MAKING NO BONES ABOUT IT: BONE MINERAL DENSITY CHANGES SEASONALLY IN A NONHIBERNATING ALASKAN RODENT

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High-latitude voles and lemmings undergo strong seasonal changes in their behavior and physiology, which may lead to concurrent changes in bone mineral density (BMD). We tested whether the BMD of northern red-backed voles (*Myodes rutilus*) in Alaska changed seasonally, and if so, whether these changes in their weight-bearing bones were correlated with seasonal changes in photoperiod (a mediator of activity and concentrations of reproductive hormones in high-latitude voles and lemmings), body mass, body length, or a combination of these. We used dual-energy X-ray absorptiometry to measure the BMD of the femur and humerus of voles collected in different seasons. BMDs increased dramatically from the start of spring to their peak level in early summer, and then decreased gradually to their lowest point in late winter. BMDs were significantly lower in fall and winter than in spring and early summer. BMDs of long bones were significantly correlated with both body mass and photoperiod, which accounted for 46.2% and 45.7% of the variation in the BMDs of femur and humerus, respectively. The strong changes that we observed in BMD are likely to be due, in part, to the combined effects of strong seasonal changes in body mass, activity, and baseline levels of reproductive hormones.

Key words: activity, Alaska, Arvicolinae, body mass, bone mineral density, high latitude, *Myodes rutilus*, osteopenia, seasonality, winter

Arvicoline rodents (voles and lemmings) in high-latitude regions exhibit strong seasonal changes in their behavior and physiology that could affect bone mineral density (BMD). Breeding begins in spring under increasing photoperiod in most species and is marked by notable increases in activity (Stebbins 1974), home-range territory (West 1977), body mass (Nay et al. 2007; Sealander 1967; Zuercher et al. 1999), and concentrations of sex steroids (Wallen and Schneider 2000). Winter is the reverse, and breeding typically ends under decreasing photoperiod. The spring–summer breeding season of most high-latitude voles and lemmings is generally fast-paced and includes the production of multiple litters. In fact, some animals born in summer may even reach adulthood and breed within the same year of their birth (Prendergast et al. 2001; Whitaker 1996). In winter, nonhibernating arctic and subarctic mammals remain active, but exhibit physiological acclimatiza-tion (Nay et al. 2007; Sealander 1967, 1972; Zuercher et al. 1999), changes in social behavior (West 1977; Wolff and Lidicker 1981), and increased energy expenditure (Holleman et al. 1982) to offset thermoregulatory costs.

The winter reductions in body mass, movement, and gonadal sex steroids described above could contribute to either a seasonal osteopenia (a condition of reduced bone density below normal peak BMD) or seasonal osteoporosis (a more severe weakening of bone due to excessive loss of protein and mineral content) in the weight-bearing long bones. Bone is a dynamic tissue that is constantly reshaped by osteoblasts, which build bone, and osteoclasts, which resorb bone. In mammals, reductions in bone density can result from restricted movement and a lack of mechanical stress on bones (disuse osteoporosis—Blouin et al. 2007; Resnick 1988), prolonged spaceflight (a special case of disuse osteoporosis—LeBlanc et al. 2000; Milstead et al. 2004), changes in diet or mineral uptake (Demigne et al. 2006; Gennari 2001; Rodriguez-Martinez and Garcia-Cohen 2002), reductions in baseline concentrations of gonadal steroids and growth hormone (Christmas et al. 2002), or changes in life-history stage (Bonnick 2006; Genarri 2001).

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Although arvicoline rodents remain active year-round in the subnivean space (Getz et al. 2005; Holleman et al. 1982; Stebbins 1974), their activity and home range are severely reduced in winter. Even at lower latitudes, both meadow voles (*Microtus pennsylvanicus*) and prairie voles (*M. ochrogaster*) restrict movement in winter, sometimes covering a distance 2–3 times less than that covered in other seasons (Getz et al. 2005). The free-living arctic–subarctic northern red-backed vole (*Myodes* [formerly *Clethrionomys*] *rutilus*) has been described as having an activity pattern that is moderately high in spring, extremely high in summer, and extremely low in winter (Stebbins 1974), and Tavernier et al. (2004) have shown that the activity patterns of this species in a laboratory setting are strongly linked with photoperiod. These photoperiod-induced reductions in activity could drive changes in bone density.

