments of heat flow are adequate to maintain a constant body temperature. Over this range of temperatures, there is little temperature-dependent increment of energy expenditure producing a "zone of least thermoregulatory effort" (Gebrehmedin 1987), classically known as the thermoneutral zone.

Below the range of the thermoneutral zone, heat flow from the body has been minimized but still exceeds the minimum rate of metabolic heat production. To maintain a constant body temperature, energy must be expended to produce sufficient heat to compensate for the undesirable heat loss. As ambient temperature continues to fall, the energetic cost of thermogenesis rises.

When heat load exceeds the rate at which heat can be dissipated by passive means, a mammal must expend energy on active heat dissipation or allow the body temperature to rise. Numerous large ungulates allow their body temperatures to rise during heat stress but all must maintain the brain at a constant temperature. This is accomplished by cooling blood in the nasal sinus and immediately circulating it to the brain (Taylor and Rowntree 1972).

Active heat loss usually involves muscular activity and is most commonly seen as panting. The respiration rate of most ungulates rises as ambient temperature rises above some critical temperature. This critical temperature differs between species, seasons, and body sizes. While ambient temperature remains below body temperature, elevated respiration allows greater direct heat loss through warming of expired air. Meanwhile, the opportunities for evaporative heat loss from the surfaces of the respiratory tract are enhanced by the increased volume of passing air (Albers 1977).

Elevated ventilation rates result from increased activity of respiratory muscles, primarily the diaphragm and intercostal muscles. This increased muscular activity generates more heat that the body must dissipate. However, this inefficiency may be offset by the elasticity of the rib cage. The the elastic properties of the rib cage afford it a resonant frequency at which, the muscular work of panting is reduced (Crawford 1962). Northern ungulates in prime winter coat are faced with extreme variation in their need to conserve or dissipate heat. During periods of extreme cold or wind and minimal activity, heat loss must be minimized. Conversely, during exertion, as occurs when fleeing from a predator, great quantities of metabolic heat must be dissipated. This variety of thermal regimes has led to the evolution of highly labile mechanisms to regulate heat transfer to the environment.

Objectives and hypotheses

This study attempts to assess the impact of winter tick infestations on some energy transactions of experimentally-infested, captive moose. It is restricted to assessment of energy expenditure on maintenance and thermoregulation. Although the other pathways may be affected by tick infestation, they remain to be studied. The project addresses four major objectives:

1. To experimentally demonstrate and assess the impact of _D_. _albipictus_ on the Fasted Metabolic Rate (FMR) of moose.
2. To assess the impact of tick-induced alopecia on the thermoregulatory energy expenditures of moose.
3. To assess the extent to which moose adjust respiratory heat exchange to compensate for premature, tick-induced loss of insulation.
4. To assess the impact of tick infestation on the winter weight dynamics of captive moose.

The following hypotheses will be tested:

H1. Fasting metabolic rates of infested moose are equal to those of uninfested moose.

H1a Fasting metabolic rates of infested moose differ from those of uninfested moose.

Prediction: Minimum metabolic rates of moose may be elevated by the activity of the immune system and by the replacement of lost blood and damaged tissue.

H2. Metabolic rates of infested and uninfested moose exhibit the same response to ambient temperatures outside the thermoneutral zone.

H2a Metabolic rates of infested and uninfested moose exhibit different responses to ambient temperatures outside the thermoneutral zone.

Prediction: The loss of surface insulation should shift the thermoneutral zone upwards resulting in depressed metabolic rates of infested moose at temperature above the thermoneutral zone and higher metabolic rates of infested moose below the lower critical temperature

H3. Respiratory minute volumes of infested, alopectic moose and of uninfested moose exhibit the same response to ambient temperatures.

H3a Respiratory minute volumes of infested, alopectic moose and of uninfested moose exhibit different responses to ambient temperatures.

Prediction: As hair loss proceeds, infested moose may attempt to offset increased heat loss from the skin by reducing respiratory minute volume, thereby reducing respiratory heat loss.

H4. Mean rates of weight change of infested and uninfested moose are similar throughout the winter.

H4a Mean rates of weight change of infested and uninfested moose differ throughout the winter.

Prediction: If tick infestations increase the rate at which moose expend energy and that increase is not offset by increased feed intake, then the resulting depletion of energy stores may be reflected as reduced weight gains or accelerated weight loss by infested moose.

Overview

The results of this work suggest that the relationship between winter ticks and the energy budget of moose is very complex. A subtle increase in the minimum metabolic rates of moose was produced by tick infestations. Insufficient cold conditions during the trial periods prohibited the demonstration of detrimental effects of tick-induced alopecia on energy expenditures at cold temperatures. However, a reduction of respiratory heat loss accompanied the progressive, premature loss of winter hair. Infestations produced no detectable effects on weight changes. The discussion suggests that although moose do suffer some negative consequences of tick infestations, they are able to offset much of the additional energetic costs, allowing them to successfully inhabit areas of high enzootic tick populations.

CHAPTER II.

CALVES EXPOSED TO 30,000 TICKS

METHODS

Animals

All animals used in this study were bottle-reared in captivity. In May and June 1984, 11 moose calves (5 males and 6 females) were acquired from the wild in central Alberta, with the assistance of Alberta Fish and Wildlife personnel. A twelfth (female) was acquired from the University of Alberta, Ministik Wildlife Research Station in mid-June. The moose were reared at the Ellerslie Research Station, near Ellerslie, Alberta using the techniques presented by Welch et al. (1985). Calves were weaned onto a pelleted alfalfa ration at about 80 days of age.

Animals were handled extensively and habituated to the routines of data collection to minimize the effect of handling stress on future metabolic measurements. Beginning in early July, each animal was haltered for about one-half hour daily. Each animal was also fitted with a gas mask for a similar length of time. By early August, only six (Mo73,Mo74,Mo75,Mo76,Mo77,and Mo79) seemed to be habituating to wearing the mask. Thereafter, training efforts were concentrated on those six. After weaning, those six animals were masked and haltered several times weekly until metabolic measurements began in October.

Throughout most of the study, the moose were kept at the Ministik Station, but during autumn, the transmission period for D. albipictus, the moose were moved to the Ellerslie Station to prevent natural infestation. In November 1984, eight calves(Mo73, Mo74, Mo75, Mo76, Mo77, Mo79, Mo81 and Mo83) were moved to the Ministik station. There, infested and control moose were kept in separate pens and fed the same pelleted alfalfa ration throughout the remainder of the winter.

All ticks used in this study were offspring of female ticks collected from experimentally-infested moose at the Ellerslie station the previous spring (see Drew 1984 for complete history). After collection, the ticks were reared in the laboratory at the University of Alberta.

Engorged female ticks were placed individually in glass vials (10 ml) with cloth covers or in groups of 50 in plastic containers (300 ml) with mesh covers. The vials were held in cardboard flats, in an environmental chamber at 21°C. A pan of water was placed at the bottom of the chamber to maintain a high level of humidity. In July, the ticks were moved to a larger environmental chamber at 18°C to accommodate other studies. A shallow pan at the bottom of the chamber was filled with water at all times. Mounted in the top of this larger chamber was a fan for continuous air circulation.

During September, larvae for the infestations were counted with a miniature aspirator (Drew 1984). Three separate vials of 10,000 ticks each were counted for each moose. Each vial of counted ticks was immediately suspended in a desiccation chamber over water. In order to mimic autumn temperatures, the desiccators containing the ticks were placed in a cold chamber at 4°C until they were applied to the moose.

Treatment groups

Two treatment groups, infested and control, were established. After the first series of metabolic rate measurements, the six mask-trained moose were paired by sex and metabolic rates (Table 1). One animal from each pair was assigned to each group. One remaining moose was assigned to each of the two treatments groups.

Experimental infestations

An infestation level of 30,000 ticks per calf was chosen in order to preserve comparability with the studies of Glines (1983) and Drew (1984) in which calves were experimentally infested with 31,000 and 30,000 tick larvae respectively. Intensities of 30,000 ticks per moose were well within the range of 13,000 to 45,000 ticks reported on free-ranging moose calves in Alberta by Samuel and Barker (1979).

Table 1. Fasted weights (kg) and Fasted Metabolic Rates ($kJ/hr/kg^{0.75}$) of paired moose calves prior to infestation.

Infested				Control			
ID	Sex	Weight	FMR	ID	Sex	Weight	FMR
MO73	M	170	18.97	MO77	M	161	11.25
MO74	F	154	16.36	MO79	F	166	22.24
MO75	F	136	11.20	MO76	F	141	14.36
MO83	F	---	--[a]	MO81	M	---	--[a]
means		153	15.51			156	15.95

[a] Mo83 and Mo81 were used for respiration rate measurements but not for metabolic rate measurements.

On 29 October 1984, four moose (Mo73, Mo74, Mo75, and Mo83) were each infested with 30,000 D. albipictus larvae. For a single infestation, ticks were separated into 3 approximately equal clumps. While each calf stood teathered, the hair along the dorsal midline was parted. One cluster of ticks was placed deep in the parted hair on the withers, the second at mid-back, and the third above the rump. The parted hair was returned to its normal orientation and the moose remained tethered for an additional 10-15 minutes to prevent immediate grooming.

Fasting

To allow Fasting Metabolic Rate (FMR) measurements, the experimental moose were fasted for 48 to 72 hours, approximately monthly from October 1984 until May 1985 (Table 2.). While at Ellerslie (Oct. and Nov. 1984), the moose were fasted in several cement-floored pens. After moving to Ministik, the moose were fasted by removing all feed from the troughs; little natural forage was available in the pens throughout the winter. For the April and May trials, the moose were fasted in two 10 m x 10 m corrals, devoid of vegetation. Fresh water or snow was always available during the fasting period.

Table 2. Dates, duration, and ambient temperatures of fasting metabolic rate trials in 1984-85.

Dates	Duration (hr)	Ambient Temp.(°C) min.	Ambient Temp.(°C) max.	Notes
26-29 Oct 1984	72	-16.0	-12.0	pre-infestation
6 - 8 Nov	48	-5.0	-3.0	
13-15 Dec	48	-25.0	-1.0	
15-17 Jan 1985	48	-25.0	1.0	
12-14 Feb	48	-14.0	0.0	
12-14 Mar	48	1.0	5.5	
21-23 Apr	48	5.0	15.0	
7 - 9 May	48	15.0	19.0	

At the completion of each fasting period, the animals were gradually returned to <u>ad libitum</u> diet to prevent rumenitis. Animals were first given medium-quality or low-quality hay and natural browse. Once they had fed to satiation (4-8 hr), 2-3 kg/animal of pelleted ration was fed. Throughout the next 2-3 days, the amount of pelleted ration was gradually increased to <u>ad libitum</u>. During the entire refeeding period, hay, water, and natural browse were always available.

Measurement of metabolic rates

Metabolic rates were measured once at the commencement of the fast, again at about 24 hours of fasting, and twice on the final day using indirect calorimetery. Each moose was led into a 1 m x 3 m stall (Figure 3), tethered, and allowed to adjust to confinement. Once the animal was calm, a collection mask was placed over its nose. The was mask connected to a collection system fitted with one or more weather balloons. The collection system was purged by venting gases from the distal end of the system for approximately 1 minute. The vent was then closed and expired gases were collected for 10 minutes. If the collection balloons filled in less than 10 minutes, as often happened when ambient temperatures rose above 15°C, the collection was terminated and duration of the collection was recorded.

Figure 3. Collection of expired respiratory gases from Mo73 for determination of fasting metabolic rate.

During each collection, the animal's activity was subjectively scored from 1 (motionless) to 10 (violent movements). This index of activity was used to assess the effect of activity on metabolic rate measurements and later to remove estimates of metabolic rate that were unduly elevated by activity. Ambient temperature at the time of each measurement was read from an alcohol thermometer inside a Stevenson Screen located 20m from the metabolic stall. Wind and precipitation were recorded but occurred too infrequently to contribute additional insight to later analysis. Within one-half hour of collection, the expired air was analyzed to determine oxygen content and total volume. At the completion of every fasting trial, each moose was weighed to determine fasted weight for use in weight-specific metabolic rate calculations.

