ARE PIKAS EXPOSED TO AND AFFECTED BY SELENIUM DEFICIENCY?

Authors: Palmer, K. M., Stanton, N. L., Ben-David, M., Mionczynski, J., and Williams, S. E.

Source: Journal of Wildlife Diseases, 43(3) : 475-484

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-43.3.475

Journal of Wildlife Diseases, 43(3), 2007, pp. 475–484

ARE PIKAS EXPOSED TO AND AFFECTED BY SELENIUM DEFICIENCY?

K. M. Palmer,[1] N. L. Stanton,[1] M. Ben-David,[1,4] J. Mionczynski,[2] and S. E. Williams[3]

[1] Department of Zoology and Physiology, 3166, 1000 East University Ave., University of Wyoming, Laramie, Wyoming 82071, USA
[2] Wildlife Consultant, 70 Three Forks Road, Atlantic City, Wyoming 82350, USA
[3] Department of Renewable Resources, 3354, 1000 East University Ave., University of Wyoming, Laramie, Wyoming 82071, USA
[4] Corresponding author (email: bendavid@uwyo.edu)

ABSTRACT: Regional extirpations of pikas (*Ochatona princeps*) within the last few decades have been attributed to global warming. Other recent global alterations such as increased nitrogen (N) deposition and associated selenium (Se) deficiency may further stress pika populations. In 2003 and 2004, we live-trapped pikas from three populations in Wyoming and measured Se values in their hair. We also sampled hair and liver from museum specimens collected throughout the Northern Rocky Mountains in 1987 and 1988. Our results suggest that liver and hair values were related, and that pika hair reflected the Se concentrations of the geologic parent materials. We determined that animals residing in several remote areas in the Rocky Mountain region could be Se deficient and that increase in N deposition correlated with an increase rather than a decrease in Se values in pika hair. In addition, we found no relation between Se contents in hair and body condition index, suggesting that low Se levels may not have negative effects on individual pikas. Whether Se levels influence reproductive success of pikas is unknown and should be the focus of future studies.

Key words: Alpine tundra, geologic parent material, hair, liver, nitrogen deposition, *Ochatona princeps*.

INTRODUCTION

Since the end of the Wisconsin glaciation (10,000–12,000 yr ago), North American pikas (*Ochotona* spp.), which are small lagomorphs restricted to talus slopes in alpine habitats (Lawor, 1998; Beever et al., 2003), have experienced range reductions, isolation, and localized population extirpations due to increased summer temperatures and reductions in available habitat (Brown, 1971; Greyson, 1977, 1987). Studies of *O. princeps* within the last few decades suggested that this declining trend is accelerated because of global warming (Clinchy et al., 2002; Beever et al., 2003; Franken and Hik, 2004) as increased summer temperatures may exceed the thermoregulation capacity of pikas (MacArthur and Wang, 1973; Hafner, 1993; Beever et al., 2003).

In addition to potential direct effects associated with global warming, micronutrient deficiency may be an emerging problem in remote alpine habitats (Flueck, 1994). In particular, selenium (Se) deficiency is known to decrease glutathione peroxidase activity. This enzyme protects cellular membranes against oxidative damage (Ohlendorf, 1996; Arthur et al., 2003). Selenium deficiency can also compromise the immune system (Sheehan and Halls, 1999; Arthur et al., 2003) and reduce reproduction (Combs and Combs, 1986; Flueck, 1994; Güvenc et al., 2002). Population impacts associated with Se deficiency have been reported for a Rocky Mountain bighorn sheep (*Ovis canadensis candensis*) herd in the Wind River Range of Wyoming. This herd displayed signs of nutritional muscular dystrophy (NMD), a disease often associated with Se deficiency in domestic ungulates. Approximately half of this herd died and the problem was subsequently alleviated through Se dietary supplementation (Hnilicka et al., 2002).

Selenium bioavailability largely depends on the Se content in the soils, which usually reflects the Se content of the parent geologic material (Meyer and Burau, 1995). High concentrations of Se are found in sedimentary rocks like shales, sandstones, and phosphate rocks (Adriano, 1986; Ohlendorf, 1996; Dhillon and Dhillon, 2003). Lower levels usually occur in granites, rhyolites and rhyolitic pumices, limestones, and dolomites (Combs and Combs, 1986; Berrow and Ure, 1989; Ihnat, 1989). Under conditions of increased soil nitrogen (N), soil microorganisms are capable of depressing Se bioavailability either by reducing Se to forms unavailable to plants or volatilizing it into the atmosphere (Thompson-Eagle et al., 1991; Dhillon and Dhillon, 2003). Maximum Se volatilization occurs in moist soils (Thompson-Eagle et al., 1991). Thus, increased deposition of N from anthropogenic sources in recent decades (Wolfe et al., 2001), coupled with high summer precipitation, may reduce bioavailability of Se to plants and herbivores even in remote alpine habitats. Reduced bioavailability of Se may be exacerbated for pikas that inhabit areas with a high percentage of talus where soils are shallow (Clayton et al., 1991) and are readily saturated with atmospheric N deposits (Baron et al., 1994). If pikas are sensitive to Se deficiency, anthropogenic increases in N deposition may have an added detrimental effect on their already stressed populations.

