

# PHENOTYPIC VARIATION IN MOOSE: THE ISLAND RULE AND THE MOOSE OF ISLE ROYALE

Rolf O. Peterson<sup>1</sup>, John A. Vucetich<sup>1</sup>, Dean Beyer<sup>2</sup>, Mike Schrage<sup>3</sup>, and Jannikke Råikönen<sup>4</sup>

<sup>1</sup>School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931; <sup>2</sup>Michigan Department of Natural Resources and Environment, Northern Michigan University, 3001 New Science Facility, Marquette, MI 49855; <sup>3</sup>Fond du Lac Resource Management Division, 1720 Big Lake Rd. Cloquet, MN 55720; <sup>4</sup>Swedish Museum of Natural History, Department of Contaminant Research, Frescativägen 44 P.O. Box 50007, S-104 05 Stockholm, Sweden.

**ABSTRACT:** There is strong empirical support for the *island rule*, whereby body size in insular populations of animals tends toward gigantism in small-bodied species and dwarfism in large-bodied species (>10 kg). For large-bodied species, underlying reasons for dwarfism in insular populations include lack of predation and resource limitation. We found that metatarsal length of moose (*Alces alces*) from Isle Royale National Park in Lake Superior (North America) was significantly shorter than that of mainland moose in Minnesota and Michigan. On Isle Royale, moose body size was inversely related to moose density at the time of birth, illustrating the resource limitation that is influential where average moose density is 5-10 times higher than on the mainland. Reduced body size probably developed in Isle Royale moose within a half century of their establishment, prior to the arrival of wolves (*Canis lupus*), and subsequently body size should be shaped by the countervailing influences of resource limitation and predation by wolves. Bones provide an excellent basis for spatio-temporal comparisons of body size among moose populations. With additional data on metatarsus length from moose in Alaska and Sweden, we illustrate important considerations such as sample size, sex differences, and biases arising from source of bone collections.

ALCES VOL. 47: 125-133 (2011)

**Key words:** *Alces alces*, body size, bones, growth, metatarsus, nutrient limitation, predation, skeletal.

Reduced species diversity in insular environments produces a novel suite of selective pressures which has informed scientific understanding of evolution since the time of Charles Darwin. The most pervasive alteration of phenotype involves body size change in island fauna, termed the *island rule* (Van Valen 1973). Initial efforts to describe the variety of patterns evident around the world led to taxonomic groupings of phenotypic change in insular species, for example, dwarfism in carnivores and gigantism in rodents (Foster 1964). More recent analyses have found it fruitful to consider body size change in insular faunas as occurring along a body size gradient (Lomolino 2005), with small

bodied fauna (<0.1 kg) increasing in size and large bodied fauna (>10 kg) exhibiting reduced size. Miniature species of hippopotamus and elephant occurred on islands in the Mediterranean Ocean (Simmons 1999) and dwarfed mammoth species developed on Wrangel Island in the Arctic Ocean (Vartanyan et al. 1993) and the Channel Islands off the coast of California (Agenbroad 2005). The discovery of dwarfed hominids (*Homo floresiensis*) on the Island of Flores in Indonesia (Lieberman 2009) has renewed interest in this phenomenon. A recent review cited the need for detailed studies of particular species in specific insular situations, in order to provide better understanding of factors influencing

evolution and assembly principles for biotic communities (Lomolino 2005).

Ungulate populations on islands typically evolve smaller body size, with the dominant interpretation being that resource limitation and reduced predation together lead to dwarfism. For ungulates in mainland populations, the evolution of large body size is assumed to be driven by greater success in evading predators, but on islands lacking predators, other environmental factors tend to select for smaller body size. In spite of the prominence of moose (*Alces alces*) and their evolutionary predecessors in paleontology (Bradshaw et al. 2003) and the significance of body size evolution among cervids generally (Geist 1998), it is surprising that basic data on change in body size for insular moose populations is totally lacking.

In this study we gathered bone length data from moose in Isle Royale National Park and several mainland populations to evaluate the extent and rate of change in body size for an island population of moose. While Isle Royale harbors a high density of moose, there have also been gray wolves (*Canis lupus*) present for the past 60 years, thus providing a unique insular environment where we expect that opposing selective forces may influence body size. We sought to clarify, to the extent possible, the relative roles of resource limitation and lack of predation in shaping moose phenotype.

