

Bioenergetic Consequences of Alopecia Induced by *Dermacentor albipictus* (Acari: Ixodidae) on Moose

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ABSTRACT Fasting metabolic rates, respiration rates, respiratory minute volumes, and fasted weights were measured on three yearling moose (*Alces alces* (L.)) (Artiodactyla: Cervidae) infested with 50,000 winter ticks, *Dermacentor albipictus* (Packard) (Acari: Ixodidae), and on two uninfested controls. Infestations produced no detectable effects on fasting metabolic rates or weight changes. The influence of tick-induced alopecia on lower critical temperatures could not be assessed because of warm temperatures during the winter and spring trials. Destruction of winter hair accompanied a reduction in respiratory minute volumes and respiration rates of heat-stressed moose.

KEY WORDS: Arachnida, *Dermacentor albipictus*, moose, alopecia

PREMATURE LOSS of the winter hair coat of moose (*Alces alces* (L.)) (Artiodactyla: Cervidae) infested with the winter tick, *Dermacentor albipictus* (Packard), is well documented (Glines & Samuel 1984, McLaughlin & Addison 1986, Samuel et al. 1986). This tick-induced alopecia develops primarily in March and April and, in western North America, occurs only in the southern half of moose range (Samuel 1989). Infestations of this parasite have been implicated as mortality factors for moose (Cowan 1951, Berg 1975), but data that unequivocally support these suggestions are lacking (Lankester 1987). McLaughlin & Addison (1986) found reduced visceral fat stores in infested moose and hypothesized that this loss of energy stores resulted from escalated heat loss from the denuded skin. We undertook this study to quantify the bioenergetic consequences of tick-induced alopecia.

Materials and Methods

Moose used in this study were raised from neonates at the University of Alberta Ellerslie Research Station in the summer of 1984 (Welch et al. 1985). They were housed in tick-free enclosures throughout the autumn to prevent natural infestation. On 15 September 1985, each of four moose were infested with approximately 50,000 larval ticks. Ticks for a single infestation were separated into three approximately equal clusters. Then, each moose was partially immobilized with xylazine (Rompun; Haver-Lockhart, Miles Laboratories, Rexdale Ontario, Canada), and the hair along the dorsal midline was parted. Individual clusters of ticks were placed deep in the parted hair over the withers, at middle of the back, and 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 min thereafter.

In November, four infested moose and four uninfested controls were moved to the Ministik Field Station, where infested and uninfested moose were kept in separate outside pens and fed a pelleted alfalfa ration. Although all animals were trained to stand tethered, only five remained calm enough to provide reliable measurements of metabolic parameters. Thus, most results are based on three infested and two uninfested moose. Respiration rates of all bedded moose were recorded opportunistically throughout the study.

Moose were not fed for 48-72 h, approximately monthly from January until June 1986. During these fasting periods, metabolic rates of the moose were measured at 6-h intervals using indirect calorimetry; metabolic rates measured after a minimum of 30 h of fasting were included in fasted metabolic rate measurements. While each moose stood tethered in an outside stall (1 m by 3 m), a collection mask connected to one or more weather balloons was placed over its nose. To purge the collection system, gasses were vented from the distal end of the system for approximately 1 min. The vent was then closed, and expired gases were collected for 10 min. If the collection balloons filled in <10 min, as often happened when ambient temperatures rose above 15°C, the collection was ended and the length of the collection period was recorded. A collection was abandoned if the moose was active or became alarmed. Ambient temperature at the time of each measurement was read from an alcohol thermometer inside a Stevenson screen located 20 m from the metabolic stall.

Expired air was analyzed to determine total volume and oxygen content. 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

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Fig. 1. Tick-induced alopecia on moose. Approximately 35% of vi-

Corporation, Sussex, UK). Gas temperature within the gas meter a mercury manometer and an aneroid. Water vapor pressure was measured with a wet-dry bulb thermometer.

At the completion of evening measurements, each moose was weighed, and an anemometer was determined. The percentage of the torso covered by areas of alopecia was used as an index of hair loss. Photographs of each side were taken and a detailed diagram of the alopecia was traced. Because the head and lower legs were covered by hair, those areas were excluded from the analysis. Areas of damaged hair were traced with a digitizer (Bit pad two; Stratistics, Fairfield, Conn.).

