MOOSE ANTLER MORPHOLOGY AND ASYMMETRY ON ISLE ROYALE NATIONAL PARK

Kenneth J. Mills[1,3] and Rolf O. Peterson[2]

[1]Department of Biological Sciences, Michigan Technological University, Houghton, Michigan, USA 49931; [2]School of Forestry and Wood Products, Michigan Technological University, Houghton, Michigan, USA 49931.

ABSTRACT: Isle Royale National Park, an island archipelago in Lake Superior, supports moose at higher density (1–4/km²) relative to most other North American sites. We compared antler size and asymmetry measurements from Isle Royale moose that died of natural causes to measurements available for other regional moose populations in published literature. We used these comparisons to test predictions that antlers of Isle Royale moose would be smaller and more asymmetric that other regional populations due to the high population density and the resulting ecological conditions on Isle Royale. Moose on Isle Royale follow the same patterns of antler development as elsewhere, reaching maximum size at 7–8 years of age with slight declines after age 10–12. However, these moose develop antlers that are much smaller than all measured North American subpopulations. Antler size was most comparable to moose from Scandinavia where moose exist at comparably high population density. Boone and Crockett score, which is commonly used to compare antler size, performed poorly at ranking individuals with large antlers suggesting that more biologically relevant measures such as antler volume should be considered for comparisons of antler size. Pedicle constriction was found to be a reliable indicator of senescence among old bulls. Antler asymmetry was negatively related to antler size and was more extreme than asymmetry measured in Alaskan moose. Moose age had no detectable effect on the degree of antler asymmetry. In general, bull moose on Isle Royale develop smaller, more asymmetric antlers than other North American subpopulations which exist at lower density, consistent with the hypothesis that these qualities are related to nutrient limitation caused by high population density. Results, however, may also reflect genetic differences and artifacts of sampling.

Moose (*Alces alces*) develop large antlers during a relatively short growing period, requiring an intake of nutrients and expenditure of energy above that required for maintenance of basal functions (Stewart et al. 2000). The ability to acquire and allocate resources necessary for antler development is influenced by factors such as age, body size, nutrition, genetics, and population and environmental conditions (Sæther and Haagenrud 1985, Clutton-Brock and Albon 1989, Markusson and Folstad 1997, Stewart et al. 2000, Strickland and Demarais 2000, Bowyer et al. 2001, Schmidt et al. 2001). As secondary structures in sexually dimorphic cervids, antlers have significance in sexual selection and are correlated with social dominance and mating success (Clutton-Brock and Albon 1989, Bartoš 1990, Solberg and Sæther 1994, Pélabon and Joly 2000, Stewart et al. 2000). These developmental, morphological, and sociobehavioral attributes allow antlers to be useful parameters in ecological research.

[3]Present address: Wyoming Game and Fish Department, PO Box 850, Pinedale, WY, 82941. kenneth.mills@wyo.gov

Antler size typically increases until bulls reach maximum body and antler size between the ages of 5 and 10 years (Stewart et al. 2000, Bowyer et al. 2001). After age 10, antler size tends to decline (Sæther and Haagenrud 1985, Bubenik 1990, Bubenik 1998, Stewart et al. 2000, Bowyer et al. 2001), and simultaneously there is increasing evidence of physical senescence (Hindelang and Peterson 1994). Age and body mass, then, both influence energetic investment in antler development (Scribner and Smith 1990). Antler development patterns of Isle Royale moose that die of wolf predation and other natural causes will reflect overall nutritional condition as well as the culling influence of mortality factors. Also, the large number of relatively old moose in the population (Peterson 1977) should illuminate the poorly understood influence of senescence on antler development (Bubenik 1998).