Expired respiratory gases were analyzed using one of two similar analyzing systems. Most of the measurements were made with the analyzing system at the Ministik Station (Figure 4). Total volume was measured with a gas-meter. Oxygen content of dried respiratory gas samples was measured with an oxygen analyzer (Servomex model 750B, Servomex Corp, Sussex UK). Gas pressure and temperature within the gas meter was measured with a mercury manometer and an electronic thermometer. A wet-dry bulb thermometer installed in the system allowed calculation of water vapor pressure. A similar gas analyzing system was constructed

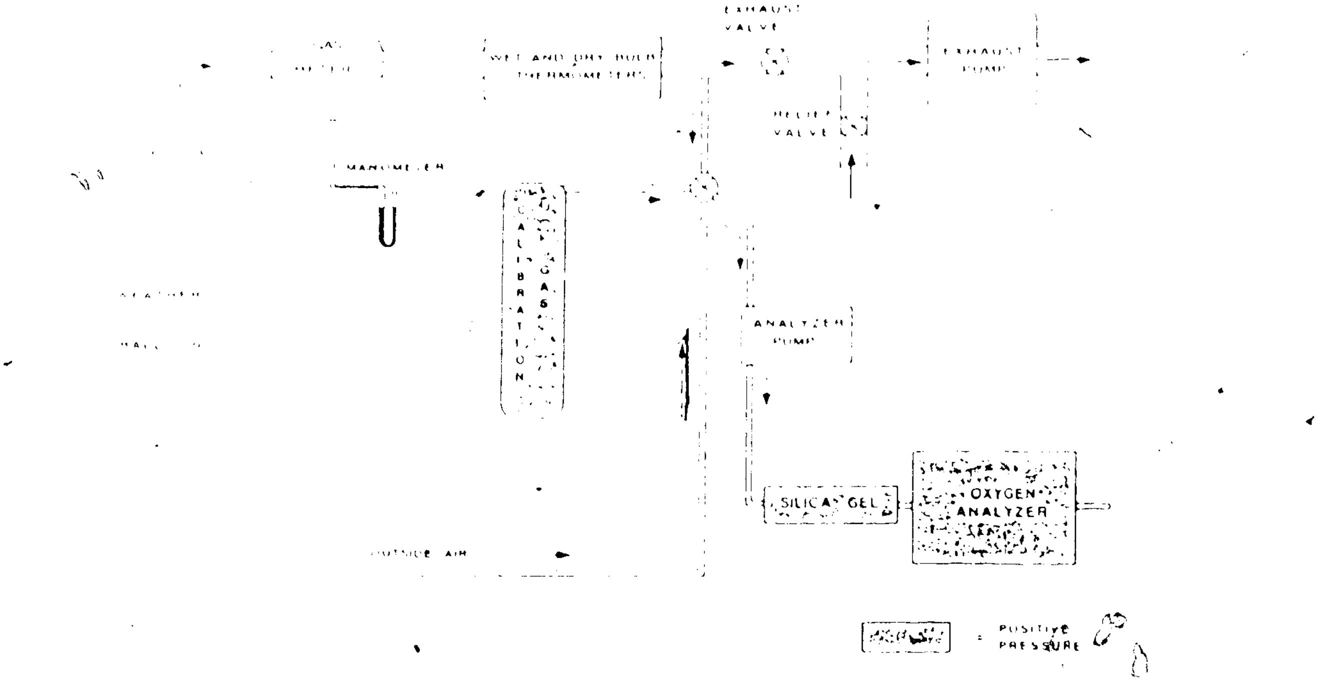

Figure 4. Respiratory gas analyzing system used to estimate metabolic rates of moose at Ministik Research Station.

at the Ellerslie station with a Beckman oxygen analyzer (M7000, Beckman Inc) for use during October and November.

Calculations

Volumes of expired air were first corrected to standard temperature and pressure (STP - 273^0K, 101.325kPa). Thereafter, oxygen consumption, energy expenditure, and finally weight-specific metabolic rate were calculated. For lack of CO_2 mesurements, Respiratory Quotient (RQ) could not be calculated and was, therefore, assumed to be 0.70 for a fasted animal (MacLean 1970).

Correction of gas volumes to STP was achieved by applying the following relationship (Weast 1980):

$$\frac{Ps\ Vs}{Ts} = \frac{Po\ Vo}{To}$$

Ps, Vs, and Ts represent pressure in kPa, volume in liters, and temperature in ^oK respectively, of a gas sample, and Po, Vo, and To represent pressure, volume and temperature at STP. Pressure of the sample gas was calculated as:

$$Ps = Pa - (Pd + Pwv)$$

Pa represents atmospheric pressure; Pd represents the pressure differential between gas inside the meter and atmospheric pressure and was read from the manometer. Pwv is the vapor pressure of water in the sample and is calculated by the formula (modified from Blaxter et al. 1972):

$$Pwv = \frac{4.74 + 0.817Tw - 0.5Td + 0.0081Tw^2 + 0.000387Tw^3}{-7.5006}$$

where Tw and Td are wet-bulb temperature and dry-bulb temperatures respectively in degrees Celsius.

The volume of oxygen that had been consumed from the sample (VO_2) was computed for each sample period using the formula:

$$\dot{V}O_2 = \frac{(VO_2air - VO_2ex)}{100} \times Vo$$

where VO_2air represented the percent of atmospheric oxygen (20.95%) and VO_2ex was the measured percent of oxygen in the expired air sample.

Energy expenditure (E) was estimated by assuming an RQ of 0.70 and incorporating MacLean's (1970) value of 20.46 kJ/l O_2 into the formula:

$$E = \frac{VO_2 \times 20.46}{t / 60}$$

where t represents the duration (time) of collection in minutes. From this value, weight-specific metabolic rate, in $kJ/hr/kg^{.75}$ was calculated:

$$WSMR = \frac{E}{Wt^{0.75}}$$

where Wt represents the weight, in kilograms, of the moose at the end of the fast.

Other data

Respiration rates of bedded moose, determined by counting flank movements for one minute, were recorded opportunistically throughout the winter. At the time of these observations, ambient temperature was recorded.

The extent of hair-loss was estimated for each moose at the time of each fast. Color photographs were taken of each moose at the time of each trial. Later, diagrams of the patterns of hair loss and destruction were drawn from those photographs. These patterns were classified and measured with a digitizer, and a crude index of insulation loss was calculated (See Chapter III, page 57-62 for detailed description of hair classifications and calculations of this index).

Statistical analysis

The criteria for Fasting Metabolic Rate are a post-absorptive state and an absence of psychological stress or activity (Gessaman 1973). Metabolic rates of ruminants decline rapidly after the onset of fasting, then reach a relative plateau (Marston 1948). Adult moose reach this plateau after 40 (Renecker and Hudson 1986a) to 40 (Regelin et al. 1985) hours of fasting. Based on results from the initial series of metabolic measurements, 30 hours seemed to be adequate time for younger moose to reach this plateau. Thereafter, a post-absorptive state was assumed after a minimum of 30 hours of fasting.

The activity score, recorded at the time of each metabolic measurement, was used as a criterion to remove measurements that were unduly elevated by activity. Metabolic rate measurements associated with activity scores of 5 and above showed greater variation than those associated with activity scores of 1 to 4. Therefore, all metabolic measurements accompanied by an activity score of 5 or greater were excluded from statistical analysis. The lack of psychological stress is difficult to assess. However, elevated activity seemed to accompany most apparently stressful situations. Beyond removal of measurements during elevated activity, no attempt was made to remove the effects of psychological stress from the dataset.

Hypotheses were tested using methods of Sokal and Rohlf (1981). For all tests, a probability (P) of 0.05 was used unless otherwise stated.

Differences between mean metabolic rates were tested with a nested Analysis of Variance of individuals within treatments within trial number.

Metabolic and respiratory responses to ambient temperature can be influenced by the state of the animal's surface insulation. For most tick-infested moose, little damage to the pelage occurs prior to March 1; thereafter, hair destruction and loss progress rapidly (Samuel et al. 1986, McLaughlin and Addison 1986). Therefore, the relationships between ambient temperature and fasting metabolic rate and respiratory rate were examined for two discrete periods: prior to March 1, and after March 1.

Responses of metabolic rates and respiration rates of infested and control moose, to a range of ambient temperatures, were compared by analysis of covariance. Respiration rates and respiratory minute volumes were log-transformed to linearize the relationships. The response of the two treatment groups was assumed to differ if either the slope or the adjusted means differed.

Rates of weight changes between consecutive metabolic trials were computed for each animal by dividing the weight gained or lost by the number of intervening days. A paired students t-test was employed to compare weight changes of infested and control calves.

RESULTS

Experimental infestation of calves with 30,000 larval ticks produced only mild parasitism. During the summer, many ticks in the lab colony died, apparently from dehydration resulting from the continuous circulation of air in the chamber; the use of an aspiration counter may have further impaired the viability of the ticks applied to the experimental animals. Despite the apparent lethargy of the ticks that did survive, most larvae disappeared from the original site of application within minutes of being placed in the hair of the moose. No difference was observed in the viability of the ticks used on different moose. Although no attempt was made to assess the survival of the ticks on the hosts, the scarcity of nymphs in the hair in January, and the paucity of engorged female ticks found on moose and in bedsites suggest that the true intensity was well below 30,000 ticks per moose. No ticks were found on the control animals or in bedsites in their pen.

Hair loss

All experimentally infested calves showed some degree of tick-induced alopecia. Grooming was first noted in mid-February; shortly thereafter, Mo75 began to exhibit some mottled hair damage on portions of her hind quarters. At that time, no disturbance of hair was visible on the uninfested animals. By March 14, Mo74, Mo75, and Mo83 had denuded or severely broken hair on their shoulders, producing hair loss indices of 14, 11 and 7 respectively. On April 20, those three showed similar states of alopecia (Table 3). Over a large triangular area encompassing the neck, shoulder and hump, the hair was severely damaged or absent. Extensive areas along the back, rump and posterior of the hind quarters were ruffled or mottled. Meanwhile, Mo73 showed only a small area of severely damaged hair on his neck and slight breakage of hair over his shoulder.

Weight changes of moose

Weight changes were similar for all calves, infested and control, throughout the winter (Figure 5). Some weight loss occurred in October and December. All animals experienced slight weight gains throughout most of the winter but lost weight in April and May. Differences between the rates of weight change of the two treatment groups were not significant ($\underline{t}=0.087, \underline{P}>0.9$).

Table 3. Insulation Loss Index of infested and control moose calves on April 20, 1985.

Infested		Control	
ID	Hair Loss Index	ID	Hair Loss Index
Mo73	3.6	Mo77	3.4
Mo74	29.8	Mo79	10.9
Mo75	35.4	Mo76	0.0
Mo83	29.9	Mo81	0.0[a]

a - no photograph taken, no hair-loss noted.

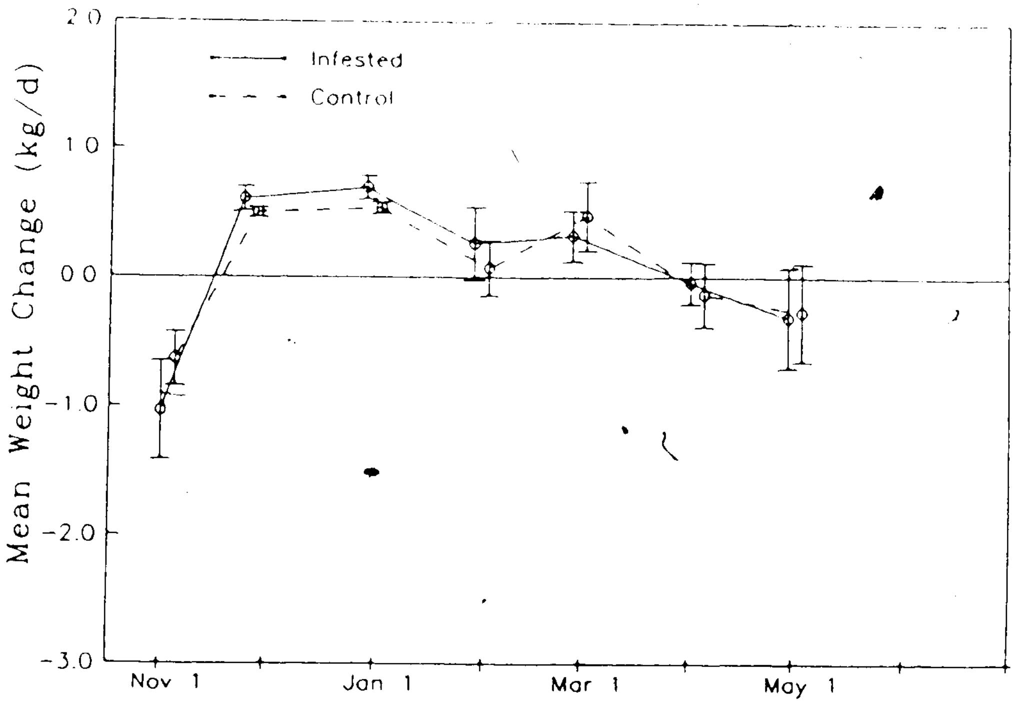

Figure 5. Weight changes of 3 fasted moose calves infested with 30,000 D. albipictus larvae, and of 3 uninfested controls. (mean ±1SD)

Metabolic rates over time

Differences between the mean fasting metabolic rates of infested and control moose were not significantly different. Although fasting metabolic rates (FMR) of infested calves averaged 9.0% higher than that of their uninfested controls (Figure 6). Analysis of variance showed fasting metabolic rates differed significantly between months ($F=7.43$, $P<0.01$) and individuals ($F=4.43$, $P<0.05$) but not between treatment groups ($F=2.39$, $P=0.11$).

Metabolic and respiratory responses to ambient temperature

prior to March 1:

Fasted metabolic rates (FMR) of infested and control moose were positively correlated with ambient temperature (T) (Figure 7). The relationships are approximated by the following equations:

$$\text{FMR(infested)} = 23.02+0.32T$$

$$\text{FMR(control)} = 22.41+0.36T$$

Neither the slopes ($F=0.042$, $P>0.75$) nor the adjusted means ($F=0.608$, $P>0.25$) of these lines differed. Due to the small number of satisfactory data points, comparison of infested and control pairs was not possible.

