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ECOSYSTEMS

A Geochemical Trophic Cascade in Yellowstone's Geothermal Environments

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ABSTRACT

We contrast the geochemistry of the Madison drainage, which has high concentrations of geothermal features, with the Lamar drainage of Yellowstone National Park, USA, and trace the consequences of geochemical differences through abiotic and biotic linkages in the ecosystem. Waters in the geothermal-dominated drainage contained anomalously high levels of fluoride (F) and silica (SiO_2). Soils, stream sediments, and surface waters that interact or mix with geothermal waters, in turn, had elevated F and SiO_2 concentrations compared to similar samples from the Lamar drainage. The geochemical differences were reflected in the chemistry of forage plants, with some plants from geothermally influenced areas containing four- to eightfold higher concentrations of F and SiO_2 than similar plants in the Lamar drainage. Geothermal heat reduced snowpack, and we found that elk *(Cervus elaphus)* concentrated in these refugia as snowpack increased each winter. The consequent high dietary intake of F in animals associated with the geothermal areas was confirmed by the finding that bone samples from elk living in the Madison drainage contained sixfold higher concentrations of F than samples collected from animals wintering in the Lamar drainage. High F exposure resulted in compromised dentition due to fluoride toxicosis, which was undoubtedly exacerbated by the abrasive action of silica. The consequent accelerated and aberrant tooth wear resulted in early onset of senescence, reduced life span, and an abbreviated age structure. We speculate that these altered demographics, combined with spatial heterogeneity of snowpack, will result in increased vulnerability of this large herbivore population to wolf predation and less resiliency to compensate demographically for predation.

Key words: demography; fluoridosis; food web; population dynamics; silica; senescence; snowpack; survival; toxicology; trophic interactions.

INTRODUCTION

The west central portion of Yellowstone National Park contains a 2000 km^2 volcanic caldera with 2-M- to 60-M-y-old, predominantly rhyolitic, rocks that produce relatively infertile soils. The caldera area also contains thousands of geysers, fumaroles, hot springs, and mud pots; thus, it represents one of the largest concentrations of active geothermal features in the world. In contrast, geothermal features are rare in the Lamar River drainage, in the northeastern portion of the park, where the dominant exposed rock type is andesite, providing a geochemistry for more fertile soils (Keefer 1972). Large herbivores are an important component of the Yellowstone ecosystem, and both river drainages support separate populations of elk (Singer and others

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1991). A nonmigratory elk herd, estimated at 500–800 animals, resides primarily within the volcanic caldera in the upper Madison River drainage within the west central portion of the park. This drainage includes the Firehole and Gibbon rivers, which join to form the main Madison River that then flows westward for approximately 24 km to the border of the park. The Lamar Valley in the northern portion of the park serves as a wintering ground for the large (10–16,000) migratory Northern Range elk herd, which has been the focus of numerous ecological studies (Houston 1982; Frank and McNaughton 1992; Coughenour and Singer 1996). Here we contrast the differences in these two areas of rock, stream sediment, and water chemistry, and of geothermal heat, and trace the ecological consequences of these differences through the plant–herbivore–carnivore trophic chain. Top–down effects of carnivores on similar trophic chains have recently been documented (McLaren and Peterson 1994; Post and others 1999). The results presented here demonstrate the importance of a bottom–up ecosystem structure through a unique geochemical trophic cascade.

METHODS

Sediment and Plant Collections

Samples of active stream sediment were collected between 1996 and 1999 at 91 widely dispersed sites in the Lamar River watershed and at 46 similar sites in the Madison River watershed, and multiple subsamples were composited from several localities within a 30-m radius of each collection site. The analyses for a given stream sediment sample give a good approximation of the integrated chemistry of the material eroding from all rock exposures upstream of the sample sites and thus define the chemical environment of the area. A mean value calculated for all samples for each chemical variable in a given drainage area provides an estimate of the regional concentration level. The mean values can thus be used to identify broad chemical differences between areas.