Asymmetry, defined as random deviations from perfect bilateral symmetry, is present to varying degrees in all bilateral morphological traits (Palmer and Strobeck 1986, Bubenik 1990, Bowyer et al. 2001). Antlers are bilateral secondary structures and, therefore, portray differential degrees of asymmetry which depend on developmental stability, environmental quality, and individual fitness (e.g., nutritional status, inbreeding, injury, parasite load, age) and thus may be useful for comparisons between individuals and populations (Palmer and Strobeck 1986, Clutton-Brock and Albon 1989, Solberg and Sæther 1994, Alados et al. 1995, Folstad et al. 1996, Møller et al. 1996, Markusson and Folstad 1997, Pélabon and van Breukelen 1998, Pélabon and Joly 2000, Bowyer et al. 2001, Schmidt et al. 2001). Antler asymmetry has an inverse relationship with antler size for many cervid species, which may be indicative of relative individual fitness regardless of age (Markusson and Folstad 1997, Pélabon and van Breukelen 1998, Bowyer et al. 2001,

Ditchkoff et al. 2001). Population wide stressors, such as reduced nutrition, may also manifest themselves through patterns in antler asymmetry and thus measures of antler asymmetry at broader scales may also be useful for comparisons between populations.

Reduced predator species diversity has allowed moose population density to reach uncommonly high levels on Isle Royale National Park compared to most other North American subpopulations (Peterson 1995, Karns 1998, Peterson et al. 2003), where a relative shortage of nutrition could reduce individual fitness and limit the ability of bull moose to allocate excess energy toward antler development (Brown 1990). Nutritional restriction due to high density may also manifest itself in the degree of antler asymmetry at the scale of the individual and the population (Pélabon and van Breukelen 1998, Pélabon and Joly 2000, Bowyer et al. 2001). Likewise, wolf predation and starvation are the only significant sources of mortality for moose on Isle Royale (Peterson 1977, Peterson 1999), so age structure and thus antler characteristics likely differ from other populations where antler morphology has been studied (Gasaway et al. 1987, Nygrén 2000, Stewart et al. 2000, Bowyer et al. 2001). Therefore, antler characteristics may provide a basis for comparing condition and nutritional status of moose at Isle Royale and other geographic sites (Bowyer et al. 2001).

Herein we assess antler size relative to age and antler asymmetry relative to age and antler size for bull moose collected on Isle Royale National Park. We predict that patterns of antler development and asymmetry will follow similar general patterns measured for other North American populations. However, we also expect that antlers for moose on Isle Royale will be smaller and more asymmetric than other North American populations due to the nutritional

restriction caused by high population density (see also Peterson et al. 2011).

STUDY AREA

Moose have existed on Isle Royale (544 km^2) for the past century and in the last half-century they have been cropped by an unmanipulated population of gray wolves (*Canis lupus*). Both species have been protected since the establishment of Isle Royale National Park in 1940 (Mech 1966). Wolf and moose populations have been counted each year since 1959. Both predator and prey exist at relatively high density, with moose fluctuating from about 500 (1/km^2) to over 2,000 (4/km^2) animals during 1959–2002, with a mean of 2.03 ± 0.11/km^2 (SE; range = 0.92–4.45/km^2) during that period (Peterson 1999, R. Peterson, unpublished data). Population densities for moose in other regions of North America are generally below 1/km^2 (Karns 1998). Likewise, moose populations located on the nearest mainland in Southwest Ontario and Northeast Minnesota, the likely source for moose on Isle Royale, generally range from 0.20–0.40/km^2 (Mech 1966, Karns 1998, Ontario Ministry of Natural Resources, unpublished data).

METHODS

Skulls of male moose with polished antlers were collected during field studies at Isle Royale during 1970–2001. Ages of moose were estimated from counts of annular cementum lines. Antler size was measured in accordance with the Boone and Crockett Club (B&C) scoring system (Boone and Crockett Club 2011, Gasaway et al. 1987). A net dry score for each set of antlers, tallied in inches, was calculated as follows: [spread + (2 × smallest palm length) + (2 × smallest palm width) + (2 × smallest beam circumference) + (2 × least number of points)] (see Boone and Crockett Club 2011 for details on scoring methods).