Respiratory responses of infested and control moose did not differ prior to March 1. Respiration rates of calves in both treatments increased gradually as ambient temperature increased over a range of -10 to 12°C (Figure 8). Respiration rates of the two treatments are

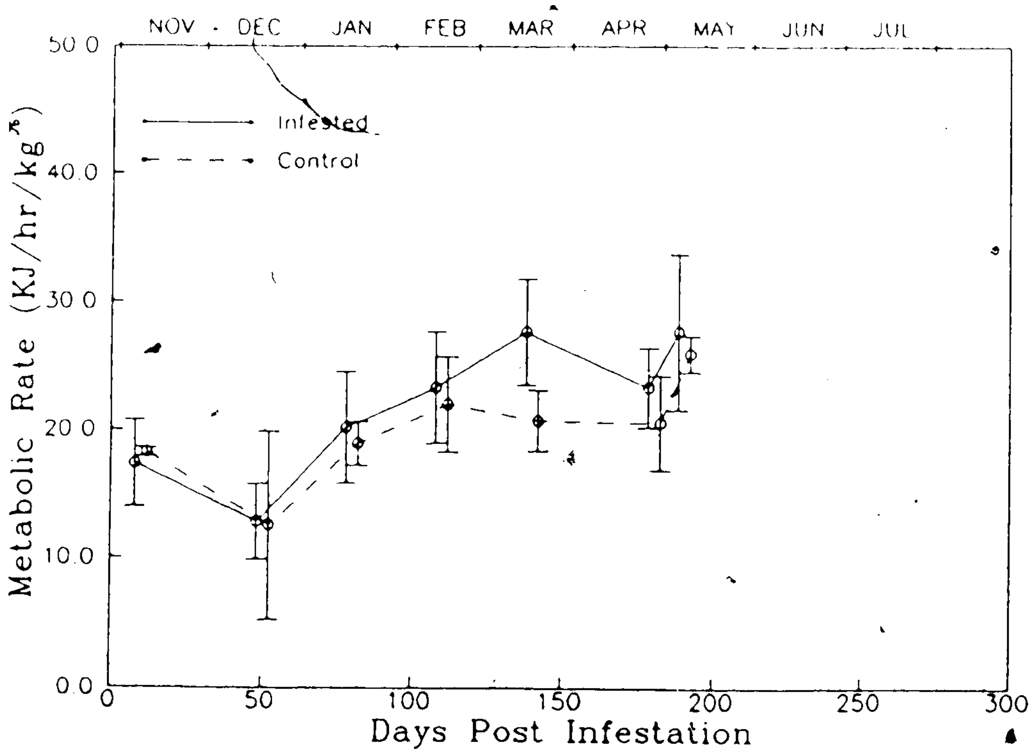

Figure 6. Fasted metabolic rates of 3 moose calves infested with 30,000 D. albipictus larvae, and of 3 uninfested controls. (mean ±1SD)

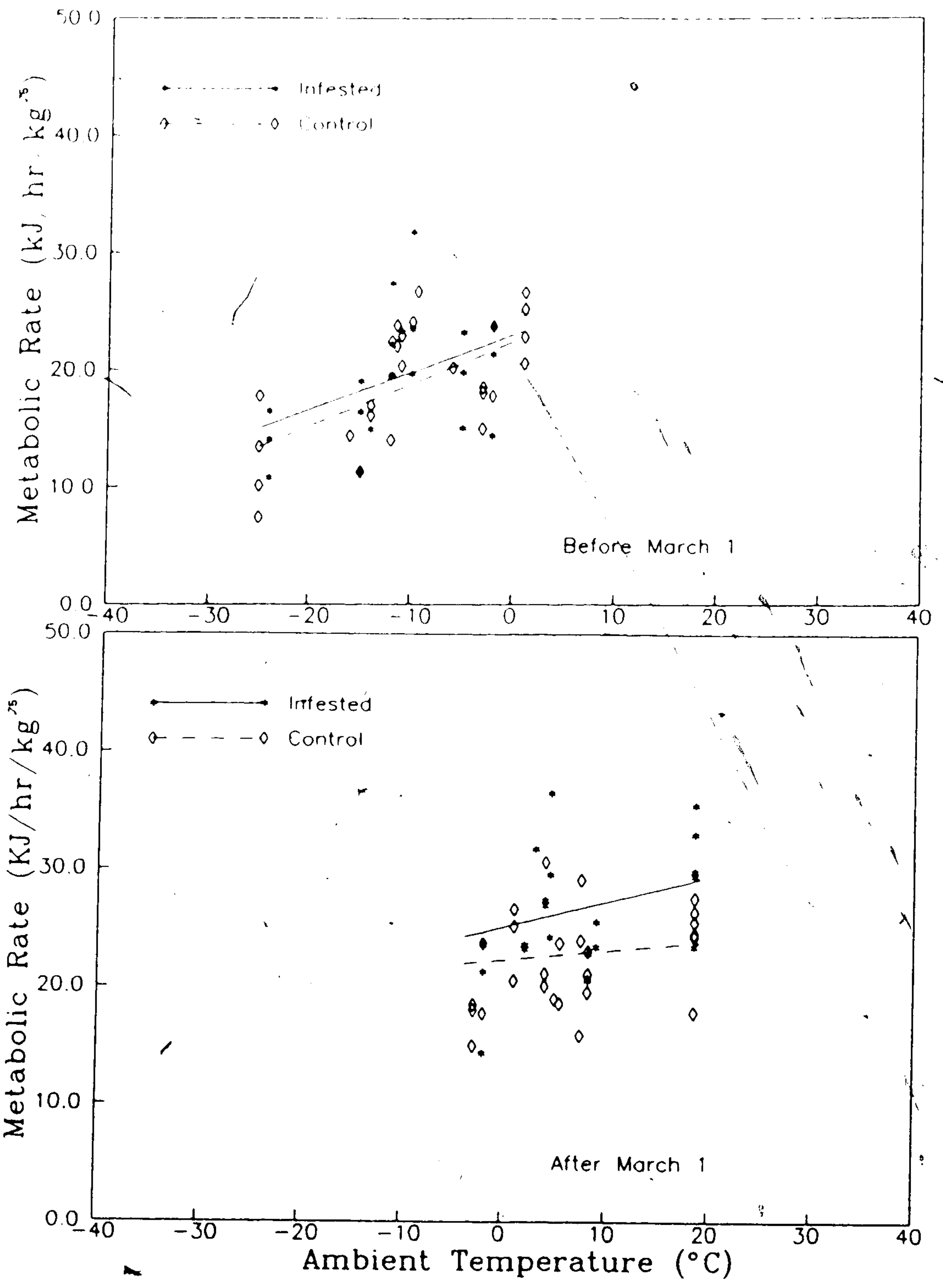

Figure 7. **Fasted metabolic rates of 3 moose calves infested with 30,000 D. albipictus larvae, and of 3 uninfested controls at a range of ambient temperatures.**

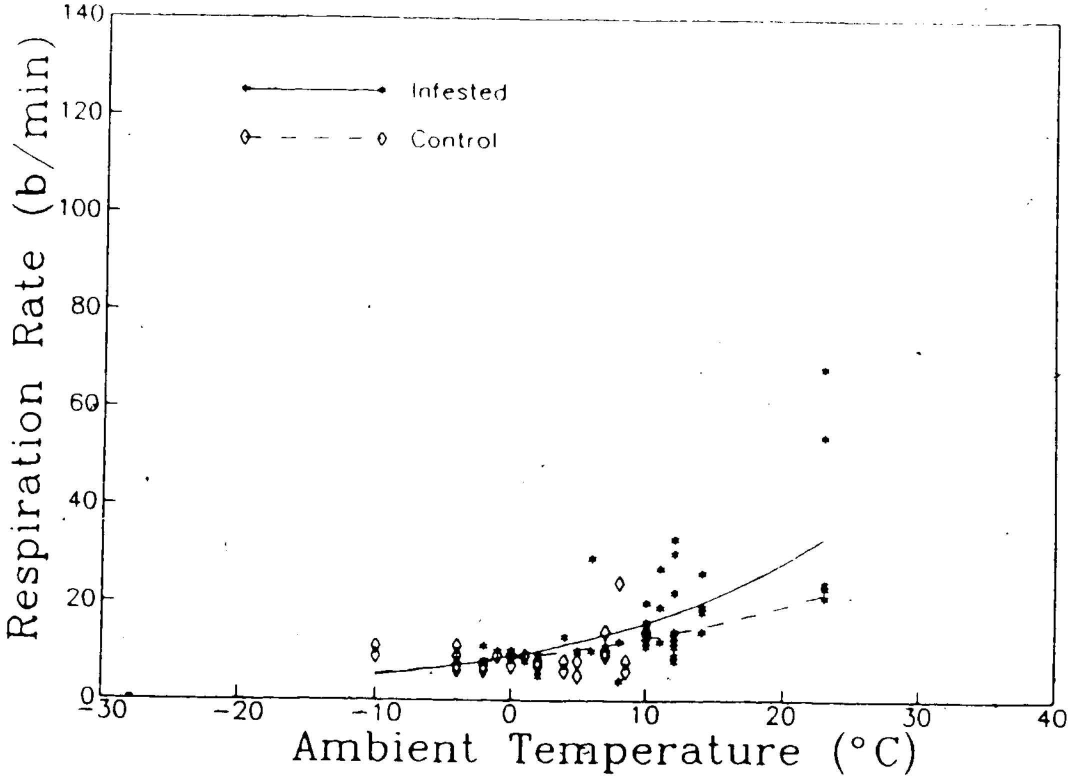

Figure 8. Respiration rates of 4 bedded moose calves infested with 30,000 D. albipictus larvae, and of 4 uninfested controls as a function of ambient temperature.

described by the following formulae:

$$RR(\text{infested}) = 9.58e^{0.087T}$$

$$RR(\text{control}) = 10.49e^{0.035T}$$

Neither the slopes ($F=3.825$, $P>0.05$) nor the adjusted means ($F=0.341$, $P>.25$) differ between the two equations. A malfunction of the gas collection system resulted in unreliable estimates of respiratory minute volume thereby preventing the use of that parameter to further test for differences in respiratory function.

after March 1:

After March 1, metabolic rates of animals in both treatment groups increased as ambient temperature increased (Figure 7). Once variation due to temperature was accounted for, the metabolic rates of infested moose were higher than those of their uninfested control. The relationship between fasted metabolic rate and ambient temperature for each treatment group is represented by the following equations:

$$FMR(\text{infested}) = 25.17+0.21T$$

$$FMR(\text{control}) = 22.30+0.08T$$

the slopes of the two regressions did not differ ($F=0.325$, $P>0.50$), however, the adjusted means for infested moose were significantly higher than those of the controls ($F=8.35$, $P<0.01$). For two of the three pairs, adjusted fasting metabolic rates the infested moose (Mo74, Mo75) were significanly higher than those of their uninfested counterparts (Mo79, Mo76) (F=6.27,7.05, $P<0.05$). For the remaining pair (Mo73, Mo77), adjusted metabolic rates did not differ (F=1.76, $P=0.21$).

During March, April and May, respiration rates of all calves increased exponentially with increasing ambient temperature (Figure 8). Infested calves showed a more rapidly increasing respiration rate than did their uninfested counterparts. The following equations describe that divergence:

$$RR(\text{infested}) = 9.03e^{0.066T}$$

$$RR(\text{control}) = 8.33e^{0.050T}$$

Slopes (F=18.48, $P<0.001$) and adjusted means (F=4.46, $P<0.05$) of the two equations differ. As noted earlier, no reliable measures of respiratory minute volume were available to corroborate this elevation of ventilatory function.

DISCUSSION

Few estimates of the survival rates of winter ticks on experimentally infested moose are published, probably because of the lack of a technique for reliably estimating the number of ticks on a live moose. Barnard and Morrison (1985) present a technique for estimating the numbers of *Amblyomma americanum* on cattle. That technique entails a inspection of specific regions of the animal for ticks. Owing to the depth of hair on moose, and the high densities of D. albipictus, their technique would probably be inadequate for estimating D. albipictus numbers on moose. Glines (1983) reported that of 31,000 ticks applied to each of her experimentally infested calves, 22,890 were present on a calf that died accidentally in November, and 9,870 remained on a calf that was killed in February. The latter animal suffered very severe hair loss and may have lost many ticks along with its hair coat.

Noticeably fewer ticks were visible on calves in this study than on calves in the studies of Glines (1983) or of Drew (1984) (W.M. Samuel pers. comm.). Nothing in the histories of these calves suggests that they should be less suitable hosts than the moose used in the previous two studies. Moose calves for all three studies were acquired from a variety of locations across Alberta. Techniques for rearing and feeding differed only slightly (see Welch et al. 1985 for complete details). Protocol for infesting the moose was similar to that used by Drew (1984) to "mass-infest" animals.

Two possible explanations remain for the presumed poor survival of the ticks in this study. The most probable explanation is that many of the larvae, although alive at the time of infestation, were too weakened by dehydration to feed and molt. A second explanation may be that ticks were applied to the moose too late in the autumn (October 29). Peak of transmission of this tick occurs in September and early October in central Alberta (Drew and Samuel 1985). Although tick larvae can survive in the field into December (Drew and Samuel 1985), and in the laboratory until April (Samuel unpubl. data), no studies have examined the ability of these ticks to survive when applied to a host.

Depth of the hair coat was not measured in the present study; therefore, an attempt was made to determine the comparability of the insulation loss index computed in this study and the measurements of lost hair volume made by McLaughlin and Addison (1986). Those authors present 2 photographs of an experimentally infested moose calf, the first taken on 5 March and the second on 13 April, accompanied by estimates of 8% and 44% loss of hair volume respectively. Applying the techniques used to estimate hair loss in this study ~~to those~~ photographs yields Insulation Loss Indices of 6.3 and 45.2. The reasonable correspondence between the reported volume of lost hair and our Insulation Loss Index suggests that the Index may be a satisfactory indicator of lost hair volume.

