

VARIATION IN METATARSAL MORPHOLOGY AMONG SUBGROUPS OF NORTH AMERICAN MOOSE (*Alces alces*)

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ABSTRACT: The objectives of this study were to characterize variation in dimensional data from the metatarsus of 4 different subpopulations of North American moose (*Alces alces*) that are known to differ in stature, and to determine if specific metatarsal width measurements (proximal, middle, distal) can be used to accurately predict metatarsal length in these subpopulations. We found that subpopulations differ in the dimensions of their metatarsal bones. Alaskan moose (*A. a. gigas*) are significantly larger in the length and width of the metatarsus than non-Alaskan moose. Moose from Isle Royale have significantly shorter metatarsal bones than the other groups which is associated with a proportional reduction in the middle metatarsal width; the ratio of middle width:length was similar across groups in contrast to the proximal: and distal width:length ratios. These dimensions were not reduced proportionally in Isle Royale specimens as these ratios were greater in the Isle Royale moose than in other groups. Predictive equations for estimating metatarsal length from each of the 3 width measurements were developed. The length could be predicted accurately from each of the width measurements if separate predictive equations were developed for specimens collected from Isle Royale versus the other subgroups. These data indicate that considerable variation exists in the dimensions of a single bone, the metatarsus, in subgroups of the same species. Valid predictive equations developed using data sets from one subgroup may not provide accurate predictions when applied to other subgroups of the same species.

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Estimating the body size of individuals is an important part of any population assessment. Direct measures (e.g., shoulder height, heart girth, body weight) of large species are often difficult to obtain in the field, and estimates of body size are often made from extrapolations of other body parts. Foot length is correlated with live or carcass weight in many ungulate species (Bandy et al. 1956, McEwan and Wood 1966, Roseberry and Klimstra 1975, Martin et al. 2013) including moose (*Alces alces*) (Franzmann et al. 1978, Lynch et al. 1995, Jensen et al. 2013). For ungulates, both living and

recently deceased, this is most often measured along the plantar surface from the calcaneal protuberance to the tip of the longest toe. For animal remains that are collected after significant decomposition, it may be more convenient and consistent to measure the length of the metatarsus itself, commonly referred to as the cannon bone. The length of the metatarsus is correlated with body size across mammalian species (McMahon 1975, Alexander et al. 1979). For example, the length of the metatarsus is correlated with body weight and growth rate in cattle (Coble et al. 1971b), and length and width

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of the metatarsus were smaller in female than male cattle (Coble et al. 1971a), a clear indication of sexual dimorphism. The length of the metatarsus is an excellent indicator of fetal age in sheep (Santucci et al. 1993), the length of the metatarsus in growing lambs is directly related to maternal nutrition during gestation (Pálsson and Vergés 1952), and the heritability of metatarsal dimensions is relatively high (Coble et al. 1971a).

The length of the metatarsus has been used as an indirect measure of body size in moose (*Alces alces*; Peterson 1977). In the field, it is quite common to find metatarsal bones from moose that have been broken or damaged in such a way that an accurate length cannot be determined. However, portions of the metatarsus are often intact permitting accurate measurement of the width at some point along the length of the bone. Recognizing that metatarsal dimensions are of great utility in field research with moose and that there is considerable size variation among subpopulations of moose, our first objective was to characterize the length and 3 specific width measurements of metatarsal bones collected from 4 groups of moose: 1) Isle Royale National Park (subspecies undetermined, either *A. a. americana* or *A. a. andersoni*), 2) extant Alaskan moose (subspecies *A. a. gigas*), 3) fossilized Alaskan moose (subspecies undetermined), and 4) mainland, excluding Alaska (includes subspecies *A. a. americana*, *A. a. andersoni*, *A. a. shiras*). Our second objective was to determine if specific metatarsal widths (proximal, middle, distal) can be used to accurately predict metatarsal length of North American moose, and to determine if the relationships between length and specific widths vary among the 4 subgroups.

METHODS

Quantitative measurements of metatarsal morphology of adult North American moose were made on 4 subgroups. The first sub-

group consisted of 420 moose from Isle Royale National Park (48°06' N, 88°30' W; Peterson 1977) located in Lake Superior approximately 30 km from the Ontario, Canada coastline. The precise origin of moose on Isle Royale is unknown, but the founding animals could be either *A. a. americana* or *A. a. andersoni* subspecies; however, Isle Royale moose are morphologically different from both subspecies (Peterson et al. 2011). These metatarsal specimens are currently housed at Michigan Technological University's (MTU) Ford Center in Alberta, Michigan.

