BEHAVIORAL AND THERMOREGULATORY RESPONSES OF MOOSE TO HIGH AMBIENT TEMPERATURES AND INSECT HARASSMENT IN ASPEN-DOMINATED FORESTS

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ABSTRACT: Heart rate and insect annoyance were studied in hand-reared adult moose (*Alces alces*) cows released into a 65-ha enclosure in April, May, July, and October. Radiant heat load exerted the greatest influence on heart rates of bedded moose in all months. Wind and insects had lesser, but significant effect during April and May, respectively. Respiratory rate was related to ambient temperature showing a dramatic increase above 14°C.

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Moose are well adapted for the cold winters of their northern range. Large body size offers considerable thermal inertia which, combined with effective insulation (Irving, 1966; Parker and Robbins, 1985), provides extreme tolerance to low temperatures. However, even moderately warm temperatures can induce heat stress in moose during both winter and summer (Renecker and Hudson, 1986). The upper critical temperature of white-tailed deer (*Odocoileus virginianus*) (Holter *et al.* 1975), mule deer (*O. hemionus*) (Parker and Robbins, 1984), wapiti (*Cervus elaphus*) (Ward and Cupal, 1979; Parker and Robbins, 1984), and reindeer (*Rangifer tarandus*) (Yousef and Luick, 1975; Ryg, 1983) generally is higher than for moose (Renecker and Hudson, 1986).

Insect activity in northern latitudes is usually associated with warmer temperatures of spring and summer. Biting flies seriously affect activity budgets of caribou (Fancy, 1983; Downes *et al.*, 1986; Murphy and Curatolo, 1987), wapiti (Gates and Hudson, 1981), and horses (Duncan, 1985). Black flies (*Simulium* spp.) (Pledger, 1978) and moose flies (*Haematobosca alcis*) (Lankester and Sein, 1986) disturb moose but, little is known about their impact on daily activity, habitat selection, or physiological responses.

The annual energetic cycle of moose in the aspen-dominated boreal forests of central Alberta has been described earlier using heart rate telemetry (Renecker and Hudson, 1989b). This paper explores the effects of heat and insects on the behavior and heart rate of moose.

METHODS AND MATERIALS

Study Area

The study was conducted at the Ministik Wildlife Research Station, 48 km southeast of Edmonton, Alberta, Canada. The station is on the Cooking Lake glacial moraine within the aspen-dominated boreal forest zone (Rowe, 1972). Surface till deposited by the most recent glacial advances of the Pleistocene has formed an undulating complex of hills and closed depressions. There are numerous seasonal and permanent bodies of water. These wetlands form incomplete drainage systems throughout the area.

Most of the area is poplar forest comprised of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) with lesser amounts of white birch (*Betula papyrifera*). The main understory shrub is beaked hazel (*Corylus cornuta*). Ecotones between communities support balsam poplar, chokecherry (*Prunus virginiana*), saskatoon (*Amelanchier alnifolia*), soapberry (*Shepherdia canadensis*), and western snowberry (*Symphoricarpos occidentalis*).

Sedge (*Carex* spp.) meadows and willow (*Salix* spp.) stands dominate the perimeter of wetlands and sloughs. Stands of cattails (*Typha latifolia*) dominate wetland communities. Upland grasslands are floristically diverse areas in various stages of old-field succession and with clonal growth of trembling aspen and balsam poplar.

Although winters are typically cold and dry, summers are generally warm with a mean June to September temperature of 15°C with daytime maximums of >30°C (Olson, 1985).

Animals

Two hand-reared cow moose were maintained within a 2 ha pasture on a pelleted aspen-concentrate ration (Schwartz *et al.*, 1985) supplemented with hand-cut browse. Their weights ranged from 262 to 387 kg during the study. The animals were both approaching 3 years of age when trials began.

The moose were released into a 65 ha enclosure during April, May, July, and October 1983, to monitor heart rate, respiratory rate, and activity. Before each trial, they were allowed an average of 4 weeks for digestive and spatial adjustment to natural habitats and forage. A total of four 24-hr behavior scans (April 2 and 8, May 27 and 29, July 14 and 12, and October 18 and 8 for moose no. 211 and 727, respectively) were recorded for each animal.

Heart and Respiratory Rates

Heart rate from each moose was obtained from an implanted radio transmitter (model HR13, Wyoming Biotelemetry, Inc.) that relayed a signal to a transceiver neck collar (Model RRF-3, Wyoming Biotelemetry, Inc.). Telemetered signals were monitored by a receiver (TRX-48A, Wildlife Materials, Inc.) and digital data processor (TDP-2, Telonics) connected to a pulse-period to pulse-rate converter (J. Cupal Consulting Engineering) which was installed in a dual channel recorder (TDR-1, Telonics) and was programmed to generate a moving average of heart rate over either 2, 4, or 8 pulses. The setting choice was dependent on signal strength (for example, a moving average of 2 heart rate pulses was selected if the signal was interrupted occasionally after <2 minutes of recording.