If Insulation Loss Index can be equated with lost hair volume, then the alopecia produced in this study was less severe than that produced by 42,000 ticks and within the range of alopecias produced by 21,000 ticks reported by

McLaughlin and Addison (1986). Tick-induced alopecia on calves in this study was considerably less extensive than that reported by Drew (1984) for similar levels of infestation. The 3 females in this study developed alopecia slightly less severe than that reported by Glines (1983) on Mo23, the moose that experienced lthe least hair-loss in that study.

Upon infesting a moose in autumn, larval ticks engorge within 10-14 days (Drew 1984), molt into nymphs and enter a diapause lasting until February (Glines 1983, Drew 1984). During this period, the relatively inactive ticks cause little if any additional energy expenditure by their host. If ticks do not feed during this diapause, then little irritation and no stimulation of the immune system occurs. The minimal increase of grooming during this period requires little additional energy expenditure, and does not greatly alter the insulative property of the fur. In the absence of tick-induced alterations to either the heat production (MR) or heat loss (insulation), no respiratory compensation for heat loss would be expected.

From late-February through April, tick-induced alopecia and hair destruction progress rapidly in conjunction with engorgement of nymphs and adult ticks (Glines 1983, Glines and Samuel 1984, Samuel et al. 1986, McLaughlin and Addison 1986). During the feeding of these advanced instars, moose can experience hypoalbumenaemia (Glines 1984), and anemia

(Glines 1984, Fenstermacher and Jellison 1933). Closely related ticks, D. andersoni, feeding on guinea pigs have been shown to inject antigenic substances, stimulating a histamine reaction in the skin (Wikel 1981); although a similar injection and resulting cutaneous reaction probably occurs when D. albipictus feed on moose, it has not been demonstrated experimentally. The replacement of lost blood constituents and the synthesis of immunoglobulins and histamines requires some energy expenditure, inducing a temperature-independent increase in metabolic rate.

The increased heat production resulting from elevated metabolic rates of infested moose was not compensated for by accelerated heat loss due to alopecia. Moose respond to cold stress by reducing respiratory rates and, thereby, respiratory heat loss (Renecker and Hudson 1986a). If infested moose were faced with greater heat loss, then heat conservation mechanisms such as a depressed respiration rate should accompany elevated thermoregulatory heat production. This phenomenon did not occur; instead the elevated respiration rates of infested moose suggested that infested moose were faced with the need to shed excess heat rather than generate it to maintain homeothermy.

Respiration rates of infested moose may increase in response to one, or both, of two demands. First, an elevated metabolic rate necessitates greater assimilation of oxygen into the body and greater elimination of CO_2.

Moose may achieve increased gas exchange by increasing the volume of air respired or by improving the efficiency of gas exchange. The efficiency of oxygen extraction by infested animals was relatively low (1.5-2.5%) compared to the levels achieved by moose calves at -25°C (3-4%) (Welch unpubl. data). This low extraction implies that moose could reduce respiration rate and achieve some reduction of respiratory heat loss while maintaining adequate levels of gas exchange.

Demands for gas exchange are not the sole determinants of respiration rates in mammals. Higher respiratory rates of infested anmials probably resulted from the need to shed additional heat generated by the elevated metabolic rate. riendeer (Hammel et al. 1961), white-tailed deer (Jacobsen 1973), elk and mule deer (Parker and Robbins 1984), as well as moose (Renecker and Hudson 1986a) elevate respiration rates in response to elevated heat loads. This phenomenon is not unique to cervids and applies to most mammals (Whittow 1971).

Thermogenic costs appeared to be negligibly elevated by tick-induced loss of insulation between -9 and +19°C. Reduction in the depth of the fur increases the rate of heat loss from the skin (Gebremedhin 1987). This does not however, represent an increased heat loss from the entire body. Thermogenic energy expenditure is necessary only if heat loss from the entire body exceeds heat produced by all other metabolic processes (Stevens 1972). Because the minimum metabolic rate was elevated by tick infestations, infested moose were faced with the need to shed heat rather than produce it. That respiration rates of infested moose exceeded those of controls infers that the additional heat loss incurred by the loss of approximately 25% of insulation was insufficient to dissipate the additional metabolic heat resulting from other aspects of the tick infestation.

Ultimately the significance of a parasite to its hosts depends on its influence on the survival and production of the host. No study of moose experimentally infested with _D. albipictus_ has demonstrated a consistent depression of the weight gains of infested moose calves. Glines (1984) reported that one of two infested calves lost weight during nymphal and adult engorgement (Mar 12-May 21); four of five controls and the remaining infested calf gained weight during the same period. Drew (1984) demonstrated no difference in the weekly weight changes of infested and control calves. McLaughlin and Addison (1986) were not able to statistically verify an apparent difference between the weight gains of calves with extensive hair loss and of those showing little or no hair loss.

Only McLaughlin and Addison (1986) have demonstrated a difference in body condition attributable to tick infestation. They report that two condition indices (pericardial fat weight : heart weight and visceral fat weight : body weight) were lower in experimentally infested calves showing extensive hair loss. Because visceral fat indices are more sensitive indicators of condition, such techniques might have discerned different body conditions in this study.

Increased metabolic rate, unless offset by greater feed intake or increased digestive efficiency, results in a more rapid depletion of fat stores in late winter. Glines (1983) did not find a difference in the feed intakes of infested and control pair-fed animals. No studies have been undertaken to assess the effects of ticks on the digestive efficiency of moose.

CHAPTER III.

YEARLINGS EXPOSED TO 50,000 TICKS

METHODS

Animals

Moose used in this study were raised from neonates at the Ellerslie Station in the summer of 1984 (Welch et al. 1985). Most of the yearlings in this study had been used as calves for metabolic studies in the previous year (Chapter II). After the conclusion of metabolic trials in May 1985, the moose were released into a 70 ha enclosure at the Ministik Station. In August of 1985, they were returned to the Ellerslie Station and remained there throughout the autumn to prevent natural infestation. In November, eight yearlings (Mo73, Mo74, Mo75, Mo76, Mo77, Mo80, Mo81, and Mo84) were moved to the Ministik Station. Throughout the remainder of the second experiment, the moose resided at the Ministik Station. There, infested and control moose were kept in separate pens and fed the same pelleted alfalfa ration. In February 1986, fiber in the ration was increased in an attempt to prevent diarrhea in the animals.

All ticks used in this study were progeny of female ticks, collected from bedsites in the moose pens at the Ministik Station the previous spring. The ticks were placed individually in glass vials (10 ml) with cloth covers or in groups of 50 in plastic containers (300 ml) with mesh covers. To ensure a stable, high level of humidity, 50 to 75 vials were suspended in each of 5 desiccation chambers containing 1 to 2 cm of water. Ticks were kept at 2°C until early June. Thereafter, half were kept at 19°C while the other half were kept at 24°C.

The necessary number of ticks for infestations was approximated by weight rather than exact count. A technique similar to that reported by Stiller et al. (1981) was employed. Each of 20 aliquots of between 2000 and 4000 tick larvae were weighed then counted to determine the average weight of the larvae. This estimate was then used to measure groups which approximated 50,000 ticks.

Treatment groups

Several changes were necessary in the treatment groups for the 1985-86 season (Table 4). Mo79 (control female) died in June 1985, and was replaced with Mo84 (spare female). Attempts to halter-train and mask-train the replacement moose were unsuccessful, leaving only two control moose from which metabolic rate measurements could be taken. Mo83 (infested female) was replaced with Mo80 (spare male) because of her poor condition in autumn.

Table 4. Weights (kg) at the time of infestation (September 15, 1985) of yearling moose pairs studied during 1985-86.

	Infested			Control	
ID	Sex	Weight	ID	Sex	Weight
MO73	M	296	MO77	M	294
MO80[a]	M	326	MO81[a]	M	347
MO75	F	284	MO76	F	284
MO74	F	300	MO84[a]	F	283
means		302			302

a - not usable for metabolic rate measurements

Neither Mo83 nor her replacement could be used for metabolic rate measurements.

Experimental infestations

An infestation level of 50,000 ticks/yearling was chosen to produce an infestation of approximately equal magnitude to that of 31,000 ticks/moose used by Glines (1983), and of 30,000 ticks used by Drew (1984). Intuitively, the magnitude of an ectopatasite infestation should be a function of parasite density rather than of absolute number. At the inception of the experiment, no published estimates or reliable data were available on the relative surface areas of moose calves and yearlings. Therefore, an infestation level of 50,000 was selected somewhat arbitratily. Intensities of 50,000 ticks per moose were within the range of 21,000 to 57,000 ticks per moose reported from free-ranging yearlings in Alberta by Samuel and Barker (1979).

On 15 September 1985, each of three moose (Mo73, Mo74, and Mo75) were reinfested and a tick-naive moose (Mo80) was infested, with approximately 50,000 larval ticks each. The technique used to apply the ticks was similar to that used on calves. First, ticks for a single infestation were separated into 3 approximately equal clumps. Then, each moose was mildly sedated with Xylazine (Rompun, Haver-Lockhart, Rexdale OT) and the fur along the dorsal midline was parted. One cluster of ticks was placed deep in the parted hair over the withers, the second at mid-back, and the third above the rump. The parted hair was then returned to its normal orientation. Each moose remained sternally recumbent during the infestation and for 10-30 minutes thereafter.

Fasting

Moose were fasted for 48 to 72 hours, approximately monthly from January until June 1986 (Table 5). Two holding pens (10 m x 25 m), constructed in autumn 1985 and cleared of all live and cured vegetation, were used for all trials in 1986. Protocol for fasting and refeeding was similar to that followed the previous year.

Measurement and calculation of metabolic rates

Attempts were made to measure metabolic rates in November and December, 1985, but proved futile. Because the moose had not been handled extensively throughout the summer and autumn, they could not be tethered or masked. Retraining the moose entailed repeatedly enticing them into the metabolic stall and tethering them for 3 to 6 hours. Once the moose were again accustomed to standing in the stall, the mask, with valves removed, was placed over the muzzle and left there for up to one hour. Receptivity of the moose to this retraining varied: Mo76 and Mo75 required

Table 5. Dates, duration, and ambient temperatures of fasting metabolic rate trials in 1986.

Dates	Duration (hr)	Amb[illegible] Temp. ($^{\circ}C$) min.	 max.	Notes
23-26 Jan	72	-6.0	-1.0	incomplete trial
18-20 Feb	48	-28.0	-23.0	
11-13 Mar	48	-2.0	3.0	
1-3 Apr	48	-4.0	9.0	
25-27 Apr	48	3.0	14.0	rain
27-29 May	48	17.0	33.0	
28-30 Jun	48	11.0	28.0	

only 2 and 5 such sessions while Mo73 required 9 before he calmly accepted the routine.

Metabolic rates were measured at 6-hour intervals during the fasting trials from January to June, 1986. The procedures followed for collection and analysis of respiratory gases were identical to those used on calves in the previous year (see Chapter II, p 25-28 for details). Metabolic rates were calculated acording to the formulae presented in Chapter II (p 29-31).

Respiration rates of bedded moose were observed and recorded between February and June, as described in Chapter II.

Hair loss

Hair loss was estimated for every moose at the time of each fast in 1986. Color photographs were taken of both sides of each moose. Later, one photograph of each side was projected on a paper and a detailed diagram of the silhouette and hair types was traced. Naturally molting hair was classified as 1 of 3 categories: (Figure 9)

e. Winter Full encompasses all areas of undisturbed hair that had not begun to molt. The winter coat of moose is composed of two hair types: "pile", the long, light-coloured guard hairs with dark ends; and "fur", the fine, wooly undercoat

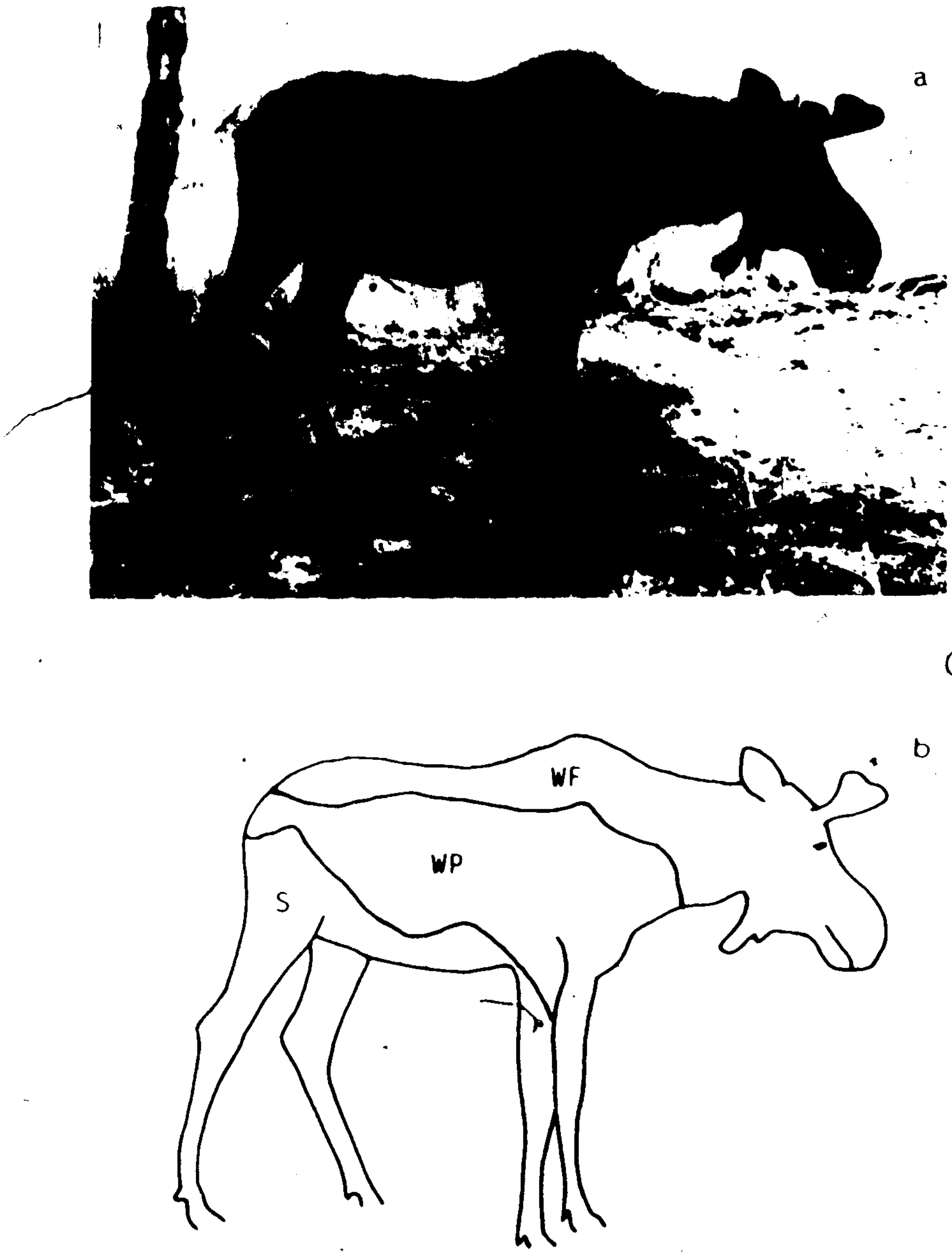

Figure 9. **Hair-loss categories on the torso of a** partially moulted, uninfested **moose (a), and a** schematic classification of **moulting hair (b).** WF = Winter Full, WP = Winter Pile, S = Summer.

