ECOTHERMIC RESPONSES OF MOOSE (*ALCES ALCES*) TO THERMOREGULATORY STRESS ON MAINLAND NOVA SCOTIA

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ABSTRACT: The size of the mainland Nova Scotia moose (*Alces alces*) population has declined precipitously over the last several decades and their current distribution is discontinuous. In recognition of the state of its moose population, Nova Scotia declared moose as 'endangered' under Nova Scotia's Endangered Species Act in 2003. A variety of factors have been attributed to the decline, and the goal of this project was to determine whether thermoregulatory stress may be impacting the viability of the moose population. Location and temperature information were collected from GPS-collared moose to test predictions related to whether moose behaviour changes in response to high temperatures. Overall, our results suggest that moose exhibit behaviours (i.e., ectothermy) that are consistent with thermoregulatory stress, but the actual impacts of this, if any, on population productivity requires further study. The greatest response occurred in the summer during both day and night, when moose moved to areas of lower ambient temperature. Further, overall movements were significantly reduced during periods of high temperatures.

The incidence of population declines are increasing due to a variety of factors, most notably overexploitation, habitat destruction, and food chain disruption (Campbell and Reece 2002). Large mammals are highly vulnerable to human exploitation and it has been estimated that less than 21% of the earth's terrestrial surface contains all the large mammals it once did (Morrison et al. 2007). In the northern hemisphere, populations along the southern extent of their species range are particularly vulnerable to climate change (Renecker and Schwartz 1997, Lenarz et al. 2009) and may eventually shift north in response to warming temperatures. These and a suite of other threats have been identified as negatively impacting North American moose (*Alces alces*) populations. Although some North American moose populations are stable or increasing, population declines have occurred in Alaska (Timmerman 2003), Minnesota (Murray et al. 2006), Manitoba (V. Crichton, Manitoba

Natural Resources, pers. comm.), and Nova Scotia (Pulsifer and Nette 1995) which has had closures of hunting seasons as a result (Parker 2003).

The southern range limit of moose may be determined by thermoregulatory stress (Renecker and Hudson 1986) and links between declining populations and increased ambient temperature associated with climate change have been suggested (Murray et al. 2006, Lenarz et al. 2009, 2010; but see Lankester 2010). Marai and Haebb (2010) define heat stress as "the state at which mechanisms activate to maintain an animal's body thermal balance, when exposed to untolerable (uncomfortable) elevated temperatures." Although the initial response may be physiological, behavioural modifications can reduce these physiological stressors (e.g., movement to cooler areas in response to heat stress).

Of all the extant boreal ungulate species, moose are the most likely candidate to suffer

from heat stress due to their relatively low, upper critical temperature limit (-5° C in winter and 14° C in summer; Karns 1997, Renecker and Hudson 1986). In addition to panting to ameliorate thermal stress (Renecker and Hudson 1986), moose often use aquatic areas (Renecker and Schwartz 1997) or forest stands that buffer from extremes in temperature, a form of ectothermy. Such areas of thermal cover (Dussault et al. 2004, Mysterud and Ostbye 2008) could provide conditions that may be as much as 7° C cooler than forest edges (Chen et al. 1995). Demarchi and Bunnell (1995) and Dussault et al. (2004) found that nocturnal activity of moose increased in summer and fall as ambient temperature increased, and use of thermal cover was lower at night suggesting that activity of moose may be inversely related to temperature and/or exposure to solar radiation. In late winter heat stress strongly influenced cover selection as moose tend to avoid areas where the temperature exceeds 8° C (the temperature when panting begins to dissipate heat from the body in the late winter months; Schwab and Pitt 1991). Leblond et al. (2010) suggested that when temperatures are cooler, moose chose areas that had less thermal cover and higher amounts of solar energy. Contrary to these studies however, Lowe et al. (2010) did not find a behavioral response by moose to temperatures in Ontario. They suggested that, within their study area, there were no obvious thermal refugia and that moose either were not impacted by the temperature range to which they were exposed, or the resolution of their measurements were not fine enough to detect a response.

Prior to European settlement of Nova Scotia, it was believed that the local moose population was large (≈15,000; Parker 2003). Approximately 100 years ago, the population on Cape Breton Island was extirpated and the current population was founded by the introduction of moose from Alberta (Pulsifer and Nette 1995). Today, the remnant native population on the mainland has a discontinuous distribution with a crude population estimate of 1000 (Parker 2003). On the mainland, the most significant populations occur in Cumberland-Colchester counties, Pictou-Antigonish counties, and in the Tobeatic Wilderness Area. The last hunting season for mainland moose was held in 1981 (Parker 2003), and in 2003 the population was classified as endangered under the Nova Scotia Endangered Species Act. Currently, there are no reliable demographic estimates or other data that could be used to justify management decisions. Some of the factors believed to be affecting population growth include: parasites such as *Parelaphostrongylus tenuis*, deterioration in the quantity and quality of moose habitat, poaching, predation, and thermal stress (Brannen 2004, Beazley et al. 2006).