The remaining measurements were recorded in centimeters (Gasaway et al. 1987). The largest diameter of both left and right pedicles on each skull was measured to study how this skull character varies with age. Some pedicles showed an apparent constriction at the point where the antler joins the pedicle, which has not been described previously in the scientific literature (Fig. 1). Therefore, both constricted and unconstricted pedicle measurements were taken for these individuals in order to quantify this morphological trait. The constricted measurement was taken at the area of greatest constriction just before the antler base, while the unconstricted measurement was taken directly medial to the constricted area. Scoring systems such as B&C may have limitations that affect the results of comparative studies (Gasaway et al.

Fig. 1. Constriction of the pedicle (outlined in white) just medial to the base of the antler was evident for many antlered bulls collected from Isle Royale National Park.

1987, Bubenik 1998). Therefore, we also determined antler volume to directly measure antler size using water displacement. Prior to measurement, each antler was saturated in water until all air pockets were filled prior to measurement. In order to measure the accuracy of this technique, we determined volume for 10 antlers, 3 times each. Each individual measurement for each antler was compared to the mean of the 3 measurements for that antler to determine the error of each measurement. Finally, the total mean error of the 30 measurements was calculated to confirm that the error was within acceptable limits (i.e., < 5%). We then compared two of the most used measures of antler size, B&C score and spread (Boone and Crockett Club 2011), to the respective total volume measurement for each individual to determine the degree to which these scores accurately estimate antler size using exponential regression.

Second-order polynomial equations were fitted to data relating antler character size to moose age to evaluate variation in antler size with age and age-related growth of antlers compared to that of Alaskan moose as measured by Bowyer et al. (2001). A Dunnett's test (Zar 1999) was used to determine if the mean maximum sizes for the 20 largest Isle Royale moose for both B&C score and spread were smaller than the same measurements from multiple subpopulations of North American moose, as determined by Gasaway et al. (1987), and moose from Finland as determined by Nygrén (2000). We also plotted comparative growth curves for Isle Royale moose, selected North American subpopulations, and a Swedish subpopulation of moose as adapted from Gasaway et al. (1987). Growth curves were determined by using 3-year running averages except for the oldest and youngest age classes, which are presented as actual means. We pooled individuals in

the 14 year age class and older for the Isle Royale subpopulation.

Relative antler asymmetry was determined by taking the difference between the large and small side of each measured antler parameter for each individual (i.e., palm width, palm length, beam circumference, number of points, pedicle diameter, and volume) divided by the respective large side for each measured antler parameter for that individual (e.g., [large palm width – small palm width] ÷ large palm width = relative asymmetry of the palm width for that individual moose). We then assessed the relationship between relative asymmetry and moose age using linear regression. We also used linear regression to measure the relationship between relative asymmetry and the mean size of the respective antler parameter. We used a one-sample t-test to compare the mean relative asymmetry for palm width, palm length, beam circumference, and number of points for Isle Royale moose to the mean relative asymmetry of the respective measures for Alaskan moose as determined by Bowyer et al. (2001). We tested whether asymmetry was fluctuating or directional for each lateral antler character using a Wilcoxon signed-rank test (see Palmer and Strobeck 1986, Zar 1999, Pélabon and Joly 2000, Bowyer et al. 2001).

