SKELETAL INTEGRITY IN MOOSE AT ISLE ROYALE NATIONAL PARK: BONE MINERAL DENSITY AND OSTEOPATHOLOGY RELATED TO SENESCENCE

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ABSTRACT: We analyzed the relationships between skeletal condition and senescence using bones of moose (*Alces alces)* collected at Isle Royale National Park between 1958-1995. We found a significant decline in bone mineral density (BMD) in the cancellous bone of the metatarsus in male and female moose with age, and a significant relationship between low BMD in the long bones and osteoporotic skull lesions, indicating a pervasive loss of bone mass. Furthermore, we found an increase in the prevalence of osteoarthritis, periodontal disease, and osteoporosis after 7 years of age when decline in age-specific survival accelerates. Males experience an earlier decline in survival and an earlier increase in osteopathologies. From an evolutionary perspective, bone status at the time of death may be a consequence of behavioral and physiological strategies that maximize fitness during the prime reproductive years.

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The mobilization of minerals for annual antler growth in cervids is a major metabolic activity. Large amounts of calcium are deposited in the antlers each year from dietary and skeletal sources regulated by metabolic and hormonal control (Bubenik *et al.* 1975). Because antlers play an important role in reproductive success, cervids release minerals into circulation by erosive destruction penetrating the periosteum of bone, producing profound osteoporosis (Meister 1956, Parfitt 1981).

Annual mobilization of minerals for antler growth, and a similar mechanism in females to meet the demands of pregnancy and lactation, create a reversible mineral deficit or "cyclic physiological osteoporosis" (Parfitt 1976: 1033) in the skeleton. Minerals are replenished through nutritional sources when reproductive demands are minimized (Banks *et al.* 1968, Parfitt 1984). Similar changes in the bird skeleton accompany egg-laying when calcium is needed for shell formation (Meister 1951), and during the molt when significant resorption of the bone marrow cavity occurs (Murphy *et al.* 1992). The processes that regulate the form and function of bones and teeth are genetic, gravitational (or mechanical), nutritional, and hormonal (Palmer 1993).

Life-history strategies of organisms involve physiological trade-offs and unselected consequences (Rollo 1994). In many species, longevity is accompanied by senescence, with a decline in survival and fecundity (Promislow 1991). Rollo (1994) stated that senescence is a general and continuous deterioration in phenotypic performance. Theories of senescence predict that the cumulative effects of bone remodeling over a lifetime exhibit themselves as disabilities in individuals that live into old age (Sacher

1978, Comfort 1979, Hayflick 1985), but from an evolutionary perspective, the bone status present at the time of death may be interpreted as a reflection of the trade-off between reproductive investment during peak reproductive years and long-term maintenance of healthy bones.

The purpose of this study was to analyze the relationships between age-related skeletal condition and age-specific survival from skeletal remains of moose (*Alces alces*) in Isle Royale National Park, MI. In a previous study, we reported osteoporotic skull lesions as an age-specific pathology which increased in prevalence in males during peak antler growth years and in females after the cumulative effects of calf-bearing years (Hindelang and Peterson 1996). Here, we analyze changes in bone mineral density related to the occurrence of osteoporotic skull lesions and pathologies of teeth and bones as they relate to sex and age. We hypothesized that there is a relationship between the occurrence of osteoporotic lesions in the skull and low bone mineral density (BMD) in the metatarsal bone, and moreover, that there is a relationship between the occurrence of skeletal pathologies and a decline in age-specific survival. Prevalence of disease and life table construction in this study were based on recovery of skeletal remains of moose, and generally represent the very young and old (Waldron 1994).

METHODS

Moose skeletal remains were collected in Isle Royale National Park, an island of 544 km^2 in Lake Superior (48°N, 89°W), from 1958-1995. Bones from over 2,500 individual moose have been retrieved. One metatarsal bone, the skull and mandibles, and any bones exhibiting pathology or abnormality were collected. Sex was determined by the presence or absence of antlers or antler pedicles on the skull, and age was estimated from counts of *cementum annuli* in teeth (Wolfe 1969). Skeletons were examined for osteoarthritis, periodontal disease, osteoporotic skull lesions, and other osteopathologies (Peterson 1977, Hindelang 1996). Other data collected included tooth wear class (Passmore *et al.* 1955), season of death, cause of death, and bone mineral equivalent density of a sample of metatarsal bones determined by quantitative computed tomography (QCT) (Hindelang and Maclean 1997).

