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The implications of selenium deficiency for wild herbivore conservation: a review

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Abstract Selenium (Se) is required at a fundamental physiological level in all animals. Adequate levels of Se are necessary for proper bone metabolism, iodine metabolism, immune function, reproductive success, and recruitment. Selenium is a component of enzymes which scavenge oxidative free radicals that would otherwise degrade cell membranes. Severe deficiency results in obvious symptoms such as white muscle disease in ungulates. However, more frequently, deficiency may be chronic and subclinical. Individuals then display no obvious signs of malady, yet performance suffers until their populations decline without

apparent cause or through proximate factors which obscure underlying primary factors. Although well known in domestic stock, the link between population performance and Se deficiency in wild populations has been difficult to firmly establish. Confounding factors include the role of vitamin E, which also acts as an antioxidant to mitigate the need for Se under some circumstances; changing Se requirements at changing times in animal life history; changing Se requirements in relation to pollution levels and other factors causing oxidative stress; and the non-uniform distribution of Se in its various chemical forms in the environment. The latter point is especially important to wild populations that have been reduced to remnant portions of their previous range. Here, we have reviewed the literature of Se in wildlife as well as provided an introduction to Se in physiology and Se behavior in the environment for the wildlife researcher and manager. We conclude that unrecognized Se deficiency may often impede optimal population performance, and we provide recommendations for habitat analysis with regard to Se which can be used in future research. Finally, evidence that the amount of available Se in the environment is decreasing from anthropogenic causes is shown.

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Introduction

Selenium (Se) has been identified as an essential micronutrient in all animals. It is required at the most fundamental physiological level as a component of the 21st amino acid, selenocysteine. Adequate levels of Se are vital to proper reproductive performance, bone metabolism, immune function, and iodine

metabolism. Yet, Se is a relatively rare element and is often present at low concentrations in soil and vegetation. It has the lowest concentration in igneous bedrock of all the nutrient elements and is unevenly distributed in the landscape and frequently at deficient levels for terrestrial herbivores. Selenium deficiencies are widespread in domestic stock and are unavoidable in some wildlife populations. This may be especially true for populations confined to high-elevation ranges or on areas with granitic bedrock or volcanic soils with low Se content or that have lost access to Se-enriched parts of their ranges such as mineral licks or low-elevation winter range. The condition may be exacerbated by increased levels of oxidative stress. Herbivores acquire their Se primarily from plants. As plants do not require Se, their levels depend on geological and climatic factors, that is, on the environmental chemistry of Se and its chemical speciation in the environment.

Because our understanding of Se as a micronutrient is relatively new, many wildlife managers are unaware of the element's importance in physiology and population dynamics. Severe deficiency in ungulates results in obvious symptoms such as white muscle disease (WMD). More frequently, deficiency is chronic and subclinical. Individuals then display no obvious signs of malady, yet performance suffers until their populations decline without apparent cause. While mysterious population declines are not always due to Se deficiency, the wildlife manager should be aware of the possibility. Furthermore, animal requirements for Se are not static and depend on life stage, levels of pollution, and other factors causing oxidative stress. Therefore, this review not only presents a summary of the wildlife literature regarding Se nutrition but also looks at the role of Se in mammalian physiology and the environmental chemistry of this important element which affects its availability to wildlife.

Discussion

Selenium in physiology

Biochemical roles

Although Se was long known to have toxic effects at high doses, it was not until 1957 that it was found to have an essential physiological role in mammals, when it was shown to mitigate liver necrosis in rats (Schwarz and Foltz 1957). Shortly thereafter, it was also shown to prevent muscular degeneration in lambs (Schubert et al. 1961). It is now known that Se is crucial to all aerobically respiring organisms and is so fundamental that the genetic code was expanded following the recognition of the 21st naturally occurring amino acid, selenocysteine. This Se-containing amino acid is essential in all mammals (Tate et al. 1999;

Hatfield and Gladyshev 2002). Some 35 selenoproteins have now been identified in animals and humans, all containing selenocysteine in their active sites (Arthur 2000; Kryukov et al. 2003; Raymond and Ralston 2004). A review of the selenoenzymes and other selenoproteins was provided by Stadtman (1990), and the number of functional selenoproteins as well as the range of biological roles for individual selenoproteins continue to expand (Reeves and Hoffmann 2009).

The most important known functions of selenoproteins are in antioxidant defense, including the elimination of active oxygen species such as hydrogen peroxide, hydroperoxides, and oxygen-containing free radicals—the toxic products of aerobic respiration (Shchedrina et al. 2010). These reactive oxygen species react with unsaturated lipid compounds, causing the degradation of cell membranes. Four glutathione peroxidases (GPX) as well as thioredoxin reductase and other selenoproteins act as oxidant scavengers in various tissues. Sakuma et al. (2008), for example, demonstrated that rats denied Se exhibited low liver Se concentrations, low GPX activity, and higher bile hydrogen peroxide and oxidative stress levels. Similarly, 65 domestic cattle with initially 0.058 mg/kg wet weight (ww) liver Se and GPX activity of 35 IU/g hemoglobin, when treated with Se boluses, exhibited an increase in liver Se to 0.070 mg/kg (ww) and GPX activity of 263 IU/g (Hidiroglou et al. 1987). Similarly, 20 domestic lambs with WMD were found to have low mean liver concentrations of 0.088 mg/kg (ww) Se and GPX activity of 22.3 IU/g vs. 0.515 mg/kg (ww) Se and 34.0 IU/g for healthy lambs ($P < 0.001$) (Beytut et al. 2002). Selenium deficiency also has effects on the blood and blood formation. Oxidative stress causes the denaturation of the globin subunits of hemoglobin, and Se deficiency makes erythrocytes osmotically fragile, increases erythropoietin levels, and leads to inefficient erythropoiesis (Kaushal et al. 2011).

Selenoprotein synthesis is important to early mammalian development, as illustrated by the findings of Serdaru et al. (2004) who reported that even during periods of Se deficiency, domestic cattle dams continued to supply high-Se colostrum to their calves through depletion of their own reserves. Genomic studies have identified a protein homologous to selenoprotein N that is unique to vertebrates (Rederstorff et al. 2006), and mutations in the gene *SEPN1* cause a form of congenital muscular dystrophy. Sequencing of the gene from patients affected with this muscular dystrophy have identified several mutations, establishing for the first time a connection between a selenoprotein and a human genetic disorder (Rederstorff et al. 2006). Congenital muscular dystrophy causes muscle pain and rigidity of the limbs and spine. Also, at least six selenoproteins are residents of the endoplasmic reticulum, revealing an important role in its function which is only

beginning to be understood. These selenoproteins are mainly involved in protein folding and the disposition of misfolded proteins (Shchedrina et al. 2010). Four of these selenoproteins are nearly exclusive to vertebrates (Reeves and Hoffmann 2009; Shchedrina et al. 2010).

Although this review highlights Se, the element also interacts with iodine by affecting its role in thyroid hormone metabolism; a brief summary of these affects is warranted here. Selenium deficiency causes secondary iodine deficiency in vertebrates (Zagrodzki et al. 1998; Arthur et al. 1999; Köhrle 2005; Duntas 2010). Iodine deficiency results in abortions, stillbirths, reduced fetal weight, weak neonates, increased neonatal mortality, prolonged gestation, and infertility (Kalkus 1920; Schlumberger 1955; Barry 1983; Wilson et al. 2002; Sivertsen 2004; Ebert et al. 2008). Juvenile growth—even under subclinical iodine deficiency—is impaired (Choudhury and Gorman 2003), neurological development is aberrant, plus various other less specific symptoms (Potter et al. 1982; Matamoros et al. 2003).

Selenium is necessary for the conversion of the inactive thyroid hormone thyroxine (T_4) into its more active counterpart, triiodothyronine (T_3), via the action of one of three Se-containing deiodinase enzymes (Wichtel et al. 1996; Köhrle 2000). The hormone T_3 is required for normal growth and development, and for energy production and oxygen consumption in cells. Selenium supplementation in deficient cattle results in higher T_3 activity and higher immunoglobulin concentrations in colostrum (Voudouri et al. 2003; Pavlata et al. 2004), and Se-deficient lambs have been shown to have low levels of T_3 and GPX, which are possibly responsible for a high incidence of stillbirths and neonatal deaths (Kozat 2007; Dalir-Naghadeh and Rezaei 2008). For example, Dalir-Naghadeh and Rezaei (2008) compared 35 domestic lambs suffering from the Se deficiency malady WMD with 30 healthy lambs and found that the mean erythrocyte GPX activity was higher in the healthy lambs (132 vs. 45 IU/g hemoglobin) and that the mean serum T_4 concentration was lower in healthy lambs (58 vs. 77 nmol/L). Meanwhile, serum T_3 concentration was higher in the healthy group (1.9 vs. 1.4 nmol/L, $P < 0.001$). Thus, Se deficiency can cause symptoms of hypothyroidism, including extreme fatigue or mental slowing, and may thus influence even basic metabolic and cold stress survival rates (Suttle 2010). The thyroid gland employs at least 11 selenoproteins, including selenoperoxidases, to protect it from hydrogen peroxide (Arthur et al. 1999; Beckett and Arthur 2005; Reeves and Hoffmann 2009).