The goal of this study was to determine if there is any evidence that moose on mainland Nova Scotia exhibit signs of heat stress. Specifically, our hypothesis was that moose would alter their behavior to reduce physiological stress in response to high temperatures. To assess this hypothesis, we tested 2 emergent predictions: 1) during periods of high temperature moose would select cooler areas, and 2) during periods of high temperature movement would be reduced relative to times when it was cooler. To test these predictions we used data from GPS-collars deployed on moose on the mainland of Nova Scotia, 2002-2006. If our hypothesis is supported, our results may lend justification for further study to quantitatively characterize the population level impacts of increasing temperatures on moose, including population recovery in Nova Scotia.

MATERIALS AND METHODS

Location and temperature data from 12 GPS-collared adult moose from Cumberland-Colchester Counties (n = 5), Antigonish County (n = 1), and the Chebucto peninsula of Halifax County (n = 6) were provided by the Nova Scotia Department of Natural Resources (NSDNR). The GPS collars (Lotek

GPS 2200L; Lotek Wireless Inc., Newmarket, Ont., Canada) were programmed to acquire and store location and temperature data every 2-4 h. Although GPS collars have the advantage of greater location accuracy and resolution in movement dynamics data relative to conventional telemetry (Girard et al. 2002), the ability to record a location at pre-determined times is reduced if the animal is under dense forest cover (Rempel et al. 1995, Moen et al. 1996, Rodgers et al. 1997, Dussault et al. 1999) or on steep slopes (Gamo and Rumble 2000); hence, there is potential for location bias. Regardless, location accuracy was expected to be within 10 m under most conditions and times.

Location data were imported into ArcGIS geographic information system (GIS), version 9.1 (ESRI, Redlands, California) and each location was assigned to 1 of 4 cover types using land-use and forest resource inventory data for the region (interpreted from 1:10,000 aerial photos; NSDNR). The 4 cover types included softwood (75% softwood species by basal area), mixedwood (26-74% softwood species by basal area), hardwood (<25% softwood species by basal area), and other (water and all other land use types that were not forest cover types).

For each prediction we controlled for time of day and season effects by conducting separate analysis during the day and night for each of 3 seasons (summer: 15 June-15 September; early winter: 16 November-14 January; late winter: 15 January-15 April). Further, because individuals were likely to respond to temperature variations in different ways (e.g., due to differences in age, body condition, location, gender, and reproductive status), data collected from each individual were analyzed separately, but global inferences were based on the results from all individuals.

To test our first prediction regarding whether moose selected cooler stands when temperatures were high, we determined the magnitude of the difference between the temperature recorded by the collar and the temperature recorded by the nearest Environment Canada weather station (collar temperature minus weather station temperature; called ΔT) for each record. Positive or negative ΔT values indicated that the animal was in a location warmer or cooler than the temperature recorded at the weather station, respectively. However, complicating this measure was the fact that it was possible that the temperature as recorded on the collar was affected by radiant heat and variation in the degree of shading from the animal. We predicted that the impact of shading might vary between day and night, regardless of season but be relatively consistent all year. Further, we expected the impact of radiant heat would be consistent for these endothermic homeotherms across the range of temperatures experienced by the animal in any one season. However, the impact of radiant heat should be greater in the summer due to the lower insulative potential offered by the summer coat. Therefore, independent analyses were conducted for day and night as well as during the summer, early winter, and late winter to minimize bias. Because of radiant heat, we expected that the collar temperature would be a positively biased measure of local temperature and therefore the power to detect selection of cooler areas based on temperature is reduced. Therefore, we expected our results to be conservative. We did not analyze spring and fall data because of our inability to control for variation in the growth or shedding of the winter coat (Samuel et al. 1986).

To be further conservative and minimize the impacts of equipment malfunction, within each dataset (e.g., summer day data) we first sorted data by ΔT and deleted 5% of the data on each extreme of the continuum so that we only worked with 90% of the data. For prediction 1, we regressed ΔT on the temperature data from the nearest Environment Canada weather station recorded at the same time, or within an hour, for each individual moose. We predicted that if moose were selecting cooler areas during periods of warmth that

there would be a significantly negative slope. Assumptions of regression were confirmed for all analysis via an examination of residuals for normality and homoscedasticity (Sokal and Rohlf 1995).