The second group of specimens was from 170 modern Alaskan moose and included specimens housed at 1) the Museum of the North, University of Alaska, Fairbanks, Alaska (collected from Denali National Park; 63°20' N, 150°30' W; n = 65), 2) the MTU Ford Center (collected in the Kenai National Wildlife Refuge [KNWR] at 60°20' N, 150°30' W; n = 95), 3) the American Museum of Natural History (AMNH), New York, New York (collected throughout Alaska; n = 6), and 4) the Field Museum of Natural History (FMNH), Chicago, Illinois (collected throughout Alaska; n = 3).

The third group of 49 metatarsal bones was fossil material from the late Pleistocene age that was collected from several sites 10–35 km north of Fairbanks, Alaska (65° N, 147°40' W) (Frick 1930, Wilkerson 1932) and was part of the Frick collection at the AMNH (n = 49); these are presumed from the subspecies *A. a. gigas*. The fourth set of 34 specimens, referred hereafter as mainland moose, was collected from a variety of sites in Canada and the United States (excluding Alaska) and included subspecies *A. a. americana*, *A. a. andersoni*, and *A. a. shiras*. These specimens are housed at the 1) MTU Ford Center (collected by the Michigan and Minnesota Departments of Natural Resources (n = 20), 2) the AMNH (n = 7), 3) the FMNH (n = 1), 4) Brown

University (n = 1), 5) Harvard University (n = 2), and 6) the University of Kentucky (n = 3). All specimens were from moose either killed by hunters or vehicular collisions.

Specimens collected in Isle Royale National Park, Denali National Park, or the KNWR were obtained from animals that died of natural causes. On Isle Royale, the majority resulted from predation by wolves (Peterson 1977); as a result, animals that were more susceptible to predation (due to age, injury, disease) may be overrepresented. The sex of specimens was determined from examination of soft tissue (when present) and morphological characteristics of the associated skull (when present). A general age was determined by the size of the remains and the complement of deciduous and permanent teeth (Peterson et al. 1983). When necessary, tissue from the metatarsal bones was removed manually with a knife and/or by prolonged immersion in hot water (>80 °C).

Quantitative measurements of the cannon bone were made using 2 sizes of manual vernier calipers. The length was measured using a 24-inch, Cen-Tech aluminum caliper (Harbor Freight Tools Inc., Camarillo, California, USA) that was modified by adding a vertical fence to each side, extending the height to approximately 2.2 cm (Fig. 1). The width of each metatarsus was measured at the proximal end, midpoint, and distal end with a standard 5-inch manual caliper (Helios, Germany; Fig. 2a). The width at the proximal end was measured at the widest point, typically within 1 cm of the end (Fig. 2b). The width at the distal end was also measured at the widest point, but the precise location varied; in some, it was very close to the end at the lateral and medial edges of the corresponding articular condyles, and in others it was proximal to the condyles, in the approximate location of the epiphyseal

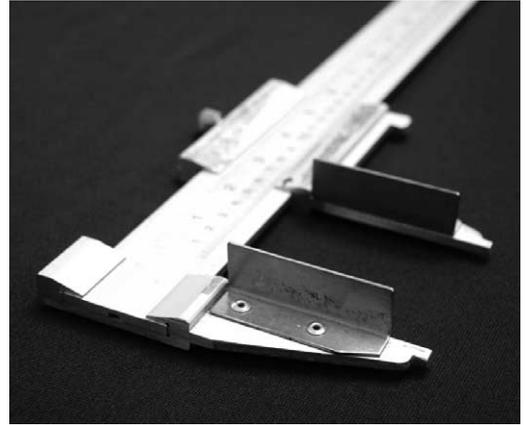


Fig. 1. The modified vernier caliper used to measure the length of the cannon bone. Note that vertical fences were added to each of the ‘jaws’ of the caliper to extend the height.

plate (Fig. 2c). These measurements were used to calculate width:length ratios for each width (i.e., proximal, middle, and distal). The condition of the epiphyseal plate was classified as either unfused or fused. The unfused classification included specimens in which the 2 portions of the metatarsus were separable, and specimens in which the 2 portions were not separable but a distinct suture was clearly visible (Fig. 3). Specimens were classified as coming from adults only if the distal epiphyseal growth plate was no longer visible.