While on pasture, heart rate was sampled for at least 10 min (when possible) during each occurrence of a behavioral category on one day using the running average of the strip-chart recording. The speed of the strip-chart was 2.54 cm or one major division/min. Each major division was subivided into 10 subdivisions and a data point was recorded at every crossing of the heart rate trace and a subdivision line. Alternatively, visual sampling of interpulse periods from the digital data processor for a minimum of 1 min was used (each replicate included 10 samples or 1 value for each 10 min except when the activity was <10 min in duration). Mean heart rates in beats per minute (bpm) for specific activities were normalized to body weight-0.25 (Brody, 1945).

Respiratory rates of bedded moose were monitored opportunistically by observation of the expansion and contraction of the thoracic region. Heart rate, behavioral, and environmental measurements were determined concurrently with one min averages of respiratory rate.

Upper critical temperature in this study was defined as the temperature at which metabolism increases in response to heat (Parker and Robbins, 1984). The initial indication of heat stress was defined as that temperature at which respiratory rate increases for the purpose of evaporative cooling (Renecker and Hudson, 1986).

Activity

Activities of each animal were monitored by continuous time-sampling (Jacobsen and Wiggins, 1982) during the eight 24-hr scans. Activities were classed as bedded-ruminating, bedded-dozing, bedded-insect annoyance, bedded-other, feeding, standing, standing insect-annoyance, walking, running, and other

(Renecker and Hudson, 1989b). Insect annoyance was ranked subjectively as: (0) no insects present or on the animal, (1) insects present, however, no apparent influence as indicated by behavior, (2) insects present that cause animal to brush head, flick ears, or shake head to avoid insects but no abrupt change of activity or habitat, and (3) apparent discomfort as displayed by extreme behavior; animals stomp feet, change activity patterns, alter pattern of habitat use, or travel rapidly in attempt to avoid the discomfort of insects. Continuous daily movements of moose were plotted on a 1:5,000 map and then measured at the termination of the 24-hr sample period.

Environmental parameters

During each 24-hr observation period, ambient and black-globe (as described by Renecker and Hudson, 1986) temperatures, wind velocity, precipitation, and a visual estimate of cloud cover were recorded every hour and/or when a behavioral change occurred where the animal was located.

Statistical analysis

From 6 to 11 replicate measurements per animal were used depending on the total number and duration of bedded periods during each 24-hr observation interval. Data from the two moose were pooled in each of the four months. More than one replicate per bedded activity bout was accepted as an independent observation if the bedded period exceeded 1 hr (1/hr) and/or a change in meteorological parameters or insect annoyance were observed

Forward selection, stepwise, multiple regression analysis (Anon., 1986) was used to summarize the relationships between heart rate or respiratory rate with environmental conditions and with insect annoyance. A curvilinear regression was used to describe the relationship between respiratory rate and ambient temperature (Anon., 1986).

RESULTS

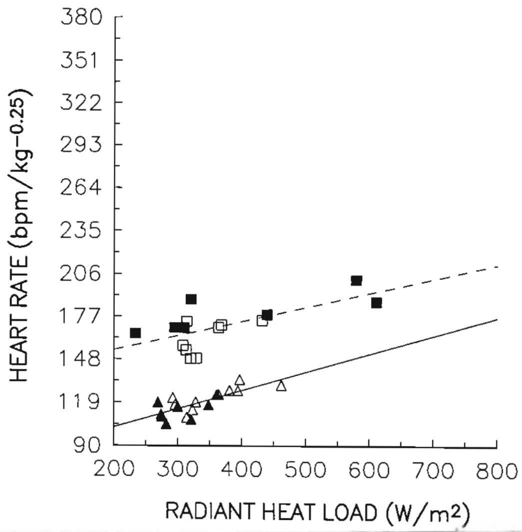
Radiant heat load provided the greatest influence on change in heart rate of bedded moose cows during all months (Fig. 1). Wind ($P = 0.02$) and insect activity ($P = 0.03$) exerted a lesser but significant influence on bedded heart rates during April and late May, respectively. Stepwise multiple regression equations for April and late May were as follows: for April, $Y = 0.15X_1 - 11.95X_2 + 69.8$, $r^2 = 0.73$, $P < 0.01$, $N = 18$, where X_1 = radiant heat load and X_2 = wind velocity; for late May, $Y = 0.127X_1 + 3.97X_2 + 158.4$, $r^2 = 0.80$, $P < 0.01$, $N = 20$, where X_1 = radiant heat load and X_2 = insect activity.

Other measured environmental parameters did not significantly ($P > 0.05$) affect heart rates. Upon stepwise multiple regression of pooled data (animals and months), ambient temperature was the only variable that significantly ($P < 0.001$; $r^2 = 0.69$, $N = 22$) influenced respiratory rate (Fig. 2).