Vitamin E, also acquired by herbivores from the plants they eat, plays an important antioxidant role protecting membrane lipids by inhibiting hydroperoxides and reducing GPX requirements (McDowell 1989). Both dietary vitamin E and Se protect against membrane lipid peroxidation, with vitamin E acting as a lipid-soluble, membrane-bound

antioxidant and Se in GPX as a scavenger of oxidative free radicals and hydrogen peroxide in aqueous solution (Combs and Scott 1977). While the two would thus act cooperatively to protect all types of cells from reactive oxygen species, the vitamin can reduce the physiological requirement for Se and complicate the interpretation of the effects of Se deficiency. For example, Brady et al. (1978) found that when captive white-tailed deer (*Odocoileus virginianus*) were supplemented with vitamin E, the incidence of WMD in their young was decreased even when the animals were maintained on a Se-marginal (although not necessarily deficient) diet of 40 ppb. However, Dierenfeld and Jessup (1990) reported that vitamin E deficiency alone was not sufficient to cause mortality in white-tailed deer. In that work, most mortality occurred when Se was also deficient. Since the production of reactive oxygen species is increased under stressful conditions, the need for Se and vitamin E is also increased under such conditions.

Deficiency maladies

The most overt malady associated with Se deficiency is WMD, also called nutritional muscular dystrophy. Well known from domestic livestock, it has also been reported in wild populations. It typically occurs in Se-deficient young at 3–6 weeks. Sometimes called “stiff lamb disease” or “weak fawn syndrome,” it results in muscle stiffness and respiratory distress. Symptoms include slumped shoulders and a stiff-legged gait, poor growth, and high respiratory rates with nasal secretions and coughing and general unthriftiness. The skeletal and cardiac muscles may be affected, and myocardial necrosis may lead to sudden death (Suttle 2010). For wildlife, the decreased ability to move freely would be expected to lead to increased predation losses, as reported by Hnilicka et al. (2004). This applies particularly to neonates as females may suffer from small udder size, low milk production, and thus causing early weaning (Hnilicka et al. 2004).

Subclinical deficiency has less overt effects. Since it functions at a very basic biochemical level, Se deficiency may be expressed in myriad ways, and only pronounced deficiency is lethal (Rucker et al. 2008; Rederstorff et al. 2006). Under conditions of deficiency, the less essential selenoproteins are lost first, with those involved in survival to maturity and reproduction being conserved (McCann and Ames 2011).

In all animal species studied, prolonged Se deficiency impairs the reproductive performance of both males and females. It affects litter size, conception rate, embryonic mortality, birth weight, age of first breeding, neonatal mortality, and growth rate and also causes the retention of placentas (Allen and Ullrey 2004; Bogden et al. 2006; Kumar et al. 2009). Selenium deficient ewes in New

Zealand and Australia, for example, were found to have a 20–50 % infertility rate with high lamb losses (Suttle 2010). Ren et al. (2011) showed that successful completion of meiosis in the testes of offspring depends on both maternal and dietary Se supply. For Se-deficient males, sperm count and fertility are sharply reduced even though some sperm motility may persist, and damaged DNA in the sperm also affects the health of the offspring (Pfeifer et al. 2001; Allen and Ullrey 2004; Rederstorff et al. 2006). Maternal Se nutrition during gestation affects the efficiency of growth in offspring irrespective of postnatal management (Neville et al. 2010).

Furthermore, Se deficiency in postnatal and adult animals impairs bone metabolism, causing osteopenia and osteoarthritis (Moreno-Reyes et al. 1998, 2001; Köhrle et al. 2005; Ebert and Jakob 2007; Ren et al. 2007; Ebert et al. 2008), including Kashin–Beck disease in humans (Downey et al. 2009). Selenium deficiency in ruminants has similarly been shown to be an underlying factor for periodontitis, mandibular thickening, premature tooth shedding, and reduced bone density (Andrews et al. 1968; Porter et al. 1970; Van Reenan 1980). Examples of Se-related periodontal abnormalities in wildlife have been reported for wild sheep (Hnilicka et al. 2004) and, apparently, for huemul deer (Flueck and Smith-Flueck 2008).

Selenium is also fundamental for proper immune function and infectious disease resistance, and the pathogenicity of several disease organisms is likely based on the sequestration of Se from host cells (Taylor et al. 1997; Kasaikina et al. 2011). It significantly affects response to viral infections in its role as an antioxidant (Levander et al. 1995). The discovery of selenocysteine as the 21st amino acid led to predictions and later confirmation that a selenoprotein gene in HIV was a virally encoded homolog of GPX (Taylor et al. 1997). Similarly, the role of coxsackievirus in human Keshan disease has parallels to Se deficiency in coxsackievirus-infected mice and triggered a similar cardiomyopathy, called “viral myocarditis.” Intriguingly, even a “benign” strain of coxsackievirus becomes virulent in Se-deficient mice, where it mutates into a more virulent strain that can produce myocarditis even when transferred to normal mice that are not Se-deficient (Levander et al. 1995; Taylor et al. 1997). Thus, these viral mutations are consistent rather than stochastic, and long-lived (Harthill 2011). Similarly, Se-deficient hosts were more susceptible to *Listeria* infections (Wang et al. 2009).

In addition to infectious diseases, Se deficiency also affects cancer prevention, aging processes, and, as discussed above, iodine metabolism (Arthur et al. 1999; Hatfield and Gladyshev 2002; Allen and Ullrey 2004). Primary deficiency can be due simply to living at high elevation and be associated with multidimensional stressors including

hypoxia, cold and heat exposure, nutrition, and disease state, all of which raise oxidative stress (Iyengar and Gopal-Ayengar 1988; Bakonyi and Radak 2004).

Selenium deficiency can elicit epigenetic effects; marginal deficiency can lead to up- or downregulation of certain enzymes, underscoring how sensitive organisms are to changes in Se homeostasis. For example, Mueller et al. (2010) found that target gene expression was upregulated in the intestine, possibly because it is in the first line of defense from the food side. In contrast, moderate Se deficiency resulted in the downregulation of genes involved in inflammation and heme biosynthesis, pointing to a disturbance in inflammatory response (Kipp et al. 2012). Selenium even influences the expression of multiple genes that code for non-selenoproteins. Selenium can prevent cysteine insertion into selenoproteins and thereby maximize its own enzymatic activity. For mice maintained on a Se-deficient diet, the ratio of selenocysteine/cysteine was ~1:1, while on an adequate diet it was 9:1. Cysteine was not detected in mice selenoproteins on an enhanced diet (Turanov et al. 2011).

Heavy metal scavenging

The deposition of atmospheric mercury and cadmium has doubled between the beginning of the nineteenth century and 1990; from 1977 to 1990, the atmospheric concentration of mercury has increased by 1.5 % per year in the Northern Hemisphere, with the anthropogenic flux being about 2.5-fold larger than the natural one (Berger et al. 1989; Slemr and Langer 1992; Jackson 1997). Consequently, increased levels of heavy metals in wild herbivores have been documented (Backhaus and Backhaus 1983). The exposure of mammals to heavy metals increases the physiological need for Se because these metals may sequester Se (Sørmo et al. 2011). For example, in Se-depauperate Lake Mjøsa, Norway, Sørmo et al. (2011) found that the Se/Hg ratio in brown trout (*Salmo trutta*) muscle tissue was a good predictor of the metallothionein concentration. Metallothionein is a cysteine-rich protein which scavenges mercury and cadmium; fish with low Se levels required more of it to scavenge mercury. Similarly, cadmium mobilization was much more efficient in Se-adequate than in Se-deficient rats (Kotyzová et al. 2010). Therefore, Se can be used to counteract the toxicity of heavy metals (Frost 1987; Whanger 1992) through complexation with selenoprotein P (Suttle 2010) or by reaction with Se itself to produce insoluble selenides (Sørmo et al. 2011). Numerous studies in many species have shown that Se supplementation counteracts the neurotoxicity, fetotoxicity, and developmental toxicity associated with mercury exposure (Raymond and Ralston 2004; Usuki et al. 2011). Furthermore, exposure to methylmercury induces Se deficiency by sequestering Se within hours and affecting epigenetically the expression of Se-dependent

enzymes. The UGA codon for selenocysteine is then no longer recognized, resulting in incomplete protein synthesis (Usuki et al. 2011). The mercury–Se interaction has been implicated in low reproductive success for endangered leatherback turtles (*Dermodochelys coriacea*; Perrault et al. 2011). In addition to heavy metals, chlorinated hydrocarbon exposure has also been implicated in raising Se requirements (Combs and Scott 1977).

