PECULIAR ANTLER CAST BY MOOSE ON THE COPPER RIVER DELTA, ALASKA

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ABSTRACT: Forty percent of cast moose (*Alces alces gigas*) antlers ($n = 25$) collected from the west Copper River Delta, Alaska had from 2.0-7.6 cm of assumed pedicle bone beyond the normal abscission point at the coronet. We examined the hypothesis that high levels of iron (Fe) in aquatic plants eaten by moose formed an insoluble complex with phosphorous (P), resulting in weak pedicles. Significant differences (MANOVA $F_{6,42} = 2.53$, $P = 0.035$) among antler samples were due to greater concentrations of P and Fe in pedicle samples than in shaft material of antlers with or without extra pedicle. Calcium:P ratios were equal for all samples. However, the P:Fe ratio was smaller for pedicle material than shaft material from both antler types. The ratio of cancellous to compact bone was the same for the shafts of both antler types, but the pedicle material was composed entirely of cancellous bone. Our results confirmed the assumption that an extreme amount of pedicle material was being cast with some antlers. Mineral imbalances associated with aquatic foraging may be responsible for this unusual antler casting. However, alternative explanations include a genetic or hormonal anomaly, as well as an extreme convex seal in prime animals in high quality habitat. Examination of these alternatives leads to the conclusion that the ultimate factor is genetic, but the actual physiological mechanism producing the abnormal antlers is unknown.

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Abnormalities in antlers have either genetic, systemic, or traumatic origins (Goss 1983). Ten of twenty-five cast moose (*Alces alces gigas*) antlers (40%) from the west Copper River Delta (CRD), Alaska had from 2.0-7.6 cm of what was assumed to be pedicle bone attached to the antler (Fig. 1). In contrast to the surface of normal seals, i.e., uniform with fine-grained pores (Bubenik, A. 1982*b*), the point of detachment from the skull was irregular and coarse. Data on diet selection, and forage and feces mineral concentrations suggested that imbalances in mineral metabolism, a systemic cause, may be responsible for this unusual antler casting (MacCracken 1992). During April-July, a period of rapid antler growth, moose on the CRD eat emergent aquatic plants (MacCracken et al. 1993). The 3 most important aquatic forages (*Equisetum* spp., *Menyanthes trifoliata*, and *Carex* spp.) averaged 45 ppm iron (Fe) at that time in contrast to 7 ppm for the major browse species (MacCracken 1992:139). Elevated levels of Fe in feed can form an insoluble complex with phosphorous (P), and P deficiencies can result in reduced skeletal growth and strength (Robbins 1983). If an insoluble Fe-P complex was formed, it should be excreted in the feces. April-July feces of moose on the CRD had concentrations of Fe and P that were 82% and 53% greater, respectively, than the average for late summer-fall and winter fecal samples (MacCracken 1992). These data supported the Fe-P hypothesis stated above.

To further investigate this hypothesis, the chemical composition and the proportion of cancellous and compact bone of cast antlers collected from the west CRD was estimated. In addition, we examine the evidence applicable to alternative explanations for this unusual casting pattern.

STUDY AREA AND METHODS

The CRD is located in coastal southcentral Alaska immediately east of Prince William Sound. It encompasses about 3200 km^2 and is the largest contiguous wetland remaining on the Pacific coast of North America. MacCracken (1992) described the climate, topography, geology, and vegetation of the CRD in detail. The CRD was divided into east and west portions by the Copper River.

During 1987-1989 cast moose antlers were collected from the west CRD and stored indoors. The antlers were divided into 2 categories for analysis: those with extra pedicle bone (abnormal) and those without (normal). Samples for chemical analysis were taken from the shaft about 1 cm distal to the coronet from both antler types. The pedicle material posterior to the coronet on abnormal antlers was also sampled. Samples were obtained by drilling 2-3 holes that were about 7-mm in diameter into the antlers (Bernard 1963) with a hand-held high speed drill at the locations described above (Fig. 1). Shavings and dust from the drillings were collected and submitted to the analytical laboratory in the Department of Range Science, Colorado State University for analysis. The material was analyzed for ash, nitrogen (N), calcium (Ca), iron (Fe), and phosphorous (P) content using standard procedures. These analyses were on a dry weight basis with ash and N reported as percent and the minerals as parts/million.

The pedicle material was composed entirely of cancellous bone. However, the ratio of cancellous to compact bone was estimated for the shaft of both antler types. The shafts were cross-sectioned with a band saw near the point of the drillings. The cross-sections were then photocopied and the area (cm^2) estimated with a leaf area index meter. The area of cancellous bone was then cut out of the photocopy, its area determined, and the ratio calculated. Antler nomenclature followed Bubenik, A. (1982*b*).