RESULTS
The total number of skulls in the sample was 106, but not all parameters could be measured for some specimens because of weathering prior to collection. Antlers for Isle Royale moose were smaller than Alaskan subpopulations in palm width, palm length, beam circumference, number of points and spread (Fig. 2, 3). For B&C score and spread, Isle Royale moose were smaller than all other North American subpopulations measured (all P <0.05; Table 1). Antler spread from Isle Royale
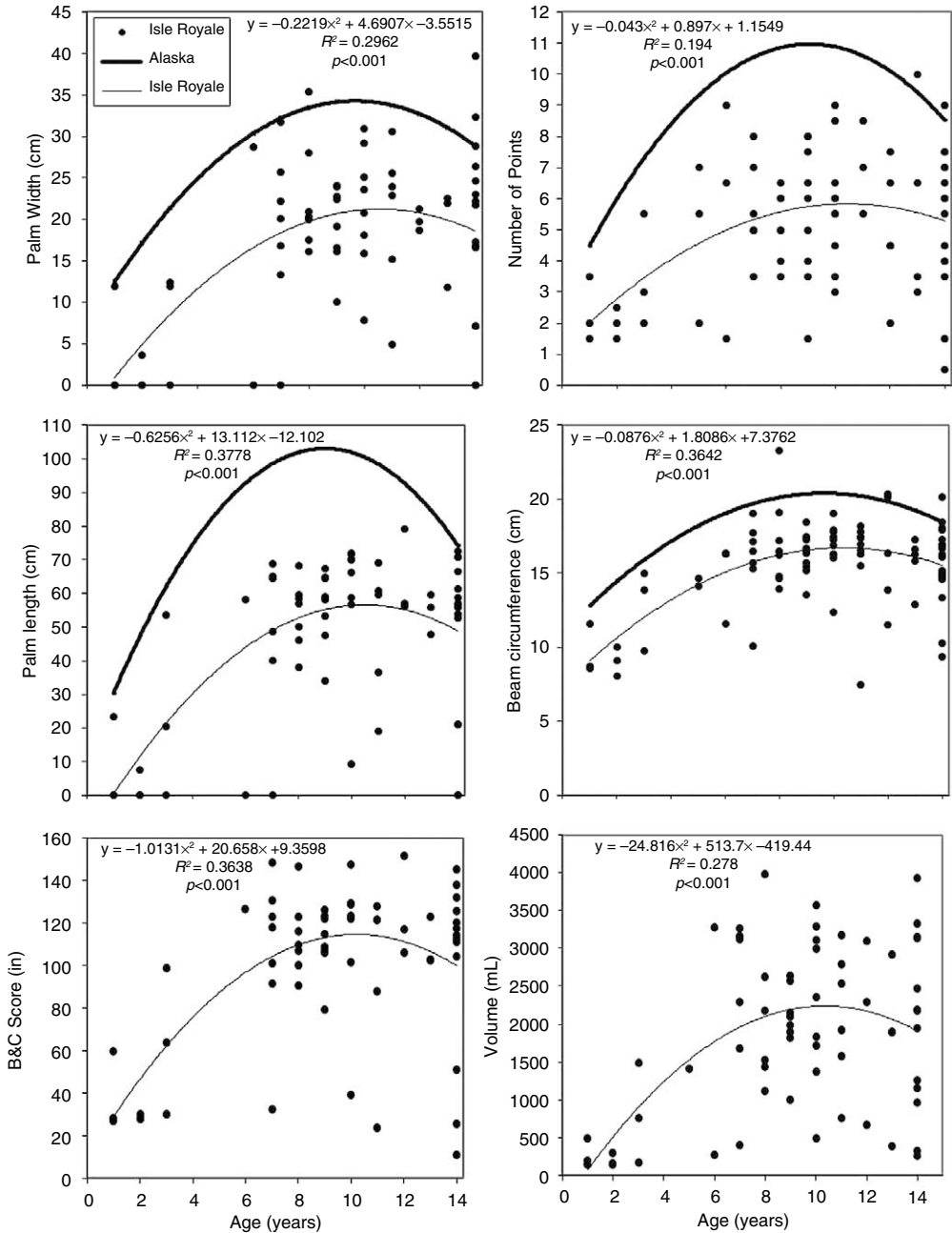
Fig. 2. Regression analyses of antler characteristics in relation to age of bull moose collected from Isle Royale National Park. Raw data was used to generate a second order polynomial regression equation for Isle Royale moose. Regression lines for Alaskan moose were obtained from Bowyer et al. (2001). Sample sizes for the Isle Royale sample are as follows: palm width, n = 68; number of points, n = 74; palm length, n = 67; beam circumference, n = 91; B&C score, n = 64; volume, n = 68.
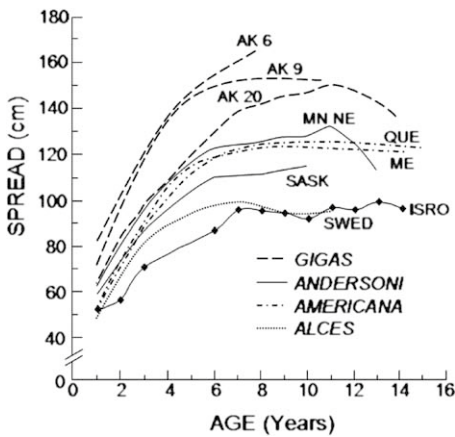
Fig. 3. Comparative growth curves for selected North American subpopulations and a Swedish subpopulation of moose as adapted from Gasaway et al. (1987). Curves are plotted by using 3-year running averages except for the oldest and youngest age classes, which are actual means. For the Isle Royale National Park subpopulation (n = 76), individuals in the 14 year age class and older are pooled.