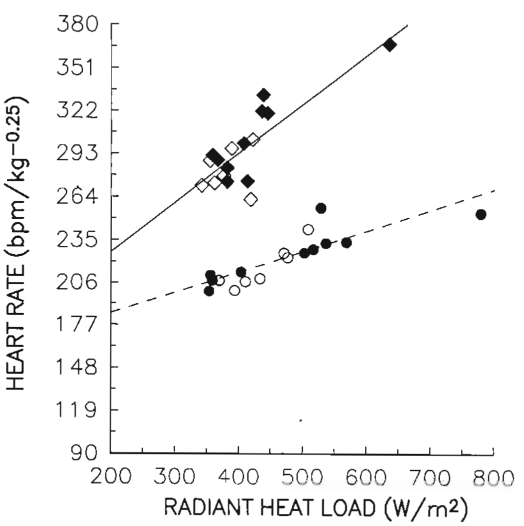
During late May, warm dry weather increased annoyance by horn flies (*Haematobia irritans*), horse flies (*Tabanus* spp.), and deer flies (*Chrysops* spp.) during daylight hours. In response, bedded-dozing heart rates increased by 22%.

During July, heat and insects (primarily mosquitoes) (*Culicidae* spp.) influenced standing, walking, and running activities. Although moose generally were inactive when it was hot, mosquitoes occasionally discouraged bedding or feeding. This harassment was of considerable importance during the brief bedded period, representing a 52% increase in heart rate above bedded-dozing behavior. Insects also forced animals to walk more rapidly while foraging and spend more time walking or running away from areas of high mosquito annoyance. Warm temperatures during midday increased the time spent standing in wetlands. Time engaged in standing, walking, and running behaviors during July (27 ± 1 min/bout of activity) was greater ($P < 0.05$) than the mean of 9.5 ± 3 min/bout

Fig. 1. Relationship between heart rate while bedded in two nonpregnant-lactating free-ranging moose cows and radiant heat load. Open and closed symbols represent data from moose no. 211 and 727, respectively.



a. On April 1 (△) and April 8 (▲) and October 18 (□) October 8 (■) 1983, equations are as follows: for April, —— $Y = 77.51 + 0.123X$, $SE_b = 0.026$, $r^2 = 0.59$, $P < 0.0001$, $N = 18$, for October, --$Y = 135.02 + 0.096X$, $SE_b = 0.029$, $r^2 = 0.46$, $P < 0.01$, $N = 15$.



b. On May 27 (○) and May 28 (●) and July 14 (◇) and July 12 (◆) 1983, equations are as follows: for late May, —— $Y = 156.99 + 0.140X$, $SE_b = 0.020$, $r^2 = 0.73$, $P < 0.0001$, N = 20, for July, -- $Y = 160.59 + 0.331X$, $SE_b = 0.060$, $r^2 = 0.67$, $P < 0.0001$, $N = 17$.

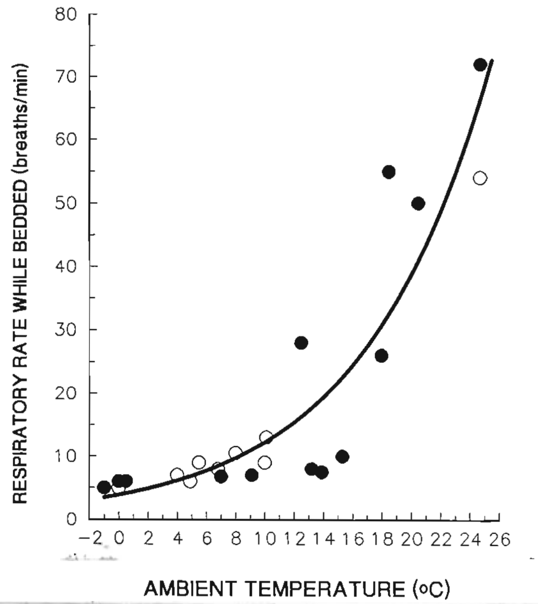


Fig. 2. Relationship between respiratory rate while bedded in two nonpregnant-lactating, free-ranging moose cows and ambient temperature during April, late May, July, and October 1983. Open and closed symbols represent data from moose no. 211 and 727, respectively. Equation is as follows: $Y = 3.868e^{0.115X}$, $SE_b = 0.013$, $r^2 = 0.84$, $P < 0.0001$, $N = 22$.

observed for the April, May, and October sample periods.

