

ANTLER SIZE RELATIVE TO BODY MASS IN MOOSE: TRADEOFFS ASSOCIATED WITH REPRODUCTION

Kelley M. Stewart¹, R. Terry Bowyer¹, John G. Kie^{1,2}, and William C. Gasaway^{3,4}

¹Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA; ²United States Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA; ³Alaska Department of Fish and Game, Fairbanks, AK 99701, USA

ABSTRACT: Body size and age are highly correlated with antler size, fighting ability, and reproductive success in male cervids. Production of antlers requires energy above that for maintenance of basal functions, and is especially demanding of minerals. In addition to producing antlers, young cervids also incur the cost of completing body growth. Large-bodied males with large antlers invest more in antler development and reproduction at the expense of body condition than do young males. Young males are constrained by the need to complete body growth to attain the body size necessary to compete effectively for females when mature and, hence, invest less in antlers. We tested the hypothesis that adult male moose (*Alces alces*) produced larger antlers relative to their body mass than did younger males. We used regression to compare the ratio of antler length per unit body mass (antler length: body mass) with age. Regression analysis indicated a strong curvilinear relationship ($R_a^2=0.961$) between antler length per unit body mass and age. Young males invested less in antlers than older males that had reached a sufficient size to compete effectively for mates; consequently, there was a tradeoff between body growth and antler size. Young males must produce antlers to gain experience in aggressive encounters and establish dominance relationships among their cohort, although investment in antlers is less than that of mature adults. Delaying investment in mating until physically mature and able to compete for females with other large-antlered males is the most successful strategy for maximizing mating success and achieving the greatest fitness in male moose, as well as among other cervids.

ALCES VOL. 36: 77-83 (2000)

Key words: age, *Alces alces*, antlers, body mass, cervids, mating success, moose, reproduction

Although several hypotheses have been forwarded to explain the function of antlers, most researchers agree that horn-like structures evolved as weapons for intraspecific combat (Geist 1966, Clutton-Brock 1982, Lincoln 1992). Among polygynous cervids, males compete vigorously for access to females during rut, which favors the evolution of sexual dimorphism and large fighting weapons, including antlers (Geist 1966, Lincoln 1994, Lundgren 1996, Weckerly 1998). The reason often proposed for this association between polygyny and sexual dimorphism is that mating success varies more

widely among males from polygynous species compared with monogamous ones, leading to more intense competition for mates and stronger sexual selection among males (Darwin 1871, Alexander *et al.* 1979, Clutton-Brock 1987, Weckerly 1998).

Body size, antler size, and social dominance are positively correlated across an array of cervids (Anderson and Medin 1969, McCullough 1969, Bowyer 1986, Van Ballenberghe and Miquelle 1993). Clutton-Brock *et al.* (1982) used regression to compare mean antler length against mean shoulder height as an index of body size, and

⁴William C. Gasaway passed away on 15 July 1998 in Stockton, CA, USA.

reported a positive relation between increasing antler and body size. Body size and age are strongly correlated with antler size and mating success (McCullough 1979, Clutton-Brock *et al.* 1982). Fighting success in red deer (*Cervus elaphus*) peaked between 7 and 10 years old, and declined rapidly in older animals (Clutton-Brock *et al.* 1979, 1982). Male reproductive success in white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*) was greatest after 5 years of age (McCullough 1969, 1979; Noyes *et al.* 1996).

Production of antlers, and supporting their large mass, requires energy above that for maintenance of basal functions in mature males, and may be especially demanding of minerals (Ullrey 1983). Both young and old-aged animals have less energy to invest in antlers because of the necessity of completing body growth in young animals, and declining body condition with senescence in old-aged individuals (McCullough 1979, Clutton-Brock *et al.* 1982, Ullrey 1983, Brown 1990). Such relationships, however, have not been demonstrated for moose (*Alces alces*). We hypothesized that antler growth was a lower energetic priority than body growth and maintenance in younger moose than in older ones; thus, extensive investment in the production of antlers was unlikely until adult body mass was achieved. We examined the relation between patterns of antler size with age, and tested for a correlation between antler length and overall antler size using data from Gasaway *et al.* (1987). We then used data from Prieditis (1979) to test the hypothesis that adult male moose produced larger antlers relative to their body mass than did younger males.

METHODS

We obtained data on age of adult moose in addition to their antler characters including right and left palm length, beam length,

number of points (tines), and total spread from Gasaway *et al.* (1987). We used principal component analyses (PCA; SAS Institute Inc. 1987) based on correlations among variables to reduce the dimensionality of those data, and obtained a single variable, principal component 1 (PC1) that indexed size. Following PCA, we compared antler size, as indexed by PC1, with age using regression analysis (Zar 1996).