The effects of subgroup and/or sex on quantitative measurements (length and width of the metatarsus, width:length ratio) were evaluated with analysis of variance using the GLM procedure of SAS (1985). The relationships between the length of the cannon bone and the 3 width measurements were evaluated with linear regression using the REG procedure of SAS (1985). The accuracy of the regression equations in predicting metatarsal length from width measurements was evaluated with paired T-test using the MEANS procedure of SAS (1985).

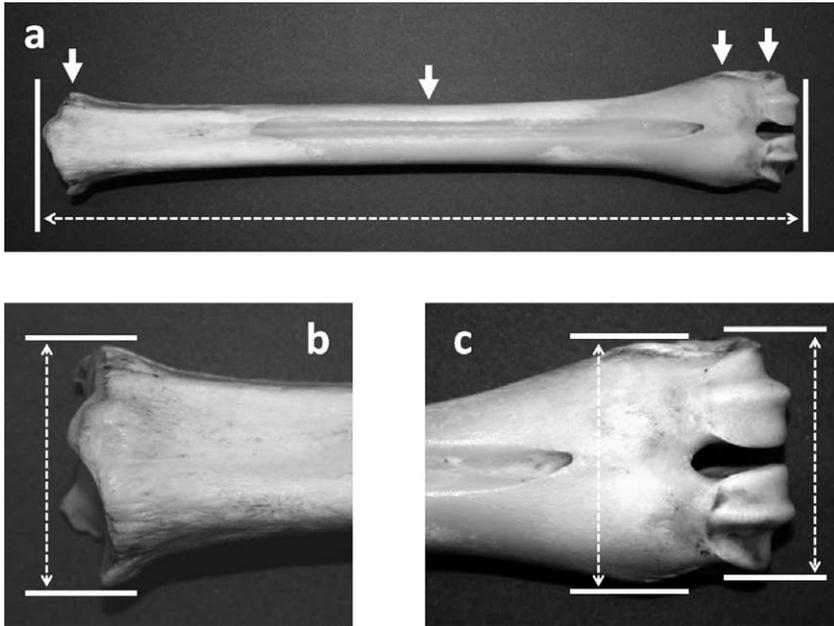


Fig. 2. Dorsal view of the cannon bone with points of measurement indicated. Panel a shows the measurement of length (dashed line) and proximal, middle, and distal widths (vertical arrows); 2 possible points for measure of the distal width are indicated. Panel b shows a detailed view of the proximal end indicating the point of measurement more precisely. Panel c shows a more detailed view of the distal end and the 2 possible points for measurement.



Fig. 3. The dorsal view of the distal end of the cannon bone from an adult (panel a) and a juvenile animal (panel b). Although not separable, the epiphyseal plate is clearly visible on the juvenile specimen (arrow).

RESULTS

Metatarsal Length and Width

The length of the metatarsus was different for each of the subgroups ($P < 0.01$; Fig. 4a). The fossil metatarsal bones from Alaskan moose were the longest, followed by those of modern Alaskan moose, mainland moose, and lastly Isle Royale moose. The width of the metatarsus at the proximal end was greater in the 2 Alaskan subgroups than in the other subgroups ($P < 0.01$; Fig. 4b); the Alaskan subgroups did not differ ($P = 0.10$), nor did the non-Alaskan subgroups ($P = 0.64$). The ratio of proximal metatarsal width:metatarsal length was different among groups ($P < 0.01$; Fig. 4c). Among all subgroups the ratio was highest