In Alaska, both *M. rutilus* and the taiga vole (*Microtus xanthognathus*) display pronounced midwinter aggregation (communal nesting) that is associated with severely restricted movement and home range (West 1977; Wolff and Lidicker 1981). Communal nesting may occur as a result of reproductive cessation, reduced aggression, clumped food resources, a scarcity of overwintering sites, thin snowpack, low temperatures, or other factors (West and Dublin 1984). It also can provide advantages, such as food sharing, thermoregulatory benefits from huddling, and cooperative defense (Wolff and Lidicker 1981). When voles huddle together in 1 large "vole complex" in a nest, it allows them to lower their energy maintenance requirements. While huddled as a unit, they gain the corporate benefits of a lower surface area-to-mass ratio and shared thermoregulatory costs, but they also retain the individual benefit of a lower overall maintenance metabolism by decreasing body mass and internal organ masses during what is likely a nutrient-poor season (Nay et al. 2007; Sealander 1967; Zuercher et al. 1999). In winter, movement of individuals is likely to be inhibited or restricted by snow and ice accumulation, the possibility of increased conductive and convective heat loss, the energetic cost of tunneling through the subnivean space, and a higher risk of predation above the snow. If food quality and mineral content are consistently poor but consistently available throughout the environment, it would seem advantageous for small, nonhibernating mammals to restrict movement, as well as tissue, organ, and body mass as much as possible in winter.

Additionally, a photoperiod has a strong effect upon the endocrine function of voles and lemmings. The hypothalamus–pituitary–gonad axis is affected by melatonin release, which is triggered by changes in day length (Goldman and Nelson 1993; Kriegsfeld and Nelson 1996; Kriegsfeld et al. 2000; Meek and Lee 1994; Wallen and Schneider 2000). Although little research has been conducted on bone densities of free-living rodents, a large body of clinical evidence suggests that these changes likely have some influence on BMD. In male human subjects, for instance, the interaction of growth hormone and testosterone promotes bone growth, whereas estrogen replacement and growth hormone supplementation have been shown to slow bone loss in menopausal women (Christmas et al. 2002). However, growth hormone does not appear to be affected by photoperiod in other tested mammalian species (Bartke et al. 1980; Borer et al. 1982; Kendall et al. 2003; Klemcke et al. 1983). The aim of this study was to test whether the BMD of a high-latitude species, the northern red-backed vole, changed seasonally, and if so, whether seasonal changes in BMD in its weight-bearing bones were correlated with seasonal changes in body morphology and photoperiod.

MATERIALS AND METHODS

Adults of *M. rutilus* were collected from Chugach State Park, Alaska (61°17′43″N, 149°32′10″W), between November 2004 and January 2007 and were grouped into 6 seasons similar to those of Zuercher et al. (1999). Seasons were designated as spring (April–May), early summer (June–July), late summer (August–September), fall (October–November), early winter (December–January), and late winter (February–March). For comparisons between sexes, we followed Zuercher et al. (1999) by collapsing early winter and late winter into 1 category ("winter") and early summer and late summer into another category ("summer") to eliminate the seasons with the smallest adult sample size (late summer and late winter).

During the study period, breeding in Chugach State Park began in mid-April and ceased between late August and early September, with peak reproduction occurring in spring and early summer seasons (Nay et al. 2007). Like other arvicoline rodents, northern red-backed voles mature rapidly, weaning after approximately 19 days (Tavernier et al. 2004) and reaching adulthood at around 45 days (Prendergast et al. 2001; K. T. Stevenson, pers. obs. on *M. rutilus*). A mass threshold of 17.5 g has historically been used to distinguish adults from younger individuals in early and late summer. Outside of these seasons, all animals have been considered to be of adult age (Whitney 1976; Zuercher et al. 1999). To exclude any possibility that animals of adult age retaining juvenile characteristics might be included in our analyses, we excluded animals weighing <20 g in these seasons. We did not observe any animals in breeding condition during winter, nor did we see any evidence of young born in winter.

Carcasses were weighed at the time of capture and were frozen at −20°C. We later dissected each vole, determined sex by the presence of either testes or ovaries, and removed the left humerus and femur. The length of each bone was determined using digital calipers accurate to the nearest 0.01 mm. Bone densities were determined using a PIXImus2 dual-energy X-ray apparatus (Lunar/GE, Madison, Wisconsin) that was known to accurately predict bone measurements in rodents (Nagy and Clair 2000) and that had previously been validated for use in determining the body composition of *M. rutilus* (Stevenson and van Tets 2008). Up to 16 bones were scanned at 1 time, and each was individually measured using the PIXImus2 software. The whole bone was used for each scan, and each bone was placed in the same position and orientation on the dual-energy X-ray apparatus scanning surface.

