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The spatial variation of extreme tooth breakage in an herbivore and potential age structure effects

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Teeth are essential in mammals for the capture, handling and processing of food and self-defense. The rate of deterioration may affect longevity and indicate certain environmental conditions. The goal of this study was to characterize tooth conditions of moose (*Alces alces*) from multiple regions and to make inferences of possible causes of variation. An assessment of > 5500 moose incisors, found that the frequency of breakage and rate of decline in incisor integrity, with age, was much higher in Cape Breton and Newfoundland (breakage from 6% to 47%) than in New Brunswick, Ontario, New Hampshire, Vermont, and Yukon (breakage from 1% to 6%). Incisal degradation, among jurisdictions, differed significantly though population age structures did not appear different. The two jurisdictions most affected by incisal deterioration, Cape Breton and Newfoundland, are inhabited by genetically distinct subspecies, at higher densities than other regions; therefore, breakage may be linked to local environmental conditions.

Introduction

Teeth have evolved for the purposes of self-defense, capturing prey, and for the handling and processing of food (Orr 1961). Tooth form varies among vertebrates because of differences in feeding adaptations (Romer 1962, Peyer 1968, Popowics & Fortelius 1997). In mammals, teeth are classified as incisors, canines, premolars or molars. Incisors, being in the front of the mouth, are used by herbivores for clipping and gnawing vegetation. Carnivores possess highly developed canine teeth used for securing prey and tearing flesh (Orr 1961). Premolars and molars, collectively termed cheek teeth, display extensive variation in number and shape because of differing food habits (Hildebrand & Goslow 2001).

The ability to acquire food resources and, in some cases, defend against predators is highly dependent upon the presence and condition of teeth; therefore, tooth condition is associated with animal senescence and there is strong selection pressure on teeth to withstand normal wear and tear (Van Valkenburgh 1988, 2009, Fenton *et al*. 1998, Patterson *et al*. 2003). Teeth must maintain foraging and chewing efficiency over the expected lifespan of the species (Janis & Fortelius 1988, Young & Marty 1986, Hindelang & Peterson 1994) and the condition of teeth is influenced by factors such as diet and age (Solounias *et al.* 1994, Fenton *et al.* 1998) and tooth wear is, therefore useful for aging purposes in many species (Fancy 1980, Hindelang & Peterson 1994). Rate of deterioration of teeth varies by species, tooth type, gender and by geographical location due to dietary influence and major and trace element availability (Young & Marty 1986, Van Valkenburgh 1988, 2009, Bibby & Losee 1970, Curzon & Cutress 1983).

Tooth breakage is distinct from wear because the tooth may or may not remain to be effective and may also occur as a result of multiple environmental factors such as diet and usage patterns. However, it is generally accepted that tooth breakage occurs more frequently in carnivores, especially predators that consume bone material (Van Valkenburgh 1988). Plant material consumption does not place as much stress on teeth, thus herbivores have a much lower potential for tooth breakage (Van Valkenburgh 1988).

In Cape Breton, Nova Scotia, a high frequency of incisor tooth breakage has been observed in moose (*A. a. andersoni*) (Clough *et al.* 2006). Though incisor breakage has been documented in Alaskan moose (*A. a. gigas*) for nearly two decades (Smith 1992, Stimmelmayr *et al.* 2006), this was the first report of breakage outside of Alaska and the first report in the *A. a. andersoni* subspecies of moose.