We examined the relationship between age and BMD from 180 metatarsi representative of all age groups, presence and absence of pathologies, and both sexes. We compared this to the metatarsus BMD from moose with osteoporotic skull lesions. Relationships between occurrence of osteoporotic skull lesions were tested using contingency tables and chi-square analyses. Life tables were compiled from the skeletal remains for adults by sex from the entire 37 years of the study to characterize age-specific survival (Deevey 1947, Caughley 1977, Nesse 1988).

Because determination of disease prevalence in dead populations can be confounded by missing data, we consistently used the equation for calculating prevalence as: prevalence = number of cases found/total examined (Waldron 1994). To achieve adequate sample size, age-specific osteopathologies were determined for 4 adult age groups, <7, 7-10, 11-14, >14 years (which roughly correspond to young adults, prime breeders, senior breeders, and old adults), and were compared by sex. Age-specific odds ratios (the ratio of the presence of pathology to the absence of pathology, among those observed) were estimated to compare prevalence by sex (Kahn and Sempos 1989, Waldron 1994).

RESULTS AND DISCUSSION

Bone Mineral Density

The mean BMD of metatarsal cancellous bone of moose without osteoporotic skull lesions exceeded the mean of those with lesions (P = 0.08) (Table 1). The significantly lower BMD mean (SE) for males, 341.1 (16.0), than females, 402.4 (17.2), is indicative of the greater demands that antler growth places on bone mineral. Mean BMD in females with normal skulls was significantly greater (P = 0.04) than in females with osteoporotic lesions. The mean BMD for males with normal skulls was not significantly greater (P = 0.25) than those with osteoporotic skulls. The fact that the proportional difference between BMD in moose with normal skulls and porotic skulls is much greater in females than males suggests that males are close to minimum levels.

In a comparison of means of cancellous BMD by age group (Table 2), both males and females showed a significant decline with age ($P < 0.01$), being greater in males. Our finding of decline in cancellous bone BMD with age is consistent with studies in humans (Parfitt 1984, Ruff and Hayes 1988). Hindelang (1996) found that cortical bone area increased with age in Isle Royale moose, suggesting that changes in bone geometry through remodeling is an adaptive mechanism for increasing cortical bone strength as bone mass declines. Banks *et al.* (1968) found cortical thickening in deer costal bone after antlers were shed, and Buckwalter *et al.* (1995) emphasized the important role that mechanical loading and vigorous physical activity play in strengthening and remodeling bone throughout life.

When we evaluated declines of bone mineral over time, we found that for moose > 14 years old at the time of death mean bone mineral content in cancellous bone of males was reduced by 37%, and in females by 13% compared to moose < 7 years old (Table 2). The lower BMD threshold for fracture-risk, specific for sex and age group, is considered 1 standard deviation below the mean based on the human model (Cann *et al.* 1985).

Season of Death and Cause of Death

We predicted that moose that died in winter would have a low mean BMD, reflecting the depleted status of bones after antler growth and during pregnancy in a season of poor nutritional replacement (Flynn *et al.* 1980, Schwartz *et al.* 1988). BMD mean (SD) for moose that died in summer or fall was 456 (109), and for those that died in winter 389 (151) (Table 3). However, the sample size for summer/fall was low, and the difference was not statistically significant (P = 0.12). An analysis of BMD by the cause of death of moose (Table 3) indicated that moose that died by accident or necropsy had a significantly higher mean BMD, 488

Table 1. Bone mineral density (mg/cm^3) for metatarsal cancellous bone in moose skeletal remains from Isle Royale.

	n	Min	Max	Mean	SD	SE
Females	83	69.5	716.6	402.4	156.8	17.2
Females with normal skulls	42	89.2	716.6	432.5	164.0	25.3
Females with porotic skulls	41	69.5	624.5	371.5	144.6	22.6
Males	96	35.3	723.5	341.1	157.2	16.0
Males with normal skulls	48	47.2	723.5	351.0	179.4	25.9
Males with porotic skulls	48	35.3	609.8	330.6	134.4	19.4

Table 2. Bone mineral density (mg/cm³) for metatarsal cancellous bone in moose skeletal remains from Isle Royale by sex and age group.