We used SPSS (version 14.0; SPSS Inc., Chicago, Illinois) statistical software to analyze the data. Multivariate analysis of variance (MANOVA) with Tukey's honestly significant

TABLE 1.—Seasonal values for body mass of adult *Myodes rutilus* in south-central Alaska. Combined data from 2004 to 2006 are shown, and means $\pm$ *SE* of body mass (g) are presented.

Season	$n = 97$	All voles	$n = 52$	Males	$n = 45$	Females
Spring	21	20.1 $\pm$ 0.7	12	20.8 $\pm$ 0.9	9	19.2 $\pm$ 0.9
Summer	21	26.4 $\pm$ 0.9	8	25.3 $\pm$ 1.5	13	27.1 $\pm$ 1.1
Early	14	27.0 $\pm$ 1.0	6	25.9 $\pm$ 1.8	8	27.9 $\pm$ 1.3
Late	7	25.2 $\pm$ 1.5	2	23.5 $\pm$ 3.1	5	25.9 $\pm$ 1.8
Fall	35	17.1 $\pm$ 0.3	20	17.4 $\pm$ 0.4	15	16.7 $\pm$ 0.4
Winter	20	13.4 $\pm$ 0.4	12	13.5 $\pm$ 0.4	8	13.2 $\pm$ 0.8
Early	14	13.4 $\pm$ 0.4	8	13.6 $\pm$ 0.5	6	13.0 $\pm$ 0.7
Late	6	13.4 $\pm$ 0.9	4	13.2 $\pm$ 0.8	2	13.7 $\pm$ 2.8

difference (HSD) post hoc test was used to determine whether there was an effect of season, sex, or the interaction term on the BMDs of the femur and humerus. We also used MANOVA to test for within-sex differences. Multiple regression analysis with stepwise variable entry was used to determine whether the independent variables of body mass, photoperiod, or body length explained a significant portion of the variability in the BMD of long bones. Mass and photoperiod were both included as entered variables because long-bone density changes proportionally with weight-bearing activity and photoperiod is strongly correlated with activity for *M. rutilus* (Stebbins 1974; Tavernier et al. 2004; West 1977). Body length was included as a test variable as an index of frame size to control for the effect of variation in body size independently of body mass. Both body-mass and body-length measurements were log transformed to eliminate allometric effects. Animals were captured and treated following procedures approved by the American Society of Mammalogists (Gannon et al. 2007), and all procedures were approved by the University of Alaska Anchorage Institutional Animal Care and Use Committee, the Chugach State Park Service, and the Alaska Department of Fish and Game.

RESULTS

Voles captured in winter were found in pairs or groups, consistent with the midwinter aggregation described by West (1977), and the expected seasonal change in body mass was observed (Table 1). Changes in the BMDs of the weight-bearing bones of adult voles followed a seasonal pattern characterized by a rapid increase in spring, peak levels in early summer, and a gradual, continual decrease from highest values in early summer to late winter (Fig. 1). The mean bone density was significantly higher in spring and early summer than in fall and winter seasons for both bones (MANOVA with Tukey's HSD test, $P < 0.05$; $F = 13.65$, $d.f. = 94$, $P < 0.001$ for femurs; $F = 11.88$, $d.f. = 94$, $P < 0.001$ for humeri according to univariate tests over 6 seasons; Fig. 2), and minimum and maximum bone densities also appeared to follow this trend (Fig. 1). Mass and photoperiod explained 46.2% and 45.7% of the total variation in BMDs in femurs and humeri, respectively (Table 2), with mass as the stronger predictor for femurs (body length was excluded from the model).