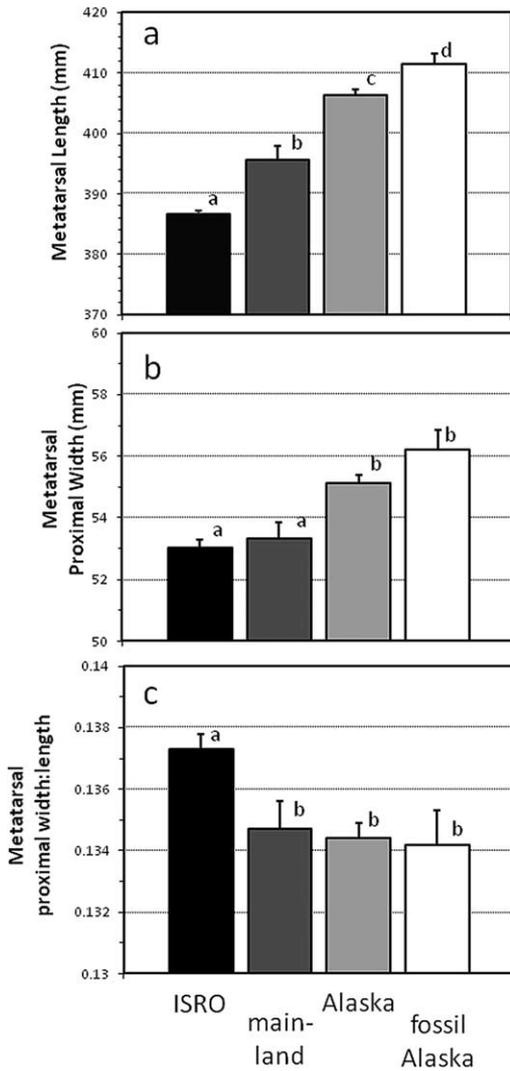


Fig. 4. The effect of subgroup (Isle Royale [ISRO], mainland [non-ISRO from the lower 48 contiguous United States and Canada], Alaska, and fossil Alaska) on metatarsal length (a), proximal metatarsal width (b), and the ratio of proximal metatarsal width to metatarsal length (c). Bars with different letter superscripts are different ($P < 0.05$).

in specimens from Isle Royale ($P < 0.05$); the ratio among the other 3 subgroups did not differ ($P > 0.70$).

To further examine the relationship between proximal width and length, the effect of width and subgroup on metatarsal length was determined ($n = 285$). Proximal

width had a significant effect ($P < 0.01$), but subgroup did not ($P = 0.06$). There was an interaction between proximal width and subgroup on metatarsal length ($P = 0.01$). Since the ratio width:length appeared to be different for Isle Royale moose compared to the other subgroups, a second analysis was conducted without Isle Royale moose. Again, the effect of proximal width was evident ($P < 0.01$), but not subgroup ($P = 0.27$) or the interaction term of proximal width and subgroup ($P = 0.20$), implying that the Alaskan and mainland subgroups are similar and a different relationship exists for Isle Royale moose.

Middle ($n = 226$) and distal width measurements ($n = 224$) were not available from the fossil specimens; therefore, comparisons could only be made among the modern subgroups. The width of the metatarsal at the midpoint was greater in Alaskan moose than those from non-Alaskan subgroups ($P < 0.01$; Fig. 5a); this width was similar in Isle Royale and non-Alaskan subgroups ($P > 0.30$). The ratio middle width:length was not different among subgroups ($P = 0.44$; Fig. 5b). As with the proximal metatarsal width, the distal metatarsal width was greater in the Alaskan subgroup than non-Alaskan subgroups ($P < 0.01$; Fig. 5c). The ratio distal metatarsal width:metatarsal length also differed among subgroups ($P < 0.01$; Fig. 5d). The distal width:length ratio was greater for Isle Royale moose than the other groups ($P < 0.01$); the other groups did not differ ($P = 0.12$).

The effect of sex on metatarsal dimensions was analyzed with all specimens in which sex could be determined, which excluded the fossil subgroup. The length of the metatarsus was greater in males than females ($P < 0.01$; Fig. 6a). As in the first analysis, the length of the metatarsus differed among subgroups ($P < 0.01$), and metatarsal length was longer in males than females in all subgroups. A significant interaction