Moose (*Alces alces*) are generalist browsers that consume leafy plants and aquatic vegetation in the summer and woody plants and shrubs in the winter (Renecker & Schwartz 1997, Schwartz & Renecker 1997). To aid in food selection, moose have a narrow muzzle, a prehensile tongue and lips (Renecker & Schwartz 1997). Moose consume browse by placing it into their mouth with their prehensile tongue, cropping it between the bottom incisors and a tough, keratinous pad on the upper lip (Bubenik 1997). Moose have the dental formula (top/bottom jaw) of 0/3 (Incisors) + 0/1 (Canines) + 3/3 (Premolars) + 3/3 (Molars) × 2 sides for a total number of 32 teeth (Bubenik 1997). They have brachydont dentition meaning that the crowns of the cheek teeth are low to accommodate continuous mastication of browse and foliage, including in the winter when browse is often frozen which leads to progressive wear as the individual ages (Bubenik 1997). Browsing and chewing efficiency decreases with excessive wearing and breakage; possibly limiting life span (Bubenik 1997, Ericsson & Wallin 2001).

Previous research on cervid dentition has focused on the progressive wear of molar teeth and the associated life history consequences (Skogland 1988, Hindelang & Peterson 1994, Bubenik 1997, Kojola *et al.* 1998, Ericsson & Wallin 2001, Mysterud 2001, Loe *et al.* 2003, Carranza *et al.* 2004, Loe *et al.* 2006, Veiberg *et al.* 2007a, Veiberg *et al.* 2007b, Carranza *et al.* 2008). A consensus among many of these studies is that tooth condition is suggested to be an important determinant of longevity and senescence (Skogland 1988, Hindelang & Peterson 1994, Ericsson & Wallin 2001, Loe *et al.* 2003, Carranza *et al.* 2004). Individuals with severely degraded incisal conditions likely incur a reduced ability to obtain sufficient forage (Skogland 1988, Kojola *et al.* 1998, Ericsson & Wallin 2001), potentially impairing reproductive success (Ericsson & Wallin 2001) and in the most severe cases leading to gradual malnutrition and increased mortality relative to age (Fortelius 1985). Offspring survival may also be impacted by the inability of a reproductive female, with degraded dentition, to obtain sufficient food resources (King *et al.* 2005) or to maintain sufficient fat reserves (Kojola *et al.* 1998).

The goal of this study was to determine whether effects on survivorship are seen in Cape Breton moose as a result of an increased frequency of incisor breakage. To do so, as historical data are unavailable, we will quantitatively characterize incisor tooth breakage from several North American moose populations. We will examine whether the spatial variation in rate of deterioration of incisors with age and sex can result in significant variation in population age structures. We hypothesize that any interregional variation in population age structure can be explained, at least in part, by rate of deterioration of tooth condition. We assume minimal hunting pressure bias on age structure among these populations. With the exception of a male-only moose harvest regime in the Yukon, hunting strategies within the studied regions (New Brunswick, Cape Breton, Newfoundland, Ontario, New Hampshire, Vermont, and the Yukon) are similar; hunting licences may be issued for either sex or

Fig. 1. The moose incisor characterization conditions categorized by presence or absence of condition; tooth S1420 demonstrates the presence of cracking, S1428 is worn along the occlusal surface as visible by a darker line along the worn edge, S954 is broken.

any age. The given populations are also likely subjected to minimal predatory pressure, with wolves (*Canis lupus*) being absent in all studied populations except Ontario and Yukon, and brown bears (*Ursus arctos*) present only in Yukon (T. Nette pers. comm.). Although we recognize that hunter-derived data are not ideal for the compilation of population age structures they seem appropriate for our study given the following assumptions: (1) hunting biases that may exist are similar among regions, and (2) age-specific mortality threats do not significantly differ among regions (Begon *et al*. 1996).

Additionally, we discuss our results in relation to possible effects of deteriorated tooth condition on reproductive success as well as differences in environmental conditions among regions such as population density and food resource availability.

Materials and methods

Incisors from moose of known age and gender were provided by wildlife officials from Newfoundland, New Brunswick, New Hampshire, Nova Scotia, Ontario, Vermont and the Yukon Territory. The age of each animal was determined by cementum annuli analysis (Sergeant & Pimlott 1959), performed at an external laboratory. The average moose density (moose/km^2), as observed for the 2005 hunting season, was reported for each region.