(Sokolov 1982). By late winter, the sun has bleached the tips of the pile hairs to a brown or gray colour, imparting a grizzled appearance to the winter coat.

f. Winter Pile includes areas where the underlying fur has been shed. The underlying fur on the torso begins to molt first on the belly and flanks. The margin of this molt, visible as a line of shaggy wool interspersed with loose pile hairs, progresses forward and dorsally leaving behind only winter pile (Samuel et al. 1986). Areas resembling winter coat but lying posterior and ventral to the advancing line of molted fur were classified as winter pile.

g. Summer contains all areas covered by the new hair that replaces the shed winter hair. Pile hair is the last to molt, leaving behind fine, black summer hair which begins to emerge from the skin before the entire winter coat is shed. The abundant oils secreted by moose in spring and summer impart the summer hair with a glossy black appearance.

Groomed hair was classified as 1 of 4 categories: (Figure 10)

a. Slightly Damaged encompasses hair exhibiting only broken tips. As moose begin to groom an area of the body, the fur becomes ruffled. Licking

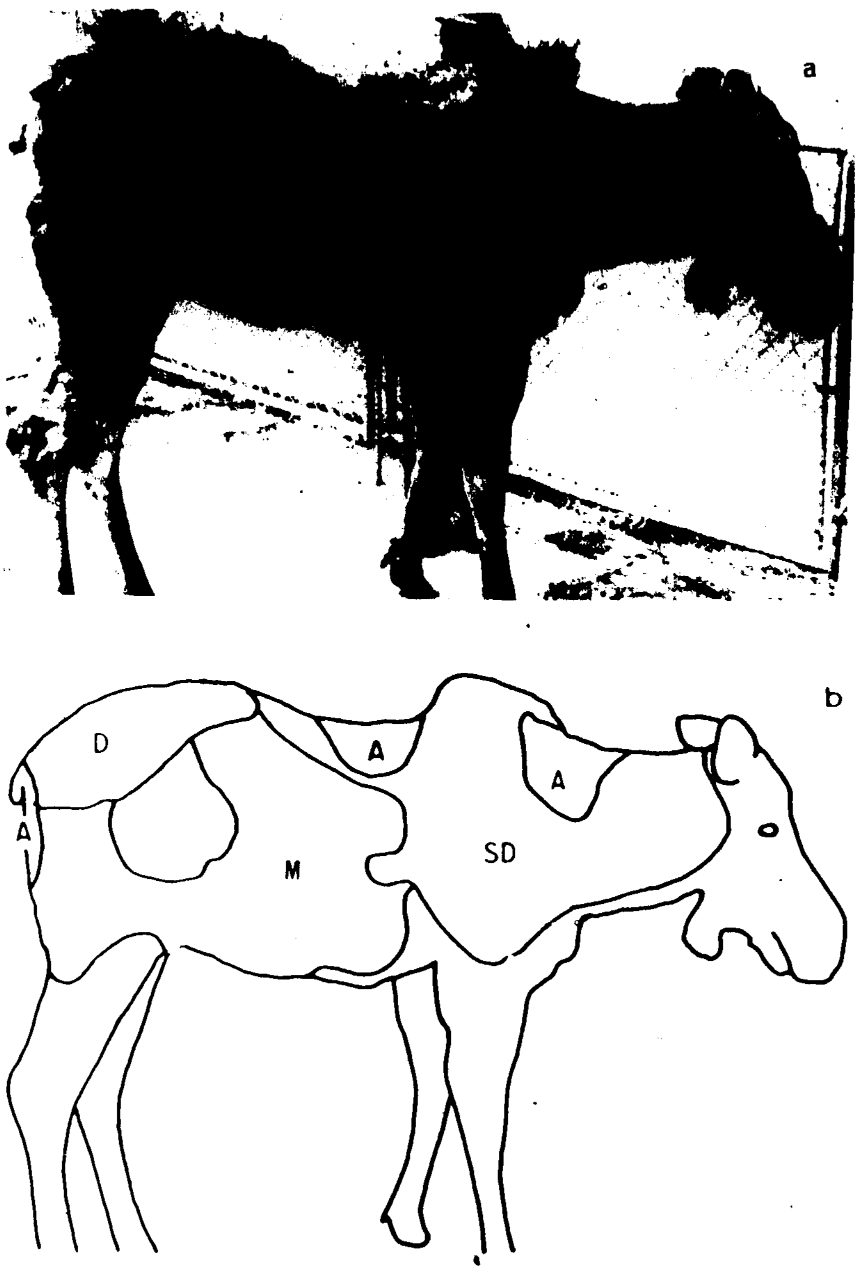

Figure 10. **Pattern of hair destruction on the torso of a moose infested with 50,000 D. *albipictus* larvae (a), and a schematic classification of damaged hair (b).**

D = Disturbed, M = Mottled, SD = Severely Damaged,

A = Absent.

produces distinctive swirls. Rubbing and scratching break the tips of the pile hairs; such hair appears black or dark brown in contrast to the grizzled, sunbleached tips of the undisturbed hair in late winter.

b. <u>Mottled</u> includes regions of hair exhibiting a "spotty" pattern of alopecia. As grooming proceeds, discrete foci of complete hair loss, seldom exceeding 5 cm^2, may result. Typically, little damage beyond ruffling occurs to the surrounding hair resulting in a dappled appearance.

c. <u>Severely Damaged</u> encompasses areas where most hair shafts are broken at mid-shaft. Scratching with hooves or teeth and rubbing against stationary objects breaks the hair shafts at uniform lengths, exposing the grey mid-shafts of the pile. Hair damaged to this extent is clearly visible and exhibits a white or light grey colour.

d. <u>Bare</u> includes all areas of skin denuded of hair. Extensive grooming can break the hair shafts at the skin surface or pull the shaft entirely out of the follicle. Further grooming occasionally results in abrasion of the skin itself. Such areas appear pink immediately after removal of the hair and gradually change to dark gray. Open wounds and scabs may also be visible.

Because hair types on the head and lower legs were difficult to determine, these areas were excluded from total and partial area measurements. Area of the planar view of the torso and the portion of the silhouette covered by each hair type was measured with a digitizer (Bit pad two - Summagraphics, Fairfield CT) using digitizing software (Sigma-Scan - Jandel Scientific, Sausalito CA).

Overall loss of insulation was approximated with a crude Insulation Loss Index (H). In the absence of information on heat flow through partially destroyed hair, several simplifying assumptions are made. Absent, summer, and severely damaged categories are assumed to be a complete loss of fur insulation. Mottled and winter pile categories are assumed to be only a partial (50%) loss of insulation. The insulation loss index was calculated as:

$$H = Acl + Apl/2$$

where Acl is the percent of the silhouette of the torso covered by areas of complete insulation loss, and Apl is the percent of the silhouette of the torso covered by areas of partial insulation loss.

Statistical analysis

Hypotheses were tested using methods of Sokal and Rohlf (1981). For all tests, a probability (*P*) of 0.05 was used unless stated otherwise.

Differences between mean metabolic rates were tested with a nested Analysis of Variance of individuals within treatments within trial number. Metabolic and respiratory rates were analyzed for two discrete time intervals, prior to March 1, and after March 1, allowing comparison of treatments before and after the onset of alopecia. Metabolic rates and respiratory minute volumes, over a range of ambient temperatures, were analyzed by analysis of covariance. Respiratory rate and respiratory minute volume were natural-log transformed. Where sufficient data existed, the responses of metabolic rate, respiration rate, and respiratory minute volume also were examined by stepwise multiple regression. The variable in question was regressed against ambient temperature, ambient temperature squared, treatment code (control=-1, infested=+1), and Insulation Loss Index. A variable was included in the final model only if the coefficient associated with it differed significantly from zero.

Mean fasted weight changes of infested and control moose were compared by a paired Students *t*-test.

RESULTS

Exposure to 50,000 larval *D. albipictus* produced a substantial degree of parasitism on all experimentally infested yearlings. Viability of the larvae appeared good at the time of infestation and numerous ticks were visible in the fur of the infested animals throughout the winter. During March and April, 10 to 20 engorged female ticks could be found by carefully searching the leaf litter in and around a single bedsite in the infested animals' pen. Several hundred engorged females were collected in this manner during March and April. Control moose remained almost entirely free of ticks. Two engorging females and one male were removed from the ear of Mo77 (control male) on April 10; no other ticks were found on the control moose or in their pen.

Hair loss

The first evidence of grooming was noted on October 10, 24 days after infestation, when Mo74 and Mo75 showed areas of ruffled hair along the back and rump. The ruffled appearance of the hair did not persist and little grooming or signs thereof were noted again until February.

Infestation with ticks induced a premature loss of the winter hair coat on all infested yearlings (Figure 11). From late February through June, hair loss proceeded rapidly on all four infested yearlings; controls experienced no alopecia and showed no signs of molt until early May. Alopecia on infested moose began as a region of broken hair on the neck, around the anus, and on the shoulder. As the areas of hair destruction enlarged and coalesced, hair on the lateral surface of the shoulders was

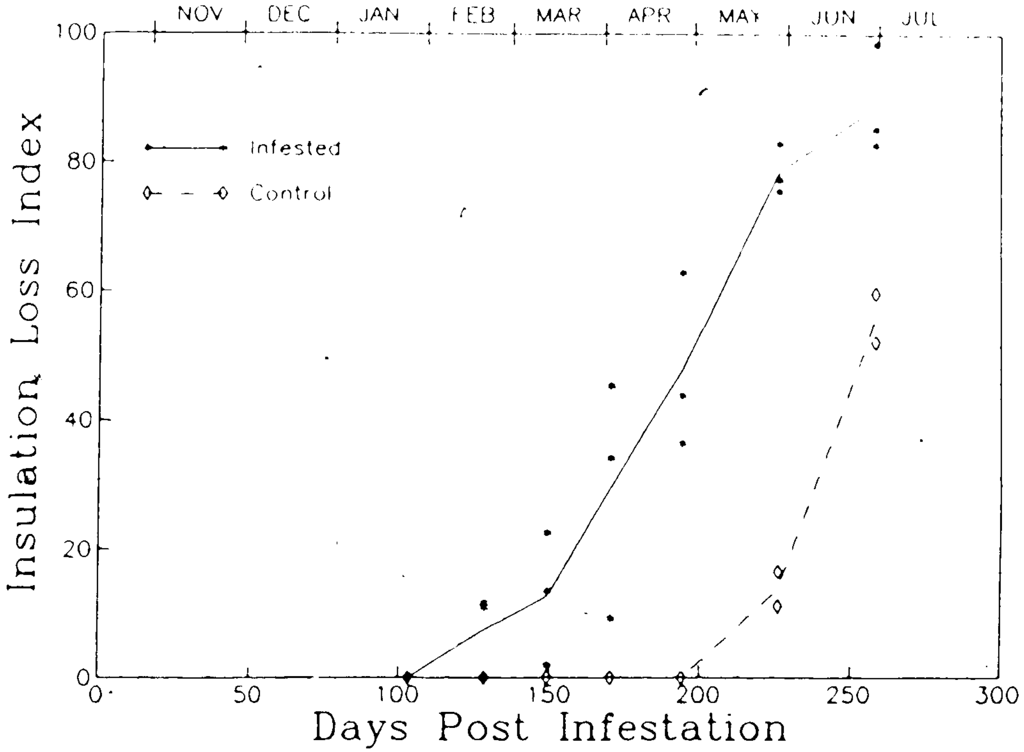

Figure 11. Insulation Loss Index of 3 yearling moose infested with 50,000 D. *albipictus* on September 15, and of 2 uninfested controls.

removed entirely. Two moose (Mo74, Mo75) experienced greater hair loss on one side than the other during the early stages of alopecia. Mo74 showed considerably greater loss of hair on her left side than on her right; meanwhile, Mo75 experienced much more rapid alopecia on her right side. By late April, the disparity between the two sides had lessened for both animals. The influence of this asymmetry on the estimate of Hair Loss Index was lessened by averaging the two sides.