Because bones from each individual do not vary in length after the initial juvenile growth phase is complete, they may be superior to body mass as a basis for comparing body size in different populations. We used the metatarsal bone, as it has a high growth priority *in utero*, and much of the variation in adult length of metatarsus can be attributed to nutritional plane before and shortly after birth (Palsson and Verges 1952). In cervid research, it was initially used to evaluate size of insular black-tailed deer (*Odocoileus hemionus*) on Coronation Island in southeast Alaska (Klein 1964).

## STUDY AREA AND METHODS

Isle Royale National Park, located in Lake Superior about 25-30 km from the nearest mainland, has supported moose since the early 1900s. The size of the primary island at Isle Royale is 544 km<sup>2</sup>, and its long and narrow topography is entirely forested by 3 distinct forest communities: spruce-fir (*Picea glauca*-*Abies balsamea*) in nutrient poor regions, especially at the eastern portion of the island, 75-year-old post-fire spruce-birch-aspen (*Betula papyrifera*-*Populus tremuloides*) in the middle of the island, and “climax” stands of yellow birch (*B. allegheniensis*) and sugar maple (*Acer saccharum*) with extensive white cedar (*Thuja occidentalis*) swamps on the island’s western half. All forest stands at Isle Royale are at least 75 years old, and those stands with highest moose density exceed 150 years in age. Additional information on moose habitat at Isle Royale is available from Krefting (1974) and Peterson (1977).

Gray wolves have coexisted with moose on Isle Royale since the late 1940s (Mech 1966), and moose mortality from wolf predation is generally highest for young-of-the-year and individuals >10 years of age (Peterson 1977). The influence of wolf predation was dramatically manifested when moose increased at least four-fold after wolves were limited by disease during the 1980s (Peterson et al. 1998). During 1971-2009, mean annual predation rate (i.e., mortality rate due to predation) was 9.90% and the interquartile range was 6.25-12.50% (Vucetich et al. 2011). Moreover, for every 1% increase in predation rate there tends to be at least a 1% decline in moose population growth rate (J. A. Vucetich and R. O. Peterson, unpubl. data).

Mainland study areas where moose skeletal material was collected include northeastern Minnesota and the central portion of the Upper Peninsula of Michigan. These areas are completely forested with tree species typical of the Upper Great Lakes and not unlike those found on Isle Royale. Compared to Isle

Royale, mainland areas have relatively more pine stands (*Pinus strobus*, *P. banksiana*, and *P. resinosa*) and fewer mature stands of spruce-fir (cf. Karns et al. 1974).

Metatarsals from moose in Sweden were available in museum collections with dates of origin that spanned more than a century. Moose habitats in Sweden are forests of primarily pine (*P. sylvestris*), spruce (*P. abies*), and birch (*B. verrucosa* and *B. pubescens*). Published data were available from moose from the Kenai Peninsula in Alaska (Peterson et al. 1982) where forested moose habitat is very similar to Sweden except that pine is absent (Peterson et al. 1984).

In Isle Royale National Park, metatarsal bones were collected from moose that died of natural causes, especially wolf predation, during the period 1970-2007. Samples from moose in Minnesota and Michigan were collected in 2004-2009; cause of death was either natural, accidental, or harvest. In Sweden metatarsal length was determined from museum collections derived over a century of mortality from a variety of causes. Published data on moose from the Kenai Peninsula in Alaska (Peterson et al. 1982) was also evaluated; these were moose that mostly died of wolf predation or starvation. In all cases moose age was estimated from counts of cementum annuli in teeth, and gender was evident from external genitalia or presence/absence of antlers or antler pedicels on the skull.

In this study metatarsal bones came from many populations that span a wide spectrum of moose population density. At Isle Royale, average moose density ranged from 1.5-3 moose/km<sup>2</sup>, about an order of magnitude higher than adjacent mainland areas (Dodge et al. 2004, Lenarz 2010). Density of moose on the Kenai Peninsula, Alaska has been relatively high at 0.8 moose/km<sup>2</sup> (Peterson et al. 1984). In Sweden, where collections spanned more than a century, moose density ranged from probably <0.1 moose/km<sup>2</sup> in the 19<sup>th</sup> century to 2-3 moose/km<sup>2</sup> after 1970 (Cederlund and

Markgren 1987).