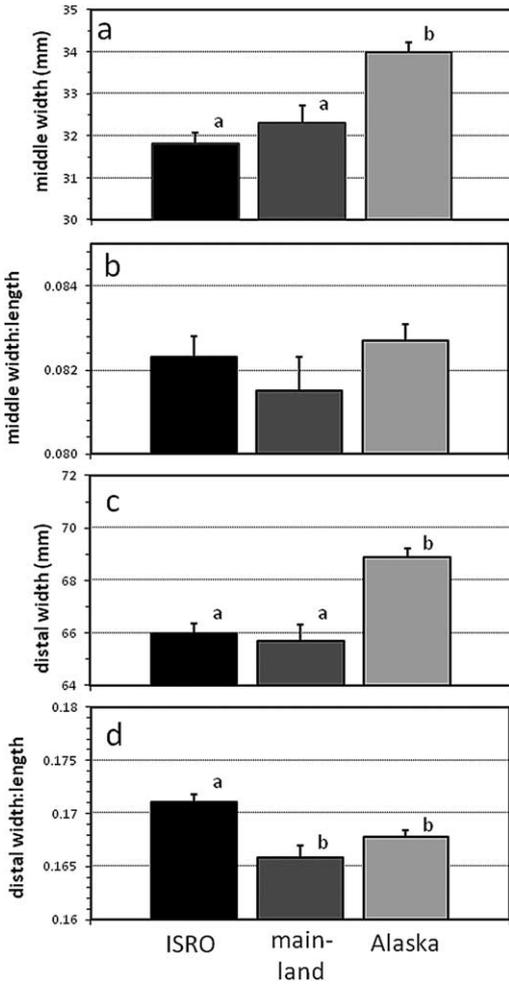


Fig. 5. The effect of subgroup (Isle Royale [ISRO], mainland [non-ISRO from the lower 48 contiguous United States and Canada] and Alaska) on middle metatarsal width (a), the ratio of proximal metatarsal width to metatarsal length (b), distal metatarsal width (c), and the ratio of distal metatarsal width to metatarsal length (d). Bars with different letter superscripts are different ($P < 0.05$).

between sex and subgroup was also found ($P < 0.01$). This interaction was strongest in Alaskan moose that had the longest metatarsal length and largest difference between males and females.

The effect of sex on the relationship between each of the 3 width measurements and metatarsal length was examined

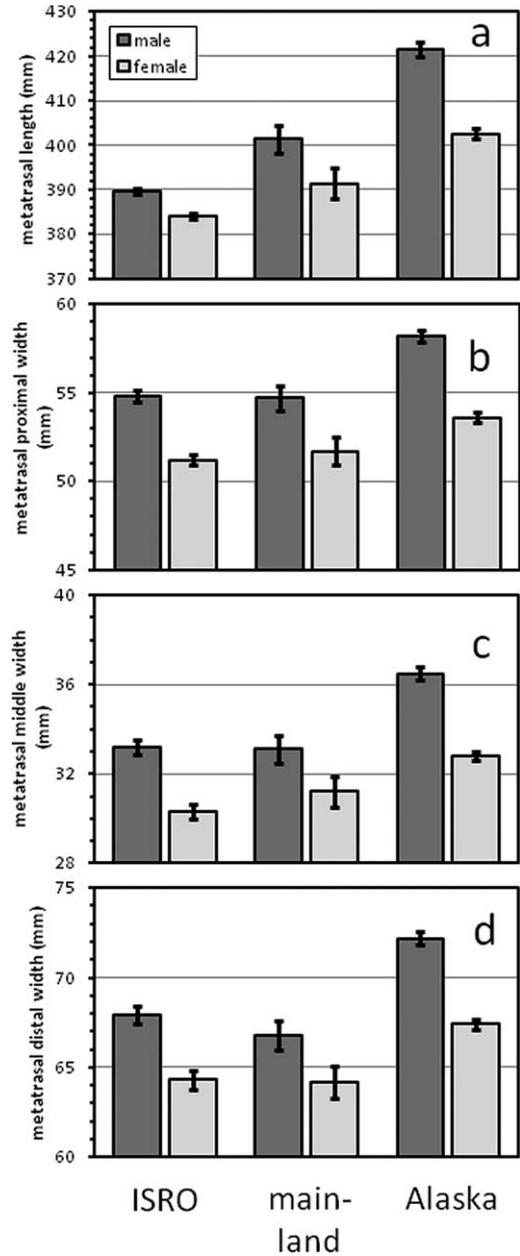


Fig. 6. The effect of sex and subgroup on metatarsal dimensions: length of the metatarsus (panel a) in which effects of sex, subgroup, and their interaction were observed ($P < 0.01$). Proximal, middle, and distal width of the metatarsus is shown in panels b, c, d. Effects of sex and subgroup on all 3 width measurements were observed ($P < 0.01$) but not of their interaction ($P \geq 0.09$).

separately in the Isle Royale and non-Isle Royale subgroups. In both cases, the effect of proximal width was evident ($P < 0.01$; Table 1). Sex had no effect on length that was not already accounted for by proximal width ($P > 0.21$). The interaction term of sex with proximal width on metatarsal length was also not significant ($P > 0.20$) in either the Isle Royale or non-Isle Royale subgroups. Similarly, there were no effects of sex or the interaction of sex and width on the relationship between middle or distal width on the length of the metatarsal (Table 1).

Predictive Equations for Metatarsal Length Based on Widths

A quantitative description of the relationship between proximal width and

metatarsal length was investigated with linear regression. Separate regression analyses were conducted for the Isle Royale and non-Isle Royale subgroups using the following simple model:

$$\text{metatarsal length} = m \times \text{proximal metatarsal width} + b + e \quad (1)$$

where:

- m = slope,
- b = y-intercept, and
- e = error term.