In summary, subclinical Se deficiencies are generically expressed as reduced immune function, reduced systemic growth and reproductive potential, and behavioral changes due both to Se deficiency malady and, possibly, secondary impairment of iodine metabolism. These subtle affects are not easily recognized, but will affect population performance. The absence of clinical signs has long been considered inappropriate as evidence for adequate mineral nutrition (Hebert and Cowan 1971a). Although subclinical deficiencies are probably widespread, they are rarely recognized in wildlife (Robbins 1983; Flueck 1994; Sargison et al. 1998; Mincher et al. 2008) or in extensive animal production systems (Johnson et al. 1979; Jones et al. 1987). Unfortunately, subclinical deficiency is not easily detected and requires production trials for its verification (Sargison et al. 1998; Grace and Wilson 2002).

Selenium in wildlife

General considerations

Although overt symptoms of deficiency are seldom reported for wild populations, the selenium status of wildlife populations has been studied around the globe, often due to suspicions about its subclinical effects. Typically, liver or whole-blood concentrations are sampled, although the value of comparisons between studies may be limited. It must be recognized that the mineral status of an individual animal may depend on age, sex, species, season, reproductive status, and the level of oxidative stress. As previously mentioned, high levels of vitamin E may mitigate the need for elevated Se. Furthermore, differing sampling and analytical techniques may affect Se measurement results. For this discussion, all reported liver values have been converted to wet weight for ease of comparison, assuming that wet weight concentrations are a factor of 4 lower than dry weight (Galgan and Frank 1995). Values originally referred to in parts per million are reported here as milligrams per liter, while the occasional value reported as milligrams per liter is given as reported in the original. For whole blood, values less than 0.040–0.050 mg/L result in nutritional muscular dystrophy in livestock (Flueck 1994 and references therein). Puls (1994) provided reference values of 0.080–0.500 mg/L plasma. When compared to livestock standards, the levels of Se in wildlife and wildlife forage

have often been reported as deficient. Table 1 summarizes the wildlife Se values reported in the examples in the following discussion and in additional studies.

Suggested selenium reference values

There are no standard recommended values for Se in wildlife. The minimum domestic stock liver recommendations are 0.120 (Van Metre and Callan 2001) to 0.150 mg/kg (ww) (Galgan and Frank 1995), and 0.063 mg/kg (ww) was reported as critically low by McDowell et al. (1995). Puls (1994) recommended criteria of deficiency when liver Se < 0.15 mg/kg (ww), 0.15–0.22 mg/kg (ww) as marginal, and > 0.22 mg/kg (ww) as optimal in cattle. Pollock (2005) concluded that 0.150 mg/kg (ww) liver represented deficiency in white-tailed deer, and values < 0.050 mg/kg (ww) are considered severely deficient by the National Veterinary Council of Sweden (Galgan and Frank 1995). Wilson and Grace (2001) reported that young red deer (*Cervus elaphus*) with WMD had liver Se concentrations < 0.035 mg/kg (ww).

Scandinavia

In examples from Scandinavia, Vikøren et al. (2005) reported a mean liver concentration of 0.110 mg/kg (ww) for 245 hunter-killed Norwegian red deer, while Galgan and Frank (1995) reported a mean of 0.250 mg/kg (ww) and with a median of 0.150 mg/kg (ww) for 2,080 Swedish moose (*Alces alces*). The mean reported values are frequently higher than the median values as a handful of individuals from any sample often have exceptionally high Se concentrations. These means are marginally adequate to deficient levels based on the standards above. Norwegian moose had a mean liver Se of 0.468 mg/kg (ww), reindeer (*Rangifer tarandus*) had 0.218 mg/kg (ww), and roe deer (*Capreolus capreolus*) had 0.168 mg/kg (ww), reflecting a concentration gradient due to the greater aerial deposition of the element in coastal areas (Vikøren et al. 2011). This study also found that an inland moose population with compromised condition and reduced productivity had deficient Se levels, with some individuals having liver concentrations below the detection limit. The environmental conditions that lead to a higher coastal deposition of airborne Se are discussed later; however, it can be seen that populations may exist along a gradient from source to sink areas (Flueck and Smith-Flueck 2011a). In another example, Frøslie et al. (1984) reported that moose liver values ranged from 0.080 to 0.92 mg/kg (ww), depending on concentrations in moss and the levels of aerial deposition. Although 50–60 % of the sampled Swedish moose fell below 0.100 mg/kg (ww) of liver (Galgan and Frank 1995; Pollock 2005), these populations did not display clinical signs of deficiency.

Table 1 Selenium status for wild, unsupplemented herbivores

Species	Locality	N	Conc.	Indications	Reference
Liver (mg/kg, ww)					
Suggested reference values: <0.15, deficient; 0.15–0.22, marginal; >0.22, adequate					
Red deer	Norway	245	0.11±0.09	nr	Vikøren et al. (2005)
Red deer	Norway		0.20	nr	Frøslie et al. (1984)
Red deer	Poland	73	0.09±0.08 ^c	nr	Pilarczyk et al. (2009)
Red deer	Poland	23	0.095±0.018	nr	Pilarczyk et al. (2011b)
Red deer	Poland	20	0.063±0.033	ch	Jarzyńska and Falandysz (2011)
Red deer	Croatia	19	0.241±0.053	nr	Lazarus et al. (2008)
Elk	WA, USA	9	0.070±0.066	nr	Fielder (1986)
Moose	Sweden	2,080	0.250±0.288	nr	Galgan and Frank (1995)
Moose	Norway	422	0.47±0.69	nr	Vikøren et al. (2011)
Moose	Norway		0.42	nr	Frøslie et al. (1984)
Moose ^a	Norway	57	1.20	nr	Ytrehus et al. (1999)
Moose ^a	Norway	63	0.13	nr	Ytrehus et al. (1999)
Moose	MN USA				
ag habitat		47	0.68 ^c	dp	Custer et al. (2004)
Bog/forest		32	0.30 ^c	dp	Custer et al. (2004)
Roe deer	Poland	96	0.16±0.14 ^c	nr	Pilarczyk et al. (2009)
Roe deer—spring	Poland	17	0.08±0.03	nr	Pilarczyk et al. (2011a)
Roe deer—winter	Poland	21	0.05±0.02	nr	Pilarczyk et al. (2011a)
Roe deer—male	Poland	10	0.093±0.025	nr	Pilarczyk et al. (2011a)
Roe deer—female	Poland	13	0.097±0.027	nr	Pilarczyk et al. (2011a)
Roe deer	Germany	11	0.27±0.07	nr	Humann-Ziehank et al. (2008)
Roe deer	Norway	280	0.17±0.14	nr	Vikøren et al. (2011)
Reindeer	Norway	73	0.21±0.07	nr	Vikøren et al. (2011)
Reindeer	Norway		0.50	nr	Frøslie et al. (1984)
Reindeer/caribou	Greenland	126	0.253	nr	Aastrup et al. (2000)
Mule deer	WA, USA	10	0.121±0.057	nr	Fielder (1986)
Mule deer	SD, USA	38	0.64±0.05	ch	Zimmerman et al. (2008)
White-tailed deer	MI, USA	8	0.24±0.02	nr	Brady et al. (1978)
White-tailed deer	FL, USA	139	0.191 ^c	nr	McDowell et al. (1995)
White-tailed deer	SD, USA	42	0.81±0.05	ch	Zimmerman et al. (2008)
White-tailed deer	VA, USA	60	0.08±0.03	id	Sleeman et al. 2009, (2010)
Pronghorn adult	OR, USA	17	0.12±0.03	pr	Dunbar et al. (1999)
Pronghorn	ID, USA	55 ^b	0.13±0.04 ^c	wfs	Stoszek et al. (1980)
Pronghorn	MT, USA	55 ^b	0.30±0.05 ^c	nr	Stoszek et al. (1980)
Mt. goat	WA, USA	10	0.022±0.020	nr	Fielder (1986)
Sheep	NV, USA	38	0.173±0.029	cm	Cox (2006)
Wild boar	Poland	172	0.190±0.09	nr	Pilarczyk et al. (2010)
Blood (mg/L)					
Suggested reference values: <0.05, blood extremely deficient; 0.08–0.50, plasma adequate					
Elk	WA, USA	118	0.086	nr	Hein et al. (1994)
Moose	AK, USA	20	0.12±0.013	nr	Stephenson et al. (2001)
Moose	AK, USA	22	0.12±0.03	pr	O'Hara et al. (2001)
Moose	WA, USA	2	0.015	nr	Hein et al. (1994)
Mule deer	WA, USA	6	0.081	nr	Hein et al. (1994)
Black-tailed deer	CA, USA	135	0.037±0.030	pr	Flueck (1994)
Black-tailed deer	CA, USA	10	0.089	pr	Pine and Mansfield (1983)