Forage plant samples ($n = 83$) were collected in late October 1997 from eight sites in the Lamar drainage and 10 sites in the Madison drainage. Collection sites were selected in nonforested valley bottoms representative of areas typically occupied by wintering elk. At each site on both winter ranges, we attempted to collect plant samples from four plant community types or microsites: dry meadow sites dominated by *Poa spp., Festuca idahoensis, Stipa richardsonii,* and *Juncus balticus;* transitional meadow sites dominated by *Deschampsia cespitosa, Poa pratensis, Phleum pratense,* and *Juncus balticus;* wet sedge meadows dominated by *Carex rostrata, C. aquatilis,* and *C. nebrascensis;* and riverbank sites within 1-m elevation of water surface dominated by *Carex spp., Poa palustris, Deschampsia cespitosa,* and *Juncus balticus.* We also sampled two additional unique plant community types associated with geothermal influences and heavily used by wintering elk on the Madison drainage: aquatic macrophytes, primarily *Myriophyllum spp., Ranunculus aquatilis,* and *Potamogeton spp.;* and spike rush (*Eleocharis rostellata*) communities. Collections were made by clipping a 10–15-cm^2 area of plant material 1 cm above the ground to simulate elk cropping. A minimum of four subsamples were collected within a 10-m radius at each site and composited.

Elk Telemetry

Field studies of the Madison drainage elk population were conducted from December 1991 through April 1998. A sample of 25–32 female elk, ranging from 1 to 15 years of age and instrumented with radio transmitters, was maintained throughout the study. The age of the animals was determined using cementum structures in the root of a canine tooth extracted at the time of capture (Hamlin and others 2000). Ground-based telemetry homing procedures were used to locate instrumented animals each winter between December and April. Order and frequency of animal location was determined using a restricted randomized design and resulted in each animal being located two to five times per week ($n = 7754$ locations). Late gestation pregnancy status of each instrumented animal was determined annually by collecting fecal pellets after observed defecations and assaying for fecal progestagens (Garrott and others 1998). During the first 2 years of the study, the activities of located animals not disturbed by the observer were recorded for 30 mins ($n = 1711$), which included recording the amount of time animals were observed foraging on various types of plant communities during 830 foraging bouts.

Geothermally influenced areas were identified using geographic information system databases developed for Yellowstone National Park and included a 50-m band along all streams and rivers draining geothermal areas to reflect plant communities exposed to geothermal waters. Snowpack-induced shifts in animal distribution were explored using regression to correlate the proportion of monthly animal locations recorded within geothermally influenced areas with mean monthly snowpack, as indexed by snow water equivalent measurements recorded daily at an automated weather station. Mandibles were collected from all adult elk carcasses located during field activities. Mandibles from adult elk that died on the Northern Range during the winters of 1995–97 were provided by the National Park Service. All collected mandibles were evaluated for clinical evidence of dental fluorosis (Shupe and others 1984). A sample of 12 mandibles from each herd were sectioned across the diastema region and assayed for fluoride (F) concentration.

Elk Demography and Population Projections

Age-specific survival and fecundity rates were calculated, with the biological year defined as May 1 through April 30. The general pattern for adult female survival and reproductive rates for large ungulates is that of consistently high rates throughout most of an animal's life span, with a pronounced period of senescence where rates progressively decline for the oldest age classes (Gaillard and others 2000). Based on these insights, two candidate age models were evaluated for both adult female survival and reproduction rates: age as a categorical effect, with categories corresponding to annual age increments (A_A), and a linear effect model (A_{LIN}).

Annual adult survival and reproduction were dichotomous variables; thus, we modeled these vital rates using a logit link and binomial error structure—that is, logistic regression, using the known-fate module in program MARK (White and Burnham 1999). We used a bias-corrected version of Akaike's Information Criterion, AICc, to rank the two models (Burnham and Anderson 1998), and 95% confidence intervals were used to evaluate the reliability of age-specific estimates. An l_x survivorship schedule was calculated from the age-specific survival rate estimates derived from the logistic regression with the resulting l_x estimates fitted to the generalized survivorship model for large mammals (Eberhardt 1985) using nonlinear least squares (SAS/STAT version 6, 4th ede, vol 2; SAS Institute, Cary, NC, USA).

