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EFFECT OF TRACE ELEMENTS ON POPULATION DYNAMICS: SELENIUM DEFICIENCY IN FREE-RANGING BLACK-TAILED DEER[1]

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Abstract. The effect of the trace element selenium on black-tailed deer (*Odocoileus hemionus columbianus*) was studied in northern California. The role of selenium was evaluated by supplementing free-ranging adult females with selenium, measuring fawn production before weaning, and comparing to unsupplemented controls. Whole blood selenium levels (mode = 24 μg/kg) of unsupplemented animals were low, and 95% of free-ranging deer had inadequate levels according to livestock standards. There were no differences in whole blood selenium levels among sexes, ages, or seasons. However, there were significant differences between spring blood samples over the years. Selenium supplements increased preweaning fawn survival from 0.32 fawns/female to 0.83 fawns/female. The assumption that free-ranging wild ruminants are not normally susceptible to trace mineral deficiencies because adaptations to deficiencies occur over geological time was not supported.

Key words: black-tailed deer; deficiency; Odocoileus hemionus columbianus; *population dynamics; reproduction; selenium; trace element.*

Introduction

Many ecologists assume that populations of native nonintroduced species are not limited by minerals (Fielder 1986). These ecologists hypothesize that native species should adapt to patterns of mineral availability by exhibiting a specific appetite or lower physiological requirement to compensate for locally low availability. Furthermore, acute deficiencies are rarely observed in wild populations, which leads to the conclusion that mineral deficiencies are not likely to limit populations. However, subacute and chronic selenium (Se) deficiencies may be more widespread than the distribution of obvious symptoms (Gardiner et al. 1962, Robbins 1983). Subclinical deficiencies can only be detected with experimental field trials that provide mineral supplement and monitor responses in production, such as growth or reproduction (Millar 1983).

Selenium is an essential trace element that is part of the enzyme glutathione peroxidase (GSH-Px) (Keen and Graham 1989). Whole blood Se levels and the bioactive GSH-Px are linearly associated in many mammals, including black-tailed deer (Flueck 1991). Although other non-Se peroxidases occur, including glutathione-S-transferase, they do not exhibit adaptive increases in activities under Se deficiency (Thomson et al. 1988).

Selenium deficiency primarily affects juveniles, resulting in increased mortality during the neonatal and preweaning period (Keen and Graham 1989). Se deficiency, including cases of nutritional muscular dystrophy in livestock from northern California, occurs when whole blood levels fall below 40 μg/kg in cattle and 50 μg/kg in sheep (Norman and Johnson 1976, Johnson et al. 1979, Norman et al. 1981, Williams et al. 1982, Jones et al. 1987, Nelson and Miller 1987). Most of northern California has soils indigenously low in Se due to the volcanic origin of the bedrock (Kubota et al. 1967). Locally grown feed in Shasta county contained only 10 μg/kg of Se (Johnson et al. 1979).

Selenium supplementation through metal boluses will result in an increase of GSH-Px activity for many months to several years (Handreck and Godwin 1970). Se supplemented before parturition is effectively transferred in utero and results in females and offspring having similar whole blood Se levels at parturition (Finkelstein et al. 1981, Hidiroglou et al. 1987). Additionally, Se administered to mothers is effectively transferred to the young through milk (Jenkins and Hidiroglou 1971, Fuss and Godwin 1975). This transfer appears to be most critical for colostrum, but a significant treatment effect on milk can last for at least 6 mo (Hidiroglou et al. 1987).

The importance of Se to several wild herbivores, including cervids, has been recognized previously (Brady et al. 1978, Robbins et al. 1985, Knox et al. 1987, Mackintosh et al. 1989). Based on whole blood Se levels of 1695 deer, Se deficiency (by livestock standards) appeared to exist in most deer herds and regions of California (Ros-McGauran 1989, Oliver et al. 1990). I evaluated the effect of Se supplementation on repro-

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duction by a population of black-tailed deer (*Odocoileus hemionus columbianus*) in northern California.