There were no between-sex differences in BMD under either the 6-season or collapsed 4-season model, possibly still due to small sample sizes in certain seasons. As an additional measure of the degree of seasonal change for each sex, we used a MANOVA for basic within-sex comparisons to determine whether a potential trend could be observed under the 4-season model. The test showed that although both sexes individually exhibited significant seasonal differences, males may undergo a slightly higher degree of seasonal variation. For males, BMDs of femurs were significantly lower in winter than in fall ($P < 0.05$), with levels in both of these seasons significantly lower than spring and summer (Table 3). Females may undergo a slightly weaker seasonal change, because their BMD values in fall, winter, and spring did not differ significantly, although mean seasonal values appeared to follow the general seasonal trends of the population as a whole. Interestingly, the mean
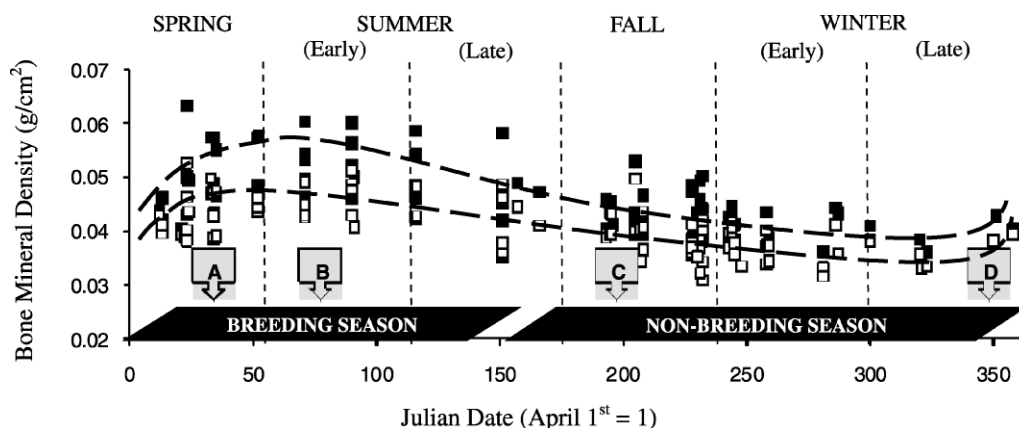

FIG. 1.—Annual pattern of change in bone density of femur (shaded squares) and humerus (unshaded squares) in a population of *Myodes rutilus* in Alaska. Bone mineral density is plotted against Julian date, and data from November 2004 to January 2007 are included. Numbers on the x-axis correspond to calendar dates beginning with the start of spring: 1 = 1 April (start of spring), 100 = 8 July (midsummer), 200 = 16 October (fall), and 300 = 24 January (midwinter). Periods of reproductive activity for this species are indicated at the bottom of the graph, and dashed vertical lines indicate the defined seasons. General characteristics of this species' life cycle are indicated by letters near the bottom of the graph: A = First occurrence of parturition, B = 1st occurrence of young-of-year reaching adulthood, C = end of lactation and weaning, D = spring equinox.
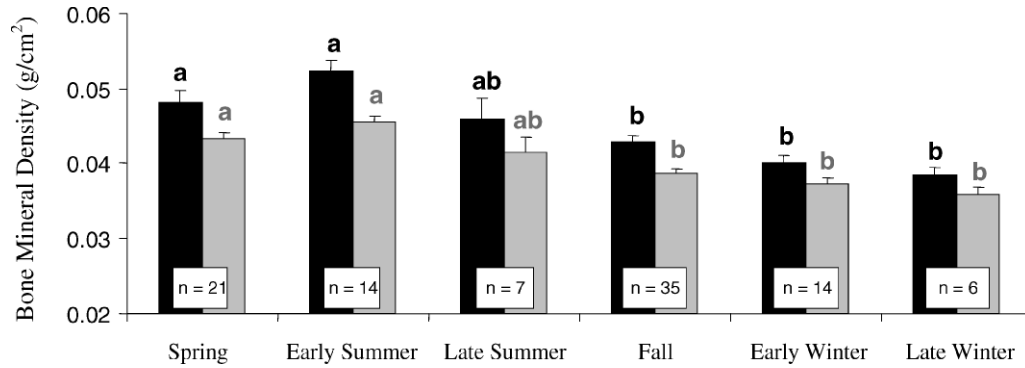
FIG. 2.—Seasonal changes in bone mineral density of femurs (black bars) and humeri (gray bars) under a 6-season model. Mean values represented by bars that share the same letter in the same color are not significantly different ($P > 0.05$).

BMDs of both bones from each sex were highest in early summer, with mean values nearly identical. However, the mean BMD values of males were slightly higher than those of females in spring and late summer seasons, whereas females retained slightly higher BMDs than males in winter.