The l_x values from the fitted equation were converted to age-specific survival probabilities, $s_x = l_{x+1}/l_x$. The age-specific reproductive rate estimates derived from logistic regression of the annual pregnancy data were fitted to a generalized m_x fecundity model for large mammals (Eberhardt 1985) using nonlinear least squares (SAS Institute). The resulting s_x and m_x schedules for the elk living in the Madison drainage were compared with those reported by Houston (1982) for the Northern Range elk population that winters in the Lamar drainage. Average life expectancies for both elk populations were calculated directly from the l_x schedules as described by Pianka (1994). The stable age distribution and estimated annual population rate of growth were calculated for both herds using the l_x and m_x schedules and Lotka's equation (Eberhardt 1985).

Chemical Analyses

The stream sediment samples were air-dried and sieved in a stainless steel sieve. The fraction passing through a sieve with 0.17 -mm or smaller openings was pulverized to less than 0.10-mm material prior to analysis. The samples were analyzed for F by a standard ion-selective electrode method. The samples were first fused with NaOH, with the resulting material dissolved in dilute HNO_3. The fluoride concentration was measured in this solution using a fluoride ion-selective electrode (Lachat Quik Chem Flow Injection Analyzer Lachat Instruments, 6645 West Mill Road, Milwaukee, WI 53218).

Dried plant and bone samples were crushed via mortar and pestle and ground in a Spex mill. Total F concentration of plant samples was determined by oxygen bomb combustion/ion-selective electrode method (ASTM 1979); total silica (SiO_2) concentration was determined by wet acid digestion and ICP-AES (Perkin-Elmer Optima 3000 Perkin-Elmer Analytical Instruments, 710 Bridgeport, Shelton, CT 06484). Bone samples were analyzed for total F by the sodium hydroxide fusion/ion-selective electrode method (Orion Research Model 96-09 Thermo-Orion, 500 Cummings Center, Beverly, MA 01915).

RESULT AND DISCUSSION

The chemistry of near-surface geothermal waters includes elements derived from magmatic sources at depth and elements leached from the rocks by circulating groundwater that mixes with the magmatic waters. The patterns of elemental enrichment in Yellowstone's geothermal waters vary from locale to locale; but F and SiO_2 are enriched in virtually all of the geothermal waters of the Madison River drainage (Figure 1). These geothermal waters drain into the major streams of the area, including the Firehole, Gibbon, and Madison rivers, and they enrich these streams in many elements, including F and SiO_2, as compared to concentrations found in surface waters within the Lamar River drainage (Thompson and others 1975; Miller and others 1997; Tuck and others 1997)(Figure 1). These differences in stream water chemistry are due partly to characteristics of the two dominant rock types in the park.