We obtained data on Eurasian moose from Prieditis (1979) to evaluate the effects of body mass (kg) and antler size with age (years). Because those data did not include measurements of all antler characters and because we did not have access to original data, we used mean antler length (cm) as our index of antler size. We confirmed that length was a reliable index to size using data from Gasaway *et al.* (1987). We employed multiple regression with an adjusted coefficient of determination (R_a^2), weighted by sample size (Neter *et al.* 1985), to compare the ratio of antler length per unit body mass (antler length : body mass) against age.

RESULTS

Principal component analyses (PCA) on antler characteristics of Alaskan moose (Gasaway *et al.* 1987) reduced the dimensionality of those data (Table 1). The first principal component (PC1) explained 73% of the variation in antler measurements. Because the eigenvector associated with the first principal component (PC1) loaded similarly (range 0.30 - 0.35) across all antler characteristics, PC1 was used in further analyses as an index of overall size of antlers. Regression analyses indicated a curvilinear relationship between antler size (PC1) and age ($R_a^2=0.60$, $P\leq 0.001$, Fig. 1). That analysis indicated large variation in antler sizes in each age class, although antlers generally increased in size until about 10 years old and then declined (Fig. 1).

We used data from Prieditis (1979) to

Table 1. Summary statistics for age and antler characteristics of 1,501 Alaskan moose from 1968 to 1983; data from Gasaway *et al.* (1987).

Variable	Mean	SE
Age (yrs)	5.4	0.08
Total spread (cm)	131.3	0.66
Right palm width (cm)	26.8	0.21
Left palm width (cm)	26.9	0.21
Right palm length (cm)	81.2	0.61
Left palm length (cm)	81.1	0.61
Right beam length (cm)	17.9	0.06
Left beam length (cm)	17.9	0.07
Right number of points	8.9	0.07
Left number of points	9.0	0.07

examine the relation between antler size per unit body mass with age. Because fewer antler characteristics were available in that data set, we used antler length as an index of size; that variable was highly correlated ($r = 0.91$) with our index of antler size (PC1) for Alaskan moose. Weighted regression analyses indicated a curvilinear relationship between antler length per unit

body mass and age ($R_a^2 = 0.961$, $P < 0.0001$, Fig. 2). We also conducted that analysis with metabolic body mass (e.g., $BM^{0.75}$), but the relationship did not improve markedly ($Y = 0.09 + 0.16X - 0.01X^2$, $R_a^2 = 0.969$, $P \leq 0.001$, $n = 11$).

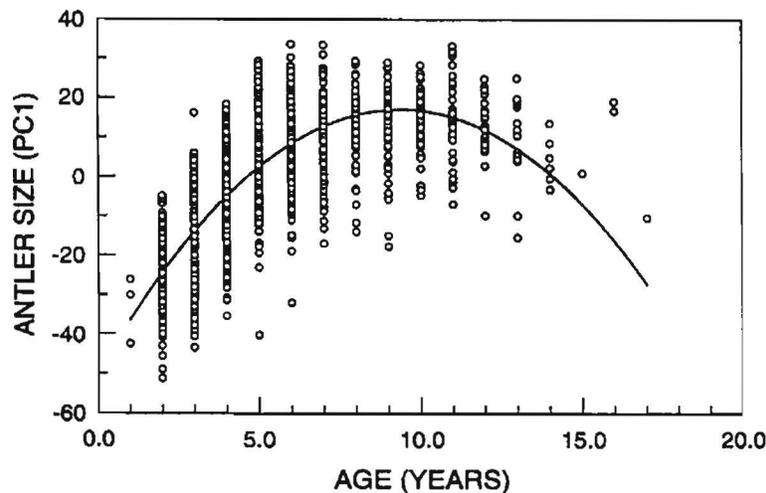


Fig. 1. Relationship between antler size (Y), indexed by principal component 1 (PC1), and age of Alaskan moose. Regression model; $Y = -49.94 + 14.30X - 0.76X^2$; $R_a^2 = 0.60$, $P < 0.001$, $n = 1,501$. Data for age and antler characteristics were obtained from Gasaway *et al.* (1987). We expected a parabolic fit because senescence of antlers in older males is common.