Comparison of the estimates of slope and y-intercept for the two groups (Isle Royale versus non-Isle Royale) indicated substantial difference (Table 2, Fig. 7). These relationships explained a high percentage of the variation in metatarsal length for Isle Royale ($r^2 = 0.47$) and non-Isle Royale specimens ($r^2 = 0.66$) (Table 2). The accuracy of the regression lines in predicting metatarsal length from proximal width was evaluated by comparing measured lengths to estimated lengths from specimens not used to derive the regression equations; specimens from both groups were included in this test. The length of metatarsal bones from both groups was more accurately predicted using the separate regression equations derived from the respective data sets (Table 3).

The same analytical procedures were used to examine the relationships between middle width and metatarsal length, and distal width and metatarsal length; middle and distal widths were not available from fossil Alaskan moose. There was no effect of subgroup or the width by subgroup interaction term, indicating consistency across all subgroups. Subsequently, regression analysis was used and prediction equations developed with the combined subgroup data (Fig. 8, 9, Table 4). Again, width measurements accounted for a large percentage of the variation in metatarsal length ($r^2 = 0.55$ and 0.53 for middle and distal widths, respectively).

Table 1. The effect of sex on the relationship between the width of the metatarsal at 3 points of measurement (proximal, middle, and distal) and the length of the metatarsal in specimens from Isle Royale and non-Isle Royale locations including Alaska (modern and fossil), Canada, and the 48 contiguous United States (excluding Isle Royale).

		Isle Royale	non-Isle Royale
proximal width	n	102	120
	width	$P < 0.01$	$P < 0.01$
	sex	$P > 0.21$	$P > 0.78$
	sex \times width interaction	$P > 0.20$	$P > 0.83$
middle width	n	65	121
	width	$P < 0.01$	$P < 0.01$
	sex	$P > 0.89$	$P > 0.79$
	sex \times width interaction	$P > 0.83$	$P > 0.84$
distal width	n	65	120
	width	$P < 0.01$	$P < 0.01$
	sex	$P > 0.82$	$P > 0.89$
	sex \times width interaction	$P > 0.86$	$P > 0.83$

As with proximal width measurements, a reasonably accurate estimate of metatarsal length was obtained from either middle or distal width (Table 5). As expected, the length of the Isle Royale specimens tended to be overestimated.

Although not justified based on the initial analysis, a more accurate estimate of metatarsal length was developed using separate equations derived from the Isle Royale and non-Isle Royale data (Table 6, Fig. 8,

Table 2. The regression parameters describing the different relationship between proximal metatarsal width and metatarsal length in specimens from Isle Royale compared to other populations in Canada and the United States including Alaska.

	Isle Royale	non-Isle Royale
Sample size	110	159
Significance level	$P < 0.01$	$P < 0.01$
Adjusted r^2	0.47	0.66
Slope (SE)	2.67 (0.27)	4.09 (0.23)
y-intercept (SE)	245 (14)	185 (13)

Table 3. Comparison of measured and predicted metatarsal lengths (mm) in Isle Royale and non-Isle Royale moose using separate predictive equations developed from proximal metatarsal lengths (mm). Non-Isle Royale moose include modern and fossil specimens from Alaska, and modern specimens from the 48 contiguous United States (excluding Isle Royale) and Canada.

	Isle Royale	Alaska	mainland
Sample size	6	6	6
Ave. proximal metatarsal width	53.6	57.7	51.6
Ave. metatarsal length	384.5	414.3	389.8
Predicted metatarsal length from proximal metatarsal width (Isle Royale)	388.2	398.9	382.7
Difference between, range, and probability that true and predicted lengths differ (Isle Royale)	-3.7 -13.6–9.8 $P = 0.40$	15.5 5.4–33.4 $P = 0.02$	7.1 -0.4–18.8 $P = 0.04$
Predicted metatarsal length from proximal metatarsal width (non-Isle Royale)	403.7	420.2	395.5
Difference between, range, and probability that true and predicted lengths differ (non-Isle Royale)	-19.2 -28.0–5.4 $P = 0.01$	-5.9 -14.7–9.0 $P = 0.15$	-5.6 -16.7–2.1 $P = 0.08$

9). Accuracy was substantially improved for the Isle Royale and Alaskan subgroups (Table 7), but not mainland moose that was a small heterogeneous group representing 3 subspecies.