Greatest length of the metatarsus was measured to the nearest mm with either calipers or a measuring board. Re-measurement of bones from Isle Royale moose showed that fresh specimens shrank by an average of 1 mm during indoor storage, so this was subtracted from fresh measurements to provide an estimate of total length when dry. Thirteen mm was added to metatarsus length reported by Peterson et al. (1982) because they measured length from the proximal to distal articulating surfaces instead of total length.

Metatarsus length was compared between populations using the two-sample *t*-test. The relationship between metatarsus length and moose density at Isle Royale was evaluated using linear regression. Body size divergence ( $S_i$ ) was expressed as the quotient of body size for moose from Isle Royale relative to the mainland, using the cubed metatarsus length after Lomolino (2005).

## RESULTS

For the sexual dimorphic moose, males are consistently larger than females, so all inter-population comparisons were restricted to moose of one gender. Mainland moose from Michigan and Minnesota were not different in size ( $P = 0.09$  for females,  $P = 0.23$  for males), so these data were pooled for subsequent analysis. For both female and male moose, Isle Royale animals exhibited significantly shorter metatarsus length than the pooled sample of mainland moose from Michigan and Minnesota ( $P = 3.49 \times 10^{-4}$  for females,  $P = 5.05 \times 10^{-12}$  for males; Table 1). Population difference between males was greater than that of females, so in effect sex dimorphism was greater on the mainland than at Isle Royale (Fig. 1). Body size divergence score between moose populations at Isle Royale and the mainland,  $S_i$ , was 0.88 for female moose but 0.93 for males.

Female moose from Alaska's Kenai Peninsula and male moose from Sweden

Table 1. Mean metatarsus length (mm) + SE (and sample size) for moose from Isle Royale (ISRO), the adjacent mainland states of Michigan and Minnesota (MI, MN), Sweden, and the Kenai Peninsula, Alaska (AK). Data from Alaska are modified from Peterson et al. 1982 (see **METHODS**). Metatarsus length of both sexes on ISRO was shorter than in MI and MN moose ( $P < 0.05$ ); metatarsus length of females from AK and males from Sweden were longer than those from ISRO ( $P < 0.05$ ).

Population	Female	Male
ISRO	381.55 ± 0.43 (546)	388.61 ± 0.42 (553)
Mainland, MI, MN	390.56 ± 2.15 (25)	406.20 ± 1.49 (25)
Sweden	394.88 ± 4.60 (8)	403.63 ± 2.38 (19)
Kenai Peninsula, AK	396.00 ± 1.23 (66)	397.00 ± 3.47 (3)

were significantly larger (non-overlapping 95% confidence intervals) than the respective gender from Isle Royale (Table 1). None of the populations from mainland areas differed in size, although this may reflect sample size limitations more than biological reality.

We were able to determine the extent of temporal change in moose size only for moose from Isle Royale. Average metatarsal length was inversely related to moose density at the time of birth ( $P = 0.05$  for females,  $P = 0.06$  for males; Fig. 2).

**DISCUSSION**

The size of moose in Isle Royale National Park presumably diverged from that of the ancestral mainland population after moose colonized the island in the early 1900s (Mech 1966). After colonization, moose density rapidly increased until public concern mounted over excessive moose density, approximately 2-6 moose/km<sup>2</sup> in the late 1920s (Murie 1934). A major population decline from starvation in winter 1934 was evidence that initial growth of the moose population was over (Krefting 1974); thereafter, moose density has fluctuated from 1-5 moose/km<sup>2</sup> (Vucetich and Peterson

2010), with average density of about 2 moose/km<sup>2</sup>.

Phenotypic dwarfing in insular ungulate populations is typically attributed to the combination of nutrient limitation (from high population density) and lack of selection pressure for larger body size (in the absence of predation). Isle Royale provides a unique environment to potentially tease apart the relative importance of nutrient limitation and low predation as ultimate causes of island dwarfism, because it supports only one species of ungulate (at high population density relative to mainland North America), and yet there is strong selection pressure from wolf predation.