Weight changes

Rates of weight change were similar for all experimental animals throughout the study (Figure 12). Weights remained nearly static, decreasing by only 0.17 kg/day until March. Through March, April, and May, moose in both treatment groups underwent more dramatic weight losses of 0.66 kg/day; by June, all moose had again begun to gain weight. Despite these temporal variations in rates of weight gain or loss, no significant differences were detected between the weight changes of 2 pairs of infested and control moose ($\underline{t}$=1.28, $\underline{P}$=0.23).

Metabolic rates

Fasted metabolic rates remained constant from January to early April then rose to a high in May, falling again in June (Figure 13). Although metabolic rates of infested

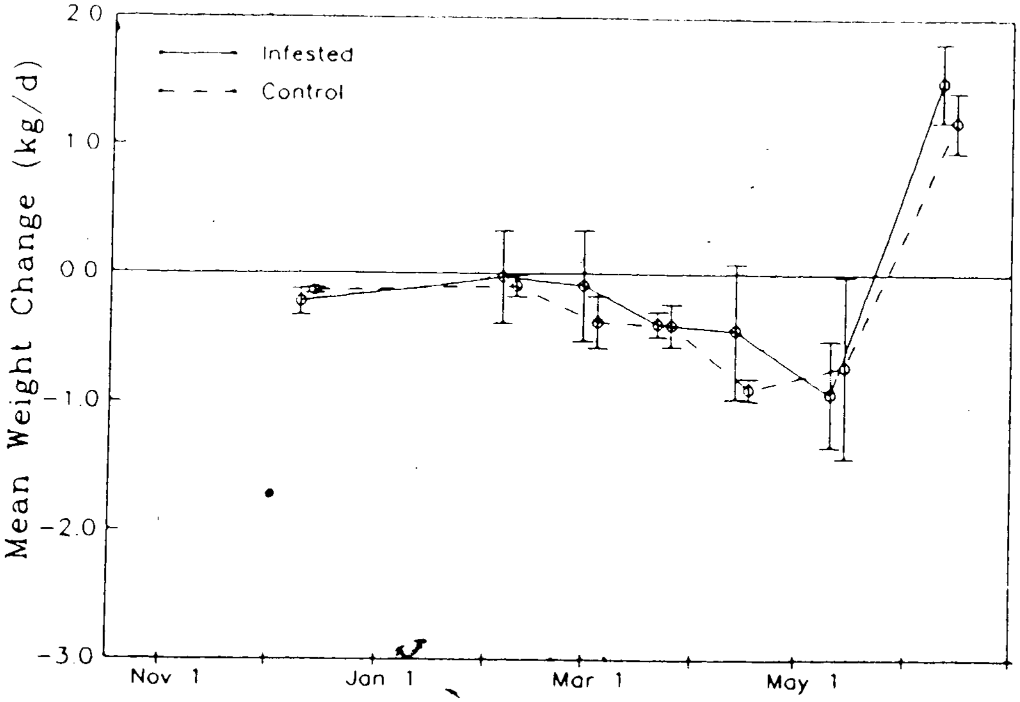

Figure 12. Fasted weight changes of 3 yearling moose infested with 50,000 D. albipictus larvae, and of 2 uninfested controls. (mean ±1SD)

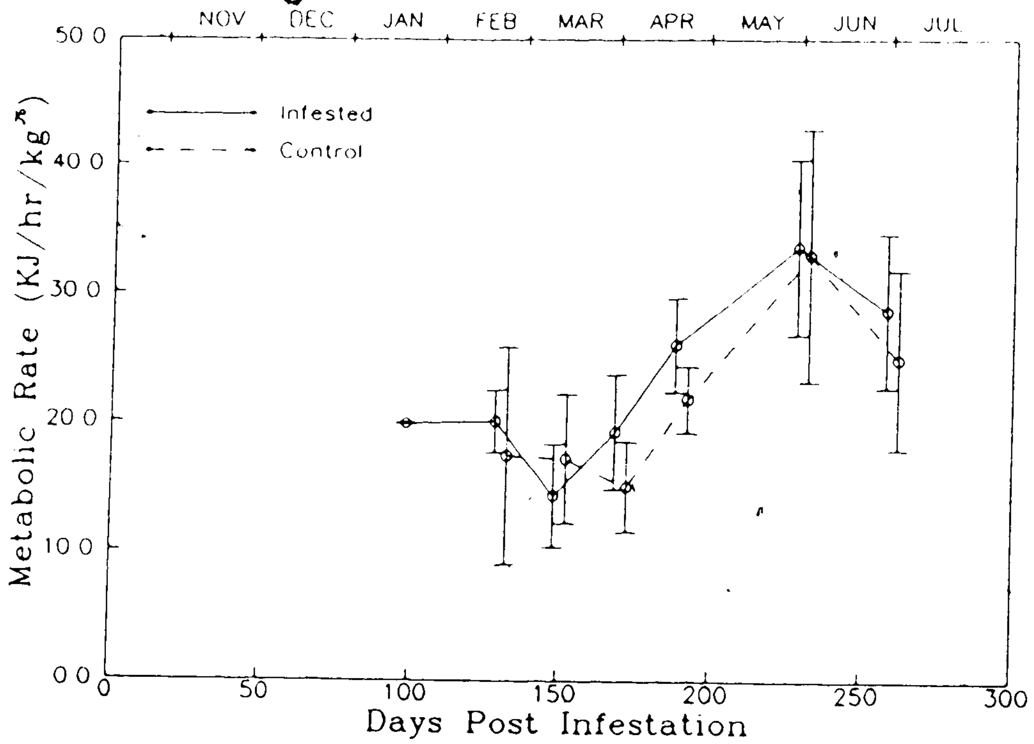

Figure 13. Fasted metabolic rates of 3 yearling moose infested with 50,000 D. albipictus larvae, and of 2 uninfested controls. (mean ±1SD)

moose averaged 10.6% higher than those of control moose, the difference could not be verified statistically. Fasting metabolic rates differed between trial periods (F=15.4, *P*<0.01) but not between treatments (F=0.766, *P*=0.62) or between individuals (F=1.64, *P*=0.5).

prior to March 1

Few measurements of metabolic rates were made at low ambient temperatures. Weather conditions were mild throughout the winter and only during the February trial were temperatures below -10°C. At that time, no difference was detected between the mean metabolic rates of the two treatments (F=0.558, P=0.26). Estimates of fasting metabolic rate during that trial, at -28 to -24°C, were variable but did not appear to differ from estimates made in March at -2 to 3°C. Respiratory minute volumes did not differ between infested and control moose during the February trial (F=1.59, P=0.25).

after March 1

After March 1, fasting metabolic rates were influenced by ambient temperature and by extent of hair loss, but not directly by treatment (Figure 14). The response of metabolic rate to ambient temperatures (T) is approximated by the following formulae for infested (FMRi) and control (FMRc) moose respectively:

$$\mathrm{FMRi} = 17.59 + 0.73T$$

$$\mathrm{FMRc} = 14.77 + 0.77T$$

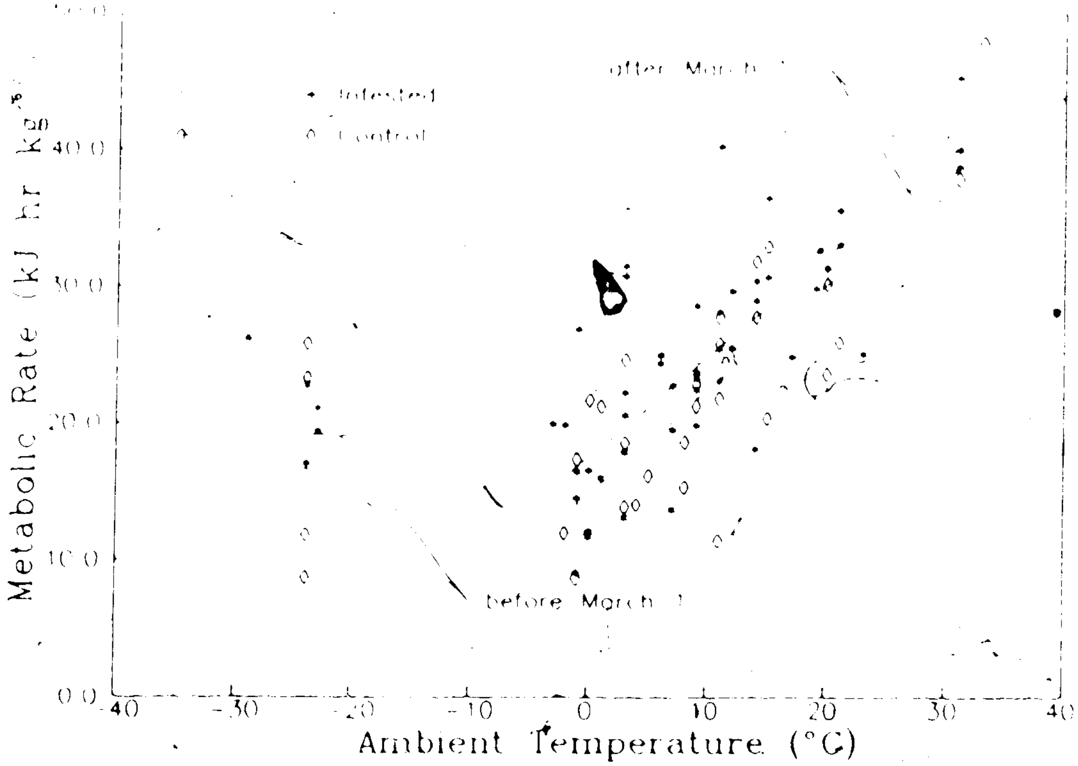

Figure 14. Fasted metabolic rates of 3 yearling moose infested with 50,000 D. albipictus larvae, and of 2 uninfested controls at a range of ambient temperatures.

Although fasting metabolic rates of infested animals appeared to be higher than that of controls, neither the slope (F=0.053, $P>.95$) nor the adjusted means (F=3.623, $P=0.07$) differed between treatments. This lack of direct treatment effect is further corroborated by multiple regression analysis of fasting metabolic rate against treatment and the square of temperature, wherein the coefficient associated with treatment did not differ from zero (T=0.10, $P=0.92$). Only hair loss index (H) (T=4.55, $P<.001$) and temperature squared (T=8.16, $P<0.001$) were significant predictors yielding the following equation:

$$\text{FMR} = 16.82 + 0.0203\text{H} + 0.0886\text{T}^2$$

Respiratory minute volumes and respiration rates of infested moose were depressed after March 1. Respiratory minute volumes of infested (RMVi) and control (RMVc) animals increased exponentially as ambient temperatures (T) rose (Figure 15):

$$\text{RMVi} = 19.30e^{0.077\text{T}}$$

$$\text{RMVc} = 24.53e^{0.069\text{T}}$$

Adjusted mean minute volumes of infested moose were lower (F=4.706, $P<0.5$) than those of controls while the slopes of the curves did not differ (F=0.99, $P=0.35$). A similar pattern of respiration rates of infested (RRi) and control (RRc) yearlings is described by the following equations (Figure 16):

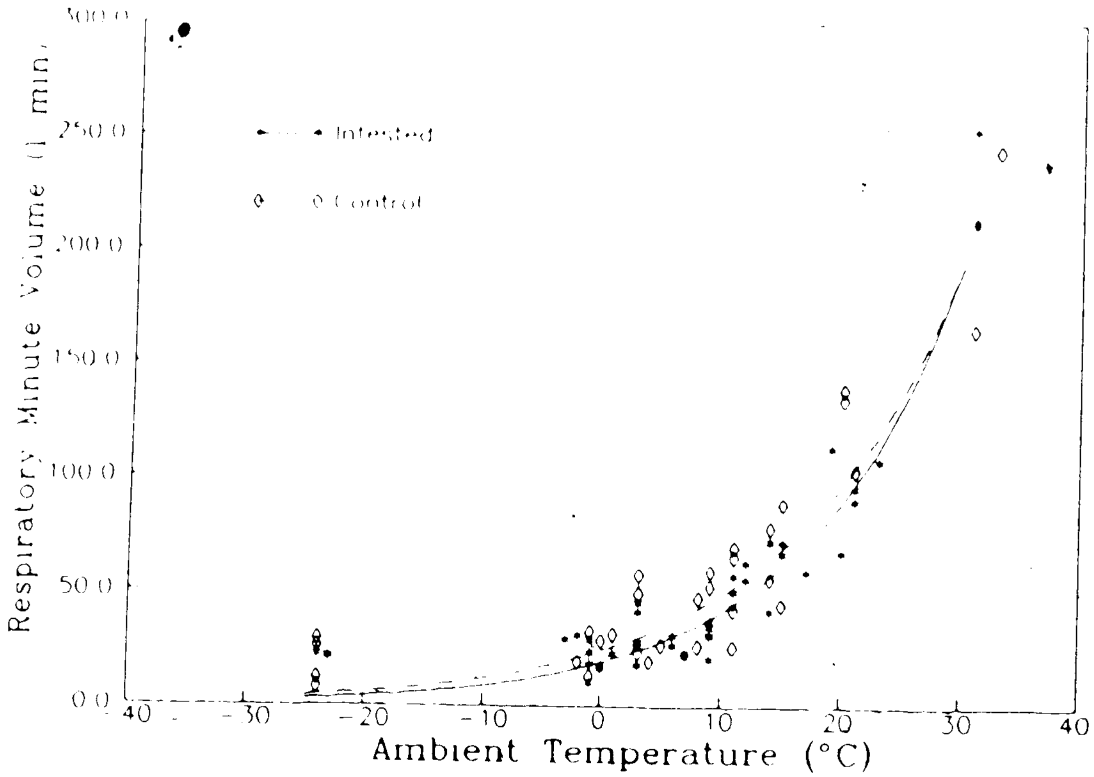

Figure 15. Respiratory minute volumes of 3 yearling moose infested with 50,000 D. albipictus larvae, and of 2 uninfested controls as a function of ambient temperature.