The primary incisor, the I1, was examined for breakage from all regions. Incisors, after cataloguing, were visually inspected for post-mortem damage which was distinguished by the presence of breakage not accompanied by smoothing and staining along the broken edge(s) of the enamel surface. Damaged teeth were excluded from further characterization. The condition of remaining incisors was characterized according to cracking, wear, or breakage along the occlusal surface (Fig. 1). Teeth with cracks which began or terminated along the occlusal edge of the tooth were recorded as exhibiting cracking. The presence of wear was recorded if tooth dentine was visible along the occlusal surface of the incisor with a characteristic band of discoloration where enamel had worn down. Breakage, distinguishable from post-mortem tooth damage, exhibited rounding of edges formed from breakage as well as staining along the newly formed occlusal surface of the tooth.

To quantitatively characterize cracking, among regions, the length of all cracks on each tooth was summed and the average total length taken, by region, for those teeth which were well formed (mature) and did not exhibit excessive wear or breakage (incisal depth between 6 and 8 mm). Though broken teeth were excluded from the measure, this restriction on incisal depth was to avoid introducing bias by measuring cracks across an incomplete occlusal surface and comparing to the sum of measures taken on a tooth with a wider, complete, occlusal surface. The length of each crack terminating along the occlusal (cropping) surface was measured with a digital caliper. Additionally, the total number of cracks present on each tooth was averaged for all

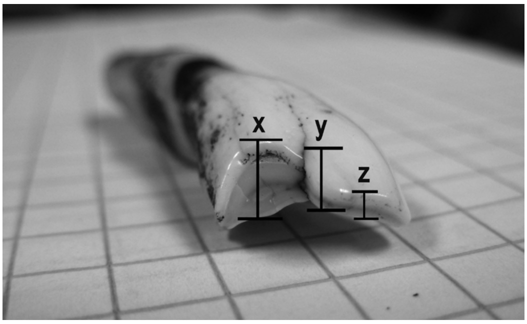

Fig. 2. Method of incisal depth quantification for use as a proxy for moose incisor tooth condition as a function of broken and worn surfaces; *x* + *y* + *z* = incisal depth (mm); measurements will be of a higher magnitude when surface is broken, as shown in *x*.

teeth within each region. An incisal depth measure was developed to quantify the functional impacts on incisor integrity of the cumulative effects of wear and breakage. Incisal depth was calculated as the sum of the depth of the tooth (front to back), 2 mm below the occlusal surface, in three locations across the surface; at 1/3, 1/2, and 2/3 the distance across the tooth's occlusal surface (Fig. 2). Larger values for incisal depths were associated with excessive wear and/or breakage; generally, a less effective tooth with compromised integrity and an uneven surface for cropping. Characterization of incisors was performed consistently for all teeth.

To test whether the rate of deterioration of incisal depth with age differed between genders, a test of single covariate homogeneity of slopes (Borich 1972) was conducted for each region using incisal depth as a dependent variable, age as an independent variable, gender as a categorical classification and an interaction term, sex × gender. If a significant interaction existed, further consideration would treat males and females independently.

To assess the spatial variation in the relationship between incisal depth and age, linear regressions were constructed for each region. The slope coefficient (β_{Age}) and associated standard error measures from each region were used in conjunction with estimates of breakage frequency to characterize the tooth condition. To formally test spatial variation we conducted test of homogeneity of regression slopes among regions. All statistics were performed using SYSTAT (ver. 11.0, Systat Software Inc., Richmond, California, USA).

The population structure, among regions, was qualitatively characterized with static survivorship curves constructed with age data from hunter-killed moose to assess whether there was any meaningful level of variation. Hunting behaviours in each region were assumed to be similar.