The relationships between metabolic rate and hair loss were examined for two periods: when hair loss was minimal, and when hair loss was progressive. Differences between treatment groups and among treatments were tested by nested analysis of variance. Use of Satterthwaite's approximation by unequal sample sizes. Metabolic rates, respiratory rates of infested moose within a range of ambient temperatures were compared by analysis of covariance (SAS 1981); the assumption of

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minute volumes, and (L.) (Artiodactyla: Cervidae) (Acari: Ixodidae) effects on fasting respiration on lower critical temperature during the winter and respiratory minute

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Fig. 1. Tick-induced alopecia on a moose 190 d after infestation with approximately 50,000 *D. albipictus* larvae. Approximately 35% of visible hair on the torso has been damaged.

Corporation, Sussex, UK). Gas pressure and temperature within the gas meter were measured with a mercury manometer and an electronic thermometer. Water vapor pressure was calculated from wet-dry bulb thermometer readings.

At the completion of every fasting trial, each moose was weighed, and an index of hair loss was determined. The percentage of the silhouette of the torso covered by areas of hair damage or loss was used as an index of hair loss. 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 damage was traced. Because hair damage on the head and lower legs was difficult to determine, those areas were excluded from all area measurements. Areas of damaged hair were measured with a digitizer (Bit pad two; Summagraphics Corporation, Fairfield, Conn.).

The relationships between ambient temperature and fasting metabolic rate and respiratory rate were examined for two periods: before 1 March, when hair loss was minimal, and after 1 March to 9 July, when hair loss was progressing rapidly or was extensive. Differences between infested and control treatment groups and among sampling periods were tested by nested analysis of variance (ANOVA); use of Satterthwaite's approximation was necessitated by unequal sample sizes (Sokal & Rohlf 1981). Metabolic rates, respiratory minute volumes, and respiration rates of infested and control moose within a range of ambient temperatures were compared by analysis of covariance (Sokal & Rohlf 1981); the assumption of parallelism was verified

statistically for each of these analyses. Respiration rates and respiratory minute volumes were log-transformed. Daily weight changes were computed for each animal by dividing the weight gained or lost between consecutive metabolic trials by the number of intervening days. A paired *t* test was used to compare fasted weight changes of infested and control moose (Sokal & Rohlf 1981). The death of one control moose left only two pairs for this comparison.

Results

Exposure to 50,000 larval *D. albipictus* induced alopecia on all infested moose (Fig. 1). From late February through April, hair loss proceeded rapidly on all infested moose. Uninfested moose experienced no alopecia and showed no signs of molt until May (Fig. 2).

Rates of weight change were similar for all experimental animals throughout the study (Fig. 3). Fasted weights decreased by only 0.17 kg/d until March. From March until early May, moose in both treatment groups underwent more dramatic weight losses of 0.66 kg/d. By June, all moose were gaining weight. Despite these temporal variations in rates of weight change, no differences were detected between the weight changes of two pairs of infested and uninfested moose ($t = 1.28$, $P = 0.23$).

Fasted metabolic rates remained relatively constant from February to early April, then rose to a high in May and fell again in June (Fig. 4). No difference was demonstrated between fasted metabolic rates of infested and control moose. Fasting

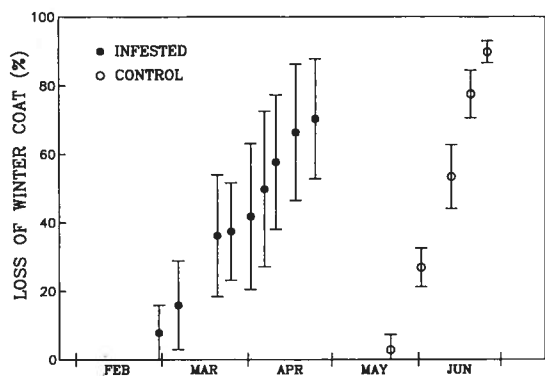


Fig. 2. Proportion of winter hair coat (\pm SD) lost by four yearling moose infested with 50,000 *D. albipictus* and by four uninfested controls.

metabolic rates differed among trial periods ($F = 14.4$; $df = 6, 6$; $P < 0.01$) but not between treatment groups ($F = 1.12$; $df = 6, 68$; $P = 0.38$).

Few measurements of metabolic rates were made at low ambient temperatures. Weather conditions were mild throughout the winter; only during the February trial were temperatures below -10°C . At that time, hair loss was minimal, and no differences were detected between the mean metabolic rates ($F = 0.558$; $df = 1, 8$; $P = 0.26$) or between respiratory minute volumes ($F = 1.59$; $df = 1, 8$; $P = 0.25$) of infested and control moose.