STUDY AREA

The summer range is represented by Latour State Forest (121°40′ N, 40°40′ E) in eastern Shasta County, California, USA. The elevations of summer range are between 1400 and 2600 m. Basic geological structures are of volcanic origin, partially overlain at some higher elevations by younger glacial deposits (Gladish and Mallory 1964). The timberline varies between 2500 and 2800 m. Free water is plentiful. The montane vegetation is dominated by coniferous trees and a dense shrub and ground cover with a history of intensive logging activity, sporadic wildfires, and open-range use by livestock. The treeline is dominated by lodgepole pine (*Pinus contorta* ssp. *murrayana*), followed at lower elevations by mixed conifer forests dominated by *Abies concolor, Pinus lambertiana, P. ponderosa, Calocedrus decurrens, Pseudotsuga menziesii,* and *Quercus kelloggii* (Major and Taylor 1988, Rundel et al. 1988). Ponderosa pine forest is found below the mixed conifer forest as a narrow belt through an elevation range of 500 m. Important understory shrubs include *Arctostaphylos viscida, A. manzanita,* and *Rhus divertiloba.* This pine forest often forms an ecotone between foothill woodland and mixed conifer forest.

The winter range incorporates the western foothills from ≈900 to 150 m elevation and the eastern portion of the Redding Basin. From the easterly crest, the land slopes to the west through a series of dissected tablelands of basaltic sheets, mudflows, and ash, capped by volcanic cones, and ends in the upper Sacramento Valley, a flat area typified by the Millville and Swede Creeks Plains. The vegetation is characteristic of an oak woodland–savanna habitat with a close floristic tie to chaparral, widely dispersed oaks with introduced annual grasses and legumes as predominant ground cover (Griffin 1988). Most of the oak woodland has been occupied by cattle ranches for over a century. Land use is characterized by livestock grazing, frequent burning regimes, and firewood cutting.

The total deer range (summer and winter) extends ≈120 km from west to east, while the north to south extent is ≈50 km.

METHODS

The reproductive rate of randomly selected, Se-supplemented females was compared to that occurring in the nonsupplemented herd. Deer were captured during their spring migration using either people or a helicopter to drive deer toward nets. The departure of adult females from the spring staging area and subsequent traversing of the capture site occurred randomly with regard to age (Smith-Flueck et al. 1990). Also, the age structure in the sample of females captured with the aid of a helicopter (n = 27) was equivalent (P = .56) to the sample from the passive trap (n = 33). Self-selection did not appear to be a source of bias since animals of all ages and sexes were caught frequently, and no consistent pattern of capture was discernible. Thus, the selection process appeared to be random, although no deliberate attempts could be made to randomize. Females 20 mo of age or older were considered of reproductive age and were included in the trial. Age determination at trapping was based on body size, mammary gland and facial appearance, and the presence of two or three cusps on the lower fourth premolar. Ages were confirmed later based on cementum annuli analysis.

Deer were physically restrained and blood samples were collected in EDTA tubes by jugular venipuncture and frozen until analysis. In 1985–1987, two Se boluses (Permasel Sheep pellets, ICI Australia Limited, now called Copper Animal Health, Melbourne, Australia) were administered orally to each adult female. The bolus consists of elemental iron and Se (9.5 g Fe, 0.5 g Se), remains in the reticulum or rumen, and releases ≈0.5–1.3 mg of Se per day (Handreck and Godwin 1970). The animals were then marked with radio transmitters and released. Preliminary studies in 1984 showed that two Se boluses were necessary to significantly increase blood Se level. Blood samples were also collected each spring from adult males and fawns that were trapped but not assigned to the test group and each autumn from unsupplemented adult females, adult males, and fawns.

