SHIVERING BY CAPTIVE MOOSE INFESTED WITH WINTER TICKS

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ABSTRACT: Occurence and rate of shivering were measured to assess thermoregulatory responses of captive moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*). Shivering was observed on 47 occasions in 5 of 8 infested moose calves from October to April; in contrast, 4 moose calves not infested with winter ticks did not shiver under identical weather conditions. Only 5 shivering bouts occurred from October to March, all on a single day. The other 42 shivering bouts occurred in April with bouts lasting 1–103 min. During the April bouts, ambient temperature was 1– 4 °C (42 of 42), maximum wind speed was ≤12 km/h (38 of 42), and it was raining (30 of 42). Shivering was associated with 23–44% hair loss in April, but not during cold weather in mid-winter despite 5–10% hair loss in March. Maintaining stable core body temperature during late winter-early spring could compromise the energetic balance of wild free-ranging moose with extensive hair loss and abundant ticks, in conditions equivalent to or worse than measured in this study.

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There are numerous studies and much conjecture as to how winter ticks (*Dermacentor albipictus*) adversely affect moose (*Alces alces*). Effects on growth, food habits, blood composition, and bioenergetics have been studied in experimentally infested captive moose (McLaughlin and Addison 1986, Glines and Samuel 1989, Welch et al. 1990, Addison and McLaughlin 1993, Addison et al. 1994, Addison et al. 1998). Samuel (2004) and Musante et al. (2007) modeled the potential blood loss from winter ticks and concluded that the elevated energy expenditure and protein imbalance associated with blood loss is deleterious to survival of moose calves with heavy infestations. McLaughlin and Addison (1986) speculated that heat loss through winter tick-induced disruption of the hair coat in late winter-early spring may cause accelerated loss of body fat as measured in well fed, captive moose. In contrast, Welch et al. (1990) suggested that hair loss may impose only nominal thermoregulatory costs on free-ranging moose and may possibly facilitate dissipation of excess heat in warm, early spring weather.

Shivering in moose is of interest because it is an involuntary form of thermogenesis that usually occurs when low ambient temperatures (T_a) require an increase in metabolic rate to maintain core body temperature (T_b) (i.e., the lower critical temperature, T_{lc}) (Hohtola 2004). Shivering at or near the T_{lc} has been observed in other cervids (Parker and Robbins 1984). Our objective was to determine under what conditions shivering occurs in captive moose calves infested with winter ticks. This information will increase understanding of the metabolic impacts during late winter and early spring weather when moribund and dead moose with severe winter tick

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infestations are most frequently observed in the wild.

METHODS

The experiments were conducted in Algonquin Provincial Park, Ontario (45° 30′ N, 78° 35′ W) where 13 of 18 calves were captured at <2 weeks of age in May 1982; 5 calves were from other areas in central and northeastern Ontario (Addison and McLaughlin 1993). Male and female calves were paired in each of 6 adjacent pens (29.6 × 16.5 m) located within a mixed forest stand with little undergrowth and a partial canopy (50% cover in summer) of white pine (*Pinus strobus*), white birch (*Betula papyrifera*), trembling (*Populus tremuloides*) and big tooth aspen (*P. grandidentata*). Calves were weaned as described by Addison et al. (1983) and from late October to the end of the experiment were fed *ad libitum* a ruminant ration containing 16% crude protein, 2.5% crude fat, and 6% crude fiber (United Cooperative of Ontario, Mississauga, Ontario, Canada).

Three treatment groups of moose were established: 4 controls without winter ticks, 4 infested with 21,000 winter tick larvae (moderate), and 4 infested with 42,000 larvae (heavy). Where possible, siblings were assigned to different treatment groups. Control moose were sprayed with acaricide (Dursban M., Dow Chemical of Canada Ltd., Sarnia, Ontario, Canada) twice in November and powdered with rotenone in December, January, and February to control accidental infestation by larval ticks. All moose were euthanized at the end of the experiment when their hair was dissolved and hides were checked for remaining ticks (Addison et al. 1979).

Moose were weighed on a calibrated platform scale (Canadian Scale Company Model 7045) approximately every 7 days from 16–325 days of age (Addison et al. 1994). These same 12 moose were used in concurrent studies of hair loss that was measured every 4–10 days from 23 January – 15 April 1983 by measuring the area of hair loss and depth of hair removed (McLaughlin and Addison 1986).