In this study, we measured the levels of Se in the hair of individual pikas from three populations in Wyoming inhabiting talus slopes derived from three different geologic parent materials. Hair has been used to assess body Se status reliably (Combs and Combs, 1986; Ihnat, 1989; Deore et al., 2002; Güvenc et al., 2002), and it is a convenient tissue to collect in remote areas because it can be stored without Se loss. Because studies of Se usually report levels in tissues such as liver, kidneys, and blood (Combs and Combs, 1986; Ihnat, 1989; Flueck, 1994; Ohlendorf, 1996), we measured Se values in liver and hair samples of 21 pika specimens provided by the New Mexico Museum of Natural History (NMMNH; University of New Mexico, Albuquerque, New Mexico). Our goal was to derive a relation between Se levels in hair and liver, so that we could use hair values to detect Se deficiency in the field samples. We also used these museum specimens to increase our sample size for exploration of effects of geologic parent material on Se values in pika hair and to evaluate the effects of increasing N deposition on Se in these animals. Finally, we investigated the relation between Se values in the hair of pikas and measures of body condition in order to determine whether Se-deficient pikas were adversely affected.

METHODS

Field sites

Pikas were live-trapped in three Wyoming mountain ranges: northern Wind River Mountains in northwestern Wyoming (43.38°N, 109.63°W), the Snowy Range Mountains (southeastern Wyoming 41.33°N, 112.33°W), and northern Big Horn Mountains in northeastern Wyoming (44.73°N, 113.74°W; Table 1). These alpine tundra habitats are dominated by perennial forbs, grasses, sedges, shrubs, and cushion plants, including alpine avens (*Geum rossii*), alpine bistort (*Polygonum viviparum*), alpine forget-me-not (*Eritrichium nanum*), alpine sagewort (*Artemisia scopulorum*), mosscampion (*Silene acaulis*), cinquefoil (*Potentilla diversifolia*), and alpine clover (*Trifolium dasyphyllum*; Knight, 1994; Scott, 1995). The mean annual temperature is below freezing and the mean annual precipitation averages 90 cm (Wyoming Climate Atlas, 2005).

Trapping

Trapping occurred from early July to mid-September during the daylight hours in 2003 and 2004 in the Wind River and the Snowy Range Mountains and in 2004 in the Big Horn Mountains. Seven to 10 collapsible Tomahawk live traps (model 102, Tomahawk, Wisconsin, USA) were set on the talus borders, prebaited during the night, and fastened open. Traps were activated at first light and checked every 2 hr. Traps were baited with either natural vegetation (cinquefoil and bistort) or dried dill.

In the summer of 2003, we captured 14 individual pikas and anesthetized them with an

TABLE 1. Geologic parent material for locations of pika trapped in Wyoming in summer 2003 and 2004 (sample size for 2004 in italics) and for museum specimens collected in 1987 and 1988 and archived at the New Mexico Museum of Natural History (sample size in parentheses). Selenium contents for these specific locations were unavailable, so values were coded based on published data for similar rock formations (Combs and Combs, 1986; Berrow and Ure, 1989; Ihnat, 1989).

Location	Geological parent material	Selenium (mg/kg)	Code	*n*
Wind River Mountains, Wyoming, USA	Igneous granite	0.02–0.09	1	7, *12* (3)
Snowy Range Mountains, Wyoming, USA	Metamorphic schist, quartzite, quartz-pebble conglomerate, and marble	12–120	4	7, *10* (3)
Big Horn Mountains, Wyoming, USA	Sedimentary dolomite and limestone	1.3–24	2	*9* (3)
Hagensborg, British Columbia, Canada	Igneous granite	0.02–0.09	1	(3)
Custer County, Idaho, USA	Volcanic rocks	10–30	3	(3)
El Paso County, Colorado, USA	Sedimentary dolomite and limestone	1.3–24	2	(3)
Cascade County, Montana, USA	Sedimentary dolomite and limestone	1.3–24	2	(3)

intramuscular injection of ketamine hydrochloride (Vetalar, BioNiche Animal Health, Belleville, Ontario, Canada). Dosages varied; but averaged 0.8 mg/kg body weight. We then implanted a sterile subcutaneous passive integrated transponder (PIT tag) between the shoulder blades for individual identification, and plucked about 0.1 g of hair from the collar region for Se analysis. All hair samples were stored in acid-washed plastic tubes with plastic lids. We also measured body mass (g), as well as total body, skull, and left hind-foot lengths (mm). After processing, each pika was placed in the trap until recovery and then released at the capture site.