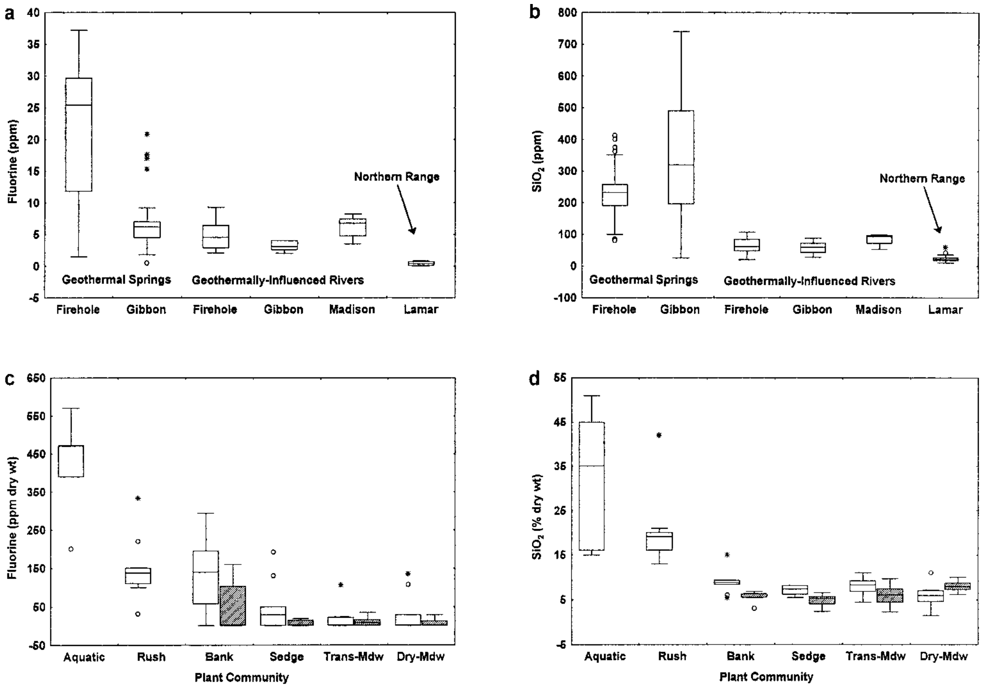

Figure 1. Contrast between water and plant chemistry for two major drainages of Yellowstone National Park, USA. The upper Madison River drainage is within a volcanic caldera and contains thousands of geothermal features, whereas the Lamar River drainage is northeast of the caldera and has few geothermal features. (**a**, **b**) Fluorine and silica (SiO_2) concentrations in various sources of surface waters sampled in the two areas ($n = 200$) (Thompson and others 1975; Miller and others 1997; Tuck and others 1997). (**c**, **d**) Fluorine and silica (SiO_2) concentrations in elk forage plants ($n = 83$) sampled along a gradient from plant communities growing in close association to surface waters to xeric communities more distant from surface waters. Open boxes represent samples collected from the upper Madison River drainage; hatched boxes represent samples collected from the Lamar River drainage. Winter aquatic macrophyte and spike rush plant communities were not present in the Lamar drainage. Boxes represent the 25–75% range; horizontal bars depict the median; whiskers describe the data range excluding outliers; open circles represent outliers; asterisks represent extreme outliers.

Rock and stream sediment samples also have contrasting chemistries that depend on the rock type dominant in a given area. Representative mean values from the literature for rhyolite are 790 ppm F, 75% SiO_2; for andesite, the mean values are 210 ppm F, 59% SiO_2 (Taylor 1969; Fleischer and Robinson 1963). Similarly, the F concentrations in active stream sediment samples collected within these two areas also reflect differences related to surface rock chemistry (Madison River drainage: geometric mean = 792 ppm, $n = 46$; Lamar River drainage: geometric mean = 283 ppm, $n = 91$). In both areas, rocks altered by geothermal activity tend to have higher concentrations of chemical variables such as F and SiO_2 than their unaltered equivalents, regardless of rock type. Thus, the fluoride and silica chemistry of stream water and stream sediment is closely related to a combination of the chemistry of exposed rock material and that of chemical additions caused by geothermal activity.

The chemical composition of plants generally reflects the chemical composition of the soil and water in which they grow (Kabata-Pendias 2001). Plants growing in the Madison River drainage on soils derived from geothermally altered rocks and/or irrigated by geothermal waters, as well as plants growing in the streams draining geothermal areas and along their banks, contained higher levels of F, and in some environments, higher SiO_2, than plants collected at similar sites in the Lamar River drainage (Figure 1). The elevated concentrations of F and SiO_2 are undoubtedly the result of a combination of absorption by the plant as well as surface contamination by soil particles (O'Reagain and Mentis 1989; Kabata-Pendias 2001). In particular, a pronounced biofilm was noted on both the aquatic macrophytes and spike rush specimens during collection. This film would have considerable potential to trap and accumulate suspended sediments in the wetland and river environments in which these plant communities are found.