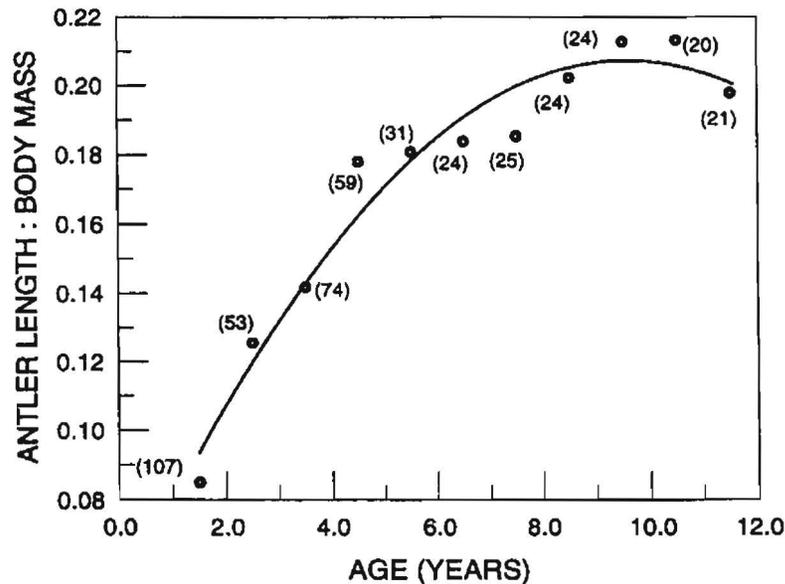


Fig. 2. Relationship between the ratio (Y) of antler length (cm) to body mass (kg) as compared with age (X) in years for Eurasian moose. Regression model; $Y = 0.04 + 0.38X - 0.002X^2$; $R_a^2 = 0.961$, $P < 0.0001$, $n = 11$, weighted by sample sizes (n). Means and sample sizes for age, antler length, and body mass were obtained from Prieditis (1979).

DISCUSSION

Male moose < 4 and ≥ 10 years old invested less in antlers than breeding-age males (Figs. 1 and 2). Moose < 4 years old had proportionally smaller antlers for their body size than individuals between 5 and 10 years of age (Fig. 2). McCullough (1979) and Clutton-Brock *et al.* (1982) reported that the greatest reproductive success was among adult males that had completed body growth, and our data supported their observations that mature males invested more in antler development than did younger age classes. Clutton-Brock *et al.* (1982) and Lincoln (1992) reported that prior to 5 years old, substantial increments in body growth were observed in male red deer, whereas rates of growth were slower in older age classes. Male moose, in Alaska, achieved maximum body mass at about 8 years of age (Schwartz 1998); our data also indicated that investment in antlers was greatest after that age (Figs. 1 and 2). Indeed, Bubenik *et al.* (1978) noted that shaft circumference

of moose antlers was greatest at 9.5 years. Fighting success of male red deer peaked between 7 and 10 years old and declined rapidly in males > 11 years (Clutton-Brock *et al.* 1982). Those observations are supported by the declining trend in antler sizes in animals > 10 years of age among male moose in our sample (Fig. 1).

Genetics, nutrition, and physical condition have substantial effects on antler characteristics (French 1956, Gross 1983, Brown 1990, Hundertmark *et al.* 1998). Moreover, antler morphometrics have been used to evaluate the performance of populations of white-tailed deer (McCullough 1982). Antler development is costly and requires substantial investment of resources; absorption of minerals, particularly calcium, from bones during antler growth has been observed in several species of cervids (Banks *et al.* 1968, Hillman *et al.* 1973, Muir *et al.* 1987). Van Ballenberghe (1983) reported that moose in Alaska completed antler growth in a shorter period than most other cervids,

which required high investment in antlers over a relatively short time. This rapid growth and potential for absorption of minerals might be especially costly for moose. Ullrey (1983) reported histological changes in the bones of white-tailed deer and mule deer (*Odocoileus hemionus*), and indicated that minerals were mobilized from bone during antler growth in adults. Indeed, the chemical composition of antlers varies with their size (McCullough 1969, Bowyer 1983) as well as the particular part of the antler (Miller *et al.* 1985). Existing models of calcium metabolism and antler development (Moen and Pastor 1998) should consider differential investment in antlers with respect to age. In addition, differences in allocation of minerals may have implications for osteoporosis in moose (Hindelang and Peterson 1996, Hindelang *et al.* 1998).