Shivering and other behaviors were recorded simultaneously from 3 observation booths positioned above the back of each of a pair of 6 adjacent pens. Three observers recorded observations of 2 moose in a single pen during a 2.5 h period, after which a second group of 3 observers replaced them. These 2 groups then alternated in successive 2.5 h periods throughout the day; all observations were in daylight hours. The 6 moose observed simultaneously included 2 from each treatment group; subsequently, the remaining 6 moose (2 per treatment) were observed the following day and this process continued until 27–30 h of observations were recorded monthly (October – April) for each moose. Behaviour was recorded in 60, 1-min intervals during 1 h observation periods; 2403 h of observation occurred from mid-October 1982 to mid-April 1983. The T_a, wind speed, and precipitation were recorded at the beginning of each observation period, and those data were attributed to each observation min in that period.

RESULTS

Female and male calves weighed 128 ± 6 and 144 ± 15 kg when 4½ months old in early October and 200 ± 17 and 218 ± 20 kg, respectively, at the end of the experiment at 11 months of age (Addison et al. 1994). The 4 control moose harbored 0, 4, 21, and 85 winter ticks at the end of the experiment, in contrast to 1179–8290 ticks recovered from the infested moose. Forty-two of 47 shivering bouts were observed in 2 individual moose in the moderate treatment group; 29 bouts were by a single moose (M4) (McLaughlin and Addison 1986).

The T_a was relatively mild on most observation days particularly in October,

Table 1. Weather characteristics during monthly observations of captive calf moose infested with winter ticks, Algonquin Provincial Park, Ontario, 1982–1983. Values represent hours of observation during specific conditions; total monthly hours per category may differ due to rounding. The proportional monthly hours of rain are in parentheses.

	OCT	NOV	DEC	JAN	FEB	MAR	APR
Ambient Temperature (°C)							
>0	64	12	10	0	0	33	50
0 to −9	1	48	26	42	19	26	10
−10 to −19	0	0	19	15	25	0	0
−20 to −29	0	0	5	3	10	0	0
−30 to −32	0	0	0	0	5	0	0
Wind Speed (km/h)							
0	7	13	7	28	22	21	25
1–9	5	8	5	5	2	16	3
10–19	24	22	28	25	21	16	21
20–29	24	19	20	2	14	1	9
30–40	1	3	0	0	0	0	0
Precipitation							
Rain	15 (56)	10 (27)	10 (28)	7 (19)	0	13 (57)	26 (84)
Snow	17	27	26	29	7	10	5

November, March, and April. In December – February (the coldest months) there were 59, 18, and 5 h of observations when T_a was −10 to −19, −20 to −29, and −30 to −32 °C, respectively (Table 1). No wind was measured in 123 h of observation, winds 20–40 km/h occurred most frequently in October – December, and there were 14 h of observations in February when wind was >20 km/h (Table 1). Precipitation during observation periods was lowest in February (Table 1). Hours of precipitation were generally similar in September – January and April, with most April precipitation as rain.

No shivering was observed from October – January and in March. One infested moose had 5 short shivering bouts within 35 min on a single day in February; T_a was −10 to −11 °C with wind speed of 12 km/h during 1 bout, and 28 km/h during the other 4 bouts. These bouts averaged 5 min, ranging 1–10 min in length. The other 42 bouts occurred in April and averaged 17.8 min, ranging from 1–103 min in length. The T_a was 1–4 °C, maximum wind speed was ≤12 km/h (38 of 42), and it rained during 30 of the 42 April bouts.

Shivering occurred when moose were standing (n = 25) or recumbent (n = 20), and when both standing and recumbent (n = 2). Other activities during shivering bouts included recumbent with head rested on the ground (n = 9), walking (n = 9), ruminating (n = 8), feeding (n = 4), defecating (n = 4), drinking or eating snow (n = 2), urinating (n = 2), grooming (n = 2), rubbing against other objects (n = 1), trotting (n = 1), and galloping (n = 1).