Table 1 (continued)

Species	Locality	<i>N</i>	Conc.	Indications	Reference
Mule deer—resident	CA, USA	563	0.103±0.1	nr	Oliver et al. (1990)
Mule deer—migratory	CA, USA	1,132	0.081±0.067	nr	Oliver et al. (1990)
Mule deer—resident	CA, USA	69	0.084	nr	Dierenfeld and Jessup (1990)
Mule deer—migratory	CA, USA	82	0.054	nr	Dierenfeld and Jessup (1990)
Pronghorn	OR USA				
Neonate	Year 1	17	0.085±0.021	pr	Dunbar et al. (1999)
Neonate	Year 2	44	0.051±0.015	pr	Dunbar et al. (1999)
Adult		20	0.099±0.036	pr	Dunbar et al. (1999)
Mt. goat	WA, USA	20	0.035±0.025	nr	Fielder (1986)
Mt. goat	WA, USA	11	0.057±0.056	nr	Fielder (1986)
Mt. goat	WA, USA	19	0.041±0.032	nr	Robbins et al. (1985)
Mt. goat	Alberta, CA	7	0.150±0.110	nr	Samson et al. (1989)
Sheep	Alberta, CA	51	0.025±0.011	nr	Samson et al. (1989)
Sheep	Alberta, CA	8	0.120±0.030	nr	Samson et al. (1989)
Sheep	WA, USA	13	0.09±0.06	nr	Coggins (2006)
Sheep	WA, USA	16	0.19±0.09	nr	Coggins (2006)
Sheep	WA, USA	17	0.21±0.07	nr	Coggins (2006)
Sheep	WA, USA	14	0.084	pr	Hein et al. (1994)
Sheep	OR, USA	27	0.11±0.07	nr	Coggins (2006)
Sheep	OR, USA	25	0.11±0.08	nr	Coggins (2006)
Sheep	WY, USA	43	0.130	pr	Hinilicka et al. (2004)
Skeletal muscle (mg/kg, ww)					
Red deer	Poland	20	0.043±0.025	ch	Jarzyńska and Falandysz (2011)
Red deer	Croatia	34	0.531±0.091	nr	Lazarus et al. (2008)
White-tailed deer	MI, USA	109	0.04±0.016 ^c	nr	Ullrey et al. (1981)
White-tailed deer	MI, USA	8	0.07±0.01	nr	Brady et al. (1978)
Reindeer/caribou	Greenland	127	0.104	nr	Aastrup et al. (2000)
Serum (mg/L)					
White-tailed deer	FL, USA	174	0.013±0.001 ^c	nr	McDowell et al. (1995)
White-tailed deer	MI, USA	32	0.11±0.005	nr	Brady et al. (1978)
Pronghorn	OR, USA	20	0.049±0.010	pr	Dunbar et al. (1999)
Hair (mg/kg)					
Elk	OR, USA	8	0.110±0.06	nr	Fielder (1986)
Moose	AK, USA	23	0.50±0.20	pr	O'Hara et al. (2001)
Mule deer	OR, USA	10	0.150±0.08	nr	Fielder (1986)
Mt. goat	OR, USA	22	0.020±0.023	nr	Fielder (1986)
Mt. goat	OR, USA	6	0.070±0.021	nr	Fielder (1986)

Values are as originally reported or the means of pooled reported values. Reference values are suggested based on the discussion in this review *ch* clinically healthy, *cm* high incidence of capture myopathy, *dp* declining population, *nr* none reported, *pr* poor recruitment, *wfs* weak fawn syndrome, *id* immune depression and disease

^a Median rather than mean values

^b Combined Idaho and Montana sample sizes=55

^c Values converted from dry weight

Europe

Elsewhere in Europe, roe deer in northern Germany were reported to have mean liver Se concentrations similar to those of domestic sheep of 0.270 mg/kg (ww), although their vitamin E levels were higher (Humann-Ziehanek et al. 2008). Seventy-three red deer and 96 roe deer sampled in Poland from 2003 to 2007 had mean liver Se levels of 0.090 and 0.160 mg/kg (ww), respectively, all without reported clinical signs (Pilarczyk et al. 2009). Kidney concentrations were higher. Polish wild boars (*Sus scrofa*) also had higher concentrations in kidney than in liver, with the mean of 172 liver values being 0.190 mg/kg (ww) and with spring values being higher than autumn (Pilarczyk et al. 2010). In continued work, Pilarczyk et al. (2011b) also demonstrated a correlation between liver Se and GPX activity ($r^2=0.73$).

North American mountain goats and bighorn sheep

High-elevation populations of mountain goats and wild sheep may be especially susceptible to Se deficiency. In North America, Fielder (1986) found that Washington mountain goats (*Oreamnos americanus*) had deficient mean liver Se levels of 0.022 mg/kg as compared to elk (*C. elaphus*) of 0.070 mg/kg and mule deer (*Odocoileus hemionus*) of 0.121 mg/kg, both from lower altitudes. Unfortunately, Fielder et al. (1986) did not report whether the liver samples were analyzed on a wet weight basis, although the values reported probably reflect wet weight analysis. Goat forage species were also analyzed for Se content, with the highest concentration reported at 0.030 mg/kg and with most falling below the detection limit, again reflecting the gradients of Se found in the environment. Hair sampling results were reported as 0.070 mg/kg for goats, 0.110 mg/kg for elk, and 0.150 mg/kg for deer. When we plotted the mean liver vs. mean hair

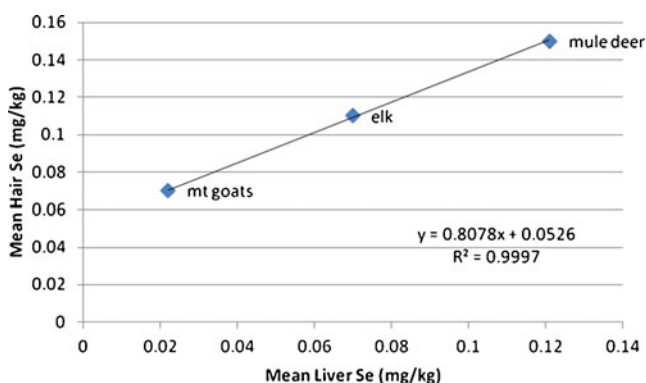


Fig. 1 Mean hair vs. mean liver Se concentrations of Table 2 in Fielder et al. (1986). The samples were from hunter-killed animals, with sample size ranging from $n=6$ for hair from goats to $n=10$ for hair from deer and liver from goats and deer

concentrations of Fielder et al. (1986), an excellent correlation was obtained, although the data set is admittedly limited. However, this suggests that hair sampling may provide a non-intrusive method for establishing the Se status of wild populations. It must be cautioned that external Se contamination on hair is not easily removed by washing prior to analysis (Morton et al. 2002). This is shown in Fig. 1, and it suggests that more work in this area would be valuable. Blood concentrations were not correlated with liver Se in those data.

White muscle disease was reported in British Columbia mountain goats following capture-related stress by Hebert and Cowan (1971b). These animals were not sampled for their Se content; however, they used forage species containing <0.050 mg/kg Se. In Nevada, Cox (2006) reported that hunter-harvested bighorn sheep (*Ovis canadensis*) mean liver Se ranged from 0.168 to 0.177 mg/kg. Although not specified in that report, these are probably wet weight values, and supplementation with mineral blocks did not raise this value above 0.203 mg/kg, perhaps suggesting that they were adequate. These levels are within the marginal range for cattle; however, many wildlife populations with lower values have been reported (Table 1). Robbins et al. (1985) established a linear relationship between whole-blood Se levels and GPX activity in Olympic National Park, Washington, mountain goats. Selenium in blood averaged 0.041 mg/L for 19 goats, although this value was heavily influenced by one high result of 0.147 mg/L. Interestingly, the GPX activity per unit Se was higher for goats than for domestic cattle, suggesting that goats are adapted to a low Se environment and have a lower physiological requirement for the element. Goats injected with Se supplements required up to 30 days to develop peak GPX activity. In contrast, Samson et al. (1989) were not able to demonstrate that GPX activity per unit Se was higher in bighorn sheep or mountain goats than for cattle.