moose was also smaller than the palmate antler category from Finland ($|q|$ = 3.1696, P <0.05), and was marginally different from the non-palmate antler category ($|q|$ = 1.9245, $P \approx$ 0.05; Table 1). Isle Royale moose also appear to have maximum antler spread similar to that of moose from Sweden, although raw data were not available for the Swedish subpopulation (Fig. 3).

For moose at Isle Royale, maximum antler size is reached between the ages of 7 and 8 years for all measured parameters, except for B&C score, which reached its maximum at 6 years (Fig. 2, 3). Generally, a slight decrease in size occurred after 10–12 years of age, with incipient physical senescence (Fig. 2). This was evident by the malformed or misshapen antlers of several senescent individuals (see Bubenik 1998).

The volume measurement technique was determined to be accurate to within a mean of 1.9 ± 0.3% (range = 0.2–5.5%).

Age-related change in antler volume was similar to other size measurements, reaching a maximum at age 7, then decreasing more slightly after age 10 (Fig. 2). The relationship between B&C score and total volume (left + right) was exponential and variable for individuals with high B&C scores (Fig. 4A). Antler spread also was exponentially related to total volume and was more variable as spread increased (Fig. 4B). Pedicle diameter portrayed the same antler development pattern as other parameters, reaching maximum size at 8 years (Fig. 5A). However, it did not appear to decline as an indication of senescence as other parameters did. Pedicle constriction was present in some moose as early as 7 years and increased with age to a maximum at 16–18 years (Fig. 5B).

The degree of relative asymmetry was not related to moose age for any bilateral antler parameter (all P > 0.458), but was negatively related to antler size for most bilateral antler categories including volume (F = 0.27, P = 0.002; Fig. 6), palm width (F = 1.61, P = 0.000), beam circumference (F = 10.82, P = 0.001), and number of points (F = 0.74, P = 0.000). Relative asymmetry had no relationship with antler size for palm length (F = 0.07, P = 0.799) or pedicle diameter (F = 0.15, P = 0.697)

The degree of relative asymmetry for Isle Royale moose was much larger than in Alaskan moose for palm length, palm width, and beam circumference but was not different for number of points (Table 2). Wilcoxon signed-rank tests showed that left and right antler sides were not different for palm length, palm width, beam circumference, number of points, volume, or pedicle diameter (Z = 0.061, P = 0.952; Z = 1.056, P = 0.291; Z = 0.002, P = 0.998; Z = −0.836, P = 0.403; Z = 0.679, P = 0.497; Z = 0.808, P = 0.419, respectively).

Table 1. Antler spread and Boone and Crockett score for the 20 largest moose from selected regions of North America and Finland. (data adapted from Gasaway et al. 1987 and Nygrén 2000).