In the summer 2004, we captured 31 new pikas; two of these were individually marked with a PIT tag and the rest were marked with a permanent ink to trace within season recaptures. Hair samples were collected at first capture only in each season.

During the two summers, six pikas died as a result of handling and carcasses were kept cold in snow until frozen at −20 C in the lab. Hair and liver samples were collected from five of these six individuals for Se analysis (one carcass was too decomposed to yield reliable estimates).

Museum specimens

We obtained 21 hair and liver samples of pika specimens from NMMNH preserved as skin, skeleton, and frozen tissues. Skin specimens were prepared with no preservatives. Partial portions of livers had been frozen immediately in the field in liquid N and subsequently stored at −80 C. Three pikas were selected from each of seven Rocky Mountain sites that represented a range of geologic parent materials (Table 1): Albany County, Wyoming (NMMNH 454, 455, and 466), Fremont County, Wyoming (NMMNH 502, 508, and 514), Big Horn County, Wyoming (NMMNH 538, 540, and 544), Cascade County, Montana (NMMNH 574, 582, and 584), Custer County, Idaho (NMMNH 646, 658, and 660), El Paso County, Colorado (NMMNH 688, 692, and 696), and near Hagensborg, British Columbia (NMMNH 986, 988, and 998). The British Columbia specimens were collected in 1988 and all others in 1987. The samples from Wyoming were collected in the same mountain ranges as the live-captured pikas, thus providing information on temporal change in Se values in relation to N deposition in these locations. We plucked approximately 0.1 g of hair from the left side of the collar region from the study skins, similar to the sampling protocol we used for field collections.

Geologic material and nitrogen deposition data

The geologic material at each location was determined using geologic maps (USGS National Geological Maps Database). Because Se

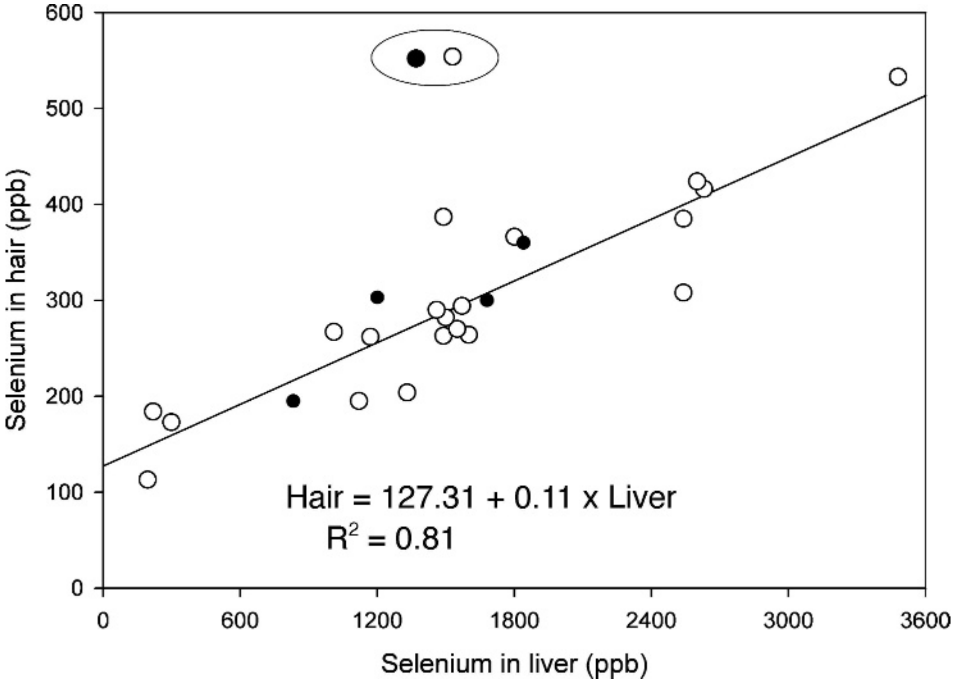

FIGURE 1. Selenium concentrations (ppb) in hair and liver of individual pikas. Samples from New Mexico Museum of Natural History collected in 1987 and 1988 are represented by open circles and field samples from Wyoming collected in 2003 and 2004 are solid circles.

values for geologic parent materials for these areas were unavailable, we developed an ordinal scale (1–4) of Se contents based on values published for similar rock formations (Table 1; Combs and Combs, 1986; Berrow and Ure, 1989; Ihnat, 1989). We obtained values of annual N atmospheric deposition (kg/ha) from the National Atmospheric Deposition Data (2006) for the Snowy Range (WY00) and the Big Horn Mountains (WY99) for 1987, 2003, and 2004. For the Wind River Mountains we used N deposition data collected by the US Forest Service at Hobbs Lake (Svalberg, 2005). We calculated ammonium-N and nitrate-N and summed those values to produce total inorganic N deposition. Because these sites usually occurred at lower elevations than our sampling sites (especially WY99), N values can only be used as an index of N deposition in our analyses rather than actual values.