Temporal variability in body size within the Isle Royale moose population seems to arise primarily from density-dependent effects of population fluctuations. Moose provide a useful species for understanding fundamental relationships among body size, population

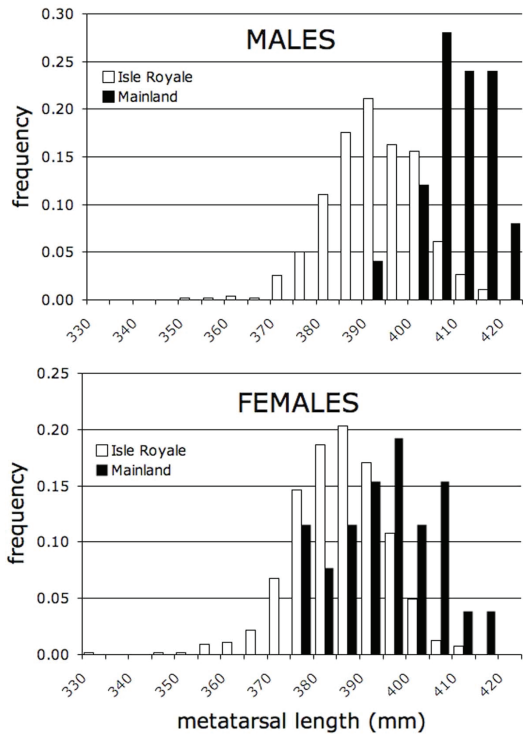


Fig. 1. Frequency distribution of metatarsus length for male and female moose in Isle Royale National Park and in adjacent mainland areas in Minnesota and Michigan.

density, and effects on vegetation, in part, because it is possible to estimate density. Although we used linear regression to evaluate the relationship between population density and body size, we do not know its precise nature. Average population density over 50 years was  $\sim 2$  moose/km<sup>2</sup>, which is very similar to the density target for the moose population in Sweden based on an understanding of biological and social carrying capacity (Cederlund and Markgren 1987). At Isle Royale, cohorts born when density was  $>2$  moose/km<sup>2</sup> showed reduced adult stature, but we could not derive a lower threshold for such density effects from the available data. Palaeoecological studies concerned with the ecosystem effects of large herbivores are often limited by the difficulty of determining animal density from assemblages of bones (Bradshaw et al. 2003), so studies of phenotypic response in modern moose may provide informative context.

Though perhaps limited by sample size from mainland moose populations, our data suggest that sex dimorphism in moose body size is reduced in Isle Royale moose relative to that of the mainland. This is relevant to the dispersal theory of Pleistocene evolution in ungulate fauna (Geist 1998), and is consistent with our current understanding of sex differences in life history strategies for large cervids. Enhanced nutrition should lead to greater body size in males than in more risk-averse females that occupy secure areas more likely to be poor in forage (Geist 2002). For 2 avian species with a life history quite different from moose, reduced sex dimorphism was also demonstrated for insular populations (Blondel et al. 2002, Roulin and Salamin 2010).

Body size divergence in moose (average  $S_i = 0.9$ ) after a century of isolation was relatively slight, compared to  $S_i$  values of 0.6-0.8 for many species of artiodactyls (Lomolino 2005) and for mammals  $<1$  kg body mass isolated in forest islands in Denmark for 175 years. Long generation time in moose would certainly retard body size change compared