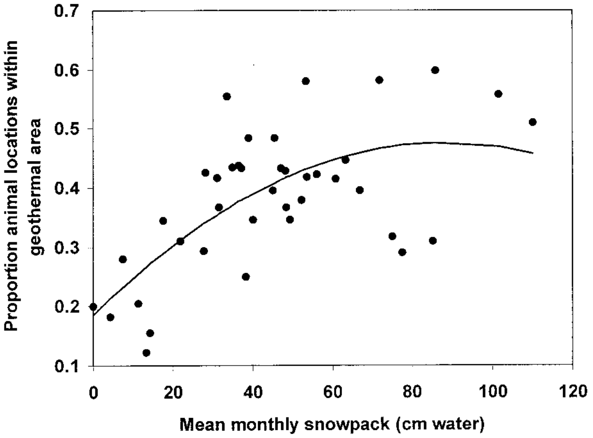

Figure 2. The interaction of winter climate and geothermal heat as it affects the propensity of elk wintering in the upper Madison River drainage to congregate in the geothermally influenced areas and feed on plants containing elevated levels of fluorine and silica. These data demonstrate an increase in the proportion of monthly elk locations recorded within geothermally influenced areas as snowpack increased throughout the winters of, 1991–98.

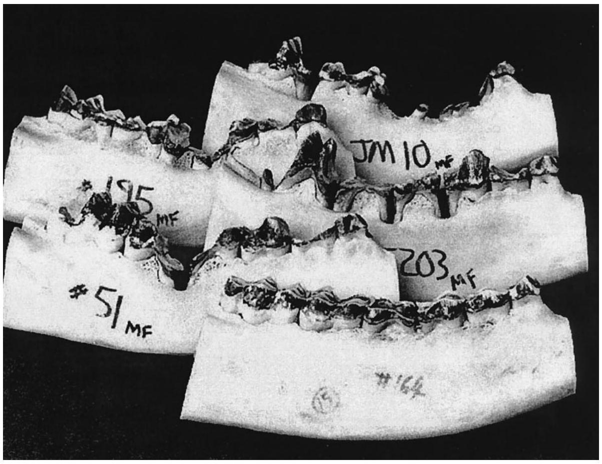

Figure 3. Elk mandibles contrasting the irregular and accelerated wear patterns and dental anomalies typical of fluorine toxicosis in four 12–15-year-old elk cows from the upper Madison River drainage that died of starvation (*background*) and a normal, relatively uniform wear pattern in the premolars and molars of a 15-year-old elk cow killed by wolves in the Lamar River valley (*foreground*). The substantial crown volume remaining in the Lamar Valley sample suggests that had this animal not been killed by wolves she would have lived substantially longer before her teeth were sufficiently worn to compromise mastication of plant material and contribute to the probability of terminal starvation.

All of the plant communities sampled were grazed by elk, but the degree to which the geothermally influenced plant communities were utilized was dependent on the interaction of climate and geothermal heat, as it affected snowpack. In high latitudes, the development of snowpack decreases the availability of forage plants and increases energy expenditures by large herbivores such as elk for locomotion and the displacement of snow to access buried forage (Parker and others 1984). Winter diets are uniformly submaintenance due to low plant quality (Hobbs and others 1981); thus, the additional energy costs of snowpack increases the depletion of body reserves, which can lead to death (Garrott and others 1997). Although the high-elevation, upper Madison River drainage routinely has deep snowpack, geothermal heat dramatically reduces or eliminates snowpack in the geothermal basins and along the banks of the rivers draining these basins (Despain 1990), providing a refuge for elk from deep snows. Data from instrumented animals indicate that elk tend to concentrate in these refugia as snowpack increases ($R^2 = 0.44$, $P < 0.001$) (Figure 2). There they feed extensively on plants containing high F and SiO_2 concentrations (meadow grasses: 32% of total observed foraging minutes; sedges: 14%; rushes: 6%; sedge–grass–rush mixture: 9%; aquatics: 6%).

Fluorine concentrates in mineralized tissues such as teeth and bones (Shupe and others 1984). Mandibles collected from elk living in the Madison drainage basin contained approximately sixfold higher levels of F (1711 ± 64 ppm, $n = 12$) than those collected from Northern Range elk (257 ± 30 ppm, $n = 12$), confirming high dietary exposure to F due to ingestion of geothermal waters, soil, and plants. Excessive dietary F ingested while permanent teeth are developing in young animals interferes with matrix formation and the mineralization of teeth, resulting in characteristic dental lesions and uneven and/or excessively rapid tooth wear (Shupe and others 1984; Fejerskov and others 1994; Kierdorf and others 1996).