Subspecies/Region		Spread (cm)				Boone and Crockett score			
		Mean	SE	Max.	Mean:Max.	Mean	SE	Max.	n
gigas									
Alaska[1]		182.6	2.64	207	0.88	247.1	0.71	255	20
gigas x *andersoni*									
Yukon and Northwest Territories[1]		170.2	2.18	191.8	0.89	232.9	1.57	247.3	20
gigas x *andersoni*									
Northern British Columbia[2]		154.7	2.64	172.7	0.90	215.7	0.91	229.1	20
andersoni									
Western Canada (except									
North British Columbia) and Minnesota[2]		154.7	2.41	178	0.87	217.3	1.27	226.9	20
andersoni x *americana*									
Ontario[2]		151.6	2.79	181.6	0.83	201.3	1.35	211.6	20
americana									
Eastern Canada and Maine[2]		154.4	2.49	181.9	0.85	202.9	2.73	238.6	19
shirasi									
Western USA[3]		133.9	2.69	151.9	0.88	188.2	1.73	205.5	20
andersoni									
Isle Royale[2]		107.0	3.18	129.4	0.83	133.4	2.04	151.7	20
alces									
Finland	palmate	114.8	0.46	149	0.77				511
	nonpalmate	111.9	0.86	139	0.81				

[1]Considered Alaska-Yukon moose by Boone and Crockett Club.
[2]Considered Canadian moose by Boone and Crockett Club.
[3]Considered Shiras moose by Boone and Crockett Club.

DISCUSSION

Population density for moose on Isle Royale, where there is predation only by gray wolves, is an order of magnitude higher than most other areas of North America (Peterson 1999), but comparable to many moose ranges in Scandinavia (0.8–1.8/km^2; Cederlund and Markgren 1987, Hörnberg 2001). Isle Royale moose, to a greater extent than other moose populations, are also subjected to strong selection by wolf predation, and are thereby more naturally regulated than other hunted populations. These two ecological characteristics make interpopulation comparisons involving moose at Isle Royale particularly compelling. However, it is necessary to address this difference in terms of sample selection when comparing datasets collected from individuals subjected to natural mortality and those collected from hunter-killed individuals. Neither sample is randomly selected; in the case of Isle Royale, individuals were collected after death from natural causes, and so probably include proportionately higher numbers of individuals in poor condition and/or older age classes. With other datasets, individuals were measured
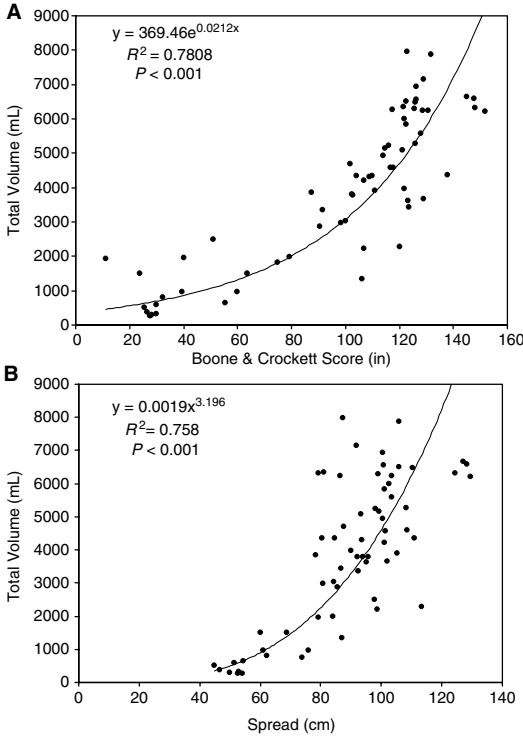
Fig. 4. Regression analyses of the relationship between total antler volume and (A) Boone & Crockett score (n = 65) or (B) spread (n = 65) for antlered bull moose collected from Isle Royale National Park.