Results

There was significant spatial variation in wearing and breakage in moose incisors among regions (Fig. 3). For example, frequency of breakage within the entire sample ranged from 1%, in Ontario, to 47%, in northern Newfoundland (Fig. 4). Wear, occurring less often than breakage or cracking, ranged from 3%–41% across populations surveyed. The frequency of tooth crack presence was high in all regions, thus the total crack length measures were more valuable in assessing regional differences. For incisors with a depth of between 6 and 8 mm, the average total length of incisor cracks ranged from 5.8 mm to 12.1 mm (Table 1). The average number of cracks per tooth in within each region ranged from 2.2 to 3.8 (Table 1). While there was a weak positive association ($r^2 = 0.107$) between average total crack length and frequency of breakage among regions, the association was stronger for total number of cracks and frequency of breakage within regions ($r^2 = 0.457$).

The homogeneity of slopes test including the gender × age interaction term indicated that incisal depth with age did not significantly depend upon the gender interaction ($p > 0.05$, in all regions). Therefore, further analysis considered males and females together in each region.

In New Brunswick, New Hampshire, Ontario, and Vermont, breakage ranged from 1% to 6% and the slope of regression lines of incisal depth with age ranged from 0.21 to 0.29, averaging 0.25 (SE = 0.05). The regions with increased frequencies of breakage, northern Cape Breton and Newfoundland, are grouped together in a plot of all regression lines (Fig. 5). The slopes of regression lines for these regions ranged from 0.40 to 0.56 (SE = 0.03).

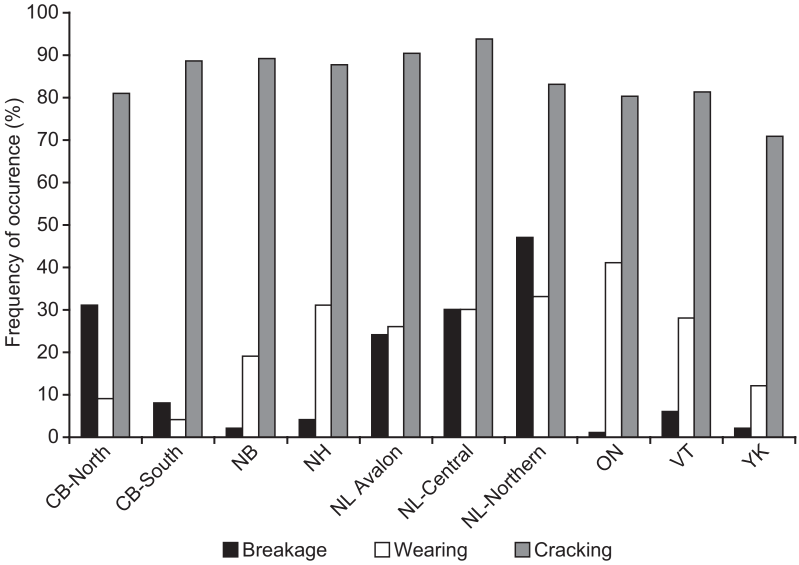

Fig. 3. The frequency of moose incisor breakage, wearing, and cracking, by region, for animals harvested from 2004–2007, with all age classes and gender combined. CB = Cape Breton, NB = New Brunswick, NH = New Hampshire, NL = Newfoundland, ON = Ontario, VT = Vermont, and YK = Yukon.