Females (n = 46, 1985–1987) from the treatment group were observed for the presence of fawns in autumn after the migration to the winter range, where visibilities often exceeded 500 m. Blood selenium levels in deficient domestic livestock rose rapidly during the 1st wk following supplementation and remained elevated for several months (Handreck and Godwin 1970, Whanger et al. 1978). Therefore, I consider the Se-supplementation in spring to have an effect during the last trimester of gestation and lasting until measurement of fawn autumn survival. Doe–fawn associations were confirmed by observing (1) a fawn nursing; (2) a fawn bedded or remaining within a few metres of the female in the absence of any other adult females; and (3) the spatial arrangement of fawns with does if moving in a group. Frequently, several observations of each doe were necessary to confirm the association. In addition, these fawn counts were corroborated by: (1) observations of the females and their fawns during the preceding summer; and (2) the lactational status of the female at necropsy.

Once the number of fawns accompanying each radiomarked female was ascertained, she was shot and bled immediately by cardiocentesis. The rumen–reticulum was opened to confirm the presence of the Se boluses.

The numbers of adult females counted in the herd in autumn included yearlings, whereas the experimental groups did not contain this age class. To adjust for this, herd composition data from the time of the spring

TABLE 1. Number of fawns and adult females (adjusted) in the selenium-supplemented groups, and the number of fawns and adult females in the unsupplemented herd, 1985 to 1987.

	Selenium supplemented			Not supplemented		
Year	Does	Fawns	F/D	Does	Fawns	F/D
1985	12	10	0.83	379	150	0.40
1986	20	18	0.90	441	149	0.34
1987	14	10	0.71	357	75	0.21
Total	46	38	0.83	1177	374	0.32

captures were used to estimate the number of yearlings present the following autumn. Fifty percent of fawns born the previous year and counted in spring were assumed to be females, which would be counted as female yearlings in the following autumn, and which were thus added proportionally to the number of experimental females (Table 1). Due to the low spring fawn counts, however, the additional number of yearlings did not influence the fit of the log-linear model ($P = .74$ vs. $P = .75$).

Fawn-to-doe ratios in autumn for the rest of the herd were recorded concurrently with observations of the Se-supplemented females. Counts were obtained from driving roads in different portions of the winter range and from observations while hiking in areas used by radio-marked females. All animals close enough to be classified with 20× spotting scopes or 10× binoculars were included in these counts. The probability of repeated counts was small, since the home ranges of experimental females were well separated. The open landscape was responsible for fawns remaining in close proximity to their mothers, and fawns were clearly smaller than yearlings due to growth rates, which on average were <50% of published growth rates of free-ranging fawns (Brown 1961, W. T. Flueck, *unpublished data*). Furthermore, detailed daily herd composition counts were also available for periods after spring migration until after autumn migration 1984–1987 for comparison (W. T. Flueck, *unpublished data*).

Whole blood Se was determined with a modified fluorometric procedure by the Veterinary Extension Unit of the University of California, Davis (Flueck 1991). The lowest detectable level for the procedure was 5 μg/kg. During a global interlaboratory study of blood Se determinations, results from this laboratory coincided with the mean of the 51 participating laboratories (Koh 1987).

RESULTS

Whole blood Se levels

The mean whole blood Se concentration of all unsupplemented deer, 1984–1987 ($n = 135$), was 37 ± 30 μg/kg (mean ± 1 SD) (Fig. 1). There were no differences attributable to age, sex, or season, but there was significant variation among spring samples of unsupplemented animals in different years ($P = .016$, one-way ANOVA). The averages in spring of 1984 to 1987 were 43 ± 30, 44 ± 30, 26 ± 20, and 34 ± 20 μg/kg, respectively ($n = 101$). According to livestock standards, 80% of the deer sampled in spring were deficient (blood Se levels below 50 μg/kg), and an additional 15% had low–marginal levels (below 75 μg/kg; Koller et al. 1983). Post-treatment (autumn) Se blood levels in Se-supplemented females ($n = 42$) averaged 121 ± 90 μg/kg, which was 3.1 times higher than pre-treatment levels ($P < .0001$).