The data on chemical composition were analyzed with a multivariate analysis of variance (MANOVA) model, contrasting the 3 samples (SYSTAT 1990). The canonical structure of the MANOVA model was examined to estimate which variables accounted for any statistical differences ($P \leq 0.05$). The data were converted to ranks (Conover and Iman 1981) prior to analysis. Comparisons between the ratio of cancellous to compact bone in the antler shafts were made with a *t*-test.

RESULTS AND DISCUSSION

Seven abnormal and 15 normal antlers were sampled for mineral content. Three abnormal antlers that appeared to be > 1 year

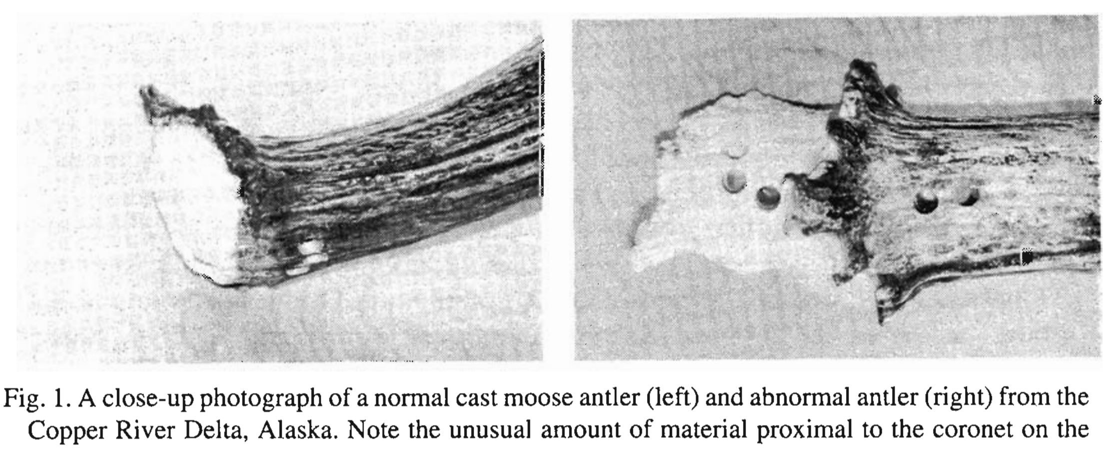

Fig. 1. A close-up photograph of a normal cast moose antler (left) and abnormal antler (right) from the Copper River Delta, Alaska. Note the unusual amount of material proximal to the coronet on the abnormal antler, and the seal characteristics of both antler types. The holes are the sites where samples were taken for chemical analyses.

old since being cast were not analyzed. Significant differences ($F_{6,42} = 2.53$, $P = 0.035$) among the samples were due to greater levels of P and Fe in the pedicle material from abnormal antlers than shaft material from either antler type (Table 1). Calcium:P ratios were the same for each sample, however, the P:Fe ratio for pedicle samples was smaller than for the shaft samples (Table 1). Ash estimates for CRD moose antler samples were within the range for moose as well as 7 other cervids as reported by Bernard (1963). However, Ca levels in this study (14.4[0.3]% dry weight, mean[SE]) were well below the minimum for moose (19.7%) and the other species examined (Bernard 1963). Concentrations of P in CRD moose antlers were also low (8.4[0.2]%), but closer to the values reported for moose (8.96%) and other species studied by Bernard (1963). Comparisons between our data and those presented by Bubenik, A. (1982*a*) for wapiti (*Cervus elaphus*) antlers followed the same trends. The lower Ca and P content of CRD moose antlers may be related to a number of factors, including variation in sample preparation methods, analytical techniques, laboratory equipment and technicians, or real biological differences among study areas, species, and seasonal changes in antler composition (Chapman 1975). In addition, all of the antlers we examined were exposed to the elements for at least 1 month. Comparisons among studies should be interpreted with caution, while within study comparisons are more definitive.

Our sample of abnormal antlers was equally divided ($x^2 = 0.40$, $P = 0.50$) between right (60%) and left (40%) antlers. In addition, the ratio of cancellous to compact bone (Table 1) in the shaft of both antler types was similar ($t = 0.12$, $P = 0.91$). Our results indicated that the assumed pedicle material on abnormal antlers differed from the antler shafts in chemical composition and structure, confirming its assumed origin. Studies comparing skeletal with antler bone have reported ash estimates that were 3-6% greater for skeletal bone (Chapman 1975, Ullrey 1982). Additionally, Ullrey (1982) presented estimates for white-tailed deer (*Odocoileus virginianus*) ribs that averaged 45.3% Ca (% of ash) with antlers averaging 43.4% Ca. However, P estimates were more equivocal, 19.9% for ribs and 20.2% for antlers (Ullrey 1982). In this study, the ash, Ca, P, and Fe content of the pedicle material was higher than the antler shaft material. Although these differences were small and in the case of ash and Ca were not statistically significant, the tendency for higher concentrations of miner-

Table 1. Mean(SE) composition of antlers cast by moose on the Copper River Delta, Alaska. Antlers were classified as abnormal or normal based on the presence of attached pedicle material on the former. Ash, nitrogen, and mineral estimates are on a dry weight basis. The cancellous-compact bone ratio is based on the area of each in antler cross-sections.