Selenium processing and analysis

Field and museum hair and liver samples were sent on dry ice to Olson Biochemistry Laboratories (South Dakota State University, Brookings, South Dakota, USA) for Se analysis. Selenium content was determined with the use of the fluorometric method described by Palmer and Thiex (1997). Biologic samples were digested (oxidized) in nitric and perchloric acids, diluted, and reduced with HCl. Following digestion and acid treatments, 2,3-diaminonaphthalene was added to form Se^{4+} 2,3-diaminonaphthalene complexes. Fluorometry was then used to measure the reaction product (Palmer and Theix, 1997). The detection limit was 80 ppb for hair samples and 50 ppb for liver samples.

Statistical analysis

Linear regression with liver as the independent and hair as the dependent variables was used to detect a possible relationship between Se concentrations in pika hair and liver (Neter et al., 1996; SPSS for Windows 15.0). Similarly, we used linear regression to evaluate the relation between geologic parent materials and mean Se values in pika hair. Means rather than individual points were used to account for differences in sample sizes (Table 1; Neter et al., 1996). To evaluate the effects of N deposition on Se values in pika hair, we

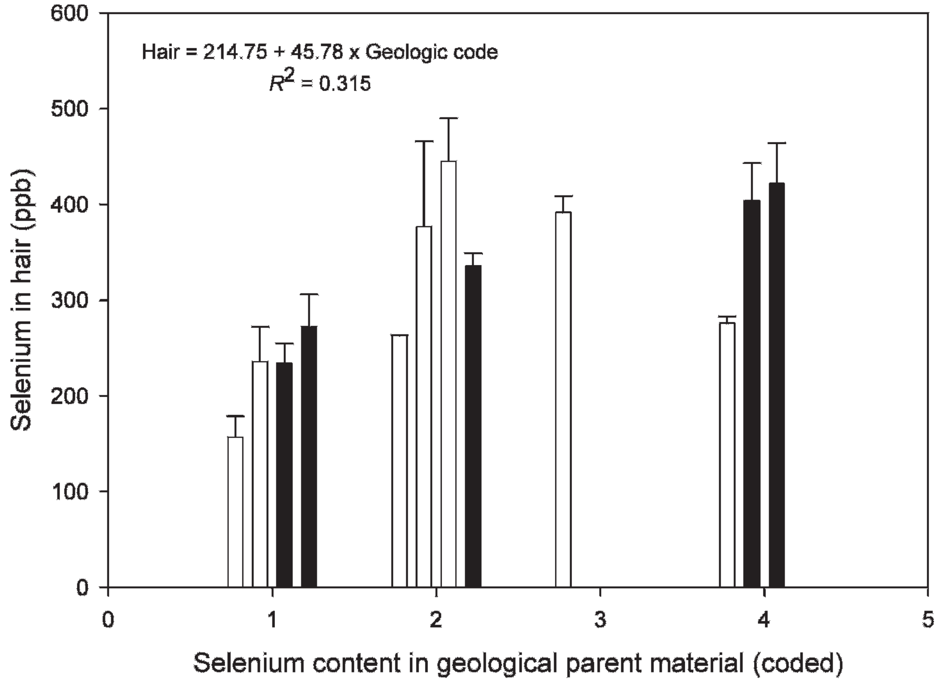

FIGURE 2. Relation between selenium contents in underlying geologic parent material (ordinal codes—see Table 1) and selenium levels (ppb; mean±SE) in hair of pikas. Samples from New Mexico Museum of Natural History collected in 1987 and 1988 are represented by open circles and field samples from Wyoming collected in 2003 and 2004 are solid circles.

calculated the difference in N deposition between every 2 yr of data (e.g., value of N deposition for Snowy Range in 1987 subtracted from 2004). Similarly, we calculated the mean difference in Se levels in pika hair for each 2 yr of data. We then regressed the difference in Se values against the change in N deposition using a linear model (Neter et al., 1996). Finally, to establish the relation between Se values and body condition, we developed a condition index. Body mass was divided by the left hind-foot length of each animal. We used linear regression with hair Se as the independent variable and body condition as the dependent variable (Neter et al., 1996; SPSS for Windows 15.0).

RESULTS

Liver Se ranged from 195 ppb to 3480 ppb; hair Se ranged from 113 ppb to 554 ppb. Two points were identified as outliers (studentized residuals >2) and excluded from the analysis (Fig. 1; Neter et al., 1996). Se values in hair increased with increased liver contents (Fig. 1; linear regression, $R^2=0.81$, $P<0.001$).

As expected Se content in pika hairs was higher in areas with enriched geologic parent material (Fig. 2; regression on means, $R^2=0.315$, $P=0.034$). Similarly, the difference in Se in pika hairs was positively related to the difference N deposition for the sites sampled in Wyoming (Fig. 3; regression on mean differences, $R^2=0.931$, $P=0.0004$).