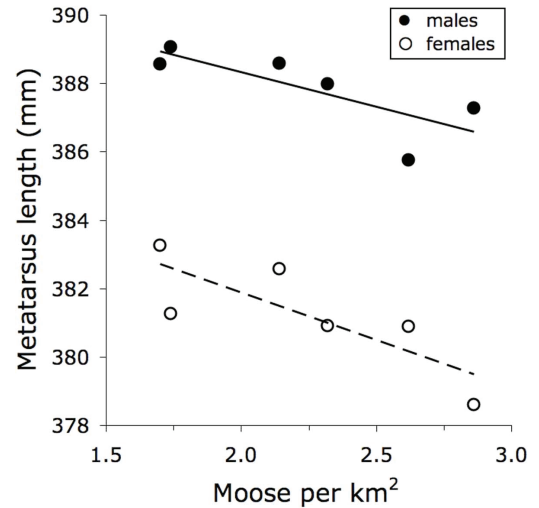


Fig. 2. Metatarsus length for moose in Isle Royale National Park declines as population density at the time of birth increases. Each data point represents mean metatarsus length and mean population density for 5-year periods from 1965-1969 through 1990-1994. For females:  $Y = 387.45 - 2.78X$ ,  $R^2 = 0.65$ ,  $P = 0.05$  (average  $n = 42$ , range = 23-53). For males:  $Y = 392.4 - 2.04X$ ,  $R^2 = 0.62$ ,  $P = 0.06$  (average  $n = 44$ , range = 24-70).

to smaller mammal species.

This study provides evidence that using the moose metatarsus could be useful in comparisons of moose populations in other areas. This bone has the advantages of easy dissection from whole carcasses, ability to withstand most carnivore feeding, ease of measurement, high measurement repeatability, and high sensitivity to nutritional plane for parturient females. Sample size needs to be adequate for population comparisons, on the order of  $\geq 20$  samples per sex. The sampled animals need to be at least 2-3 years old, or at a minimum possess a fused epiphysis, which implies that further elongation of this bone is impossible. Attention must be paid to geographic origin of museum specimens; our Swedish specimens were too few in number to illustrate how moose size varied in relation to latitude, suggested by anecdotal evidence for larger moose in more northern parts of Sweden. For fine-scale comparisons, fresh

bones should be allowed to dry indoors for one year before measurement. Finally, because all mortality factors are biased in some manner, interpretation should consider the source of mortality that provided the samples.

For example, Peterson et al. (1982) provided growth curves for moose metatarsus length that suggested continued growth for moose 2-4 years old, even though metatarsal growth is normally terminated after fusion of the epiphyseal growth plate after the second summer of growth. Continued growth for samples older than this may reflect bias toward sampling moose with small body size, to be suspected for wolf-killed moose. Furthermore, the relationship between metatarsal length and moose age among wolf-killed moose represents evidence that larger moose are less prone to predation. Specifically, metatarsal length tends to increase with moose age up to approximately 8 years (Peterson et al. 1982 and, more recently, J.A. Vucetich and R.O. Peterson, unpubl. data). This increase cannot represent physiological growth because growth of the metatarsus of any individual ceases after 2 (or 3 at the extreme) summer periods of growth (Peterson 1977). Consequently, further increase in metatarsal length with moose age represents the culling of smaller moose before they have a chance to increase in age.

Evolution of cervids generally, and moose in particular, is assumed to have been driven by intense predation pressure from large carnivores resulting in long legs and a reduced number of leg bones (Bubenik 1998). The larger of these carnivores have been extinct for several thousand years (Geist 1998), yet present-day carnivores may still influence the phenotype of moose. A meta-analysis of moose density in relation to carnivore species diversity indicates that extant carnivores (2 species of bears [*Ursus arctos* and *Ursus americana*], the gray wolf, and hunting humans) provide an important degree of population limitation (Peterson et al. 2003), implying a relationship between predation intensity and moose sur-

vival patterns. Although the gray wolf coexists with moose on Isle Royale, our study underscores the significance of nutritional limitation associated with high density as the basis for insular dwarfing in large ungulates. Reduced body size in insular ungulate populations has been viewed as an adaptation allowing early reproduction in a low-mortality environment (Lomolino 2005), but our study underscores the potential for interlinking ecological and evolutionary dynamics. Future studies of genetic change in moose from Isle Royale in relation to population density and wolf predation would be fruitful; presently there are no data available on genotypic responses in this population. At this point, our “Occam’s Razor” interpretation is that reduced selection pressure from lack of predation is neither necessary nor sufficient for reduced body size in insular ungulates, at least at short temporal scales – what is required is high population density leading to nutritional limitation. Parsing the relative roles of ecological and evolutionary responses remains a future challenge.