In Alberta bighorn sheep and mountain goats, 51 sheep had low whole-blood levels of 0.025 mg/L Se with a range of 0.005–0.045 mg/L at Ram Mountain, and eight sheep had 0.120 mg/L with a range of 0.070–0.160 mg/L at Mount Allan (Samson et al. 1989). For comparison, five captive sheep maintained on an adequate Se diet had an adequate mean concentration of 0.112 mg/L, with a range of 0.090–0.120 mg/L. In the same report, mountain goats at Caw Ridge, Alberta, had mean blood Se of 0.150 mg/L over a range of 0.069–0.330 mg/L. Although the sheep population at Ram Mountain would be considered deficient compared to livestock, once again, no clinical signs of WMD were discernible. In an Oregon sheep population, Se supplementation via salt was provided on the Lostine winter range (Coggins 2006). Since 1977, whole-blood Se levels in this population were the highest of all populations tested in the region, with an average of 0.390 mg/L for the period 1997–2005. Neighboring herds

ranged from 0.090 mg/L at Asotin, Washington, to 0.210 mg/L at Redbird, Idaho. Lostine range lamb survival was better than in the other nearby populations. Similarly, Hnilicka et al. (2004) reported improved recruitment in Se-supplemented bighorn sheep in Wyoming, while Dean et al. (2004) reported that Wyoming bighorn lambs in captivity showed a decrease from 0.190 to 0.120 mg/L whole-blood Se when maintained on a diet containing 0.020–0.030 mg/kg Se for 2.5 months. Their GPX activity also decreased; however, no clinical signs of deficiency were identified. Meanwhile, Rosen et al. (2009) reported an absence of benefit to Se supplementation of captive bighorn sheep. However, these captive sheep already had serum Se values of 0.180–0.450 mg/L, within the range considered adequate. Mincher et al. (2008) documented bighorn sheep leaving normal summer range to make bimonthly 26-km, 2,000-m elevation round-trip migrations, with the purpose of visiting Se-containing mineral licks on normal winter range. Also drawn by sodium chloride, this geophagia supplemented a summer range diet which was deficient in Se.

White-tailed deer

Among other North American studies, 139 white-tailed deer in southern Florida had a mean liver Se concentration of 0.169 mg/kg (ww), with a range of 0.035–1070 mg/kg (ww) over 4 years of sampling. Thirteen percent of these deer were considered critically deficient and another 55 % were marginal (McDowell et al. 1995). The wide range in individual values is not uncommon, and the authors commented that “some deer either live in pockets of habitat that supply substantially more selenium...or they may exhibit different feeding behavior.” As often reported, kidney Se levels were higher than for liver, but not correlated to liver Se, and liver is thought to respond more quickly to dietary changes in Se (Oh et al. 1976). When we plotted the mean serum Se data reported by McDowell et al. (1995) vs. their mean liver concentrations from seven deer populations, a linear correlation with $r^2=0.77$ was obtained. This suggests that both blood and liver Se are better indicators than kidney for assessing animal status.

Ullrey et al. (1981) reported that muscle Se concentrations with a mean value of 0.040 mg/kg (ww) and a range of 0.013–0.123 mg/kg (ww) were considered deficient in 92 % of Michigan white-tailed deer as compared to domestic animals that were demonstrably deficient. Comparing several ungulate species in Washington, Hein et al. (1994) found that Washington bighorn sheep, mule deer, and some elk populations were marginal in whole-blood Se, while moose were reported to be severely deficient at 0.015 mg/L; however, the moose sample size was very small at $n=2$.

Black-tailed deer

Flueck (1991) found a linear relationship ($r^2=0.91$) between whole-blood Se levels and GPX activity in black-tailed deer (*Odocoileus hemionus columbianus*) in California. Selenium levels in unsupplemented wild deer ranged from 0.009 to 0.119 mg/L, while deer supplemented with oral boluses had levels ranging from 0.020 to 0.307 mg/L Se in whole blood. It was also reported that supplementing wild black-tailed deer with initial whole-blood Se concentrations below 0.050–0.100 mg/L increased fawn survival over two-fold (Flueck et al. 1989; Flueck 1994). In continued California work, Oliver et al. (1990) sampled 1,695 mule deer from 15 geographically distinct herds for whole-blood Se. They reported that one third of these groups had median blood Se levels <0.05 mg/L and that individual deer were found to have a concentration less than the detection limit of 0.01 mg/L. Migratory deer, which utilized high-elevation range during summer, had lower overall levels than resident deer. Dierenfeld and Jessup (1990) also reported lower blood Se for non-migratory deer, although their vitamin E levels were higher.

In contrast to Flueck (1989, 1994), Brady et al. (1978) reported that supplementation of white-tailed deer with a diet containing 0.200 mg/kg Se, which had been previously subsisting on a usual diet containing only 0.040 mg/kg Se, did not improve juvenile mortality rates, although vitamin E supplementation did. However, serum Se levels at the onset of the experiment were in the range 0.110–0.120 mg/L Se, which may not be deficient, and liver values were 0.240 mg/kg (ww), higher than in many other deer populations.

Impaired reproduction in moose, elk, and black-tailed deer

In a study of poor neonatal survival and adult mortality of Alaskan moose, particularly females were found deficient in Se (O'Hara et al. 2001; Stephenson et al. 2001). O'Hara et al. (2001) considered whole-blood levels with a mean of 0.120 mg/L Se as marginal, for 22 animals sampled. Hair was also sampled in this study, with a value of 0.500 mg/kg (ww) for 23 females and 0.900 mg/kg (ww) for nine males. A minimum recommended level for cattle hair of 0.500 mg/kg (ww) was given by Puls (1994). Stephenson et al. (2001) reported mean whole-blood Se in Tanana Flats moose of 0.120 mg/L, with 8 of the 20 animals sampled having <0.085 mg/L, while captive moose that displayed symptoms of WMD had whole-blood Se levels of 0.160 mg/L, but critically low levels of vitamin E. These authors concluded that neonatal moose losses due to Se/vitamin E deficiency were often unrecognized. Starkley et al. (1982) speculated that the low reproductive performance of Roosevelt elk (*Cervus elaphus roosevelti*) stemmed from Se deficiency

since domestic livestock in their range require Se supplementation. Similarly, Pine and Mansfield (1983) reported a mean whole-blood Se concentration of 0.89 mg/L with a range of 0.013–0.247 mg/L for 12 black-tailed deer in California, for a herd with poor recruitment.

American pronghorn

Selenium levels in pronghorn (*Antilocapra americana*) from a declining herd in Oregon were determined to be mostly marginal to low in Se content, with nine males in the fall of 1996 having a range of 0.06–0.22 mg/kg (ww), with a mean of 0.11 mg/kg (ww) in the liver, and does in the spring of 1997 having a range of 0.10–0.15 mg/kg (ww) and a mean of 0.13 mg/kg (ww) (Dunbar et al. 1999). These animals also showed no signs of clinical deficiency, which the authors attributed to adequate spring serum levels of vitamin E in the does. For comparison, Raisbeck et al. (1996) reported that four captive pronghorns maintained on feed containing 0.300 mg/kg Se had mean concentrations of 0.50 mg/kg (ww) in the liver, 0.67 mg/kg (ww) in the kidney, and 0.21 mg/kg (ww) in skeletal muscle. In central Idaho, pronghorn Se levels in a struggling herd were compared to levels in a healthy Montana herd. Liver Se in Idaho averaged 0.13 ± 0.04 mg/kg (ww), and a minimum of ~20 % of neonate fawns showed evidence of “weak fawn syndrome” (Bodie and O’Gara 1980; Stoszek et al. 1980). Only 45 km to the east in Montana, pronghorn fawns had considerably higher survival rates, and liver Se averaged 0.30 ± 0.05 mg/kg (ww).

Patagonian huemul

In South America, the 20-year general lack of recovery of Patagonian huemul deer (*Hippocamelus bisulcus*) was hypothesized to be due to Se and iodine deficiencies based on low antler quality compared to the past, a high prevalence of osteopathy among adults, low recruitment rates, and overt Se deficiency in neighboring Chile (Flueck and Smith-Flueck 2011b). Among young adult Patagonian huemul deer, a conservative prevalence of osteopathy of 52 %, with a specific physiognomy of chronic alveolar osteomyelitis and osteoarthritis, suggested that Se–iodine deficiency was a prime etiological factor (Flueck and Smith-Flueck 2008). Se deficiency in that region is likely more prevalent in high-altitude refugia occupied by remnant populations of endangered huemul. Importantly, the inaccessibility of most traditional winter ranges and valley bottoms, elimination of migratory traditions, and concomitant elimination of source populations were suggested to contribute to current poor huemul recruitment.