	Antler type and sample origin		
	Abnormal (n=7)		Normal (n=15)
Constituent	Pedicle	Shaft	Shaft
Ash (%)	58.4(0.8)	55.6(0.8)	57.2(0.4)
Nitrogen (%)	5.8(0.1)	6.1(0.2)	5.8(0.1)
Calcium (ppm)	149317(2318)	141917(2895)	141321(2231)
Iron (ppm)	115(43)	62(17)	74(20)
Phosphorous (ppm)	87459(741)	81296(2006)	82677(1138)
Ca:P	1.71(0.5)	1.75(0.2)	1.71(0.3)
P:Fe	726(17)	1309(118)	1117(57)
Cancellous:compact	- -	0.11(0.02)	0.10(0.03)

als in skeletal bone vs. antler is consistent among the limited number of studies that have been published.

Iron and P concentrations provided the best evidence that the mineral composition of the pedicle material differed from the antler shafts. Pedicle Fe and P were 41% and 6% greater, respectively, than antler shaft material. Consequently, the P:Fe ratio for pedicle material was 37% lower than for the shaft material. The low P:Fe ratio for the pedicle material appears to be consistent with the Fe-P hypothesis. If excessive Fe in the diet interfered with P metabolism, lower levels of P relative to Fe in the pedicles would be a logical consequence. However, we could not find data on skeletal Fe to determine if the P:Fe ratio for pedicle material was unusual.

The lack of compact bone in the pedicle material from abnormal antlers would be expected. Bubenik, G. (1982) and Suttie and Fennessy (1990) reported a lack of compact bone in the pedicles of white-tailed deer immediately before casting and in fallow deer (*Dama dama*) 4 weeks following casting, respectively.

The mechanism by which a mineral imbalance resulted in abnormal antlers is unknown. Fluctuations in alkaline phosphatase, an enzyme that interacts with vitamin D_3 and Ca-regulating hormones, was closely correlated with phases of the antler cycle in white-tailed deer and fallow deer (Bubenik, G. 1990*a*). These chemicals are heavily involved in bone metabolism, particularly growth and mineralization. However, normal antler casting appears to result from the decalcification of the bone at the interface of the living pedicle and the dead antler due to osteoclastic activity (Chapman 1975). Our results suggest that the abnormal antlers may result from resorption at, or close to, the frontal bone-pedicle junction. The anomaly we observed appears to be a miscue in targeting the appropriate region of the pedicle for resorption.

The results of surgical experiments indicated that antlerogenic tissue is widespread in the area of the pedicles. Removal of the fully developed pedicle in moose and other cervids did not stop antler growth in the following years (Bubenik and Pavlansky 1965, Chapman 1975, Goss 1983, Jaczewski 1990), indicating that moose on the CRD that lost pedicle material could produce antlers the next year. However, removal experiments and observations of free-ranging animals that lost pedicle to trauma indicated that it may take from 2-4 cycles before subsequent antlers regain their species specific structure. This suggests that moose on the CRD that cast pedicle should produce malformed antlers in ensuing years; a phenomena that would be hard to assess without intensive tracking of individuals for a number of years. However, 32% of the cast antlers we collected and 50% of intact racks (n = 14) examined had some sort of atypical characteristic. Whether these characteristics were associated with previous pedicle loss could not be determined. The response to pedicle loss is highly variable and sometimes subtle, requiring an unaffected antler for comparison (Bubenik and Pavlansky 1965). In addition, information on pedicle loss and subsequent antler characteristics is primarily from removal experiments prior to antler growth, or natural breakage after antler hardening, not as a result of the casting process. Jaczewski (1990) described the surgical removal of one pedicle in the spring and the remaining pedicle in the fall in 2 red deer (*Cervus elaphus*) castrates, but only in terms of the asynchronous development of the ensuing antlers.