Except during April, May, and October, moose were harassed by mosquitoes throughout the day. Only strong winds and unseasonably low ambient temperatures provided much relief. During summer, moose travelled farthest (6,450 ± 940 m/day in July, in comparison to an average of 2,250 ± 640 m/day for April, May, and October) when harassment from mosquitoes was highest and animals moved greater distances between feeding patches. Animals moved more rapidly and longer distances to seek relief. In contrast, harassment from horse and deer flies only occurred during the warm, daylight hours of May and did not cause abrupt changes in behavior.

DISCUSSION

Because of their large body size and effective insulation, moose are extremely cold tolerant (Renecker and Hudson, 1986). This larger size conserves heat and reduces relative energy requirements during winter when the quality and quantity of available forage fail to meet maintenance requirements. However, hot weather appears to be stressful to moose in both winter and summer (Renecker and Hudson, 1986). Habitat selection is one way moose regulate energy balance. Although closed canopy aspen forest during late May and July provided shade and an abundance of high quality forage (Renecker, 1987), it also reduced convective cooling. In contrast, open wetlands imposed warmer ambient and black-globe temperatures but greater wind velocities. Wind and cool water reduced daytime energy costs.

Heat stress increases energy expenditures but suppresses activity, particularly during warm winter days, when animals have maximum thermal insulation and are habituated to cold (Renecker and Hudson, 1989a). When the ability to dissipate metabolic heat is taxed, moose feed in wetland habitats to take advantage of long appendages and the cooling effects of wind and water.

Energy expenditures for various activities were derived using a pooled exponential regression equation which described the relationship between metabolic rate and heart rate that was calibrated in another study ($Y = 4.655e^{0.00071X}$) (Renecker and Hudson, 1985). This equation predicted energy expenditure within 4.2 and 9% of actual values in the same animals and explained >88% of the variation in metabolic rate. Although the animals in this study were not used to generate the equations, heart rate provides the only practical method of monitoring instantaneous changes in specific energy costs of free-ranging animals.

Using heart rate as a predictor of metabolic rate, thermal conditions influenced energy expenditures and activities of moose, especially during warm weather. For example, while bedded-dozing in shallow water during July, calculated energy expenditures declined to 2.9 kJ/hr/kg$^{0.75}$ below the day-time average for bedded-dozing moose on land in shade. Similarly, respiratory rate declined from 26 breaths/min recorded for a bedded-dozing moose on land in shade near midday to 7.5 breaths/min when the moose was bedded-dozing in the sedge wetland. Use of water in cattail stands decreased standing energy expenditures of moose by 6.52 kJ/hr/kg$^{0.75}$ from values recorded for the same animal less than 1 hour earlier standing in nearby willow habitats.

During late May, moose bedded in open habitats exhibited open-mouthed panting (90 breaths/min; 23.3 kJ/hr/kg$^{0.75}$) when ambient and black-globe temperatures approached 26°C and 46°C, respectively. Compared with midday, respiratory rates during bedded-dozing fell to 7 breaths/min and an energy expenditure of 20.1 kJ/hr/kg$^{0.75}$ in early morning (0600 hr) when cooler ambient temperatures (10°C) prevailed. During April, bedded-dozing respiratory rates decreased to 5 breaths/min and energy cost declined to about 10.7 kJ/hr/kg$^{0.75}$ when ambient and black-globe temperatures dropped below -1 and 0°C, respectively.

Low tolerance to high radiant heat loads and ambient temperatures is paramount in daily energy balance of moose, as it can result in refusal of feed, static body weights, or weight loss (Renecker and Hudson, 1986). During summer, standing moose have an upper critical temperature of 14-20°C (Renecker and Hudson, 1986). Ambient temperatures above these limits cause dramatic increases in both energy expenditure and respiratory rate. Although moose may initially select shaded habitats with cooler ambient temperatures, eventually, high daytime radiant heat loads force moose to select wetlands as a temperature control mechanism. Use of wetlands ameliorates thermal stress (Flook, 1955;

Knorre, 1959; Kelsall and Telfer, 1974) and provides refuge from insects.

Moose rely on evaporative cooling to eliminate surplus heat from their body. Activities such as feeding, walking, and running increase levels of generated heat within the body and therefore, further tax respiratory cooling. Moose must then dramatically increase breathing rates to maintain thermoregulation. Alternatively, moose may choose to remain bedded which may result in weight loss because of reduced intake (Renecker and Hudson, 1986; Renecker and Hudson, 1990) or they may occupy wetland habitats.

Smaller ungulates, such as deer, have lower thermal insulation and have developed behavioral and physiological mechanisms for coping with cold. Wapiti avoid the maximum thermal conditions by bedding in shaded habitats (Gates and Hudson, 1981), however, they also have a higher upper thermal limit than moose (Parker and Robbins, 1984). Whereas the large body size of moose relaxes the constraints of cold environments, the stress imposed by heat limits their geographical and ecological distributions (Kelsall and Telfer, 1974). As a result, moose usually inhabit drainages or cool mountain valleys throughout their southern distribution (Telfer, 1988).

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