We have provided only snapshots of moose stature from several populations. In reality, moose phenotype is quite dynamic, as we have shown for moose on Isle Royale. Future research may elucidate the precise role of wolf predation in evolution of the moose phenotype. At Isle Royale, moose with shorter metatarsus length have lower survival rates (Peterson et al. 2010), so there is potential for evolutionary response to mortality caused by wolf predation. On the predator-free island of Hirta (Scotland, UK), free-ranging Soay sheep (*Ovis aries*) declined in body weight over a 20-year period, with phenotype apparently changing as an ecological response to changing climate rather than adaptive evolution from genetic selection (Ozgul et al. 2009).

More detailed analysis of skeletal material from moose may demonstrate if body size reduction in moose follows allometric models, a research area relevant to understanding the evolution of *Homo floresiensis*,

a recent insular hominid that stood barely 1 m tall. Unexpectedly small brain size in relation to body size has posed challenges to understanding the evolution of this relatively modern dwarf species (Weston and Lister 2009). Preliminary analysis of brain size in moose from Isle Royale suggests higher variability than the metatarsus (R. Peterson and J. Vucetich, unpubl. data), and Bubenik and Bellhouse (1985) argued that brain volume was a sensitive indicator of early nutritional plane. Future progress in this arena would be aided considerably by more systematic collections of moose skeletal material across space and time.

### ACKNOWLEDGEMENTS

Collections of moose skeletal material at Isle Royale National Park were supported by grants from Isle Royale National Park (Co-op Agreement J631005N004/0003), the National Science Foundation (DEB-042562), Earthwatch, Inc., and numerous private donors. Collections from moose in Minnesota were possible through the support of the Fond du Lac Resource Management Division and the Minnesota Department of Natural Resources, while in Michigan the support of the Michigan Department of Natural Resources and Environment facilitated this study. In Sweden the following museums provided access to collections for measurement: Museum of Natural History, Gothenburg; Malmö Museum; Museum of Zoology Lund University; Swedish Museum of Natural History. In Sweden, we thank Peter Mortensen, Karina Lövgren, and Arne Söderberg for help with specimen collection. In all study areas, numerous volunteers and staff assisted in collection and preparation of bones from moose, and we greatly appreciate their dedication and interest.

### REFERENCES

- AGENBROAD, L. D. 2005. North American Proboscideans: Mammoths: The State of Knowledge 2003. Quaternary International 126-128: 73-92.
- BLONDEL, J., P. PERRET, M. C. ANSTETT, and C. THEBAUD. 2002. Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *Journal of Evolutionary Biology* 15: 440-450.
- BRADSHAW, R. H. W., G. E. HANNON, and A. M. LISTER. 2003. A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management* 181: 267-280.
- BUBENIK, A. B. 1998. Evolution, taxonomy and morphophysiology. Pages 77-123 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington D. C., USA.
- \_\_\_\_\_, and T. J. BELLHOUSE. 1985. Volumetric measurement of braincase cavity. *Mammalia* 49: 415-420.
- CEDERLUND, G., and G. MARKGREN. 1987. The development of the Swedish moose population, 1970-1983. *Swedish Wildlife Research Suppl.* 1: 55-61.
- DODGE, W. B. Jr., S. R. WINTERSTEIN, D. E. BEYER, Jr., and H. CAMPA III. 2004. Survival, reproduction, and movements of moose in the western Upper Peninsula of Michigan. *Alces* 40: 71-85.
- FOSTER, J. B. 1964. Evolution of mammals on islands. *Nature* 202: 234-235.
- GEIST, V. 1978. *Life Strategies, Human Evolution, Environmental Design*. Springer-Verlag, New York, New York, USA.
- \_\_\_\_\_. 1998. *Deer of the World*. Stackpole Books, Mechanicsburg, Pennsylvania, USA.
- \_\_\_\_\_. 2002. Adaptive behavioral strategies. Pages 389-433 in D. E. Toweill and J. W. Thomas, editors. *North American Elk: Ecology and Management*. Smithsonian Institution Press, Washington D. C., USA.
- KARNS, P. D., H. HASWELL, F. F. GILBERT, and