following hunter harvest, which would introduce biases based on hunter selection (e.g., hunter selection for larger than average bulls, antler size restrictions imposed by wildlife management agencies). The mean:maximum ratios presented in Table 1 suggest that the regional datasets are likely similar, and therefore comparable. It is likely that the true maximum antler size realized by Isle Royale moose is larger than that presented herein, but cast antlers that are significantly larger than the largest represented in this dataset are rarely found during fieldwork on the island (R. Peterson, Michigan Technological University, unpublished data). This evidence suggests that these datasets have at least acceptable levels of comparability, but comparisons should still be considered with
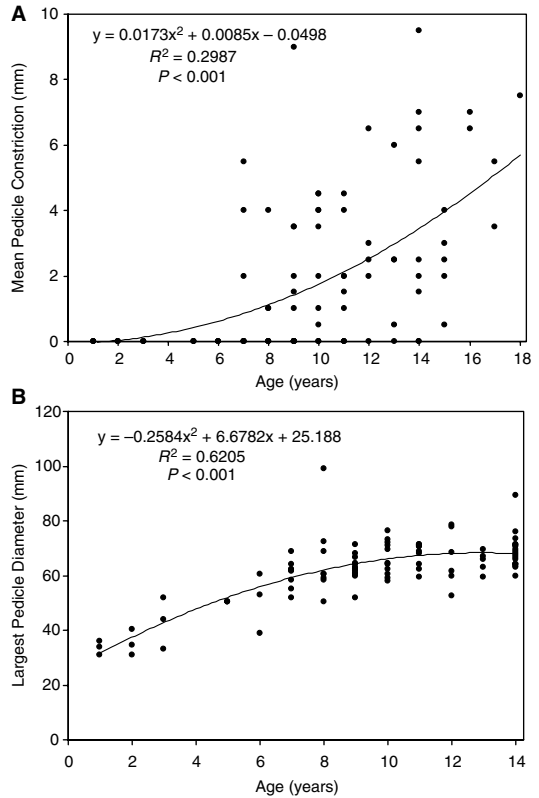

Fig. 5. Regression analysis for (A) pedicle constriction (n = 91) and (B) pedicle diameter (n = 95) in relation to age of antlered bull moose collected from Isle Royale National Park.
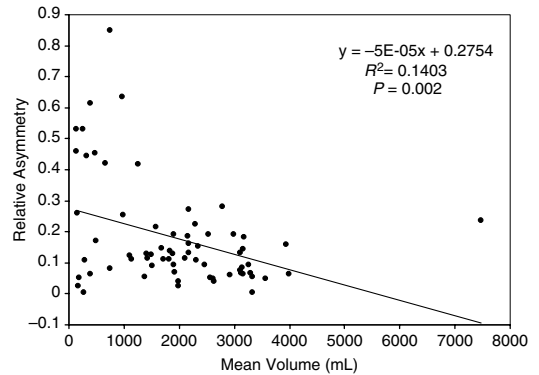

Fig. 6. Linear regression between relative asymmetry of left and right antler sides against mean antler volume for bull moose collected from Isle Royale National Park (n = 68).

Table 2. Comparison of mean relative asymmetry (RA; large - small/large) for antler characters from 1,501 harvested Alaskan moose and antlered bull moose collected from Isle Royale National Park. Data for antler characters from Alaska were obtained from Bowyer et al. (2001) and Gasaway et al. (1987).

Antler character	Alaska		Isle Royale				
	RA	SE	RA	SE	n	t	P
Palm width	0.10	0.002	0.20	0.033	67	3.04	0.003
Palm length	0.07	0.002	0.16	0.034	66	2.60	0.011
Beam circumference	0.03	0.001	0.06	0.011	100	2.46	0.016
# points	0.19	0.005	0.20	0.026	74	0.44	0.660

caution due to the potential biases caused by differences in sampling methodologies (e.g., sample sizes, sampling duration, sample collection protocols).