Values of body condition index in pikas ranged from 24.8 to 71.2. We found no relation between Se values in pika hair and this body condition index (Fig. 4; linear regression, $R^2=0.0014$, $P=0.81$).

DISCUSSION

Results suggest that values of Se in hair can be used to evaluate Se status in pikas. The occurrence of two outlying points is puzzling, because Se loading in hair is

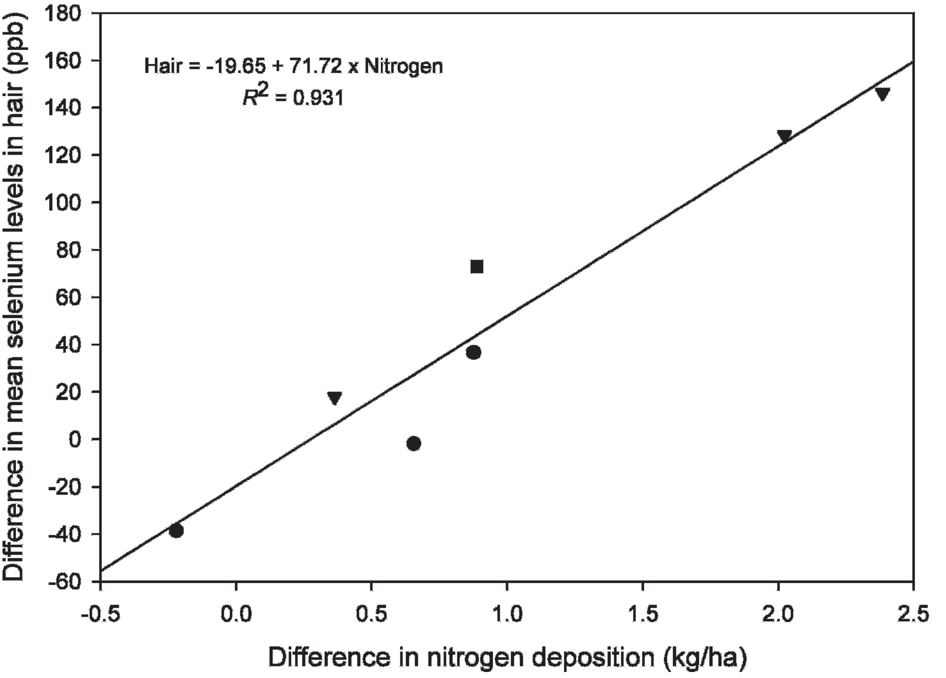

FIGURE 3. Relation between the difference in atmospheric nitrogen deposition between every 2 yr of data (kg/ha) and the difference in mean selenium levels in pika hair (ppb) for the three study sites in Wyoming. Circles represent data for the Wind River Mountains, squares the Snowy Range Mountains, and the diamond represents the Big Horn Mountains.

likely to increase only when animals have met a minimum physiological requirement (Deore et al., 2002). To determine whether some of the sampled pikas experienced Se deficiency we compared our results to published values in the literature (Table 2). With the use of the lowest reported value of adequate levels of Se in hair (350 ppb for goats; Table 2) it appears that 44 of 66 pikas may have been Se deficient. Given that for several species minimum adequate liver values can be as low as 250 ppb (Table 2), it is unlikely that so many pikas are Se deficient. Therefore, we used the regression between hair and liver Se (Fig. 1) to estimate the Se liver values for those live-captured pikas for which we only had hair Se data. Comparing these estimates and minimum adequate liver values for the phylogenetically related rabbits (900 ppb), it appears that 10 of 66 pikas (three museum specimens and seven live-captured individuals) could have been Se deficient. These 10 animals were captured in the Wind Mountain Range in Wyoming and collected in British Columbia; these areas are both characterized by granite rocks that contain low levels of Se. These results agree with our observation that the Se patterns in pika hair broadly correspond with underlying rock composition.

That the relation between rock formation and Se in pika hair accounted for about 30% of the variance is not surprising, given that we had no actual information on Se contents in the geologic parent material for our study areas. In addition, this relation was likely masked by the effects of N deposition and pika behavior. In contrast with our prediction, higher N deposition corresponded with increased Se levels in pika tissues. It is possible that this positive relation between N deposition and Se in pika hair is a result of a concurrent increase in atmospheric Se