There appear to be 2 reasons not to expect dramatic antler deformation in moose due to pedicle loss with cast antlers. Bubenik, G. (1990*c*) stated that the response to pedicle injury was more pronounced in the more evolutionary primitive cervids (e.g., white-tailed deer, roe deer [*Capreolus capreolus*], and fallow deer) relative to more advanced species (e.g., moose, red deer, and caribou

[*Rangifer tarandus*]). Furthermore, Barto (1990) defined 2 groups of cervids based on whether or not new antler growth was initiated shortly after casting. Moose fall into the group in which there is a substantial period of time (2-4 months, Van Ballenberghe 1982) between antler cast and initiation of new growth. Pedicle wounds can heal relatively quickly (Goss 1983) and enough time may elapse between antler cast and regrowth in CRD moose to replace lost pedicle, particularly if only a portion of the pedicle is lost. Bubenik and Pavlansky (1965) noted that the rate of pedicle healing was related to the amount of material excised. Another complicating factor is that most experiments and observations relating pedicle loss to subsequent antler growth have occurred on the more primitive cervids, or those in which antler cast is followed shortly by regrowth.

The characteristics of the abnormal antlers at the point of detachment from the skull suggested that a traumatic break could have been responsible. However, there are 3 conditions that are contrary to that explanation. First, the relatively high proportion of abnormal antlers in our collection seems unreasonable for what is normally a rare event. Second, the equal distribution of abnormal antlers from left and right sides would also be highly unlikely as a result of breakage. Third, if weak pedicles resulted in a traumatic break, we would expect that most breakage would occur during the rut. Broken tines resulting from rutting activities were common on the CRD and occasionally an antler was completely lost by breakage through the shaft, but there was no evidence that the abnormal antlers were associated with the rut. However, it is possible that pressure applied to these antlers at the time of casting may have resulted in a break in the pedicle. Newsom (1937) suggested that moose may actively facilitate casting when he observed them knocking their antlers against trees. However, this was a single isolated report and we did not observe this behavior in CRD moose.

The growth, mineralization, and casting of antlers is highly correlated with seasonal fluctuations in hormone levels, particularly testosterone (Bubenik, G. 1990*a*). A rapid and substantial decline in testosterone following the rut has been suggested to initiate the casting process once a threshold level has been reached (Bubenik, A. 1990). A hormonal irregularity in CRD moose could be an alternative cause of the abnormal antlers. Evidence for hormonal control of antler casting is from captive, castrated animals in which antler cast did not occur when hormones were artificially maintained at high levels, but were subsequently cast when hormone injections were discontinued (Bubenik, G. 1982, 1990*a*). These results suggest an "all or nothing" response of the casting process to hormone decline and it is unlikely that a hormonal irregularity could result in the abnormal antlers we examined.

Bubenik, A. (1990) stated that when plasma testosterone reached the threshold level that initiated casting, petrification began at the core of the pedicle and moved toward the edges. The rate at which this lateral resorption occurs results in either a convex, flat, or concave antler seal which has also been related to the condition of the animal (Acharjyo and Bubenik 1982, Bubenik, G. 1982, Bubenik, A. 1990). Abnormal antlers in CRD moose could simply be an extreme convex seal in prime animals in high quality habitat (MacCracken 1992). There are 3 observations that do not support that conclusion. First, the extra pedicle material on the abnormal antlers was far in excess of that expected for a convex seal. Measurements presented in Bubenik, G. (1990*b*) from white-tailed deer indicated that the most extreme convex seal projected only 1.5 cm beyond the coronet. Second, the relationship between antler seal characteristics and animal condition-age have been documented only in red deer and white-tailed deer (Bubenik, G. 1982). Third, the antler in Fig. 1 with the extra pedicle had a concave seal, which is not discernable from the angle at which the photograph was taken.

There may also be a genetic explanation for the high proportion of abnormal antlers in our sample. Moose were introduced to the CRD through a series of transplants from 1949-1958 (MacCracken 1992). The initial release was a single male calf in 1949. This calf was likely the dominant breeder for the next 5-7 years during which time 5 more male calves, 7 female calves, and 1 yearling female were released, about 61% of the total translocation of 23 moose. The potential for a founder effect was high. If the male originally released in 1949 possessed the tendency to shed pedicle material with antler this trait could have been inherited by most of the offspring of translocated animals; assuming that the trait was heritable. Presumably, a genetic cause would effect both left and right antlers equally. Bubenik, G. (1990*a*:279) speculated about a "... genetically fixed boundary of higher sensitivity to T [testosterone], which determines where the [pedicle] tissue will be petrified and where it will reach only the dormancy stage. This line is usually identical to the baseline of the coronet; however, cases are known where this line was either further below or above the coronet".

Given the above discussion, a genetic anomaly that became disproportionately represented in the west CRD subpopulation through a founder effect seems to be the most likely ultimate cause of the abnormal cast antlers of moose on the CRD. However, the physiological mechanism (proximate cause) that targets specific portions of the pedicle for resorption is unknown. Unfortunately, investigators studying antlerogenesis have concentrated their efforts on the initial phases of the antler cycle. The casting process has not received the attention that is warranted (Goss 1983).

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