Moose present on Isle Royale develop smaller antlers than all other reported subpopulations in North America, and their antlers are similar to or smaller than two subpopulations reported for Scandinavia. However, antler development through age follows much the same patterns as other populations, reaching a maximum size after 7 to 8 years, which is maintained until senescence at around age 12 (Gauthier and Larsen 1985, Bowyer et al. 2001). The fact that Isle Royale moose appear to have a restricted ability to produce larger antlers should be a function of ecological conditions on the island, with nutrient limitation induced by high population density being the most fundamental difference between this island population and those in mainland areas. This is demonstrated when comparing antler size of Isle Royale moose to antler measurements collected from moose in Southwest Ontario. The maximum antler spread and B&C score for Isle Royale was 22.2 cm or 49.6 in smaller than the mean of the 19 largest moose measured from the mainland Ontario population (Table 1). This analysis suggests a significant reduction in antler size in the century following moose colonization on the island, with the primary difference between these groups being population density (Karns 1998, Peterson 1999,

R. O. Peterson, unpublished data, Ontario Ministry of Natural Resources, unpublished data).

Most comparative antler studies use composite scores of linear measures such as the B&C scoring system or simply antler spread. These scores are easy to calculate, but may have significant limitations (Gasaway et al. 1987, Bubenik 1998). We determined that B&C score and spread do not accurately rank large antlered individuals, in many cases ranking larger individuals below smaller individuals (Figs. 4A and B). The B&C score, therefore, may have limited usefulness when comparing antler size between similar populations, especially when comparing primarily large antlered bulls. Volume, on the other hand, should be a more accurate measure of antler size because it is directly related to energetic investment during antler development. This suggests that researchers should consider biologically relevant morphological metrics such as volume when conducting comparative studies on antlers.

Moose numbers on Isle Royale are naturally regulated with no human interference, which allows individual moose the opportunity to reach ages when signs of senescence would be expected. In most cases, the second order polynomials used in regression estimated reductions in size for older individuals. Despite this, most measured antler parameters had only slight reductions in antler size for post-prime age individuals,

which was consistent for moose measured in Alaska (Bowyer et al. 2001). However, there was a small proportion of old and senescent individuals that developed small and drastically asymmetric antlers (see Bubenik 1998). Pedicle constriction may be a better indicator of declining reproductive vigor in older individuals. Pedicle constriction was observed in both large and small antlered individuals as well as individuals with normal and abnormal antler morphology. Constriction was first apparent in some bulls that were 7 years of age, the same age that antlers begin to reach their maximum, mature size, and it increased with age, though not all older individuals had measurable restrictions. A. B. Bubenik (pers. commun.) suggested that pedicle constriction resulted from testosterone insufficiency, which may begin well after sexual maturity and increase with reproductive senescence.

Antler asymmetry for moose on Isle Royale was fluctuating and was most pronounced among moose with small antlers at the extremes of age and development. Although some older, senescent individuals developed very small and asymmetric antlers (see Bubenik 1998), overall there was little evidence to suggest that age has any governing effect on antler asymmetry. Therefore, antler asymmetry should be a valid indicator of individual fitness and condition regardless of age, with the individuals in the best condition developing the largest and most symmetric antlers. Likewise, asymmetry may also provide a basis for comparisons of fitness and condition between populations. In this case, Isle Royale moose portrayed greater degrees of relative asymmetry than Alaskan subpopulations, the only subpopulation for which asymmetry measurements were available (Bowyer et al. 2001). High levels of antler asymmetry population-wide, as measured for moose from Isle Royale, may reflect more nutrient limitation and developmental instability.

In general, bull moose on Isle Royale develop smaller, more asymmetric antlers than other North American subpopulations, even those within the same geographic region, suggesting that these qualities are the result of nutrient limitation caused by high population density (Peterson et al. 2011). These findings are consistent with the evidence of slight dwarfism associated with high population density and lack of selection by wolf predation during the first half of the 20th century (Peterson et al. 2011). However, this correlative study did not quantify or eliminate other potential contributing factors, such as genetic founder effects and effects of sampling methodology. This study also supports the contention that antlers are useful indicators for both individual and population condition (e.g., Markusson and Folstad 1997, Pélabon and van Breukelen 1998, Strickland and Demarais 2000, Schmidt et al. 2001), although future research should attempt to specifically evaluate fitness in relation to measures of antler size and asymmetry for moose.

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