After 1 March, fasting metabolic rates were influenced by ambient temperature but not by treatment (Fig. 5). Although fasting metabolic rates of infested animals appeared to be higher than those of controls, no differences between the adjusted means were detected statistically ($F = 3.324$; $df = 1, 68$; $P = 0.07$).

Respiratory minute volumes and respiration rates of infested moose were depressed after 1 March. Respiratory minute volumes of all animals increased exponentially as ambient temperatures rose

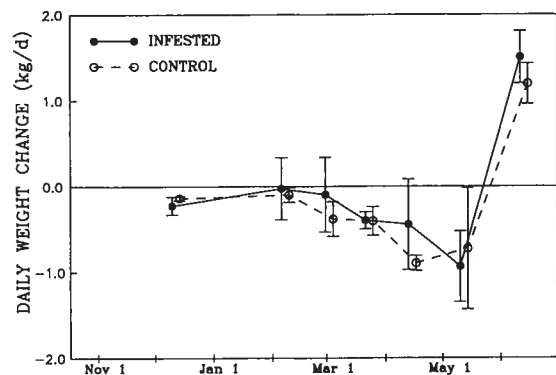


Fig. 3. Weight changes (\pm SD) of three fasted yearling moose infested with 50,000 *D. albipictus* larvae and of two uninfested controls.

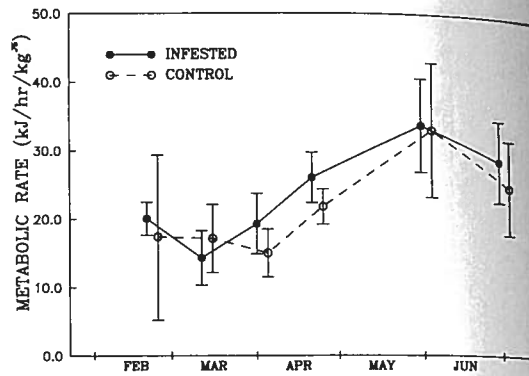


Fig. 4. Fasted metabolic rates (\pm SD) of three yearling moose infested with 50,000 *D. albipictus* larvae and of two uninfested controls.

(Fig. 6). Adjusted mean minute volumes of infested moose were lower than those of controls ($F = 4.706$; $df = 1, 68$; $P < 0.05$). Similarly, adjusted mean respiration rates of infested moose were lower than those of controls ($F = 44.2$; $df = 1, 135$; $P < 0.001$) (Fig. 7).

Discussion

At ambient temperatures of -3 to 33°C , tick-induced alopecia had no demonstrable effect on the fasted metabolic rate of moose. All our measurements of metabolic rates were made at ambient temperatures above the -5°C upper critical temperature reported for moose (Renecker & Hudson 1986). Thus, our measurements reflect conditions of mild to severe heat stress (rather than cold stress) for moose. Under such conditions, excess heat is a liability that must be dissipated; an increased loss of heat from the skin surface reduces the amount of heat that must be dissipated actively.

Depletion of energy stores has been reported in several cases of acarine-induced alopecia. Reduced

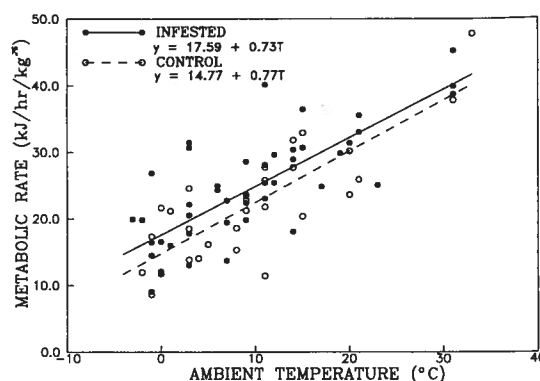


Fig. 5. Fasted metabolic rates of three yearling moose infested with 50,000 *D. albipictus* larvae and of two uninfested controls at a range of ambient temperatures.