	Females			Males		
Age Group	*n*	Mean	SD	*n*	Mean	SD
< 7	6	440.2	178.0	11	427.3	201.0
7 - 10	12	427.5	171.2	25	397.9	124.0
11 - 14	33	405.0	160.9	34	328.9	141.8
> 14	32	383.1	136.0	26	268.6	142.2

Table 3. Bone mineral density (mg/cm³) of metatarsal cancellous bone by season of death and cause of death for moose dying on Isle Royale.

	n	Mean	SD
Season of Death			
Winter	131	388.7	151.1
Summer or Fall	8	455.9	109.0
Cause of Death			
Accident	11	488.2	128.4
Wolves	105	401.0	147.8
Malnutrition	34	279.8	136.3

(128), than those that were killed by wolves, 401 (148) ($P = 0.05$). Moose that died of malnutrition had a significantly lower mean BMD, 279 (135) ($P < 0.01$) than by other causes of death.

Occurrence of Skeletal Pathologies

The prevalence of osteoarthritis (OA) was very low in animals that died before age 7, but increased steadily with age to 70% in females and 85% in males (Table 4). Periodontal disease (PD) had an earlier onset, with about 7% of moose that died before age 7 and over 70% that died after age 14 showing periodontal lesions. Osteoporotic skull lesions (OP) were rare in animals that died before age 7, but increased with age.

Age-specific ratios (disease: nondisease) allowed us to determine the relative occurrence of osteopathologies of females to males in a single value (Table 4). Osteoarthritis occurred at far lower rates in females than males in all age groups reflected by a common ratio of 0.36. Periodontal disease had the closest rate for males and females of all of the osteopathologies, with the youngest and oldest age groups nearly even at 0.92. Osteoporosis showed the greatest sexual difference among age groups with rates higher for females in the 11-14 year-old group but lowest for males in the 7-10 year-old and the >14 group. This supports the hypothesis that females exhibit greater bone mineral loss in their senior breeding years as the cumulative effects of gestation and lactation increase, but then prevalence of osteoporotic lesions declines in later years when reproduction declines (Sadleir 1987, Grasman and Hellgren 1993, Hindelang and Peterson 1996).

Because the osteopathologies identified in this population are all age-related, it is not surprising that multiple pathologies often occur in a single animal at the time of death. In a sample of 506 moose, there was a significant positive relationship between osteoporotic skull lesions and periodontal disease ($\chi^2 = 73.24$, $P < 0.001$), and between osteoporotic skull lesions and osteoarthritis ($\chi^2 = 59.07$, $P < 0.001$). This finding would be expected because osteoporosis and periodontal disease both have a strong metabolic component involving the hormonal control of calcium-phosphorus balance (Palmer 1993), while osteoarthritis is primarily a degenerative process (Jaffe 1972).

Table 4. Prevalence of osteoarthritis (OA), periodontal disease (PD), and osteoporotic skull lesions (OP) of skeletal remains examined for osteopathologies in moose from Isle Royale of known sex and age. Odds ratios of female prevalence to male prevalence calculated by age group.

	OA (n=1,117)			PD (n=1,371)			OP (n=480)		
Age Group	♀ Prev	♂ Prev	♀/♂ Odds Ratio	♀ Prev	♂ Prev	♀/♂ Odds Ratio	♀ Prev	♂ Prev	♀/♂ Odds Ratio
< 7	0.4	3.2	0.121	7.1	7.7	0.916	0.0	6.1	0.000
7 - 10	23.6	51.1	0.296	32.5	39.8	0.728	9.4	34.8	0.194
11 - 14	38.6	60.9	0.404	55.9	72.5	0.481	47.0	33.3	1.776
> 14	70.7	85.7	0.405	70.4	72.2	0.916	41.5	54.9	0.583
Totals	27.6	40.6	0.355	35.7	42.6	0.699	32.1	32.8	0.691

Survival and Osteopathologies

The life table analysis showed an accelerating rate of mortality in both sexes, beginning at age 6-7 in females and at age 7-8 in males, with a higher rate in males at each age (Table 5). This finding suggests that Isle Royale moose exhibit senescence consistent with the conclusions of Finch

Table 5. Life table for adult Isle Royale moose based on skeletal remains collected from 1958 to 1993.