DISCUSSION

We observed a pattern of seasonal change in BMD in a population of northern red-backed voles in Alaska that was characterized by dramatic increases in bone density during spring, peak values in early summer, and steady decreases in these values from early summer to late winter (Figs. 1 and 2). This pattern is likely to be related to the voles' seasonal changes in activity and breeding condition because BMDs of both bones were correlated with body mass and photoperiod (an indirect indicator of activity). Other seasonal factors also may have contributed to these changes in BMD (e.g., changes in hormone levels, appetite, food selection, life-history stage,

TABLE 2.—Predictive models for bone mineral density (BMD) in femurs and humeri of *Myodes rutilus*. Body mass influences the density of weight-bearing bones, and thus, it is directly proportional to bone strength. Photoperiod is an indirect measure of activity (Stebbins 1974; Tavernier et al. 2004). Body length was used as an additional measure of age within the adult age class.

Multiple regression	d.f.	R^2	F	P-value	Include in model?	Unstandardized coefficient (B)
Femur BMD model	96	0.462	40.326	<0.001		
Entered variables						
Log body mass				0.001	Yes	0.024
Photoperiod				0.011	Yes	<0.001
Log body length				0.869	No	
Constant				0.155		0.010
Humerus BMD model	96	0.457	39.632	<0.001		
Entered variables						
Log body mass				0.030	Yes	0.015
Photoperiod				0.030	Yes	<0.001
Log body length				0.363	No	
Constant				0.001		0.017

energy and mineral availability in the environment, and vitamin D levels). However, the strong correspondence of activity and body mass with BMD (Table 2) is consistent with Wolff's law (Wolff 1892) and other, more recent studies linking bone remodeling to weight-bearing activity (Blouin et al. 2007; Resnick 1988). When weight-bearing activity is low, whether due to low body mass, low activity, or both, BMD is low. When weight-bearing activity is high, whether due to high body mass, high activity, or both, BMD is high. The combination of these factors appears to accelerate bone mineral depletion and osteopenia from late summer to late winter, and repletion in spring and early summer.

The observed pattern of change in bone density appears to be independent of age-related effects, such as the replacement of older adults dying off in summer or fall with younger adults entering the data pool. All animals in the study were of adult age and changes in body length (an additional indicator of age within the adult group) was excluded by the model, and was therefore not a good predictor of bone density (Table 2). The observed pattern also appeared to be independent of any significant sex effects, but a larger sample size in certain seasons could prove otherwise. In high-latitude regions, winter is a period of reduced activity, body mass (Table 1), sunlight exposure, vitamin D synthesis (Hickie et al. 1982), and gonadal steroid synthesis in arvicoline rodents. Summer is the reverse. The ability to synthesize vitamin D or produce gonadal steroids in winter is likely to be particularly limited, as low photoperiod is combined with the subnivean lifestyle to further reduce exposure to sunlight. Mass may also be tied to photoperiod in this species because we have observed significant reductions in the body mass of subjects placed on manipulated photoperiods (switched from long days to short days) relative to control animals.

The positive increases in the BMDs of overwintered adults in late March that we observed just after the spring equinox (but before the onset of spring reproduction in April [Fig. 1]), may mark the beginning of internal physiological changes in voles that eventually lead to increased body mass, activity, reproductive hormone levels, and BMD. Bones increased in density throughout spring, presumably because of the photoperiod-linked increases in weight-bearing exercise and concentrations of gonadal steroids. When day length was

TABLE 3.—Within-sex comparisons of the effect of season on the bone mineral density (BMD) of *Myodes rutilus*. Seasonal means $\pm$ *SE* of BMD are presented for male and female voles in different seasons. A MANOVA of the mean values for spring, summer, fall, and winter indicated a significant effect of season on bone density for both the femur and humerus ($P < 0.05$). Mean BMD values for each sex and bone in each season that are represented by a shared letter are not significantly different ($P > 0.05$); means for femurs and humeri were never compared with one another, and males are not compared with females in this table. Within each sex, Tukey's HSD tests showed that mean bone densities were lower in fall and winter seasons than in spring and early summer seasons ($P < 0.05$).