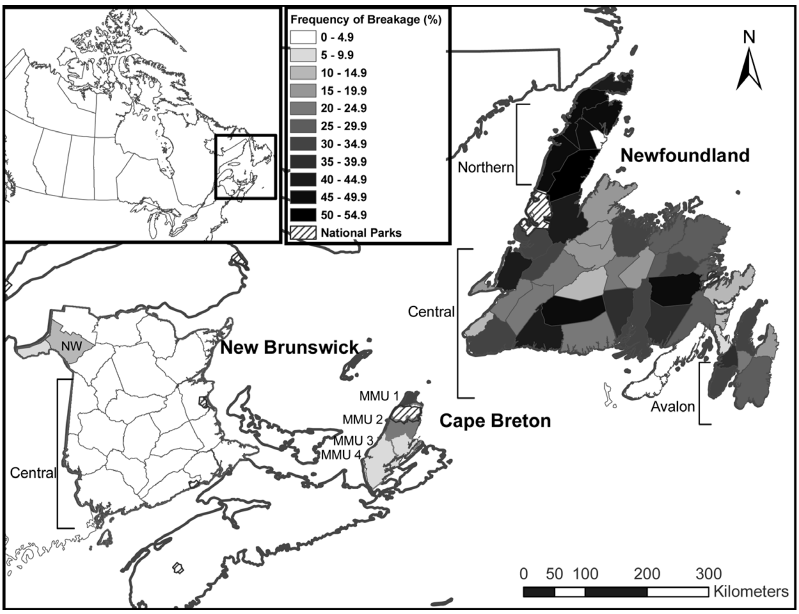

Fig. 4. The spatial variation in the frequency of moose (*Alces alces*) incisor breakage in Atlantic Canadian regions for animals harvested from 2004–2007, with all age classes and genders combined. GIS data sources: New Brunswick Department of Natural Resources, Nova Scotia Department of Natural Resources, Newfoundland Department of Environment and Conservation: Wildlife Division, and the Maritime Provinces Spatial Analysis Research Center.

The overall frequency of breakage in New Brunswick was 2%; however, in the northwest area of the province (management zones 1 and 2), a breakage frequency of 11% was present in the teeth examined. In Cape Breton, a south to north gradient of increasing tooth deterioration was present when each moose management unit (MMU) in the region was considered separately. The slope of the regression lines ranged from 0.29 (SE = 0.05) in the south to 0.51 (SE = 0.04) in the north, corresponding to an increase in breakage from 6% to 34% in the north. The slope of the relationship between incisal depth and age, in Newfoundland, ranged from 0.40 (SE = 0.03) in the Avalon region (where breakage occurred in 24% of the samples) to 0.56 (SE = 0.03) in the northern region of the province (breakage in 47% of moose). The test of homogeneity of slopes indicated that the regression slopes, representing the extent of deteriorated

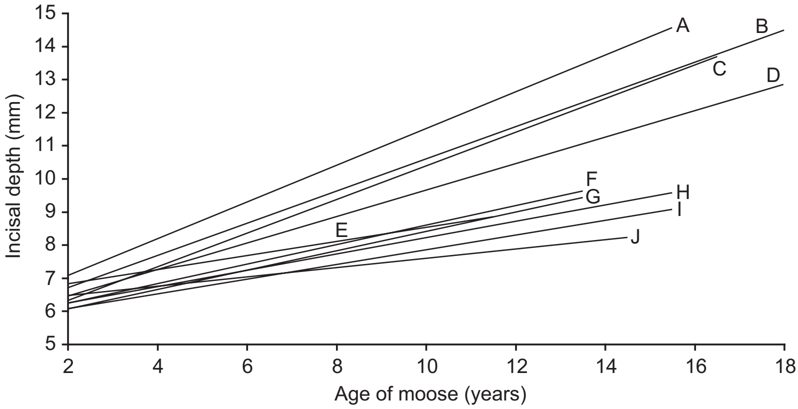

Fig. 5. Regression lines of moose incisal depth and age, by region, where A–D are areas of increased frequencies of breakage and E–J represent regions where the frequency of moose incisor breakage is < 6%. A: Newfoundland Northern, B: Newfoundland Central, C: Cape Breton North, D: Newfoundland Avalon, E: New Hampshire, F: Cape Breton South, G: Ontario, H: New Brunswick, I: Vermont, and J: Yukon.

tooth condition with age, differed significantly among regions ($p < 0.001$).

Visual assessment of survivorship curves (Fig. 6) suggest that longevity and age structure of moose among regions is similar, despite variation in inter-regional tooth condition.

Discussion

There was spatial variation in the frequency of tooth breakage among the North American moose regions surveyed (Fig. 4) that was not significantly related to cracking, wear, or gender.