African elephants

Africa provides another example of probable Se and iodine deficiency induced by habitat loss (Milewski 2002). Knysna elephants (*Loxodonta africana*) living near Cape Town were previously able to balance their nutrition by foraging over a large geographic range. However, their confinement to forests and fynbos seems to have prevented them from acquiring the micronutrients required for pregnancy and lactation. Seaweed cast up after storms originally provided the necessary iodine and Se, but Knysna elephants no longer have access to the shores. Analyzing large mineral licks used by herbivores in Tanzania, Mills and Milewski (2007) found Se concentrations to be much higher than in topsoils and suggested that animals may use the taste of sodium chloride as a clue to such zones where they are likely to find greater quantities of micronutrients, including Se. This finding is in agreement with that for bighorn sheep discussed above (Mincher et al. 2008).

Selenium deficiency in captive animals, capture myopathy, and other clinical cases

Selenium deficiency has frequently been reported among captive wildlife populations. With the advent of deer farming, Se-responsive unthriftiness in red deer and mortality rates in fallow deer (*Dama dama*) have been reported (Van Reenen 1980; Knox et al. 1987; Von Kerckerinck zur Borg 1987). Grace and Wilson (2002) reported that young red deer with extremely low liver Se concentrations of 0.002–0.009 mg/kg (ww) exhibited WMD and that there was a linear relationship between liver and blood Se concentrations ($r^2=0.86$). A higher incidence of post-capture myopathy occurred in New Zealand red deer caught in Se-deficient areas, and WMD as well as Se-responsive symptoms such as ill thrift were observed in adult deer and fawns (Van Reenen 1980). Some reports have described overt symptoms of WMD in fallow deer, red deer, and Pere David’s deer (*Elaphurus davidianus*; Alexander 1986). Matzke (1986) reported the prevention of necrobacillosis in fawns with Se and vitamin E treatment. A trial in red deer showed a linear relationship between blood Se and GPX. In that study, both periodic oral dosing with Se or a single injection of barium selenate significantly elevated blood Se and GPX levels throughout the trials (Mackintosh et al. 1989). These reports are similar to those initially reported in domestic lambs and calves (Muth 1955) and deer (Hadlow 1955). White muscle disease, accompanied by decreased immune function and susceptibility to disease, was also reported for lesser kudu (*Tragelaphus imberbus*) at the Basle Zoo (Switzerland) as compared to Se/vitamin E-supplemented kudu at the Stuttgart Zoo (Germany) (Besselmann et al. 2008). However, the Se levels in these animals were not reported.

Clinical signs including WMD have been documented in juvenile and adult captive reindeer and other ruminants: adverse effects of deficiency included failure to conceive, stillbirths, neonatal deaths, low birth weights, retarded growth, and lameness (National Zoological Park 1972, 1974; Griner 1978; National Research Council 1983). Sleeman et al. (2009) suggested that Se deficiency may have contributed to the development of paratuberculosis in white-tailed deer, with all deer considered having marginal or deficient hepatic Se levels (mean=0.086±0.03 mg/kg, ww), which may also have predisposed this population to the development of a parasitism/malnutrition syndrome (Sleeman et al. 2010). Finally, Yoshioka et al. (2000) reported hepatic lesions and cardiomyopathy similar to the human Se deficiency Keshan disease in Se-deficient farmed Sika deer (*Cervus nippon*). Of 25 Sika deer sampled, 18 had serum Se concentration less than the detection limit of 0.025 mg/L.

As seen from the foregoing discussion and in Table 1, many sampled wild populations have deficient or even seriously deficient Se status by comparison to livestock. However, overt symptoms of deficiency have only been occasionally described, possibly due to the difficulties of monitoring wild animals. While wildlife may have lower physiological requirements than livestock, this has not been conclusively demonstrated. Subclinical deficiencies in wild populations are especially difficult to recognize and may be common. Establishing a reference range, particularly regarding subclinical situations, requires production response trials which would thus also include all factors interacting in the absolute mineral requirement. In the next section, the factors that affect the amount and bioavailability of Se in the natural environment, and thus the amount in forage plants used by wildlife, are examined.

Selenium in the environment

Selenium as a component of habitat

Selenium can exist in four species, each of which has unique chemical behavior. As a chemical analog of sulfur, the reduced species selenide is often found as a contaminant of sulfide ores, such as pyrite or galena. These selenides ($\text{Se}^{2-}/\text{HSe}^-$) are non-bioavailable forms of the element found in parent rocks. Oxidation of selenides by exposure to air creates higher oxidation states and increases the bioavailability of the element. Elemental selenium (Se^0) is first produced (Thompson et al. 1956), and continued oxidation results in selenite ($\text{HSeO}_3^-/\text{SeO}_3^{2-}$ or Se^{IV}) and, eventually, selenate (SeO_4^{2-} or Se^{VI} ; Geering et al. 1968; Lakin 1972; Elrashidi et al. 1987). The presence of certain minerals or anaerobic bacteria may reduce and sorb Se (Maiers et al.

1988; Oremland et al. 1989, 1994; Myneni et al. 1997; Refait et al. 2000). However, microbial oxidizers are also known (Sarathchandra and Watkinson 1981), and a variety of mechanisms compete to establish the predominant species in an environmental setting. Available selenate and selenite taken up by plants provide the traces needed by foraging wildlife as an essential nutrient.

Although natural systems are seldom at equilibrium, the species of Se in soil will tend toward the predicted species in Fig. 2 with time (Geering et al. 1968). The regions in Fig. 2 were calculated based on thermodynamic considerations that have been confirmed by field measurements (Kubota and Cary 1982; van Dorst and Peterson 1984; Masscheleyn et al. 1990; Mincher et al. 2007). Figure 2 shows that oxidizing (dry) alkaline soil favors the available selenate and selenite species, while reducing (wet) acidic soil favors unavailable elemental Se and selenides. Low redox potentials occur in soil inundated with stagnant water, resulting in oxygen depletion and Se reduction (Yang et al. 2006; Mincher et al. 2007). For example, Gil et al. (2004) reported that low forage and deficient bovine serum Se

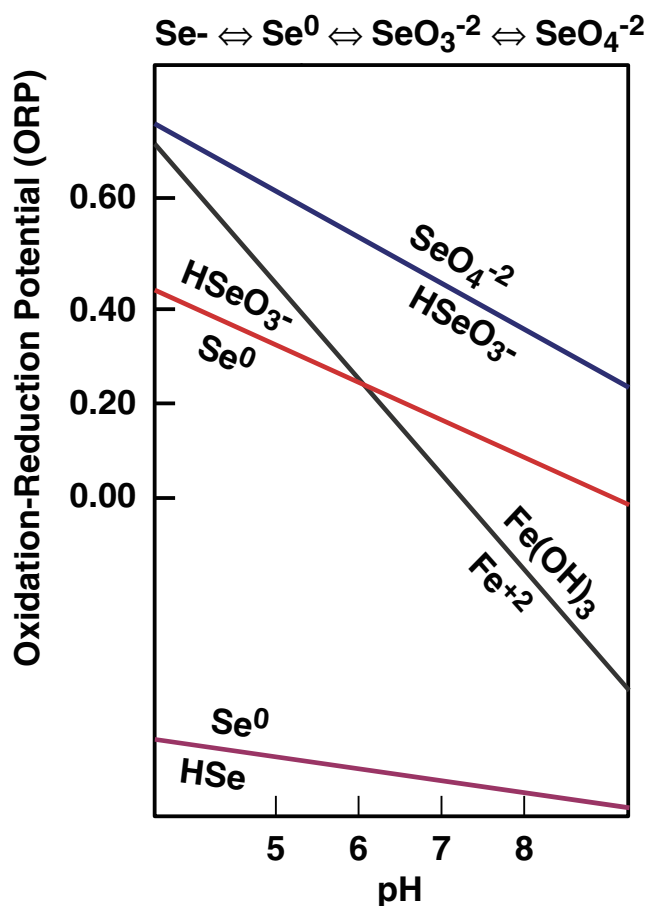


Fig. 2 The equilibrium forms of selenium to be expected in soil at various conditions of pH and redox potential. Selenide (HSe^-) and elemental Se (Se^0) are bio-unavailable, while selenite (HSeO_3^-) and selenate (SeO_4^{2-}) are bioavailable. Adapted from Geering et al. (1968)

concentrations occurred in flooded Argentina Pampas regions even though they had high soil Se.