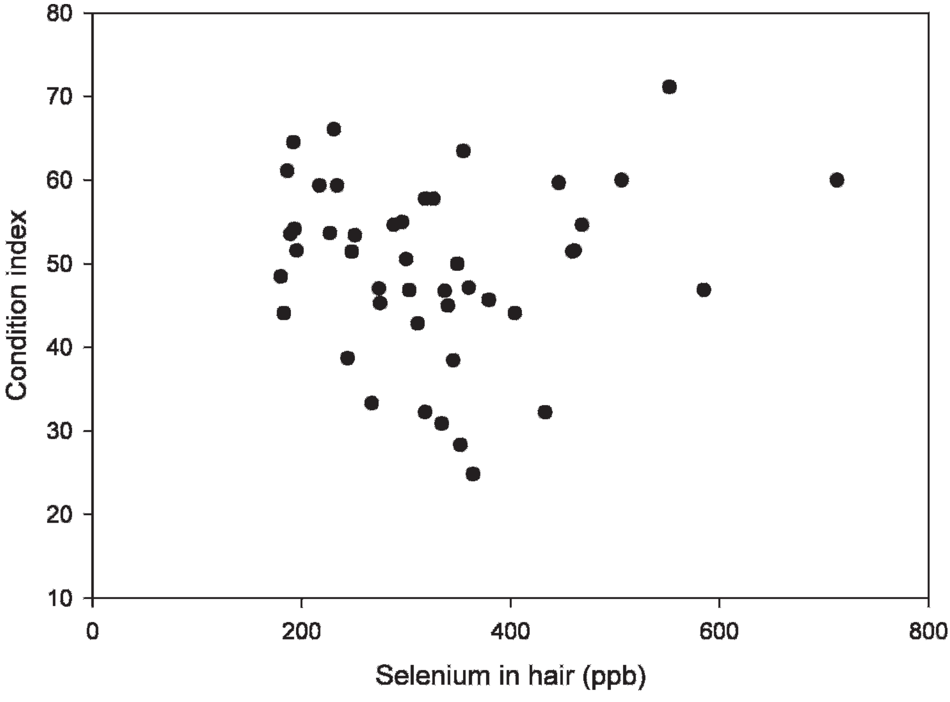

FIGURE 4. Relation between selenium levels in hair (ppb) and body condition index (mass divided by hind-foot length) for individual pikas live-captured in three study areas in Wyoming in 2003 and 2004.

deposition (Haygarth et al., 1995; Steinnes et al., 2005; Donahue et al., 2006), rather than from effects of N deposition on the activity of soil microorganisms. If this interpretation is correct, increased atmospheric deposition may ameliorate Se deficiency in areas where geologic parent material is depleted in Se. In areas rich in Se, such atmospheric deposition may lead to Se toxicity, which may negatively affect already declining pika populations.

An additional ameliorating effect to Se deficiency could stem from the behavior of pikas. Dearing (1997) found that pikas are able to choose plants rich in allelochemicals, which enhances their preser-

TABLE 2. Values of selenium deficiency, adequate selenium levels in liver, and adequate selenium levels in hair published in the literature for a variety of mammals.

Species	Source	Se deficiency in hair (ppb)	Adequate Se levels in liver (ppb)	Adequate Se levels in hair (ppb)
Goats (*Capra hircus*)	O-Hara et al., 2001; Puls, 1994	150	250–1200	>350
Horses (*Equus caballus*)	O-Hara et al., 2001; Puls, 1994	<500	300–1000	1000–3000
Cattle (*Bos taurus*)	Puls, 1994	60–230	250–500	500–1320
Pigs (*Sus domesticus*)	Puls, 1994	180–220	400–1200	400–2000
Deer (*Odocoileus virginianus*)	Puls, 1994	20–180	250–460	
Moose (*Alces alces*)	Gamberg et al., 2005		300–1600	
Rabbits (*Oryctolagus cuniculus*)	Muller and Pallauf, 2005; Puls, 1994	900–1200	900–2000	

vation in hay piles. It is possible that pikas are capable of collecting and storing Se-rich vegetation in their hay piles. For example, in a companion study on bighorn sheep in the Wind River Mountains, we found that plants collected from pika hay piles (e.g., *Carex, Geum, Potentilla,* and *Trifolium*) contained significantly more Se (75 ppb±13.69) than other forage plants (e.g., *Achillea, Cerastium, Cymopterus, Geranium, Ribes*, and *Taraxicum*) collected in alpine meadows in August 2004 (30 ppb±2.31; Mann-Whitney U, $P=0.004$; K.M.P. and S.E.W., unpubl. data).

Our results suggest that although bioavailability of Se to pikas may be reduced in some areas, it may not necessarily translate into reduced body condition. Although we used hind-foot length rather than the more commonly used body length (Bookhout, 1996), we believe our results are representative. First, several studies suggest that hind-foot length is a more reliable estimate of total body size than body length for unanesthetized animals (Pauli et al., 2006). Second, we found no relation between body condition and Se levels in hair of pikas, regardless of whether we used hind-foot, body, or skull lengths (not reported). Nonetheless, the lack of relation between Se and body condition does not indicate that pikas are not experiencing reduced immune capacity or reproduction with Se deficiency. Controlled feeding studies would be necessary to determine if pikas contract any disorders associated with Se deficiency. Also, field monitoring will be required to determine if pikas in Se-deficient populations experience low survival or recruitment.