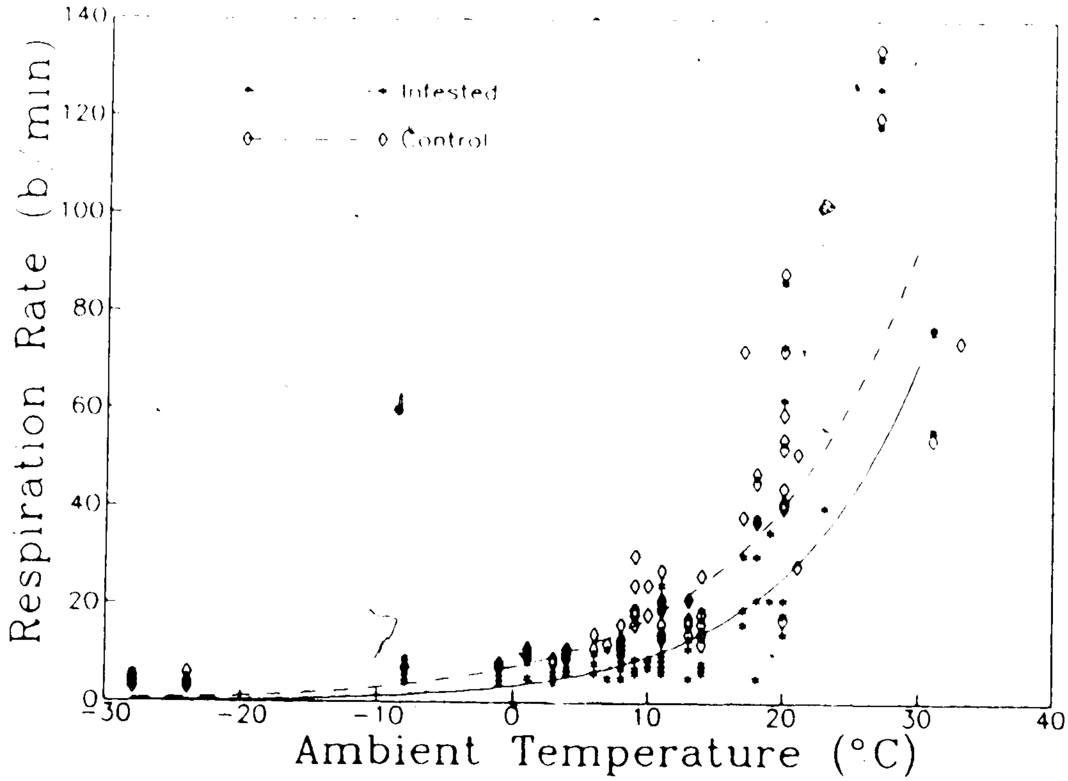

Figure 16. Respiration rates of 4 bedded yearling moose infested with 50,000 D. albipictus larvae, and of 4 uninfested controls as a function of ambient temperature.

$$RRi = 3.49e^{0.10T}$$

$$RRc = 7.39e^{0.085T}$$

As with minute volumes, adjusted mean respiration rates of infested moose were lower than those of controls (F=44.2, $P<0.001$) while the slopes of the two curves did not differ (F=2.74, $P=0.10$).

DISCUSSION

Metabolism and respiration

Metabolic rates estimated in February were the first reliable measurements of fasting metabolic rate after infestation. Hair loss was minimal and ambient temperatures low. At that time, the ticks appeared to incur neither an elevated minimum metabolic rate nor an escalation of thermoregulatory expenditures. The similarity of respiratory minute volumes and respiration rates of infested and control yearlings suggested that either no compensatory heat exchange was necessitated at that stage of the infestation or that adjustments to respiratory volume were not differentially employed by the treatments to regulate heat loss. Although acceptance of the former suggestion would be convenient, insufficient data were collected to reject the alternative explanation.

After March 1, the correlation between hair loss and metabolic rate implies a complex interaction between activity of the ticks and energy expenditure by their moose hosts. The mere presence of ticks did not elevate the metabolic rate of moose, but, as hair loss progressed, metabolic rates of control moose and of infested, alopectic moose diverged.

The first, and intuitively most obvious explanation for the influence of hair loss on metabolic rate is that as hair loss progressed, heat loss was accelerated; hence, heat production was increased to maintain thermal equilibrium. Further support for this suggestion lies in the depressed respiration rates and respiratory minute volumes of infested moose, because they experienced greater hair loss than controls. However, a valid argument can be made against this suggestion. If the elevated heat production is a response to accelerated heat loss (a form of cold stress), then, as ambient temperatures rose above the lower critical temperature, metabolic rate should stabilize, resulting in a convergence of metabolic responses of the two treatments at higher temperatures. Instead, metabolic rate of alopectic moose remained higher than controls, even at temperatures well above the 14-20°C upper critical temperature of moose in summer coat reported by Renecker and Hudson (1986a). Further criticism of this suggestion is that several recent works have shown that moose are generally limited by their ability to shed heat rather than their ability to retain it (Belovsky 1981, Renecker and Hudson 1986a).

An alternative explanation for the parallel escalation of hair loss and fasting metabolic rate is that some third factor changes as the infestation proceeds and independently elevates metabolic rate and accelerates hair destruction. Several potential candidates for this factor are tactile irritation, immunological activity, grooming activity, or some combination of these three. For example, if tactile irritation intensifies as adult ticks engorge, moose will groom more vigorously, producing an expanding alopecia. Meanwhile, the physical activity of grooming while standing can elevate the rate of energy expenditure by 60% of resting metabolic rate (Renecker 1987). The effect of activity on metabolic rate was largely removed by exclusion of any measurements made while the moose were attempting to groom. However, it is difficult to estimate the energetic cost of flicking the ears, quivering of the skin, and the general restlessness exhibited by an infested moose.

No single cause explains the relationship between hair loss, metabolic rate, and respiratory functions. Both escalation of heat loss and elevation of minimum metabolic rate interact to determine metabolic and respiratory functions. A simplified scenario of the interaction between tick infestations, immune responses, metabolic rate, alopecia and respiration can be postulated. As increasing numbers of nymphs, and adults, begin to feed, more antigenic substances are secreted into the skin of the moose. The immune system responds by producing antibodies and mounts a basophilic infiltration in the skin (Allen

1986). The production of immune compounds and the restlessness resulting from the irritation consumes energy, elevating the metabolic rate. The irritation resulting from the feeding ticks and the release of histamines around attachment sites induce moose to groom, further elevating their energy requirements and continually destroying more hair. As alopecia progresses, more heat is lost from the skin surface. In response to this accelerated loss of heat, moose reduce respiratory rates and respiratory minute volumes, and thereby reduce respiratory heat loss, to maintain a constant body temperature. The extent to which infested moose must restrict respiratory heat loss is lessened by the elevated heat production incurred by the ticks.

Thus far, respiration rates and respiratory minute volumes of controls have been considered as normal; by comparison, the lowered respiration rates and respiratory minute volumes of alopectic moose have been referred to as depressed. However, the converse perspective also merits some consideration. For most ungulates, an elevated respiration rate acts to dissipate excess heat (Whittow 1971). Hence, as ambient temperature increases, respiration rate and respiratory minute volume rise, enhancing both direct and evaporative heat loss to the environment. Because ventilation is the result of cyclic contraction of the costal and diaphragmatic muscles, an elevated respiration rate requires additional expenditure of energy. Any additional heat produced by the respiratory muscles must also be dissipated at a further energetic cost, further reducing the efficiency of respiratory heat dissipation. Alopectic moose, because of their reduced surface insulation, need to dissipate less heat across the respiratory surfaces. Because they need not elevate their respiratory rates as dramatically, alopectic moose achieve a double savings; primarily, they expend less energy actively dissipating heat, and secondarily, they are faced with less additional heat produced by the process of dissipation. Therefore, alopectic moose may be at some thermal advantage at temperatures encountered in April and May.

Hair loss and grooming

The minor hair disturbances noted 24 days after infestation (Oct 10) probably resulted from grooming elicited by engorging larvae. Drew and Samuel (1988) suggest that the majority of larvae engorge within 10-14 days after reaching a suitable host; this would result in completion of larval molt by October 1. In the ensuing weeks, the time of nymphal inactivity, the fur returned to its normal loft and showed no signs of breakage from the initial bout of grooming. Two captive moose infested for a third consecutive year did suffer some hair loss during the first weeks of the infestation (Samuel and Welch unpubl. data). However, alopecia resulting from larval engorgement must be infrequent on free-ranging moose, because alopectic moose are rarely seen or killed by hunters in autumn or sighted during mid-winter population surveys. A tentative conclusion can be forwarded that some irritation and grooming does accompany larval engorgement, but in most instances only a transient disruption of insulation results.

The reoccurrence of grooming in February and its resulting hair damage coincided with the terminus of nymphal diapause as reported by Glines(1983), Drew(1984), McLaughlin and Addison (1986), and Drew and Samuel (1988). The timing and pattern of hair loss generally followed those reported by Samuel et al. (1986), with only minor exceptions. No suitable explanation for the asymmetrical alopecia exhibited by Mo74 and Mo75 has been found. This anomaly may have resulted from disparities between densities of ticks on the two sides of each moose. Tick densities were not quantified but cursory inspections revealed numerous ticks on both the lightly and the heavily groomed sides of both moose. These same two moose also developed asymmetrical alopecia the following year after being reinfested with approximately 50,000 larvae (Samuel and Welch unpubl. data).

The extent of alopecia on all four infested yearlings exceeded that experienced by calves infested with 30,000 larvae (Chapter II). The true level of infestation on calves in the present study was probably well below the

30,000 ticks to which each calf was exposed. During the summer of 1984, as much as 75% of the lab colony of tick larvae died after being moved into an environmental chamber equipped with a fan for continuous air circulation. This unusually high rate of mortality in lab reared ticks apparently resulted from desiccation. Sufficient numbers of larvae survived to permit infestations of 30,000 ticks/moose; however, at the time of infestation, the ticks were not as active as normal larvae.

Only 1 of 3 calves infested with 31,000 larvae by Glines (1983) developed alopecia in excess of that experienced by yearlings in the present study. That animal developed very severe alopecia and was killed in February to avoid undue suffering (Glines 1983). It appeared to suffer from an immune complex disease resulting from the tick infestation. Alopecia in the present study exceeded that for Ontario moose calves infested experimentally with 21,000 or 42,000 ticks (McLaughlin and Addison 1986). As far as can be determined, this study deals with the most extensive tick-induced alopecia yet produced on healthy captive moose. Thus, the potential for assessing the impact of alopecia on energy expenditures was high. Unfortunately, mild temperatures throughout the winter precluded the measurement of metabolic rates of cold stressed moose.

CHAPTER IV.

THE IMPACT OF TICKS ON MOOSE SURVIVAL

[illegible] simplified model (Figure 17) summarizes the energy transactions of moose. Energy is acquired from forage by nutrient metabolism. This energy is then utilized for maintenance processes, activity, and production of body or fetal tissue (Stevens 1972). If rate of heat production by these processes is less than the minimum rate of heat loss from the body, or if the heat produced exceeds the maximum rate of passive heat loss, then additional energy must be expended to maintain a constant body temperature. If energy acquisition exceeds these demands, then the surplus may be stored as fat and metabolized at a time when acquisition does not meet demand. Ticks may alter the energy budget of their host by changing the net rates of energy acquisition or expenditure or by causing a reallocation of energy among various pools.