Fighting in cervids is both dangerous and costly; numerous studies have reported relatively high rates of activity and of injuries resulting from male combat during the mating season (Schaller 1967, Bowyer 1981, Clutton-Brock *et al.* 1982, Lincoln 1994). Mature adults invest heavily in antler development and reproduction at the expense of body condition (Miquelle 1990), whereas body growth appears to take precedence over antler development in growing cervids (Chapman 1975). Indeed, juvenile white-tailed deer had lower proportion of total mass in antlers than did deer > 4.5 years of age (McCullough 1982). Juvenile cervids are less likely to invest in antlers at the expense of body growth, particularly because body size is highly correlated with fighting success; and interactions between juveniles and mature adults were typically won by large males (Clutton-Brock 1982, Bowyer 1986). Hirth (1977) reported that sparring matches were performed primarily by the youngest males that were growing the fastest and were the least certain about their position in the dominance hierarchy,

whereas males in the largest antler classes participated in relatively few sparring bouts.

Investment in antlers at the expense of body development in younger age classes may result in decreased reproductive success overall, because those individuals ultimately may not be able to obtain the body or antler size needed to be competitive for females. Delaying investment in mating until physically mature and able to compete effectively for access to estrous females with other large-bodied and large-antlered males is likely the most successful strategy for maximizing reproductive success, thereby achieving the greatest fitness in moose and other cervids.

ACKNOWLEDGEMENTS

We are indebted to J. G. Cook, and B. L. Dick, for their helpful reviews of our manuscript, and to E. Rexstad for statistical advice. This manuscript benefited from helpful discussions of moose antlers with V. Van Ballenberghe, C. C. Schwartz, and K. J. Hundertmark. Funding for this study was provided by the Institute of Arctic Biology at the University of Alaska Fairbanks, and the U.S. Forest Service.

REFERENCES

- ALEXANDER, R. D., J. L. HOOGLAND, R. D. HOWARD, M. NOONAN, and P. W. SHERMAN. 1979. Sexual dimorphism, and breeding systems in pinnipeds, ungulates, primates and humans. Pages 402-604 *in* N. A. Chagnon and W. Irons (eds.) *Evolutionary Biology and Human Social Behavior, an Anthropological Perspective*. Duxbury Press, Boston, MA.
- ANDERSON, A. E. and D. E. MEDIN. 1969. Antler morphometry in a Colorado mule deer population. *J. Wildl. Manage.* 33:510-533.
- BANKS, W. J., G. P. EPLING, R. A. KAINER, and R. W. DAVIS. 1968.

- Antler growth and osteoporosis. I. Morphological and morphometric change in the costal compacta during the antler growth cycle. *Anat. Rec.* 162:387-497.
- BOWYER, R. T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. *J. Mammal.* 62:574-582.
- _____. 1983. Osteophagia and antler breakage among Roosevelt elk. *Calif. Fish Game* 69:84-88.
- _____. 1986. Antler characteristics as related to social status of male southern mule deer. *Southwest. Nat.* 31:289-298.
- BROWN, R. D. 1990. Nutrition and antler development. Pages 426-441 in G. A. Bubenik and A. B. Bubenik (eds.) *Horns, pronghorns, and antlers: evolution, morphology, physiology and social significance.* Springer-Verlag, New York, NY.
- BUBENIK, A. B., O. WILLIAMS, and H. R. TIMMERMANN. 1978. Some characteristics of antlerogenesis in moose. A preliminary report. *Proc. N. Am. Moose Conf. Workshop* 14:157-177.
- CHAPMAN, D. I. 1975. Antlers - bones of contention. *Mammal Rev.* 5:1-172.
- CLUTTON-BROCK, T. H. 1982. The functions of antlers. *Behaviour* 79:108-125.
- _____. 1987. Sexual selection in the Cervidae. Pages 110-122 in C.M. Wemmer (ed.) *Biology and management of the Cervidae.* Smithsonian Inst. Press, Washington, DC.
- _____, S. D. ALBON, R. M. GIBSON, and F. E. GUINNESS. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus*). *Anim. Behav.* 27:211-225.
- _____, F. E. GUINNESS, and S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago, IL. 378 pp.
- DARWIN, C. 1871. *The descent of man and selection in relation to sex.* John Murray, London, UK. 409 pp.
- FRENCH, C. E. 1956. Nutrient requirements for growth and antler development in white-tailed deer. *J. Wildl. Manage.* 20:221-232.
- GASAWAY, W. C., D. J. PRESTON, D. J. REED, and D. D. ROBY. 1987. Comparative antler morphology and size of North American moose. *Swedish Wildl. Res. Suppl.* 1:311-325.
- GEIST, V. 1966. The evolution of horn-like organs. *Behaviour* 27:175-214.
- GROSS, R. J. 1983. *Deer antlers: regeneration, function, and evolution.* Academic Press, New York, NY. 316 pp.
- HILLMAN, J. R., R. W. DAVIS, and Y. Z. ABDELBAKI. 1973. Cyclic bone remodeling in deer. *Calcified Tissue Res.* 12:323-330.
- HINDELANG, M., G. JAYARAMAN, and R. O. PETERSON. 1998. Biomechanical properties, osteoporosis, and fracture potential of metatarsal trabecular bone from moose in Isle Royale National Park. *Alces* 34:311-318.
- _____, and R. O. PETERSON. 1996. Osteoporotic skull lesions in moose at Isle Royale National Park. *J. Wildl. Diseases* 32:105-108.
- HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildl. Monogr.* 53. 55 pp.
- HUNDERTMARK, K. J., T. H. THELEN, and R. T. BOWYER. 1998. Effects of population density and selective harvest on antler phenotypes in simulated moose populations. *Alces* 34:375-383.
- LINCOLN, G. A. 1992. Biology of antlers. *J. Zool. Lond.* 226:517-528.
- _____. 1994. Teeth, horns, and antlers: the weapons of sex. Pages 131-158 in R. V. Short and E. Balaban (eds.) *Differences between the sexes.* Cambridge Univ. Press, Cambridge, UK.