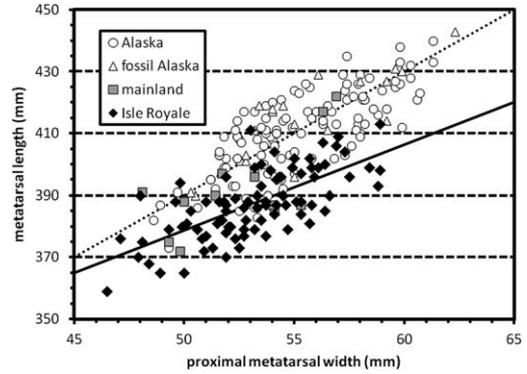


Fig. 7. Scatter plot depicting the relationship between the proximal metatarsal width and metatarsal length for the 4 subgroups (Isle Royale [ISRO], mainland [non-ISRO from the lower 48 contiguous United States and Canada], Alaska, and fossil Alaska). Regression lines for the Isle Royale (dotted) and non-Isle Royale (solid line) groups are shown.

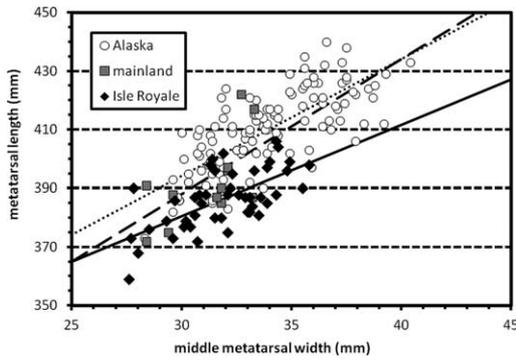


Fig. 8. Scatter plot depicting the relationship between middle metatarsal width and metatarsal length for 3 subgroups (Isle Royale [ISRO], mainland [non-ISRO from the lower 48 contiguous United States and Canada], and Alaska). Regression lines derived from ISRO specimens (dotted line), non-ISRO specimens (solid line), and for all specimens combined (dashed line) are shown.

DISCUSSION

The measurements of metatarsal length and width indicated that the Alaskan subgroups are larger in relative size. The Isle Royale subgroup is different from the other subgroups with shorter metatarsal length and correspondingly larger proximal: and distal width:length ratios. The length of the metatarsus was shorter in Isle Royale moose than the other subgroups and may reflect the trend for large herbivores to experience a reduction in size when isolated on small islands (Peterson et al. 2011), which conforms to the ‘island rule’ (Van Valen 1973, Lomolino 2005). Given this hypothesis and the short history of Isle Royale moose, these data demonstrate the remarkable speed at which this phenomenon can occur.

The metatarsal length:width ratios also provide insight into the biological mechanism by which reduction in metatarsal size occurred on Isle Royale. Long bones, including metatarsals, initially form in 3 parts, the proximal epiphysis (proximal articular surface), diaphysis (shaft), and distal epiphysis.

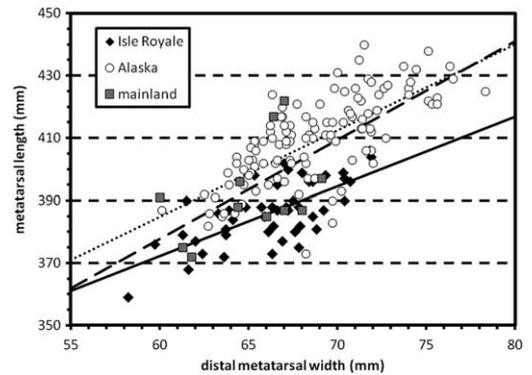


Fig. 9. Scatter plot depicting the relationship between distal metatarsal width and metatarsal length for 3 subgroups (Isle Royale [ISRO], mainland [non-ISRO from the lower 48 contiguous United States and Canada], and Alaska). Regression lines derived from ISRO specimens (dotted line), non-ISRO specimens (solid line), and for all specimens combined (dashed line) are shown.

Growth ceases when the cartilaginous epiphyseal plates separating these portions ossify. It appears that the reduced size in Isle Royale specimens is limited to the diaphysis with both the length and width of the diaphysis affected proportionally. The widths at the proximal and distal epiphyses do not appear to be reduced, particularly when compared to the mainland group. Thus, the shortening effect appears to be mediated solely through the diaphysis and this isolated effect may facilitate the identification of specific genes mediating such evolutionary action.