	Males ($n = 52$)			Females ($n = 45$)		
Season	n	Femur BMD	Humerus BMD	n	Femur BMD	Humerus BMD
Spring	12	0.050 ± 0.002 a	0.044 ± 0.001 a	9	0.045 ± 0.002 ab	0.042 ± 0.001 ab
Summer	8	0.052 ± 0.002 a	0.044 ± 0.002 a	13	0.049 ± 0.002 a	0.044 ± 0.001 a
Early	6	0.052 ± 0.002	0.045 ± 0.001	8	0.052 ± 0.002	0.046 ± 0.001
Late	2	0.052 ± 0.007	0.042 ± 0.006	5	0.044 ± 0.002	0.041 ± 0.002
Fall	20	0.043 ± 0.001 b	0.039 ± 0.001 b	15	0.042 ± 0.001 b	0.038 ± 0.001 b
Winter	12	0.038 ± 0.001 c	0.036 ± 0.000 b	8	0.041 ± 0.001 b	0.038 ± 0.000 b
Early	8	0.039 ± 0.001	0.036 ± 0.001	6	0.042 ± 0.001	0.039 ± 0.001
Late	4	0.038 ± 0.001	0.035 ± 0.001	2	0.038 ± 0.001	0.037 ± 0.001

decreasing between summer and fall, it is likely that BMD was affected by reduced activity levels associated with reductions in forage quality, ambient temperature, appetite, body mass, and reductions in the concentrations of gonadal steroids. As winter progressed and heavy snow and ice cover became established, BMD reached its lowest point (Fig. 1; Table 3), presumably as a result of further reductions in movement (Stebbins 1974) and the occurrence of communal nesting (West 1977).

Although the observed pattern of bone remodeling in *M. rutilus* occurred independent of sex effects, additional within-sex comparisons revealed that only males showed a significant difference in femur BMD between fall and winter (MANOVA with Tukey's HSD, $P < 0.05$; Table 3). Males showed rapid increases in testis mass in spring (Nay et al. 2007; see also Sealander 1967; Whitney 1976), which could contribute to intensified mate guarding or searching for females, along with greater home range. Males that are more robust (i.e., have higher BMDs) and can more quickly assimilate minerals into bone matrix after winter may have an advantage over less-robust males in mate guarding, female mate choice, and copulation success. Testosterone also may have a stronger affect on bones of males than estrogens and progestogens do on females. The potential trend toward males having a slightly higher degree of change in BMDs than females in spring (Table 3) also may indicate a greater increase in activity of males, as is found in other arvicoline rodent species (Schmidt et al. 2002). Interestingly, male and female voles had very similar bone mineral stores in early summer, which reflected their highest seasonal level. This may indicate that mineral availability is not limited in this season and that the environment allows for maximum BMDs in both sexes (Table 3). By late summer, however, the BMDs of females appeared to be reduced in comparison to males, possibly an effect of a taxing reproductive season for this sex. This comparison of the degree of change within each sex revealed a potential trend toward bones of males having lower BMDs than bones of females in winter seasons. This may convey some sexual dimorphism in activity or food selection, but could also be linked to this and other species' ability to breed in winter (Hansson 1984;

Khlebnikov 1970; Millar 2001; Moffatt et al. 1993; Whitney 1976). Winter breeding does not occur in all years, and no winter breeding was observed in Chugach State Park populations between 2004 and 2007. However, because female arvicoline rodents can be induced into ovulation by copulation, they may be more constrained to maintain bone mineral stores in winter than males. Contact or copulation with a reproductively viable male is a rare but possible occurrence for female *M. rutilus* and other high-latitude arvicoline rodents (Hansson 1984; Khlebnikov 1970; Prendergast et al. 2001), and this might induce ovulation or result in pregnancy, as it does in other species of *Myodes* (Clulow and Mallory 1970; Odberg 1984).

In summary, the northern red-backed vole, a nonhibernating, high-latitude arvicoline rodent, does not maintain constant, yearlong bone mineral stores. Voles show rapid increases in BMD of long bones in spring, peak levels in early summer, and a gradual but continual decrease in BMD from early summer to late winter. These changes correspond with seasonal changes in body mass, activity, and hormones levels, although they also may be affected by forage quality, mineral and nutrient availability, and other factors.

The overall pattern of bone remodeling in *M. rutilus* undoubtedly reflects this species' overwintering strategy and life history. As a result, bone remodeling in *M. rutilus* provides a basis for comparative studies with other small high-latitude mammals, both nonhibernating and hibernating. The late-season reduction and rapid spring increase in bone density exhibited by free-living voles may, at some level, be useful in obtaining a better understanding of human osteoporosis.

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