To test prediction 2 that moose would move less during periods of high temperatures, we divided the range of environmental temperature values for each of the 3 seasons and for day and night into 2 groups with a 7º C range (arbitrarily chosen based on the range of values in the dataset). We did not use the extremes of the temperature continuum because of low sample sizes and we omitted the records with temperature values in the middle of the distribution to ensure there was opportunity to detect variation between the 2 groups, if indeed there was meaningful variation. During the summer, the temperature ranges used were 10 to 16º C for low temperature and 20 to 26º C for high temperature. During early and late winter the temperature ranges used were -11 to -5º C for low temperature and 0 to 6º C for high temperature. When temperatures were within either the low or high range, for each animal, we calculated the average movement distance (i.e., straight-line distance between successive locations) over all 2 h periods for which we had location data. A one tailed t-test was used to test if the distance travelled during periods of high temperature was less than during periods of low temperature (for that season); we used α = 0.05 for decision-making criteria. Where we found evidence of ectothermic response to temperature, we characterized the types of sites where moose were located during these times to better understand site type selection.

RESULTS

We recorded 29,964 locations for 12 moose from 2002-2006.

Summer

We examined the temperature response of 7 moose (3 males from Halifax County and 2 females from each of Halifax and Cumberland County) but we only had 2 h movement data from 5 of these animals (all from Halifax County), as 2 individuals had collars programmed to record data at 4 h intervals.

During the daytime, the slope of the regression lines varied among animals but all were negative and different from zero (all Ps < 0.001). There was also a trend in the response to environmental temperature such that the male response (combined results: Δ T = 8.0 – 0.28 EC temp; P <0.001, df = 1732, β_0 SE = 0.39, β_1 SE = 0.02) was greater than that of females (combined results: Δ T = 4.8 – 0.20 EC temp; P <0.001, df = 1972, β_0 SE = 0.36, β_1 SE = 0.02). During the day all 5 moose moved less (all Ps <0.001) during periods of high temperature than low temperature. The average movement distance during low temperatures was 2.2 X further than during high temperatures (range = 1.8-2.6 X). During periods of high temperature there was a greater proportion of locations in softwood, and a smaller proportion in mixed wood and open areas than during periods of cooler temperatures (Table 1).

At night the slopes of the regression lines for all 7 moose were negative and different from zero (all Ps < 0.001). As in daytime, there was also a trend in the response to environmental temperature by gender, with the response by males (combined results: Δ T = 6.6 – 0.39 EC temp; P <0.001, df = 12552, β_0 SE = 0.47, β_1 SE = 0.03) greater than that of females (combined results: Δ T = 2.9 – 0.24 EC temp; P <0.001, df = 1629, β_0 SE = 0.38 β_1 SE = 0.02). There were far fewer instances (only 5-16 % as many per individual) of high temperature records than low temperature records. There was no difference (P < 0.05) in the movement distance between periods of high and low temperature for 3 of the 5 moose; 2 others (a male and a female from Halifax County) moved more during high temperatures.

Table 1. Proportion (%) of the total locations of 11 moose on mainland Nova Scotia in each of 6 site-types when the temperature recorded at the nearest environment Canada weather station was between 20-26 °C and 10-16 °C, 15 June-15 September, 2002-2006.

Site Type	Temperature		Difference
	20-26 °C	10-16 °C	
Softwood	47.6	39.5	8
Mixedwood	26.1	30.3	-4.2
Open	14.7	19.5	-4.8
Water	7	5.7	1.3
Hardwood	4.5	4.6	-0.1
Other	0.2	0.4	-0.2
# locations	1331	1359	

Early winter

We examined the temperature response of 5 moose (3 males from Halifax County and 1 female from each of Halifax and Cumberland County). During this time we only had 2 h interval location data from 4 moose (all from Halifax County) because the collar for the moose in Cumberland County was programmed to record at 4 h intervals.

During the day the slopes of the regression lines for all 5 moose were negative, but only 4 of these slopes (range of -0.11 to -0.23) were different from zero (P <0.001; the exception was a Halifax County male). One of the individuals for which we have movement data had only 6 records for 'low' temperature, therefore analysis was only conducted for 3 individuals (2 males and 1 female), each with ≥20 records for each of 'high' and 'low' temperature; there was no difference in movement distance between periods of high and low temperature (all Ps >0.05).

At night there was no consistent trend in temperature response among the 5 moose tracked. Regression lines for 2 of the 5 moose (both males from Halifax County) were not different from zero (P>0.05), whereas another male and the female from the same area had positive relationships (P<0.05); a female from Cumberland County had a negative relation-

ship (P<0.05). One of the 4 moose (a Halifax County female) moved more (P<0.05) during high temperature periods; movement distance was not different for the other 3 moose.

Late winter

We had data to examine the temperature response of 11 moose (3 males and 3 females from Halifax County, 4 females from Cumberland County, and 1 female from Antigonish County). However, only 6 animals wore collars programmed to record locations at 2 h intervals; therefore, movement analysis was conducted only with these 6 (2 males and 3 females from Halifax County and 1 female from Antigonish County).