This pathological consequence of fluoride toxicosis was evident in a comparison of mandibles collected from adult elk that died of natural causes on both of the Yellowstone winter ranges. Although several of the mandibles collected from elk on the Northern Range ($n = 34$) had minor dental anomalies, none showed signs of fluoride toxicosis. In contrast, 78% of the mandibles collected from carcasses on the Madison-Firehole winter range ($n = 74$) showed classic signs of fluoride toxicosis. Fifty-three percent of these affected mandibles were classified as severe, with extremely aberrant wear patterns, regression of alveolar processes, disfigurement, lost teeth, and localized bone apposition (Fig-

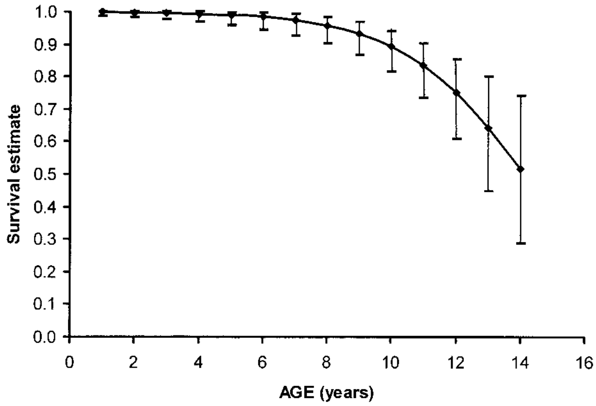

Figure 4. Age-specific survival estimates and 95% confidence intervals for adult female elk living in the Madison drainage basin. Estimates are based on 185 animal years of data and derived from logistic regression using the known-fate module in program MARK (White and Burnham 1999).

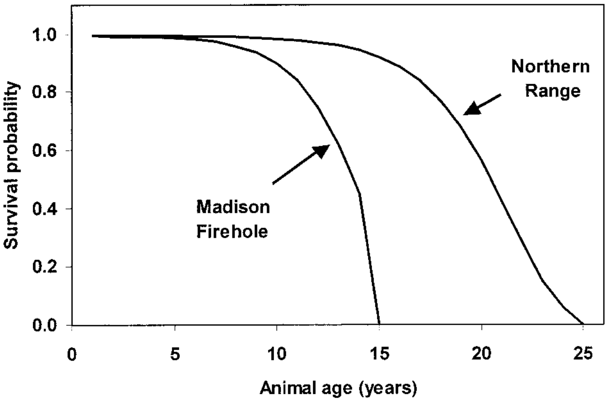

Figure 5. Differences in the generalized age-specific survival, s_x, curves (Eberhardt 1985) of the Madison drainage elk population wintering in the geothermal drainages of the upper Madison River (n = 185 animal years) and the Northern Range elk population (Houston 1982) that winters in the Lamar River valley, where geothermal features are rare. Survival data for both elk populations were collected prior to significant presence of wolves in the study systems.

ure 3). The compromised dentition of the fluorosed animals occupying the Madison-Firehole winter range was undoubtedly exacerbated by the consumption of forages with high levels of abrasive SiO_2 (O'Reagain and Mentis 1989; Vicari and Basely 1993).