The incorporation of selenite and selenate into plant tissues is inadvertent and occurs due to plant metabolic mechanisms designed to accumulate sulfur (Bell et al. 1992; White et al. 2004, 2007; Sors et al. 2005). The application of sulfur fertilizer actually decreases the uptake of Se by dilution (Allaway 1970; Hopper and Parker 1999) because sulfate (SO_4^{2-}) competes with selenate (SeO_4^{2-}) uptake by plants (Dhillon and Dhillon 2000; White et al. 2004; Sors et al. 2005; Mackowiak and Amacher 2008). Sulfur fertilization of soils has even led to the occurrence of Se deficiency disease in livestock (Schubert et al. 1961; Allaway 1970).

Selenate remains in the inorganic form in roots, shoots, and leaves, while selenite is the species readily transformed into the amino acids selenocysteine and selenomethionine (Brown and Shrift 1981). A fraction of organoselenium compounds is also volatilized from plant roots (Zieve and Peterson 1984; Zayed et al. 1998). This is lost from the soil. The form of Se, rather than the total concentration in soil, determines the amount of uptake by plants and, thus, the availability to foraging wildlife.

A selenium cycle in nature

Following the discovery of microbial Se respiration and its importance as a trace nutrient in animals, the existence of a natural biological Se cycle was proposed by Shrift (1964). A modern view of the Se cycle includes inorganic processes and may be termed the biogeochemical Se cycle (Mosher and Duce 1987). In this cycle, shown in Fig. 3, the weathering of rock produces the soluble forms of Se that are incorporated into higher plants as selenate and amino acids. Biologically produced volatile forms such as dimethylselenide are lost as gas (Fleming and Alexander 1972; Barks and Fleming 1974; Chao et al. 1976; Doran and Alexander 1976; Reamer and Zoller 1980; Zieve and Peterson 1984; Karlson and Frankenberger 1989; Zayed et al. 1998; de Souza et al. 1999; Zhang and Frankenberger 2000). In fact, the abundance of Se in coastal locations is due to the marine biological production of gaseous Se followed by atmospheric deposition (Duce et al. 1975; Lag and Steinnes 1978; Steinnes et al. 1992; Fernandez-Martínez and Charlet 2009). Mosher and Duce (1987) estimated values from major anthropogenic and natural sources including volcanoes, crustal weathering, and sea spray, reporting a total atmospheric Se flux of $(13\text{--}19)\times 10^9$ g/year, with 60 % of this thought to be of natural origin. This gaseous Se is eventually oxidized and adsorbed to aerosols, and the resulting particulate forms later deposited on the Earth's surface (Atkinson et al. 1990). Atmospheric deposition may then be

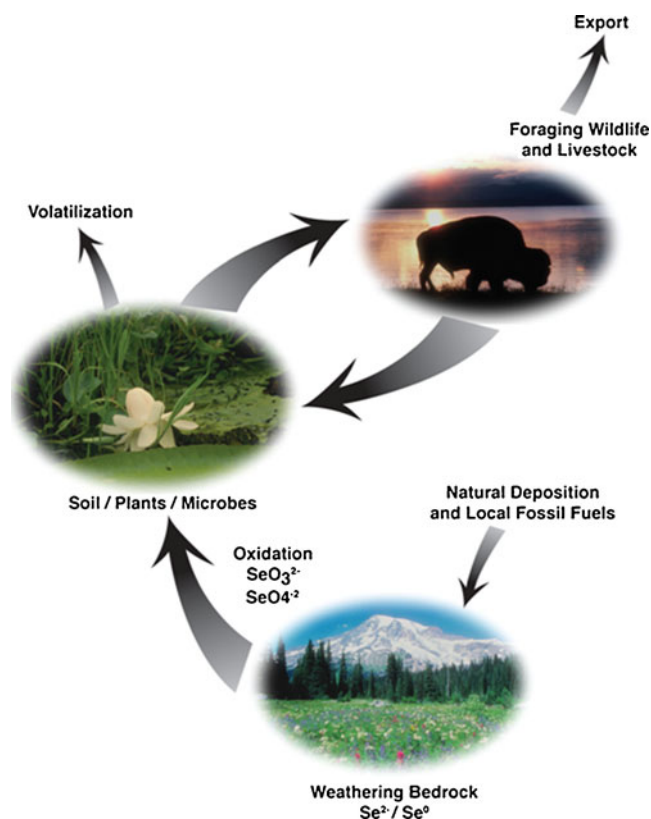


Fig. 3 Simplified view of the natural cycling of Se in the environment. The weathering of rock produces forms of the element that are taken up by plants and/or volatilized. Foraging wildlife consume Se in plants. The amount available for uptake depends on many environmental factors, discussed in the text

the most important source of Se in deficient areas (Haygarth et al. 1991, 1993a).

Loss of Se may result from plant cropping by foraging wildlife, accompanied by non-random spatial mortality patterns. For alpine species such as bighorn sheep, lambing usually occurs at high elevation with the young animals being in the nutrient accumulation stage of growth. Migration to low-elevation range later in the year with subsequent winter-related mortality results in the export of Se and other minerals from the summer range. Haygarth et al. (1991) calculated that high stocking rates of domestic lambs followed by removal from pasture represented significant losses of Se. Flueck (2009) provided an analogous example of local depletion in the element phosphorous on summer range due to high winter range mortality rates. Finally, the forms of Se excreted by animals are generally unavailable for plant uptake (Butler and Peterson 1963; Peterson and Spedding 1963; Doran and Alexander 1976; Olson et al. 1976; Joblin and Pritchard 1983). Thus, while plants convert the element to more available forms, animals convert Se mainly to unavailable forms and/or export it from key habitats. Furthermore, at higher elevations, selenite and selenate

may be lost through leaching by rainfall with subsequent transport to lower elevation. There, it often becomes concentrated in flats and flood plains (Webb and Atkinson 1965; Carter et al. 1970; Sivertsen 2004; Steinhöfel et al. 2004). An extreme example of the concentration of Se by leaching is provided by the waterfowl poisoning experienced at Kesterson Reservoir, in California, USA (Presser and Ohlendorf 1987), related to farm runoff.

Anthropogenic effects on the selenium cycle

The combustion of fossil fuels is a source of atmospheric Se of the same order of magnitude as biogenic sources (Andren et al. 1975; Mosher and Duce 1987). Archived soil and vegetation from southeast England shows increasing Se concentrations in the first half of the twentieth century, followed by declining concentrations since the passage of the clean air legislation (Haygarth et al. 1993b). Thus, industrialization seems to have increased, at least temporarily, atmospheric Se deposition in some areas. However, for remote areas, which often contain the last remaining wildlife habitat, the situation is different. Measurements of the sulfur and Se contents of both Greenland and Antarctic ice have shown that their sulfur content has increased since industrialization, while Se has not (Weiss et al. 1971). Similarly, the influence of continental sources on sulfur concentrations in the northern Pacific is greater than for Se (Mosher et al. 1987). Unlike biogenic Se, anthropogenic Se is not transported to remote locations because combustion-produced SeO_2 is readily reduced to unavailable elemental Se and deposited locally. Therefore, while total Se emissions to the environment have increased, the net result is a Se dilution effect due to competition for plant uptake by increased levels of sulfur.

To this may be added the very effective sequestration of Se by heavy metals such as cadmium, mercury, or lead (Allaway et al. 1967; Combs and Combs 1986; Frost 1987). These metals are also released continuously to the environment by fossil fuel combustion. Acid precipitation was suggested to liberate heavy metals including mercury and cadmium in Sweden, thus reducing Se bioavailability to wildlife (Borg 1987). Wild bison in Canada were also found to have deficient Se levels accompanied by elevated cadmium and mercury as compared to farmed bison (Macneil et al. 1990). Continuing declines of bighorn sheep in the Rocky Mountains have also been suggested to partially stem from anthropogenic biochemical changes in high-elevation mountains resulting in Se deficiency (Williams et al. 2002; Hnilicka et al. 2004).

Thus, the bioavailable Se concentration across the globe may actually be decreasing (Frost 1987; Ermakova and Jovanovic 2010). Fossil fuel combustion is also acidifying the general environment through the precipitation of acidic

sulfate and nitrate on the landscape. Acidity favors the reduction of Se to the reduced, biologically unavailable forms, and many authors have reported decreased Se concentrations in plants grown on acid-amended soils (Geering et al. 1968; Goldberg and Glaubig 1988; Ambe et al. 1992; Tachi et al. 1998; Wang et al. 2000). The soil acidification process may be somewhat mitigated by natural soil buffering capacity (James and Riha 1986; Clayton et al. 1991). However, the fact that these capacities can be eventually exceeded was revealed by Blake et al. (1999), who reported that soil pH at the Rothamsted Experimental Station, UK, dropped from 6.2 to 3.8 in a woodland plot and from 5.2 to 4.2 on a grassland plot between 1883 and 1999. As noted above, soil acidification also increases the solubility of the heavy metals that tie up Se as insoluble selenides. These possible implications of emissions causing acidification, a declining Se cycle, and increased exposure to heavy metals for wild ruminants were described by Flueck (1990) and Flueck and Smith-Flueck (1990).