Our study suggests that some pika populations may be experiencing Se deficiency in addition to the effects of global warming (Beever et al., 2003). Nonetheless, because pika populations are isolated, it is possible that individuals inhabiting areas with low Se in the parent material evolved physiologic adaptations in addition to behavioral ones that enable them to persist with low Se intake. Because such adaptations are likely to be genetically based, evaluating differences in the genetic makeup of pikas from different populations merits further investigation.

ACKNOWLEDGMENTS

We thank I. Abernethy, J. Hunter, R. Mares, S. Palmer, and A. Roe, for assistance in the field. The Wyoming Department of Game and Fish provided logistical support. Funding for the project was provided by the University of Wyoming Faculty Grant-in-Aid to N.L.S., the Department of Zoology and Physiology, and private donations to K.M.P. All protocols were reviewed and approved by an independent Animal Care and Use Committee at the University of Wyoming.

LITERATURE CITED

ADRIANO, D. C. 1986. Selenium. Trace elements in the terrestrial environment. Springer-Verlag, New York, New York, pp. 390–420.

ARTHUR, J. R., R. C. MCKENZIE, AND G. J. BECKETT. 2003. Selenium in the immune system. Journal of Nutrition 133: 1457S–1459S.

BARON, J. S., D. S. OJIMA, E. A. HOLLAND, AND W. J. PARTON. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implication for aquatic systems. Biogeochemistry 27: 61–82.

BEEVER, E. A., P. F. BRUSSARD, AND J. BERGER. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy 84: 37–54.

BERROW, M. L., AND A. M. URE. 1989. Geological materials and soils. *In*: Occurrence and distribution of selenium, M. Ihnat (ed.). CRC Press, Boca Raton, Florida, pp. 213–242.

BOOKHOUT, T. A. (ed.). Research and management techniques for wildlife and habitats. 5th Edition. The Wildlife Society, Bethesda, Maryland, 740 pp.

BROWN, J. H. 1971. Mammals on mountain tops: Nonequilibrium insular biogeography. The American Naturalist 105: 467–487.

CLAYTON, J. L., D. A. KENNEDY, AND T. NAGEL. 1991. Soil response to acid deposition, Wind River Mountains, Wyoming: I. Soil properties. Soil Science Society of America Journal 55: 1427–1433.

CLINCHY, M., D. T. HAYDON, AND A. T. SMITH. 2002. Pattern does not equal process: What does patch occupancy really tell us about metapopulation dynamics? The American Naturalist 159: 351–362.

COMBS, G. F. JR., AND S. COMBS. 1986. The role of selenium in nutrition. Academic Press, Orlando, Florida, 532 pp.

CURTIS, J., AND GRIMES, K. 2005. Wyoming climate atlas. http://www.wrds.uwyo.edu/wrds/wsc/climateatlas/title_page.html.

DEARING, M. D. 1997. The manipulation of plant toxins by a food-hording herbivore, *Ochotona princeps*. Ecology 78: 774–781.

DEORE, M. D., A. K. SRIVASTAVA, AND S. K. SHARMA. 2002. Blood selenium levels during different stages of selenosis in buffaloes and its evaluation as a diagnostic tool. Veterinary and Human Toxicology 44: 260–263.

DHILLON, K. S., AND S. K. DHILLON. 2003. Distribution and management of seleniferous soils. Advances in Agronomy 79: 119–184.

DONAHUE, W. F., E. W. ALLEN, AND D. W. SCHINDLER. 2006. Impacts of coal-fired power plants on trace metals and polycyclic aromatic hydrocarbons (PAHs) in lake sediments in central Alberta, Canada. Journal of Paleolimnology 35: 111–128.

FLUECK, W. T. 1994. Effect of trace elements on population dynamics: Selenium deficiency in free-ranging black-tailed deer. Ecology 75: 807–812.

FRANKEN, R. J., AND D. S. HIK. 2004. Interannual variation in timing of parturition and growth of collard pikas (*Ochotona collaris*) in the Southwest Yukon. Integrated Comparative Biology 44: 186–193.

GAMBERG, M., M. PALMER, AND P. ROACH. 2005. Temporal and geographic trends in trace element concentrations in moose from Yukon, Canada. Science of the Total Environment 351–352: 530–538.

GREYSON, D. K. 1977. On the Holocene history of some Great Basin lagomorphs. Journal of Mammalogy 58: 507–513.

———. 1987. The biogeographic history of small mammals in the Great Basin: Observations on the last 20,000 years. Journal of Mammalogy 68: 359–375.

GÜVENC, M., H. GÜVENC, F. KARATAS, A. D. AYGÜN, AND S. BEKTAS. 2002. Low levels of selenium in miscarriage. The Journal of Trace Elements in Experimental Medicine 15: 97–1001.