Maintenance energy expenditure

Ticks in the family Ixodidae secrete toxic substances into host tissue as they feed (Riek 1957b, Wikel 1982, Allen 1986). The presence of these toxins can stimulate the release of histamines from basophils in the skin (Willadsen et al. 1979, Wikel 1981) and elevate the production of serum globulins (O'Kelly et al. 1971). Engorging ticks can also cause anemia (Riek 1957a, Glines

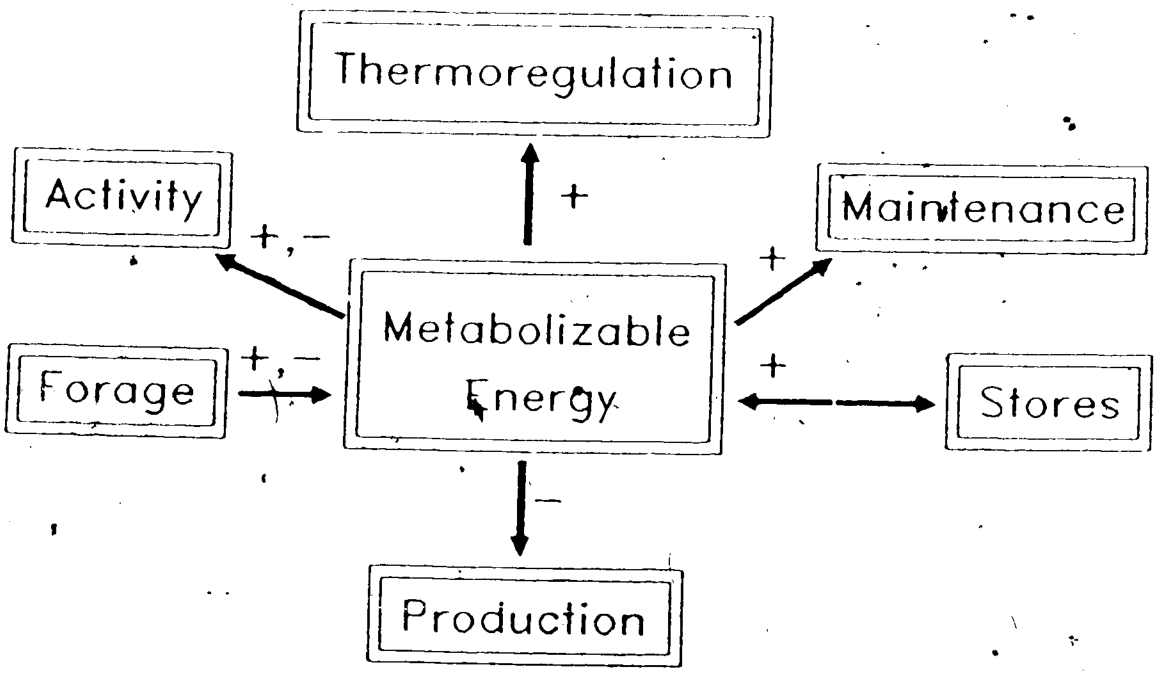

Figure 17. A simplified model of energy transactions of moose showing pathways where <u>D</u>. <u>albipictus</u> may accelerate (+) or retard (-) the rate of energy flow.

1983) and localized tissue destruction. The synthesis of immune compounds, the replacement of lost blood, and the repair of damaged tissue must incur some energetic cost. A more difficult aspect to estimate is the influence of salivary secretions of ticks on the rates and efficiencies of metabolic processes. Seebeck et al. (1971) demonstrated that approximately 2/3 of reduced weight gains of cattle infested with a similar one-host tick, <u>Boophilus</u> <u>microplus</u>, is attributable to the reduction of the hosts' appetite; the remaining weight deficit results from the "specific effects" of the tick toxin. O'Kelly et al. (1971) describe the specific effects on blood composition but provide little further insight into the energetic costs of these effects.

Ticks may elevate the minimum rate of energy expenditure in some instances but the conditions th[illegible] result in this elevation have not been determined. In this study, infestation with few ticks elevated the metabolic rates of calves at temperatures within and above the thermoneutral zone. Possibly the extensive hair loss by yearlings accompanied the removal of a greater proportion of the ticks thereby reducing the effective level of infestation below that experienced by calves. Although this suggestion may be plausible, the scarcity of ticks on the calves makes it an unlikely explanation for the differences between years in the present study.

Thermoregulation

The influence of alopecia on the energy budget of moose is largely dependent on the moose's ability to compensate for the additional heat lost from the skin surface. Below the thermoneutral zone, when heat loss is already minimized, the accelerated loss of heat can only be offset by additional heat production. If alopectic moose are exposed to temperatures within or above the thermoneutral zone, then physiological and behavioral adjustments may partially or completely offset the accelerated heat loss. Therefore, determination of the lower critical temperature of alopectic moose is essential to accurately evaluate the energetic cost of alopecia.

The lower critical temperature of moose in full winter coat probably occurs around -25 to -30 °C where Renecker and Hudson (1986a) report the first signs of piloerection. The lower critical temperature has not been determined for alopectic moose, but metabolic rates of alopectic moose in the present study did not rise when ambient temperature dropped to -9°C.

Free-ranging alopectic moose seldom experience prolonged periods of cold weather because alopecia is rare before March 1. The geographic areas where tick-induced alopecias occur lie south of the -20°C minimum and the -7.5°C maximum March isotherm (Samuel unpubl., Information Canada 1974). Thus, even at the northern reaches of winter tick range, an infested moose may only be cold stressed through part of the day. By April, when tick-induced alopecia reaches its apex, mean minimum temperatures exceed -10°C and mean maximum temperatures exceed 2.5°C (Information Canada 1974). On more southerly moose range (e.g. Alberta) where alopecia is reported most commonly, the climatic conditions are less severe generally. Hence, cold stress may only be a transient problem for moose except during unusually cold late-winter weather.

Most ungulates reduce direct respiratory heat loss in response to cold stress (Parker and Robbins 1985). As moose lose hair, they undergo a similar reduction of respiratory rate and volume. Reduction of evaportative heat loss accompanies an analogous reduction of respiration rate and respiratory minute volumes of sheep after shearing (Hofman and Riegle 1977a,b). Lowered nasal temperatures and resulting retention of evaporative heat has not been demonstrated in moose but probably does occur. Most other northern cervids restrict respiratory water loss when faced with cold stress (Parker and Robbins 1985). Although a decrease in the temperature of air expired by moose would be expected when hair loss is extensive, that relationship has yet to be demonstrated.

The response of a moose's peripheral circulation to tick-induced alopecia is entirely speculative at this time. Lack of insulation on the ears and legs probably results in little net heat loss because circulatory restriction seems to be the major avenue of heat conservation for appendages (Jacobsen 1980). The skin covering the torso, where winter hair is the thickest (Sokolov 1982) and where tick-induced alopecia begins (Samuel et al. 1986) is an uncertain and potentially large avenue of heat loss. Circulation immediately beneath the skin surface may be restricted subsequent to the loss of insulation. This peripheral vasoconstriction would cause a drop in skin temperature. The temperature of bare skin exposed to cold air may fall below that of skin underlying hair. If the skin temperature is allowed to drop, then the skin and underlying tissues form an insulating layer.

At temperatures above the thermoneutral zone, tick-induced alopecia may lessen the impact of heat stress. Uninfested moose retain full winter coats until May and do not completely molt until July (Samuel et al. 1986). During March and April, moose may be subjected to ambient temperatures between 0°C and 25°C. Under these conditions, heat stress would necessitate active heat dissipation. Alopecia may allow more heat to be dissipated from the skin surface thereby reducing thermoregulatory costs associated with respiratory heat dissipation.

Foraging and energy intake

By mitigating heat stress, tick-induced alopecia could conceivably increase the foraging capabilities of moose.

Heat stress depresses feed intake by cattle (Weston 1981). Forage intake by moose in summer is similarly limited by the moose's ability to shed heat (Belovsky 1981). It is therefor reasonable to suggest that hairless moose might be capable of greater foraging rates than are unmolted moose, particularly in April and May when ambient temperature and forage quality are high. If alopecia does enhance intake during spring, then tick-infested moose could partially compensate for earlier energetic losses to the ticks.

Ticks might also reduce net energy acquisition of moose by depressing appetite or by altering feeding behavior of the moose. Cattle exhibit a diminished appetite during infestations of B. microplus, resulting in reduced weight gains (Seebeck et al. 1971). Glines (1983) was unable to demonstrate a similar inappetence in captive moose calves infested with D. albipictus. However, these findings may not be applicable to free-ranging moose. Captive moose were fed a high quality diet (Glines 1983) and spent little time or energy in the pursuit of forage. Free-ranging moose in late winter spend 40% of their time foraging (Renecker 1987) because of the low quality of available forage (Renecker and Hudson 1985). Free-ranging, naturally infested moose at Isle Royal spend up to 12% of their time grooming during late winter, presumably in response to ticks (K. Risenhoover pers. comm.). If feeding time is compromised to allow grooming, moose must consume less forage or spend less time selecting nutritious food items.

Either of these sacrifices would result in decreased energy intake.

Activity

The activity pattern and energetic cost of activity for moose may be altered by ticks. During the engorgement of nymphs and adults, infested moose groom extensively (Glines 1983, Drew 1984). Renecker (1987) estimated that grooming in January while standing requires an energy expenditure of 60% over resting metabolism. If free-ranging moose groom 12% of their day as reported by Risenhoover (pers. comm.) and would otherwise be bedded, then as much as 33 $kJ/kg^{0.75}$ of additional energy may be spent daily (based on a resting metabolic rate of 452 $kJ/kg^{0.75}$/day reported by Regelin et al. 1985). This represents a 7% increase in daily energy expenditure. If feeding activities rather than bedding are foregone to allow grooming, the direct energetic cost may be less, but an opportunity cost of foregone energy intake is incurred.

Tick infestations may have other more insidious influences on the activity expenditure of moose. Infested captive moose remain bedded for shorter periods and spend less time bedded (Samuel pers. comm.). Bedded behavior is the least energetically expensive activity (Renecker 1987). By reducing the amount of time a moose spends bedded, ticks may further increase daily energy expenditures.

Energy stores

Weight dynamics of moose could be affected by tick-induced alterations of the rates of energy acquisition and expenditure. Weight gains of cattle infested with Boophilus microplus are suppressed (Seebeck et al. 1971, Gee et al. 1971), but a similar suppression does not appear to occur in moose infested with D. albipictus (Glines 1983, Drew 1984, McLaughlin and Addison 1986, and the present study). McLaughlin and Addison (1986) have demonstrated diminished fat reserves concomitant with extensive hair loss in moose. Because fat indices are a more direct measure of body stores, they are capable of detecting more subtle differences between conditions of individual animals than are measurements of total body weight. Apparently, infestation of D. albipictus cause some diminution of the energy stores of captive moose. However, this loss of body stores is not profound enough to be reflected in total body weight or weight change measurements. As mentioned earlier, these conclusions may not be applicable to free-ranging moose, faced with nutritional stresses.

Winter tick infestations can exert a variety of influences on the energy metabolism of moose. Net energy expenditure may be increased by elevated maintenance and activity costs and, at cold temperatures, by accelerated heat loss. Moreover, ticks may reduce the rate at which moose acquire energy by directly reducing appetite or by causing moose to spend less time feeding and more time grooming.

Several factors act to minimize the detrimental effect of ticks. Tick-induced alopecia rarely appears before March and only occurs on the southern ranges of moose. Hence, moose suffering extensive tick-induced alopecia are seldom exposed to prolonged cold. When faced with increased heat loss caused by tick-induced alopecia, moose reduce respiratory heat losses and probably restrict heat loss from appendages by circulatory or postural adjustments.

Survival of tick-infested moose

The winter tick is an important parasite of moose in North America (Peterson 1955, Anderson and Lankester 1974). Numerous authors have suggested that ticks alone can cause mortality of moose (Cameron and Fulton 1926-27, Fenstermacher and Jellison 1933, Cowan 1951, Mech 1966, Berg 1975, Addison unpubl.). The opinion inferred in most historical records from Elk Island National Park (reviewed by Blyth and Hudson 1987) is that epizootics of ticks periodically kill numerous moose and elk.

This view is not universally accepted. Ritcey and Edwards (1958) and Peterson (1977) suggest that ticks are rarely the sole cause of mortality but can cause mortality in conjunction with other stressors such as malnutrition or other diseases. This suggestion is supported by recent studies of captive, experimentally infested moose. In total, experimental infestations of 33 moose have been reported (4 by Glines 1983, 10 by Drew 1984, 11 by McLaughlin and Addison 1986, and 8 in the present study). Of these, only one death was directly attributable to tick infestations (Mo35, Glines 1983). Pneumonia, which killed one moose during the infestation and another shortly after the infestation period, may have occurred as a result of tick-induced alopecia or of the weakened state of infested animals (Glines 1983, Drew 1984). The absence of nutritional stress and the infrequency of other diseases may explain the low tick-induced mortality (~3%) in captive moose.

Depletion of energy stores and hypothermia have been suggested as mechanisms by which ticks may debilitate or kill moose (Glines and Samuel 1984, McLaughlin and Addison 1986). McLaughlin and Addison (1986) demonstrated diminished fat reserves in alopectic moose. They proposed that a 30% loss of insulation could result in a doubling of metabolic rate, but qualified their suggestion by exempting all forms of "metabolic and behavioral adaptations". In the present study, alopectic moose were not exposed to the -20°C conditions used in the aforementioned prediction. However, their calculations would predict a 65% elevation of metabolic rate at 0°C. This prediction is considerably higher than the observed elevation of metabolic rate of calves in the present study with approximately 25% hair loss or of yearlings with approximately 75% hair loss. This discrepancy emphasizes the importance of physiological adjustments in mitigating the detrimental effects of winter ticks.

For most moose, infestations of ticks do not appear to incur insurmountable energetic costs. To an individual moose, the additional energy cost of tick burdens are probably important only in conjunction with other stressors. These additional stressors may be human harassment (Addison unpubl.), severe winters (Rolley and Keith 1980), habitat degradation, and other parasites or diseases. Ample circumstantial evidence from Elk Island National Park suggests that heavy tick infestations commonly accompany high moose densities (Blyth and Hudson 1987, Samuel and Barker 1979). This relationship may arise from enhanced transmission of ticks when moose densities are high or from enhanced tick production from nutritionally stressed hosts (Gladney et al. 1973). Overbrowsing and subsequent degradation of moose forage also occurs during times of high ungulate densities (Blyth and Hudson 1987). Forage shortages coincident with heavy tick infestations may contribute to the heavy mortalities of moose that result in periodic declines of moose populations in southern Canada.

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