Effect of Se supplementation on the reproductive rate

Selenium supplementation had a significant effect on fawn survival ($P < .0001$, multiway contingency analysis for higher order interactions; Schwabe et al. 1977, Kleinbaum et al. 1982). In contrast, the interaction of

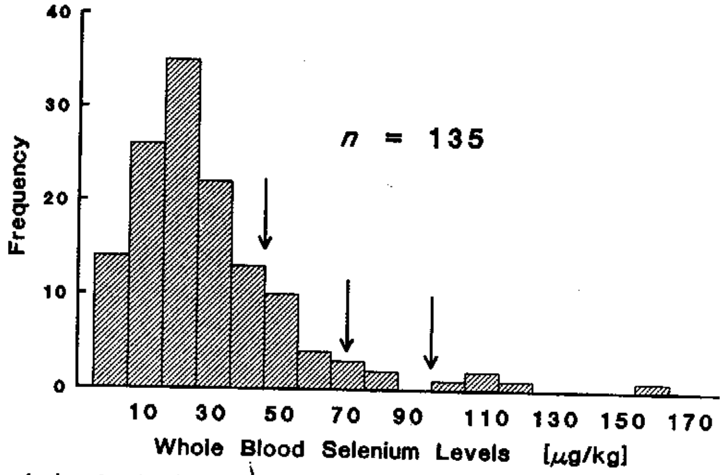

FIG. 1. Whole blood selenium levels of free-ranging black-tailed deer ($n = 135$) in California, 1984–1987. Arrows show deficient (<50 μg/kg), low–marginal (50–75 μg/kg), and marginal levels (76–100 μg/kg) for sheep (Wheatley and Beck 1988).

Se, deer, and year did not improve the model ($P = .7$), indicating that the magnitude of the Se × deer interaction was the same from year to year. Productivity due to Se supplementation was increased by 2.6 times (95% CI = 2.08–3.29 times) over unsupplemented levels and resulted in an additional 51 fawns per 100 females.

DISCUSSION

Reproduction by free-ranging black-tailed deer in Shasta County, northern California is limited by a subclinical selenium deficiency. Although total pre-weaning fawn production varied between 1985 and 1987, the effect due to Se remained constant. Contrary to Fielder's (1986) suggestion that the influence of Se deficiency on wild game production would have been present for thousands of years, there is growing evidence that anthropogenic manipulation of ecosystems can rapidly alter Se cycling and bioavailability to free-ranging herbivores (Frost 1987). Several authors have described a world-wide increase in the incidence of Se-responsive diseases in animals (Flueck and Smith-Flueck 1990).

While increased exposure to a number of substances results in an increased demand for Se (e.g., Hg [Burk et al. 1974]; Cd [Van Vleet and Boon 1981]; sulfur [Kahn et al. 1987]), there are several factors that may contribute to an apparent decline of soil Se availability to plants and animals. Plant selenium concentration or availability can be reduced by acidification of soils (Geering et al. 1968) due to acid precipitation (Fisher 1982, Mushak 1985, Frost 1987) or biomass exportation (Ridley et al. 1990). Plant fertilizers (S, N, and P) also reduce Se availability to animals (Gissel-Nielsen 1977, Millar 1983, Gupta and Watkinson 1985), a possibility also in remote areas due to aerial deposition (Ellenberg 1986). Selenium returned to the soil by ruminants is practically unavailable to plants, suggesting that intensive foraging by ruminants could reduce Se availability in time (Butler and Peterson 1963, Peterson and Spedding 1963).

I hypothesize that my study area in northern California has experienced a recent decline in bioavailability of Se through Se export and soil acidification due to biomass removal and acid precipitation (California Air Resources Board 1988, Flueck 1990). This implies that the impact of large-scale anthropogenic activities may alter Se or other trace mineral cycles in remote areas, which would reduce the effectiveness of small, isolated areas for protection of biodiversity (Flueck 1990).

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