Table 1. Moose (*Alces alces*) locations, sampling season(s), measures of tooth condition and results of simple linear regressions (β_{Age} and associated SEs) of incisal depth (ID) as a function of age in multiple North American moose regions.

Region	*n*	Frequency of breakage (%)	Frequency of wear (%)	Average cracking distance (mm)[1]	Average number of cracks per tooth	Regression		
						β_{Age}	SE	r^2
New Brunswick								
Northwest	110	11	16	5.8	2.2	0.34	0.05	0.32
Central	2350	2	20	4.4	2.3	0.25	0.01	0.36
Cape Breton								
MMU1	288	34	12	12.1	2.7	0.51	0.04	0.42
MMU2	177	25	6	12.1	3.0	0.48	0.04	0.41
MMU3	85	9	6	9.2	2.8	0.29	0.05	0.28
MMU4	72	6	3	7.8	2.4	0.30	0.06	0.26
Newfoundland								
Avalon	350	24	26	10.4	3.8	0.40	0.03	0.39
Central	927	30	30	9.2	3.4	0.49	0.02	0.38
Northern	423	47	33	9.0	3.1	0.56	0.03	0.42
Ontario	97	1	41	7.3	2.2	0.29	0.02	0.57
New Hampshire	81	4	31	6.4	2.7	0.21	0.03	0.36
Vermont	501	6	28	6.6	2.2	0.22	0.01	0.37
Yukon	41	2	12	15.5	2.4	0.14	0.04	0.24

[1] To control for breakage-induced variation, only cracks on teeth with incisal depth between 6 and 8 mm were summed and averaged by region.

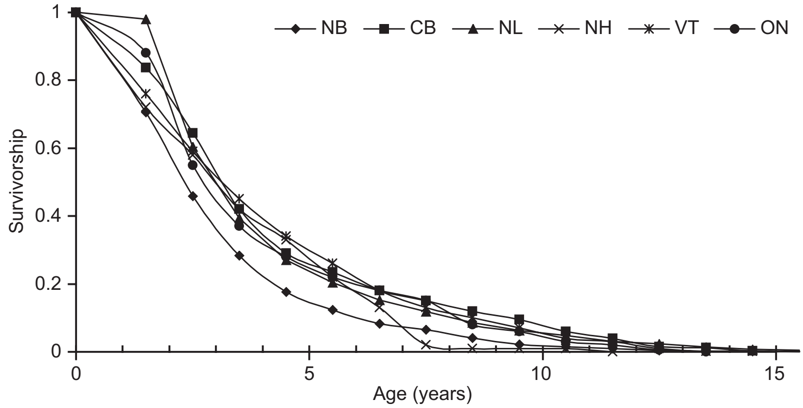

Fig. 6. Survivorship curves of moose *(Alces alces)* populations from eastern North American regions using data acquired by age determination of hunter harvested individuals from 2004–2007.

High levels of breakage had previously been reported in Alaskan and Cape Breton populations (Smith 1992, Clough 2006, Stimmelmayr 2006). In this study, we report that high levels of incisor breakage also occur in Newfoundland moose populations. The frequencies of moose incisor breakage in Newfoundland and northern Cape Breton are much higher than all other regions examined in this study and thus appear to be anomalous for a herbivorous species. Cracking and wear of the occlusal surface, increasing in severity from use over the individual's lifetime, appear to be naturally occurring processes; however, it is possible that cracks extending deep into the enamel layer of teeth may reduce the integrity of the tooth thus leading to breakage and an overall decrease in incisal condition. Also, the total number of cracks is more closely related to breakage than the total cracking distance on a tooth; multiple cracks may lead to an overall decrease in ability to withstand stress. Among regions, differences in food and nutrient sources may explain the earlier onset of declining incisal condition, extent of cracking, and the likelihood that cracked teeth become broken teeth. A comparison, among populations, of molar condition may provide insight into the differences in diet of the given populations. It may be expected that individuals with markedly worn molars may consume diets composed of foods that are unsuitable or otherwise require disproportionate mastication while individuals obtaining nutrients from sources such as mineral licks may be expected to exhibit less wear on cheek teeth.