	Females				Males			
Age (yrs)	No. Dead	d_x	l_x	q_x	No. Dead	d_x	l_x	q_x
1-2	41	64	1000	0.064	59	84	1000	0.084
2-3	24	37	936	0.040	28	40	916	0.043
3-4	22	34	899	0.038	23	33	876	0.037
4-5	17	26	865	0.031	27	38	844	0.045
5-6	16	25	838	0.030	29	41	805	0.051
6-7	34	53	813	0.065	31	44	764	0.058
7-8	36	56	760	0.074	50	71	720	0.099
8-9	45	70	705	0.099	53	75	649	0.116
9-10	47	73	635	0.115	50	71	574	0.124
10-11	45	70	561	0.125	67	95	503	0.189
11-12	41	64	491	0.130	69	98	408	0.240
12-13	71	110	428	0.258	65	92	310	0.298
13-14	45	70	317	0.221	44	63	217	0.288
14-15	36	56	247	0.226	39	55	155	0.358
15-16	43	67	191	0.350	26	37	99	0.371
16-17	28	44	124	0.350	19	27	63	0.432
17-18	24	37	81	0.462	13	18	36	0.520
18-19	15	23	44	0.536	5	7	17	0.417
19-20	8	12	20	0.615	5	7	10	0.714
20-21	4	6	8	0.800	2	3	3	1.000
21-22	1	1	2	0.643	0	0	0	-

Note: d_x = mortality (number of deaths within age interval x to x+1)
l_x = survival (proportion of original cohort scaled on 1000 that survives to age x)
q_x = mortality rate (proportion of cohort dying between x and x+1, or d_x/l_x)

(1990) who stated that when an accelerating rate of age-specific mortality is found in a population, it arises from phenotypic deterioration associated with senescence. A plot of age-specific survival with age-specific prevalence of osteopathologies (estimated as a 5-point moving average) (Fig. 1) indicated that survival declines at an accelerated rate in the 7-10 year old age group for both males and females, coincident with the increase in osteopathologies. Males exhibit an earlier decline in survival and an earlier increase in skeletal pathologies consistent with Caughley (1966), Finch (1990), and Promislow and Harvey (1990), who suggested that in many mammals males have a lower average and maximum life span.

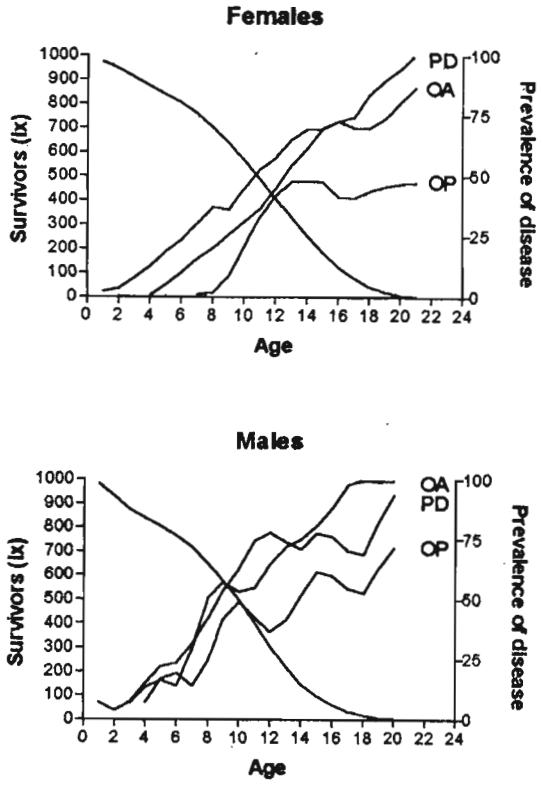

Fig. 1. Age-specific survival (l_x) and age-specific prevalence of osteoarthritis (OA), periodontal disease (PD), and osteoporotic skull lesions (OP) (estimated as a 5-point moving average) from skeletal remains of adult moose of known age and sex collected on Isle Royale from 1958-1994.

In previous studies, we demonstrated that increase in tooth wear and decline in tooth "cutting edge" also occur in the 7-10 year-old age group (Hindelang and Peterson 1993, 1994), compromising ability to forage and masticate effectively. Skogland (1988) found that tooth wear was an important proximate factor for limiting longevity in wild reindeer (*Rangifer tarandus tarandus)*, especially in food-limited situations when overgrazing of low quality food caused rapid tooth wear. He further linked foraging strategy to the life history consequences caused by tooth wear, including reduced reproductive success. Finch (1990) concluded that most ungulates have life spans of about 20 years because they are particularly vulnerable to mechanical abrasion of molars which is the major factor limiting their longevity. Our findings suggest that the optimal condition of bones and teeth peak in prime reproductive years and then declines.

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