DISCUSSION

Shivering in moose during relatively warm and often wet April weather is of special interest because it seems inconsistent with results of prior studies. The insulative properties of moose hair are as high or higher than that of any arctic mammal (Scholander et al. 1950), hence cold weather under most conditions would not cause thermoregulatory stress to moose. Increased metabolic rate indicative of moose reaching their winter T_{lc} was not observed from −25 to −30 °C (Renecker and Hudson 1986), and captive, well fed moose calves were almost as cold tolerant as adults (Renecker et al. 1978). Absence of shivering in December, January, and most of February, despite very cold weather, was consistent with metabolic measurements and predictions (Renecker and Hudson 1986). In contrast, certain of our moose had extensive hair loss in April and shivering occurred in some but not all tick-infested moose during relatively mild temperatures in April.

Insulative properties of hair are positively correlated with the depth of hair for many arctic mammals and cattle (Scholander et al. 1950, Bennett 1964). However, wet pelts and skin substantially increase heat loss (Scholander et al. 1950, Holmes 1981) and wind reduces the insulative quality of hair coats (Scholander et al. 1950, Parker and Robbins 1985). Hair loss of our moose was generally ~5% at the end of February, but for most infested moose increased to 23–44% by mid-April. Most shivering was by a single moose with 31% hair loss during rainy and moderately windy conditions in April (McLaughlin and Addison 1986).

Distinct individual variation in shivering was evident as 62 and 17% of shivering bouts were by 2 moose (moderate). It may seem anomalous that only 2 moose in the moderate group shivered the most, whereas only limited shivering was observed in the heavy treatment group. It is possible that the quantity of larval ticks applied in the 2 treatments was not different biologically. For example, hair loss was not substantially different between the moderate (23–31%) and heavy (28–44%) treatment groups. Further, hair loss in the moderate group was highly variable (2–24%) at the conclusion of the experiment (McLaughlin and Addison 1986). Moose also displayed variation in grooming and rubbing behaviors within each of the treatment groups.

Little behavioral response was evident in our tick-infested moose in Alberta during a relatively warm winter and spring (Welch et al. 1990). Only 1 trial occurred below −10 °C, and none below −25 °C, temperatures above the T_{lc} of moose (Renecker and Hudson 1986). It has been suggested that hair loss might have a thermoregulatory advantage by dissipating excess heat during warm spring weather (Welch et al. 1990). Unfortunately, variables affecting thermoregulation such as precipitation, wind, and radiant energy are seldom documented (Parker and Robbins 1985), and lack of standardization in techniques and variable diets are cause for caution when comparing bioenergetic studies of cervids (Renecker and Hudson 1986). In our study, the duration and intensity of wind and precipitation were generally similar in all months except for less precipitation in February (Table 1). The only obvious weather differences between April and the prior 4 months included more precipitation as rain in April and warmer T_a in March and April (Table 1). There was also an exponential increase in hair loss (McLaughlin and Addison 1986) and rapid growth by adult winter ticks in April (Addison and McLaughlin 1988), hence higher blood loss as estimated in previous studies (see Samuel 2004, Musante et al. 2007). Of note is that our experimental moose had >20,000 fewer ticks and much less hair loss at the end of the experiment than measured, on average, on free-ranging moose succumbing to heavy winter tick infestation in Alberta (Samuel and Barker 1979, Samuel 2004).

The greater attrition of fat reservoirs in infested than non-infested moose, despite high quality food, presumably occurred over a period of 1–2 months (McLaughlin and Addison 1986). It is unlikely that the loss of body condition in infested moose could be attributed only to energy demands of maintaining core T_b associated with hair loss. Models developed by Samuel (2004) and Musante et al. (2007) indicate that the energy cost associated with replacing direct blood loss has a substantial metabolic impact during the 2–3 week peak period of female adult engorgement. These energy costs and higher thermoregulatory costs in March and April likely contributed to the reduced body condition of the infested calves as described by McLaughlin and Addison (1986). It is also possible that due to depleted and less oxygenated red blood cells, there is less general motor activity and reduced movement, foraging, and production of body heat in heavily infested free-ranging moose.

Most moose experimentally infested with up to 42,000 larval winter ticks had limited hair loss and did not shiver during cold weather in mid-winter or even with substantial hair loss in spring. When shivering did occur it was for extended periods (hours) in spring, at or above freezing temperatures when moose were wet. The combination of rainy weather and severe hair loss from heavy tick infestation likely has more thermoregulatory impact than recognized previously. Calves with severe hair loss and reduced body fat due to heavy winter tick infestation likely have an elevated T_{lc} in late winter-early spring that could further compromise their survival.

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