- A. E. PATTON. 1974. Moose management in the coniferous-deciduous ecotone of North America. *Naturaliste Canadienne* 101: 643-656.
- KLEIN, D. R. 1964. Range-related differences in growth of deer reflected in skeletal ratios. *Journal of Mammalogy* 45: 226-235.
- KREFTING, L. W. 1974. The ecology of the Isle Royale moose with special reference to the habitat. Technical Bulletin 297-1974, Forest Series 15. Agricultural Experiment Station, University of Minnesota, Duluth, Minnesota, USA.
- LENARZ, M. 2010. 2010 Aerial Moose Survey. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA. <[http://files.dnr.state.mn.us/outdoor\\_activities/hunting/moose/moose\\_survey\\_2010.pdf](http://files.dnr.state.mn.us/outdoor_activities/hunting/moose/moose_survey_2010.pdf)> (accessed March 2011).
- LIEBERMAN, D. E. 2009. *Homo floresiensis* from head to toe. *Nature* 459: 41-42.
- LOMOLINO, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* 32: 1683-1699.
- MECH, L. D. 1966. The Wolves of Isle Royale. United States National Park Service Fauna Series Number 7, United States Government Printing Office, Washington, D. C., USA.
- MURIE, A. 1934. The Moose of Isle Royale. Miscellaneous Publication Number 25. University of Michigan Press, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA.
- OZGUL, A., S. TULJAPURKAR, T. G. BENTON, J. M. PEMBERTON, T. H. CLUTTON-BROCK, and T. COULSON. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* 325: 464-467.
- PALSSON, G., and J. B. VERGES. 1952. Effects of the plane of nutrition on growth and development of carcass quality in lambs. Part I. The effects of high and low planes of nutrition at different ages. *Journal of Agricultural Science* 42: 1-92.
- PETERSON, R. O. 1977. Wolf Ecology and Prey Relationships on Isle Royale. National Park Service Scientific Monograph Series No. 11. United States Government Printing Office, Washington, D. C., USA.
- \_\_\_\_\_, T. N. BAILEY, and J. D. WOOLINGTON. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88: 1-52.
- \_\_\_\_\_, J. M. SCHEIDLER, and P. W. STEPHENS. 1982. Selected skeletal morphology and pathology of moose from the Kenai Peninsula, Alaska, and Isle Royale, Michigan. *Canadian Journal of Zoology* 60: 2812-2817.
- \_\_\_\_\_, N. J. THOMAS, J. M. THURBER, J. A. VUCETICH, and T. A. WAITE. 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* 79: 828-841.
- \_\_\_\_\_, J. A. VUCETICH, G. FENTON, T. D. DRUMMER, and C. S. LARSEN. 2010. The ecology of arthritis. *Ecology Letters* 13: 1124-1128.
- \_\_\_\_\_, \_\_\_\_\_, R. E. PAGE, and A. CHOUINARD. 2003. Temporal and spatial aspects of predator-prey dynamics. *Alces* 39: 215-232.
- ROULIN, A., and N. SALAMIN. 2010. Insularity and the evolution of melanism, sexual dichromatism and body size in the worldwide-distributed barn owl. *Journal of Evolutionary Biology* 23: 925-934.
- SIMMONS, A. H. 1999. Faunal Extinction in an Island Society: Pygmy Hippopotamus Hunters of Cyprus. Plenum Press, New York, New York, USA.
- VAN VALEN, I. 1973. A new evolutionary law. *Evolutionary Theory* 1: 1-33.
- VARTANYAN, S. L., V. E. GARUTT, and A. V. SHER. 1993. The Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* 362: 337-340.
- VUCETICH, J. A., and R. O. PETERSON. 2010. Ecological Studies of Wolves on Isle Roy-



ale. Annual Report. Michigan Technological University, Houghton, Michigan, USA. <<http://www.isleroyalewolf.org>> (accessed ...).

- \_\_\_\_\_, M. HEBBLEWHITE, D. W. SMITH, and R. O. PETERSON. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *Journal of Animal Ecology* doi:10.1111/j.1365-2656.2011.01855.x.
- WESTON, E. M., and A. M. LISTER. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature* 459: 85-88.