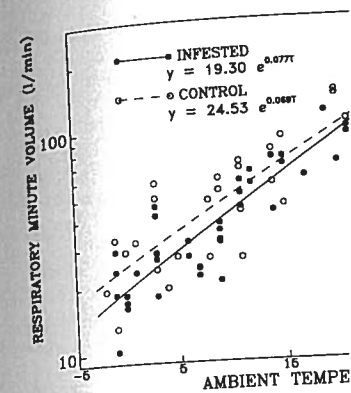


Fig. 6. Respiratory minute volume of moose infested with 50,000 *D. albipictus* larvae and of two uninfested controls at a range of ambient temperatures.

visceral fat has been reported for *Capreolus latrans* Say (Carnivora: *Capreolus*) (Acari: *Sarcoptes scabiei* (L.) (Acari: *Sarcoptes*) (McLaughlin & Addison 1986) and in moose infested with mites (*Psoroptes*) (Acari: *Psoroptidae*) (Cole & Guillot 1987). That escalated heat loss depleted reserves.

For moose that suffer from alopecia, the loss of energy stores is the result of accelerated heat loss at temperatures above -5°C , moose heat must be dissipated actively (McLaughlin & Addison 1986). The depressed respiratory minute volume noted in this study produced a reduced need for respiratory heat. A similar depression of respiration has been noted in sheep (Hofman & Riegle 1981) and in energy expenditures (e.g., acquisition (intake or digestion) by the tick infestation, but we have detected those alterations.

The temperatures at which alopecia was measured during this study were above the conditions that moose encounter in late May and early June in geographic areas where tick-induced alopecia (Samuel 1989) lies south of the -7.5°C maximum. In April, when tick-induced alopecia is common, mean minimum temperatures are -10°C and mean maximum temperatures are 2.5°C (Information from these isotherms lie near the conditions that induce alopecia, most moose encounter less severe climatic conditions).

Tick-induced alopecia increases thermoregulatory costs of moose, but infested moose is rarely

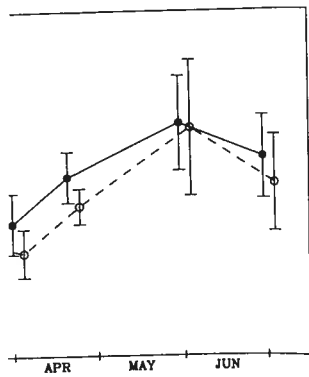


Fig. 5. Metabolic rates (\pm SD) of three yearling moose infested with 50,000 *D. albipictus* larvae and two uninfested controls.

minute volumes of infested moose were lower than those of controls ($F = 4.706$; $P < 0.05$). Similarly, adjusted mean metabolic rates of infested moose were lower than those of controls ($F = 44.2$; $df = 1, 135$; $P < 0.001$).

Discussion

At temperatures of -3 to 33°C , tick-infested moose showed a demonstrable effect on the metabolic rate of moose. All our measurements were made at ambient temperatures above the -5°C upper critical temperature of moose (Renecker & Hudson 1986). Our measurements reflect conditions of heat stress (rather than cold stress). In conditions of heat stress, excess heat is dissipated; an increased loss of heat from the surface reduces the amount of heat that must be dissipated actively.

Energy stores have been reported in moose with tick-induced alopecia. Reduced

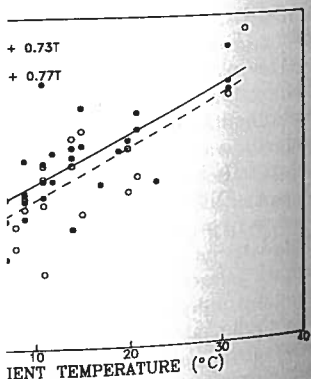


Fig. 6. Respiratory minute volumes of three yearling moose infested with 50,000 *D. albipictus* larvae and two uninfested controls at a range of ambient temperatures.

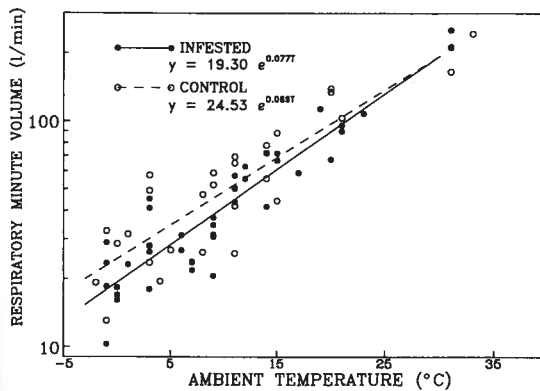


Fig. 7. Respiration rates of four bedded yearling moose infested with 50,000 *D. albipictus* larvae and four uninfested controls.

visceral fat has been reported in coyotes (*Canis latrans* Say) (Carnivora: Canidae) infested with *Sarcoptes scabiei* (L.) (Acari: Sarcoptidae) (Pence et al. 1983) and in moose infested with winter ticks (McLaughlin & Addison 1986). Likewise, holstein calves infested with mites (*Psoroptes ovis* (Hering)) (Acari: Psoroptidae) suffer reduced energy retention (Cole & Guillot 1987). Most authors suggest that escalated heat loss may account for the depleted reserves.