During the day there appeared to be minimal effects of gender in temperature response, but there was a trend with geography. Of the 6 moose (3 males and 3 females) from Halifax County, only 1 (male) had a regression line different (P <0.05) from zero (it was negative). However, each of the other 5 moose (all female; 4 from Cumberland County and 1 from Antigonish) had negative regression lines that were all similar to one another (combined results of 5 non-Halifax County moose: Δ T = 0.51 – 0.17 EC temp; P <0.001, df = 892, β_0 SE = 0.12, β_1 SE = 0.02). During the day we only had 2 h interval location data from moose in Halifax County and one animal in Antigonish. Although 5 of the 6 moose had average movement distances that were less in high temperature periods than low temperature periods, only 3 were different (P <0.05), the 2 females from Halifax and 1 from Antigonish.

There was a geographic trend in temperature response at night in that each of the 5 non-Halifax County moose (all female; 4 from Cumberland County and 1 from Antigonish) had negative regression lines (combined results of 5 non-Halifax County moose: Δ T = -0.50 – 0.145 EC temp; P <0.001, df = 914, β_0 SE = 0.132, β_1 SE = 0.016). Of the 6 Halifax County moose, 3 had regression

lines not different from 0 (P >0.05) and 3 had positive regression lines (P <0.05). During the night there was no difference in the movement distance by 5 of the 6 moose during periods of high and low temperature. One moose (Halifax County female) moved less (P <0.05) during high temperature periods relative to low temperature periods.

DISCUSSION

Annual movement patterns, home ranges, daily, seasonal, and annual temperature regimes and a number of anthropogenic factors affect moose behavior (Andersen 1991, Schwab and Pitt 1991, Courtois et al. 2002, Dussault et al. 2004). In this paper we present evidence from 2 predictions that support the hypothesis that moose on mainland Nova Scotia alter their behavior to reduce physiological stress in response to high temperatures. The extent to which this behavior is able to ameliorate the impacts of heat stress is unknown and would require further investigation. This finding is consistent with Dussault et al. (2004) who suggested that moose spend more time under cover during hot days but come out to feed during cool nights. Contrary to our results, research along the southern extent of moose range in Ontario did not support our hypothesis as moose in their study did not seem to exhibit any behavioral response to increased temperatures (Lowe et al. 2010). They found that there was little variation in temperature trends among site types such that there was minimal, if any, thermal advantage to selecting one site type over another. Instead, they found that animal movement was negatively related to snow depth.

In Nova Scotia, moose did not always display ectothermy by moving to thermal cover at the same temperature threshold or at the metabolic heat stress temperature threshold identified by Renecker and Hudson (1986). For example, during summer nights, based on individual regressions, moose moved to cooler areas when temperatures reached 14°

C, which is consistent with their findings. However, during summer days there was more inter-individual variation and many moose did not move to cooler areas until around 24° C. During early winter days moose tended to seek cooler areas as day temperatures still generally exceeded their upper critical temperature. This pattern is not reflected during early winter nights or in late winter, possibly due to the lack of microclimate variation, indicating that temperature may be similar in all cover types. Dussault et al. (2004) noted that some moose used open, deciduous, or mixed areas even when air temperatures are warm because thermal cover often offers low food availability. Given the complexity of an animal's thermal environment, factors such as wind and solar radiation in combination with ambient temperature presumably influence habitat use and movement.

The temperature patterns were not as distinct in winter as they were in the summer, but we found that moose in winter had a greater than expected use of softwood cover based on availability of this cover type in their home range during times of expected heat stress. This finding agrees with other studies which suggest that during some seasons moose will use certain types of forest cover in disproportion to availability (Cook et al. 2004). There is an assumption that closed canopy forests such as the softwood stands chosen by moose might provide areas with low snowfall amounts as well as thermal cover which makes them an even more attractive choice (Jung et al. 2009).

The moose population on the mainland of Nova Scotia is near the southern periphery of the species range in North America and is listed as 'endangered' due to its low population size. The behavioral patterns we document herein are suggestive of moose responding to increased temperature, and although may indicate heat stress, such thermoregulatory behaviour is not unexpected. Given the concern for certain moose populations at the

southern fringe of their range, it would be prudent for further investigation into the extent to which behavioural thermoregulation (i.e., ectothermy) impacts population productivity. To be cautious, forest managers should be cognizant of, and explicitly address the need to maintain appropriate thermal cover on the landscape that allows moose to use ectothermy to ameliorate the effects of high temperatures at critical times of the year. Further study may also be required to quantitatively characterize the relative ability of different cover types to buffer extremes of temperature.

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