The age structures among regions; however, were similar despite variation in incisor condition. The proportion of hunter killed moose in older age classes was also similar. As we assumed that hunter biases were similar among regions, we would have expected fewer older individuals in regions of extreme breakage if survivorship was affected by deteriorated incisal condition. Since this was not true, the hunter-derived data do not support the contention that deterioration of incisor condition reduces survivorship in Atlantic Canadian moose. In this study, we assumed that hunting and non-hunting mortality biases were similar among regions; it is possible that these age structures may, in fact, be influenced by such factors as hunter biases, differences in predation, fecundity or disease prevalence among regions.

It was hypothesized that incisor breakage would exert an effect on reproductive success only where the frequency is extremely high, such as that seen on the northern peninsula of Newfoundland. Tooth anomalies have been found to exert a larger effect on female body condition than male condition (Loe *et al*. 2006). In a healthy population, female moose fecundity has been found to decrease as the individual ages beyond 12 years (Ericsson *et al*. 2001). Therefore, the incisal depth of a 12 year old moose in a population unaffected by elevated incisor breakage may represent the upper limits of tooth quality necessary for obtaining the nutrients required to ensure reproductive success. According to linear regressions in this study, the average female moose in northern Newfoundland has an incisal depth greater than 10 mm by the age of 7, whereas females in regions without abnormally high frequencies of breakage do not exceed this depth during their reproductive years (i.e., < 12 years old). It was not found, however, that the proportion of younger individuals in regions of frequent breakage was different than the proportion found in unaffected populations. There may be multiple explanations for this. Offspring survival may not be impacted by degraded incisal conditions as nutrients required for development may not be limited, effects were not detected at this time, using these methods, or, possibly, younger individuals are overrepresented in the data set for affected regions as a result of their higher susceptibility to hunting, a potential result of higher movement rates (Courtois *et al*. 1998).

Each region affected by elevated frequencies of breakage, Alaska, Cape Breton, and Newfoundland is populated by genetically distinct moose subspecies (*A. a. gigas, A. a. andersoni,* and *A. a. Americana*, respectively). Excessive breakage was not found in this study, or reported elsewhere, to be present across the entire range of each subspecies, therefore; it appears that breakage is unlikely to be attributed to genetic factors. This suggests that environmental factors may be more important in causing the breakage patterns found in this study. Moose incisor breakage previously documented in Alaskan moose was suggested to be a result of environmental factors; more specifically, lower food quality as a result of high moose densities (Smith 1992).

We propose two hypotheses to explain the deterioration of tooth condition in Cape Breton and Newfoundland moose that are not mutually exclusive: (1) high mechanical stress is placed upon the teeth, possibly through the consumption of larger diameter browse or (2) the quality of diet is insufficient to enable the formation of strong teeth able to withstand normal use. It is possible that both hypotheses are related to high densities of individuals and the subsequent lack of suitable (easily obtained and nutritious) food resources.

Ungulate densities that exceed carrying capacity may lead to an increase in the consumption of food with lower nutritional quality or otherwise unsuitable (Vivas & Saether 1987, Freeland & Choquenot 1990, Renecker & Schwartz 1997). Tooth wear effects have been documented in other ungulates as a result of diet alterations during times of density-related food limitations (Skogland 1988, Kojola *et al*. 1998). In the regions of elevated tooth breakage, Cape Breton and Newfoundland, higher moose densities were reported from regional wildlife officials, 2.00 and 7.00 moose/km^2, respectively. Other regions, for which density information was available, are populated by moose at lower densities: New Brunswick, 0.32; New Hampshire, 0.46; Ontario, 0.15–0.40; and Vermont, 0.61 moose/km^2. The high moose densities found in the regions of declining incisal condition likely limit the availability of preferred food resources thus forcing individuals to consume less suitable supplies, perhaps those which place higher stress upon the incisors, for sustenance.