HAFNER, D. J. 1993. North American pika (*Ochotona princeps*) as a late Quaternary biogeographic indicator species. Quaternary Research 39: 373–380.

HAYGARTH, P. M., A. F. HARRISON, AND K. C. JONES. 1995. Plant selenium from soils and the atmosphere. Journal of Environmental Quality 24: 768–771.

HNILICKA, P. A., J. MIONCZYNSKI, B. J. MINCHER, J. STATES, M. HINSCHBERGER, S. OBERLIE, C. THOMPSON, B. YATES, AND D. D. SIEMER. 2002. Bighorn sheep lamb survival, trace minerals, rainfall and air pollution: Are there any connections? *In* Proceedings: Northern Wild Sheep and Goat Council, Vol. 13, Rapid City, South Dakota, G. C. Brundige (ed.), pp. 69–94.

IHNAT, M. 1989. Occurrence and distribution of selenium. CRC Press, Boca Raton, Florida, 354 pp.

KNIGHT, D. H. 1994. Mountains and plains: The ecology of Wyoming landscapes. Yale University Press, New Haven, Connecticut, 338 pp.

LAWOR, T. E. 1998. Biogeography of Great Basin mammals: Paradigm lost? Journal of Mammalogy 79: 111–113.

MACARTHUR, R. A., AND L. C. H. WANG. 1973. Physiology of thermoregulation in the pika, *Ochotona princeps*. Canadian Journal of Zoology 52: 11–16.

MEYER, R. D., AND R. G. BURAU. 1995. The geochemistry and biogeochemistry of selenium in relation to its deficiency and toxicity in animals. *In* Proceedings of a national symposium: Selenium in the environment: Essential nutrient, potential toxicant. Sacramento, California, pp. 38–44.

MULLER, A. S., AND J. PALLAUF. 2006. Down-regulation of GPx1 mRNA and the loss of GPx1 activity causes cellular damage in the liver of selenium-deficient rabbits. Journal of Animal Physiology A. Animal Nutrition 86: 273–287.

National Atmospheric Deposition Program. http://nadp.sws.uiuc.edu.

NETER, J., M. H. KUTNER, C. J. NACHTSHEIM, AND W. WASSERMAN. 1996. Applied linear statistical models. 4th Edition. Richard D. Irwin, Inc., Chicago, Illinois, 672 pp.

O-HARA, T. M., G. CARROLL, P. BARBOZA, K. MUELLER, J. BLAKE, AND V. WOSHNER. 2001. Mineral and heavy metal status as related to a mortality event and poor recruitment in a moose population in Alaska. Journal of Wildlife Diseases 37: 509–522.

OHLENDORF, H. M. 1996. Selenium. *In* Noninfectious diseases of wildlife. 2nd Edition. A. Fairbrother, L. N. Locke and G. L. Hoff (eds.). Iowa State University Press, Ames, Iowa, pp. 128–140.

PALMER, I. S., AND N. THEIX. 1997. Determination of selenium in feeds and premixes: Collaborative study. Journal of AOAC International 80: 469–480.

PAULI, J. N., S. W. BUSKIRK, E. S. WILLIAMS, AND W. H. EDWARDS. 2006. A plague epizootic in the black-tailed prairie dog (*Cynomys ludovicianus*). Journal of Wildlife Diseases 42: 74–80.

PULS, R. 1994. Mineral levels in animal health: Diagnostic data. 2nd Edition. Sherpa International, Clearbrook, British Columbia, Canada, pp. 229–252.

SCOTT, R. W. 1995. The alpine flora of the Rocky Mountains, Vol. I. The Middle Rockies. University of Utah Press, Salt Lake City, 901 pp.

SHEEHAN, T. M. T., AND D. J. HALLS. 1999.

Measurement of selenium in clinical specimens. Annals of Clinical Biochemistry 36: 301–315.

STEINNES, E., O. Ø. HVATUM, B. BØLVIKEN, AND P. VARSKOG. 2005. Atmospheric pollutants and trace gases: Atmospheric supply of trace elements studied by peat samples from Ombrotrophic bogs. Journal of Environmental Quality 34: 192–197.

SVALBERG, T. 2005. Wind River bulk deposition program: Bridger-Teton National Forest summary of 2004 data, final report. US Forest Service, Pinedale, Wyoming, 12 pp.

THOMPSON-EAGLE, E. T., W. T. FRANKENBERGER, JR., AND K. E. LONGLEY. 1991. Removal of selenium from agricultural drainage water through soil microbial transformations. *In* The economics and management of water drainage in agriculture, A. Dinar and D. Zilberman (eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands, 946 pp.

WOLFE, A. P., J. S. BARON, AND R. J. CORNETT. 2001. Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). Journal of Paleolimnology 25: 1–7.

Received for publication 12 January 2006.