The length of the metatarsus could be predicted accurately from each of the width measurements, particularly if separate predictive equations were developed for specimens from Isle Royale versus other subgroups. The greatest deviation between predicted and actual metatarsal length was only 4.3% using the specific equations; refinements to these predictive equations are presumably possible. For example, the distal width measurement was taken either at the distal

epiphysis or at the distal articular condyle, whichever was wider; however, a more accurate equation might be developed with a single, consistent measurement. Predictive equations based on middle and distal widths for the non-Isle Royale subgroups improved the accuracy of prediction for the Alaskan, but not mainland group, possibly reflecting the potential heterogeneity within the mainland group. It may indicate that separate

equations need to be developed for subpopulations within.

Finally, possible differences in the method of sample collection among data sets should be considered. The majority of mainland specimens were collected by hunters or the result of vehicular accidents, whereas specimens from Isle Royale, Kenai National Wildlife Refuge, and Denali National Park were collected from moose presumably dying of natural causes. Animals that were particularly susceptible to predation may be overrepresented in these groups. A more robust sample size reflecting consistent sampling and population variation would presumably improve the relationships presented in this paper.

Table 4. The regression parameters describing the relationship between middle metatarsal width (mm) and metatarsal length (mm), and distal metatarsal width (mm) and metatarsal length. Common equations were developed using specimens from all subgroups.

	middle metatarsal	distal metatarsal
Sample size	210	208
Significance level	$P < 0.01$	$P < 0.01$
Adjusted r^2	0.55	0.53
Slope (SE)	4.81 (0.30)	3.38 (0.22)
y-intercept (SE)	242 (10)	172 (15)

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Table 5. Comparison of measured metatarsal length (mm) and predicted metatarsal length (mm) in Isle Royale and non-Isle Royale moose based on middle and distal metatarsal widths (mm). Common predictive equations were derived using specimens from all subgroups.

	Isle Royale	Alaska	mainland
Sample size	6	6	6
Ave. metatarsal length	384.5	414.3	389.8
Ave. middle width of metatarsal	32.5	35.2	31.8
Predicted metatarsal length from middle metatarsal width	397.8	411.2	394.7
Difference between, range, and probability that true and predicted length differ (mm)	-13.3 -30.0-6.2 $P = 0.08$	3.2 -5.2-15.9 $P = 0.34$	-4.8 -9.3-0.1 $P = 0.01$
Ave. distal width of metatarsal	66.9	70.9	64.3
Predicted metatarsal length from distal metatarsal width	398.3	411.7	389.7
Difference between true length and predicted length (mm) and range (below)	-13.8 -23.3-0.0	2.7 -13.6-11.9	0.2 -11.7-12.0
Probability that the true length and the predicted length are different	$P = 0.04$	$P = 0.53$	$P = 0.96$

Table 6. The regression parameters describing the relationship between proximal metatarsal width (mm) and metatarsal length (mm) in specimens from Isle Royale compared to non-Isle Royale moose. Non-Isle Royale moose included modern and fossil specimens from Alaska, and modern specimens from the 48 contiguous United States (excluding Isle Royale) and Canada.

	Middle metatarsal width		Distal metatarsal width	
	Isle Royale	Non-Isle Royale	Isle Royale	Non-Isle Royale
Sample size	71	139	71	137
significance	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
adjusted r^2	0.41	0.54	0.50	0.54
slope (SE)	3.30 (0.47)	4.07 (0.32)	2.38 (.29)	2.91 (0.23)
y-intercept (SE)	280 (15)	270 (11)	228 (19)	209 (16)

Table 7. Comparison of measured and predicted metatarsal lengths (mm) from middle and distal metatarsal widths (mm) in Isle Royale moose with those from non-Isle Royale moose. The Alaska and mainland equations were derived from measurements from non-Isle Royale moose that included modern and fossil specimens from Alaska, and modern specimens from the 48 contiguous United States (excluding Isle Royale) and Canada.

	Isle Royale	Alaska	mainland
Sample size	6	6	6
Ave. metatarsal length	384.5	414.3	389.8
Ave. middle width of metatarsal	32.5	35.2	31.8
Predicted metatarsal length from middle metatarsal width	388.3	414.5	400.5
Difference, range, and probability that true and predicted lengths differ	-3.8 -16.2–13.7 $P = 0.50$	-0.2 -7.3–14.5 $P = 0.96$	-10.7 -15.5–5.5 $P < 0.01$
Ave. distal width of metatarsal	66.9	70.9	64.3
Predicted metatarsal length from distal metatarsal width	388.0	415.5	396.5
Difference, range, and probability that true and predicted lengths differ	-3.5 -13.5–11.0 $P = 0.47$	-1.2 -16.6–10.4 $P = 0.78$	-6.7 -16.8–6.4 $P = 0.10$

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