Lastly, increasing rates of anthropogenic biomass export due to agricultural production are also disturbing the natural Se cycle. In the natural cycle, the majority of the available Se resides in biomass (Gissel-Nielsen and Hamdy 1977; Swaine 1978; Frost 1987) in plants and litter fall (Tiedemann et al. 2000; Jobbagy and Jackson 2004). Selenium accumulates in the upper soil layers and mainly in organic material. However, biomass harvesting and export can remove Se and other nutrients in a short time, also leading to soil acidification which renders Se less bioavailable (Gissel-Nielsen and Bisbjerg 1970; Heylar et al. 1990; Gustafsson et al. 1993; Flueck 1994; Jobbagy and Jackson 2004). Extensive livestock production currently occurs over 45 million square kilometers of rangeland globally. This Se export also includes the increased biomass burning during the last several centuries (Niklasson and Granstrom 2000).

Implications for management and conservation

As wildlife habitat is encroached upon for multiple anthropogenic uses, wild animal populations lose access to important natural resources such as low-elevation range and mineral licks. This may result in loss of access to important trace minerals, including Se. If a population is suffering from severe Se deficiency, WMD would occur in deficient young at 3–6 weeks, resulting in muscle stiffness and respiratory distress. Affected muscle has visible striations upon necropsy. The malady may result in sudden death, which obviously reduces the recruitment rates or spontaneous population recovery. In adults, general unthriftiness, late weaning, and periodontal disease are common expressions. Symptoms of the deficiency may also manifest as high rates of capture myopathy or only appear after other stressful

situations, such as a severe winter. However, chronic, sub-clinical deficiency may depress population performance and be unrecognized by the wildlife manager. The following paragraphs are a guide to help managers understand under what conditions Se deficiency in wild ungulate populations is possible or even likely.

Rock of volcanic origin is typically low in Se (Carter et al. 1970; Fernandez-Martínez and Charlet 2009) because the element is volatile at high temperatures. Soils derived from granite or basalt can be expected to be well below the world average of ~400 ppb total Se (Kabata-Pendias and Pendias 1984), and plants growing over granitic bedrock will likely contain low concentrations. In contrast, plants in areas with sedimentary bedrock will contain higher amounts of Se (Dhillon and Dhillon 2000; Mincher et al. 2007). Sites at high elevation also experience losses due to leaching. For these reasons, upland range soils are often deficient (Carter et al. 1970; Ren et al. 1987; Iyengar and Gopal-Ayengar 1988; Haygarth et al. 1991; Wang and Gao 2001). If deficiency is suspected, analysis of soil may be warranted; however, as mentioned above, forage Se concentrations are related to the soil species of Se rather than its total concentration. Analyses that identify Se species rather than total Se rely on specialized and expensive techniques that are not often readily available (Pickering et al. 1995). Fortunately, it is possible to infer the likely species based on easily measured soil parameters such as redox potential (E_h , a measure of the oxidizing power of the soil) and pH (Geering et al. 1968). Both are measured with inexpensive probes amenable to field conditions. The combination of these parameters may be used to determine which Se species are most probable at a given site. Thus, risk factors for Se deficiency include high-elevation sites, granitic or basaltic geology, acidic soils, and high precipitation and/or stagnant, water-logged soils, especially at inland locations.

Should the measured soil E_h and pH suggest that soil Se is in an unavailable form, it may be desirable to sample vegetation. The total concentration of Se in plants is readily measured by many laboratories, although some provide inadequate minimum detection limits. Plant species that are actually used as forage should be sampled, and the same species should be used in repetitive sampling campaigns. Different species may accumulate Se at different rates. Some plants bioaccumulate Se to high concentrations, but are seldom used as forage. The best-known example is *Astragalus bisulcatus* which may contain Se in leaves and seeds at thousands of milligrams per kilogram (Rosenfeld and Beath 1964; Ulrich and Shrift 1968; Sors et al. 2005). Selenium accumulators have a characteristic odor produced by dimethyldiselenide. Foraging wildlife and/or livestock may actually be poisoned by eating these species.

For livestock, forage values of <0.1 ppm on a dry weight basis are considered deficient (Allaway and

Hodgson 1964). It is commonly assumed that wildlife requirements would be lower, although minimum requirements are unknown and may vary between species. The literature reviewed here suggests that forage species concentrations <0.05 ppm may indicate a risk factor. As we have already shown, a wide range of Se values may exist in individual animals, probably at least in part indicating that they feed on various species of plants or at various locations.

If some risk factors above are indicated, then sampling of the animal population itself may be warranted. Selenium in liver is the commonly evaluated metric, and as already discussed, blood and hair Se levels have sometimes been shown to be correlated with liver Se. Muscle tissue has also been used. In either case, individual animals need to be sacrificed, and this may not be practical for un hunted or endangered populations. A tissue sample of adequate size should be determined after consultation with the selected laboratory to ensure that enough material is collected to give adequate detection limits and should be kept cool, preferably frozen, and protected from cross-contamination. The sampling of hair could be conducted without the need to sacrifice animals; however, to our knowledge, a rigorous study showing the relationship between hair and liver Se has not yet been done.

Furthermore, it is difficult to determine what levels constitute deficiency. Based on the literature reviewed here, we have provided recommendations in Table 1. Should the conclusion be made that a population is performing poorly due to Se deficiency, the wildlife manager has little choice but to provide supplementation where that is possible. Mineral salt blocks with Se supplements have long been used in domestic stock nutrition and have been used to improve recruitment in wild populations. Care in the placement of blocks should be used to mitigate the possibility that unnatural congregations of supplemented animals might occur, which could introduce other management problems such as predation or disease. If deficiency was produced by loss of access to specific habitat components, it may be preferable to restore that access rather than to provide supplements. Unfortunately, habitat restoration is not always a practical alternative.

Packard's (1946) classical study on bighorn sheep elucidated the reasons for poor population performance by considering pre-Columbian distribution and migratory behavior, market hunting by settlers, extirpations of populations at low elevations, arrival of livestock, and characteristics of the high-elevation habitat where sheep still remained. He found that sheep previously used winter ranges with sedimentary bedrock and mineral licks, whereas current herds were forced to remain at high elevations. Anthropogenically caused range contraction of ungulates are heavily skewed toward loss of low-elevation ranges (Channell and Lomolino 2000; Laliberte and Ripple 2004).

Thus, loss of traditional seasonal movements has resulted in many sedentary wildlife populations and associated seasonal deficiencies in forage quality. This has been considered an important cause of declining herds and one of the largest problems challenging long-term persistence (Risenhoover et al. 1988). In situations where residual wild populations fail to respond to management or protection, the possibility that subclinical deficiency of Se or other trace elements is a factor should be considered.

Conclusions

The decline of wild ungulate populations is a worldwide recurrent problem, and the multifactorial nature of ecology, combined with the difficulties of studying elusive wild animals, tends to reveal only proximate factors like clinical disease or predation events. Underlying causes of population declines that may be more important, such as mineral and forage nutrition, are sometimes overlooked. Micronutrient deficiencies, including for Se, are especially challenging to understand because they result in a large gradient of possible effects without providing a clear and specific signature when subclinical. However, during this phase, much damage may be occurring because a slow decline in remnant populations may result in local extinctions which are difficult to document or counter. In such cases, expensive investments in habitat, restriction of hunting regulations, or predator control will probably fail to recover the affected population. The literature reviewed here suggests that subclinical nutritional Se deficiency may be common, especially at alpine locations.

From a mineral nutritional view, the most productive sites for wild ruminant herbivores are valley floors, riparian areas, flood plains, and sedimentary beds containing deeper soils and natural mineral licks. As has been shown, Se is leached to lower elevations by natural processes and has inherently higher concentrations in sedimentary soils. In addition, milder climate and other factors result in food intake of higher mineral density and low oxidative stress on animals. When access to such nutrient hot spots is no longer possible, or vertically transmitted migration behavior to get there has been eliminated through anthropogenic forces, the remaining animals are forced to live in a nutritionally marginal habitat. When a population in such circumstances fails to respond to management designed to increase its numbers, mineral nutrition deficiencies particularly of Se should be considered by the wildlife manager.

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