For moose that suffer from tick-induced alopecia, the loss of energy stores may not be simply a result of accelerated heat loss. At most temperatures above -5°C , moose are heat-stressed, and heat must be dissipated actively (Renecker & Hudson 1986). The depressed respiratory rate and volume noted in this study probably indicated a reduced need for respiratory dissipation of excess heat. A similar depression occurs in recently shorn sheep (Hofman & Riegle 1977a,b). Other forms of energy expenditures (e.g., activity) or of energy acquisition (intake or digestibility) may be affected by the tick infestation, but our methods would not have detected those alterations.

The temperatures at which metabolic rates were measured during this study may be representative of the conditions that most free-ranging alopecic moose encounter in late March and April. The geographic areas where tick-induced alopecias occur (Samuel 1989) lie south of the -20°C minimum and the -7.5°C maximum March isotherm; by April, when tick-induced alopecia reaches its apex, mean minimum temperatures over that area exceed -10°C and mean maximum temperatures exceed 2.5°C (Information Canada 1974). Because these isotherms lie near the northern extent of tick-induced alopecia, most alopecic moose probably encounter less severe climatic conditions.

Tick-induced alopecia may impose only nominal thermoregulatory costs on wild moose. Hair loss on infested moose is rarely extensive before March

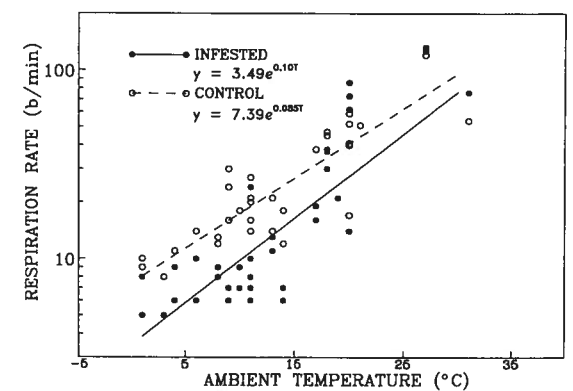


Fig. 8. Respiration rates of four bedded yearling moose infested with 50,000 *D. albipictus* larvae and four uninfested controls.

(Samuel & Barker 1979, Glines & Samuel 1984, McLaughlin & Addison 1986) and, in western North America, occurs only over the southern half of the moose range (Samuel 1989). Therefore, moose that suffer tick-induced alopecia are rarely exposed to prolonged periods of severe cold. At temperatures typical of southern moose ranges in springtime, alopecia may even facilitate the dissipation of excess heat.

Acknowledgment

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Larvae of the V ar (Sipl

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ABSTRACT The ex *Atyphloceras echis ec* lidae) from woodrat genus *Anomiopsyllus* are the adults. Among two ventrolateral set more similar in morph *sylla*, the other genus larvae found in *Neot*

KEY WORDS Inse

THE SYSTEMATICS OF FLEA known among larvae of me lometabolous insects. In the fauna, the lack of larval cha cially acute. Seminal articles val systematics discuss main taxa (e.g., Cotton 1970; Kir'ja 1971; Klein 1964; Vysotska; Wang 1956, 1988). Recent North American fauna inclu (1976) and Smith & Clay (1 large gap in the knowledge by Elbel (in press) will nee additional taxa become kno vae of only 52 of the app North American species (n struct his key of known fa tribes; unfortunately, larv representatives of a numbe and one family (Vermipsyll for examination. *Atyphloc later*, are not identifiable u of two interesting hystric woodrat nests, *Anomiopsi ner*, 1936, and *Atyphlocerc Rothschild*, 1915, are de herein. The taxonomic stat to in this paper follows th rather than that by Smit extent of the Hystrichop scriptions of hystrichopsy by Bartkowska (1965, 19 Haeselbarth (1979a,b), I (1964), and Oudemans (1 vides a good discussion o

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