The onset of survival senescence in large herbivorous ungulates is dictated by tooth wear, because as cheek teeth become severely abraded, proper mastication of forages is compromised (Laws 1981). Senescence was readily detected in the Madison-Firehole elk population (Figure 4), with the linear age model, A_{LIN}, proving more parsimonious (AICc = 74.2) than the categorical model, A_A, (AICc = 91.3). The demographic consequences of fluoride toxicosis are readily apparent in a comparison of age-specific survival schedules for the Northern Range (Houston 1982) and Madison-Firehole elk populations (Figure 5). Onset of survival senescence in animals occupying the Northern Range occurs at approximately 16 years of age, with the oldest animals surviving 20–25 years (Houston 1982). In contrast, the compromised dentition of elk living in the Madison drainage basin is responsible for a dramatically abbreviated survival schedule; the onset of survival senescence occurs at 10–11 years of age and no animals survives beyond 16 years. Age-specific fecundity schedules, in contrast, were essentially identical for the two populations through age 15. The abbreviated survival schedule for the Madison drainage elk population thus resulted in a compressed age structure with a reduced life span for animals surviving beyond their 1st year of approximately 5 years (Lamar drainage, 17.9 years; Madison drainage, 13.1 years). Other demographic consequences include a 24% reduction in the potential annual population growth rate (Lamar drainage, 11.5%; Madison drainage, 8.7%) and an approximate doubling of the proportion of the adult population in the senescent age classes (Lamar drainage, 5.8%; Madison drainage, 11.4%).

Because wolves preferentially prey on the young of the year and senescent animals (Peterson and others 1984; Mech and others 1998), the geothermally induced altered age structure of the Madison drainage elk population results in a higher proportion of the adult population being susceptible to predation by the recently reintroduced wolf population. In addition, deep snowpack can result in high wolf predation rates on ungulates (Post and others 1999). Although geothermal heat reduces snowpack in localized areas, snowpack in adjacent areas routinely exceeds 120 cm. Wolves have been observed successfully pursuing elk into these deep snow areas, where they are killed (R. A. Garrott unpublished), indicating another mechanism for enhanced vulnerability of the elk population. We also speculate that the ability of the elk herd to demographically compensate for wolf predation will be limited by a reduced population growth rate because of early senescence. Thus, the bottom–up geochemical cascade we documented extends to predator–prey dynamics at the top of the trophic pyramid (Figure 6). Given the evidence for top–down trophic cascades in similar

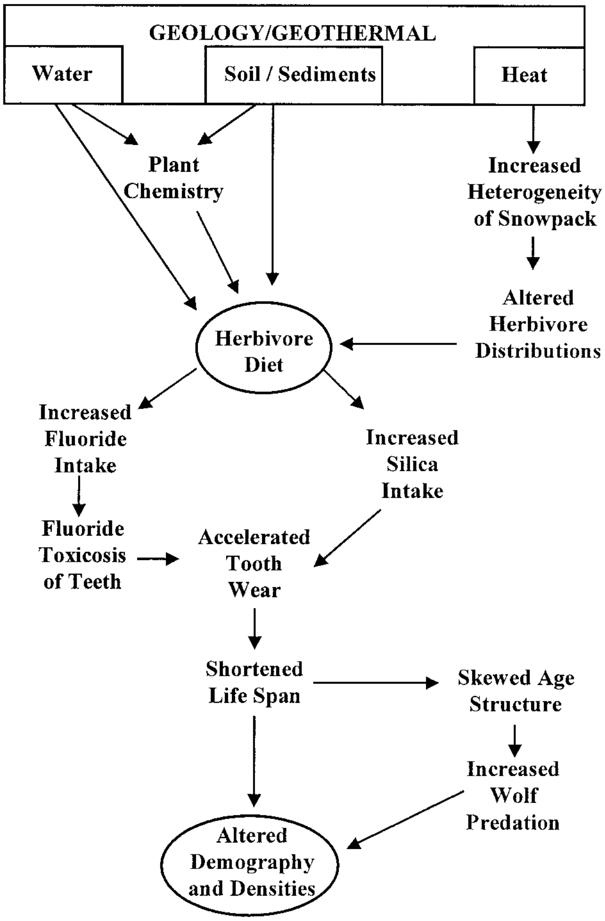

Figure 6. A conceptual model of the geochemical trophic cascade documented in the Madison drainage ecosystem associated with the major geothermal landscapes of Yellowstone National Park.

wolf–ungulate systems (Bergerud 1988), we anticipate a strong feedback cascade back down the trophic chain as the newly established wolf population begins to influence ecological processes in Yellowstone National Park.

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