When faced with limited food supplies in the winter, moose use lower quality browse by consuming bites of larger diameter, and often lower digestibility (Vivas & Saether 1987, Renecker & Hudson 1992). This may be exacerbated when competition for food increases, especially when food sources remain frozen for long periods of time. The availability of food resources is particularly important in the winter months as woody browse often represents the only form of forage available in areas with persistent snow cover (LeResche & Davis 1973). In addition, individuals may be unable to extract food resources with the appropriate nutrients when tooth condition has deteriorated (Ericsson & Wallin 2001). Moose require a range of browse species to ensure mineral requirements are met; a diet consisting of few plant species may lead to elemental deficiencies or excesses (Ohlson & Staaland 2001). Therefore, the availability of quality browse is important for the growth and maintenance of healthy teeth.

Nutritional excesses or deficiencies, either during development or throughout the lifetime, may render the composition of moose incisors in Atlantic Canada to be less conducive to typical external stresses experienced during cropping, thus, elevating susceptibility to breakage. In certain regions of Newfoundland and Cape Breton, impaired browse regeneration and limited resources have been documented to result from elevated moose densities (Mercer & McLaren 2002, Bridgland *et al*. 2007). Previous study of both incisor and molar wearing in moose, suggests that current ecological conditions, such as food quality, are important factors in incisor wearing (Veiberg *et al*. 2007a). Food resource quality and availability among regions likely, in part, explains some proportion of the tooth integrity variability that we have seen in this study. The regions most affected by incisor breakage are high density areas with decreasing supplies of suitable food resources.

Further study of Atlantic Canadian moose should examine incisal condition in relation to density effects, body condition and fecundity. Additionally, further studies should study the molar condition of individuals with compromised incisor integrity. Molar teeth are used for the continuous mastication of food resources and thus wear is generally perceived to decrease chewing efficiency, thus impacting fitness and survival (Fortelius 1985, Kojola 1988, Skogland 1988, Gaillard *et al*. 1993, Hindelang & Peterson 1994, Ericsson & Wallin 2001, Loe *et al*. 2003) though this was not supported in a recent study of red deer by Carranza *et al*. (2008). The relationship between the extent of molar wear and incisor integrity may provide insight regarding diet and feeding strategy when incisors are compromised.

Conclusion

In summary, this study characterized the spatial distribution of degraded moose incisor condition in eastern North America, in terms of cracking, wear and breakage. Potential effects on age structure were examined as was the relationship between incisal condition and gender. We found abnormally high frequencies of incisor breakage, most notably in moose of northern Cape Breton and throughout Newfoundland that were positively correlated with age. Gender was not significantly related to degraded incisal condition. This study is the first to report the occurrence of moose incisor breakage in Newfoundland, Canada, which is present, in northern regions, at extremely high frequencies. Though population age structures appear unaffected in the regions examined when using hunter derived data sets, the high frequencies of breakage found in this study are anomalous for an herbivore species.

Over time, greater selection pressure on the dentition, in a large ruminant herbivore, should be experienced by populations affected by elevated rates of incisor breakage where the animals are negatively impacted by such breakage. It may be suggested, as in the case of tooth wear in another wild ruminant (Veiberg *et al*. 2007b), that foraging conditions are more extreme in certain current habitats than where this species previously evolved. It is important to be mindful of the temporal scale of the relatively recent observation of extreme breakage in this species when making inferences to possible effects on populations in the future. A change in diet does not lead to an immediate change in enamel structure; rather, selection pressure for optimal dentition is exerted over a much longer period of evolution (von Koenigswald 1992). As such, understanding what environmental factors, which may include density, have changed in the recent past, contributing to the observed excessive breakage will be important for future studies of these impacted populations.

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