- LUNDGREN, B. 1996. Morphology of horns and fighting behavior in the family Bovidae. *J. Mammal.* 77:462-475.
- MCCULLOUGH, D. R. 1969. The tule elk: its history, ecology, and behavior. *Univ. Calif. Publ. Zool.* 88:1-209.
- . 1979. The George Reserve deer herd: population ecology of a *K*-selected species. *Univ. Mich. Press. Ann Arbor, MI.* 271 pp.
- . 1982. Antler characteristics of George Reserve white-tailed deer. *J. Wildl. Manage.* 46:821-826.
- MILLER, K. V., R. L. MARCHINTON, J. R. BECKWITH, and P. B. BUSH. 1985. Variation in density and chemical composition of white-tailed deer antlers. *J. Mammal.* 66:693-701.
- MIQUELLE, D. G. 1990. Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27:145-151.
- MOEN, R. and J. PASTOR. 1998. A model to predict nutritional requirements for antler growth in moose. *Alces* 34:59-74.
- MUIR, P. D., A. R. SYKES, and G. K. BARRELL. 1987. Calcium metabolism in red deer (*Cervus elaphus*) offered herbages during antlerogenesis: kinetic and stable balance studies. *J. Agric. Sci.* 109:357-364.
- NETER, J., W. WASSERMAN, and M. H. KUTNER. 1985. Applied linear statistical models: regression, analysis of variance, and experimental designs. Second ed. Irwin, Homewood, IL. 1127 pp.
- NOYES, J. H., B. K. JOHNSON, L. D. BRYANT, S. L. FINDHOLT, and J. W. THOMAS. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. *J. Wildl. Manage.* 60:508-517.
- PRIEDITIS, A. A. 1979. Interrelation between the body weight and horn size in European elks (*Alces alces*) of different age. *Zool. Zhurnal* 58:105-110.
- SAS INSTITUTE, INC. 1987. SAS/STAT guide for personal computers. Version 6. Cary, NC. 1028 pp.
- SCHALLER, G. B. 1967. The deer and the tiger: a study of wildlife in India. Univ. Chicago Press, Chicago, IL. 370 pp.
- SCHWARTZ, C. C. 1998. Reproduction, natality, and growth. Pages 141-171 in A. W. Franzmann and C. C. Schwartz (eds.) Ecology and management of the North American moose. Smithsonian Inst. Press, Washington, DC.
- ULLREY, D. E. 1983. Nutrition and antler development in white-tailed deer. Pages 49-59 in R. D. Brown (ed.) Antler development in Cervidae. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.
- VAN BALLEMBERGHE, V. 1983. Growth and development of moose antlers in Alaska. Pages 37-48 in R. D. Brown (ed.) Antler development in Cervidae. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.
- and D. G. MIQUELLE. 1993. Mating in moose: timing, behavior, and male access patterns. *Can. J. Zool.* 71:1687-1690.
- WECKERLY, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 79:33-52.
- ZAR, J. H. 1996. Biostatistical Analysis. Third ed. Prentice-Hall Press, Upper Saddle River, NJ. 662 pp.