Faunal isotope records reveal trophic and nutrient dynamics in twentieth century Yellowstone grasslands

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Population sizes and movement patterns of ungulate grazers and their predators have fluctuated dramatically over the past few centuries, largely owing to overharvesting, land-use change and historic management. We used $\delta^{13}C$ and $\delta^{15}N$ values measured from bone collagen of historic and recent gray wolves and their potential primary prey from Yellowstone National Park to gain insight into the trophic dynamics and nutrient conditions of historic and modern grasslands. The diet of reintroduced wolves closely parallels that of the historic population. We suggest that a significant shift in faunal $\delta^{15}N$ values over the past century reflects impacts of anthropogenic environmental changes on grassland ecosystems, including grazer-mediated shifts in grassland nitrogen cycle processes.

Keywords: stable isotope; Yellowstone; *Canis lupus*; grasslands; historic

1. INTRODUCTION

Anthropogenic habitat modification, harvest of ungulate grazers and control of their predators over the past few centuries have caused dramatic fluctuations in the population sizes and movement patterns in many large terrestrial grazers. Grazers affect ecological structure and nutrient cycling in grasslands, so their loss or extreme reduction could have repercussions throughout the ecosystem [1,2].

Yellowstone National Park (YNP) in Wyoming illustrates this phenomenon. Populations of large grazers, including bison (*Bison bison*) and elk (*Cervus elaphus*), declined owing to human harvest during the late 1800s [3]. Predator reduction programmes led to the extirpation of gray wolves from YNP and surrounding areas by 1926. As part of a trend to restore habitats

and ecosystems in some public areas, gray wolves (*Canis lupus*) were reintroduced to YNP in 1995 and 1996 [4]. In the context of carnivore restoration efforts, recent work has focused on understanding contemporary direct and indirect effects of wolves on Yellowstone prey populations and the ecosystem [5]. Implicit in these efforts is the assumption that the reintroduced wolves will fill the same ecological niche as the historic population.

Within an ecosystem, plant nitrogen isotope ($\delta^{15}N$) values generally reflect a combination of the $\delta^{15}N$ values of their source nitrogen (N) pools and the isotopic legacy of N cycle processes [6]. Carbon (C) and N in animal collagen are derived from diet, and collagen $\delta^{13}C$ and $\delta^{15}N$ values reflect time-averaged diet over multiple years prior to death [7]. We analysed bone collagen $\delta^{13}C$ and $\delta^{15}N$ values from YNP fauna from two time periods in the past century when grazer population sizes were dramatically different [3]. We investigate whether food web isotope values may serve as a proxy for broader impacts of anthropogenic environmental changes on grassland ecosystems. Further, we estimate the diet of the historic and the modern wolves through comparison of the isotope composition of wolves with their known or putative prey to test the hypothesis that modern wolves consume the same prey as the extirpated population did historically.

2. MATERIAL AND METHODS

Bone fragments from 14 historic and seven modern bison, 15 historic and 18 modern elk, two modern mule deer (*Odocoileus hemionus*), and six historic and 29 modern gray wolves from YNP were analysed (see electronic supplementary materials, table S1). The first interval is the early 1900s, when grazer populations were recovering from very low numbers in the late 1800s; the second is the late 1990s and early 2000s, when grazer numbers were high. Collagen was extracted and analysed for C and N stable isotopes as in Fox-Dobbs *et al.* [8]. Stable isotope compositions are referenced to Vienna Pee Dee Belemnite for C and air for N. The $\delta^{13}C$ values from the historic material were corrected (-1.15‰) to account for temporal change in the $\delta^{13}C$ value of atmospheric carbon dioxide [9].

Within-species changes in isotope values between time periods were assessed by one-way ANOVA. Relative contributions of putative prey to the diet of the recent wolf population were estimated using the Bayesian mixing model stable isotope analysis in R (SIAR) [10]. The only grazer available to historic wolves was elk (the small, historic bison population was fenced), and overlap between historic elk and wolf $\delta^{13}C$ and $\delta^{15}N$ distributions was assessed using MANOVA. High overlap suggests a predator–prey interaction. No historic mule deer specimens were available for this project. The same isotopic trophic differences ($\Delta^{13}C_{\text{wolf-prey}} = 1.32 \pm 0.6$‰, $\Delta^{15}N_{\text{wolf-prey}} = 4.64 \pm 0.7$‰) between wolf and prey collagen values were used in the modern and historic wolf dietary analyses [8].

3. RESULTS

The $\delta^{15}N$ values of grazers and wolves decreased significantly between the historic and contemporary intervals (one-way ANOVA): bison $F_{1,19} = 10.9$, $p = 0.004$; elk $F_{1,31} = 19.5$, $p = 0.0001$; and wolf $F_{1,33} = 44.7$, $p < 0.0001$ (figure 1*a*). Isotopic shifts that are similar in magnitude and occur simultaneously at multiple consumers and trophic levels suggest a change in the isotopic values of primary producers, not a change in consumer diets [11]. The absence of highly significant differences in faunal $\delta^{13}C$ values between time periods (bison $F_{1,19} = 3.6$, $p = 0.075$; elk $F_{1,31} = 0.13$, $p = 0.73$; and wolf $F_{1,33} = 5.0$, $p = 0.03$; figure 1*b*) is important for two reasons. It supports the conclusion that we are not tracking changes in
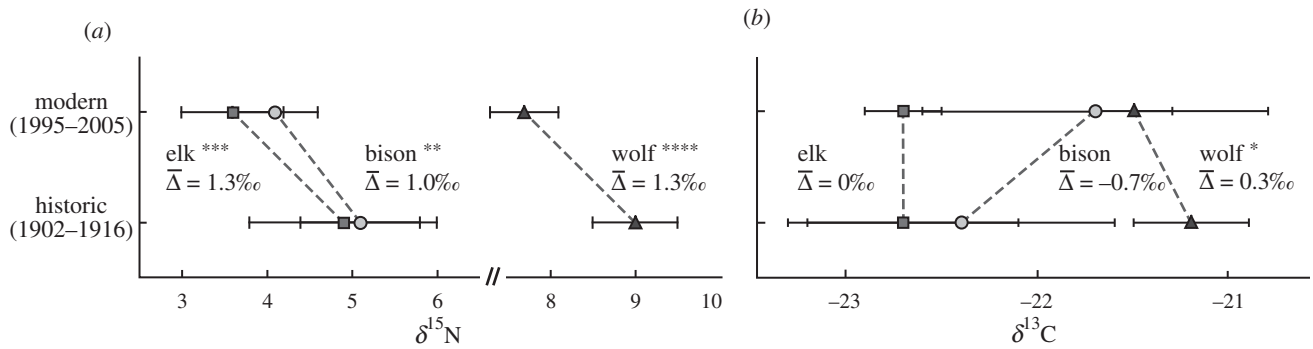
Figure 1. Mean ($\pm$s.d.) of (a) δ^{15}N and (b) δ^{13}C values (‰) for modern and historic YNP fauna. Mean differences in isotopic values between time periods (Δ) are included, and levels of significance are shown (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ****$p < 0.0001$). On average, the estimated grazer (winter) population sizes on the northern range of YNP were greater than or equal to 10 times (bison) and greater than or equal to 2 times (elk) smaller during the historic versus modern time periods [3].
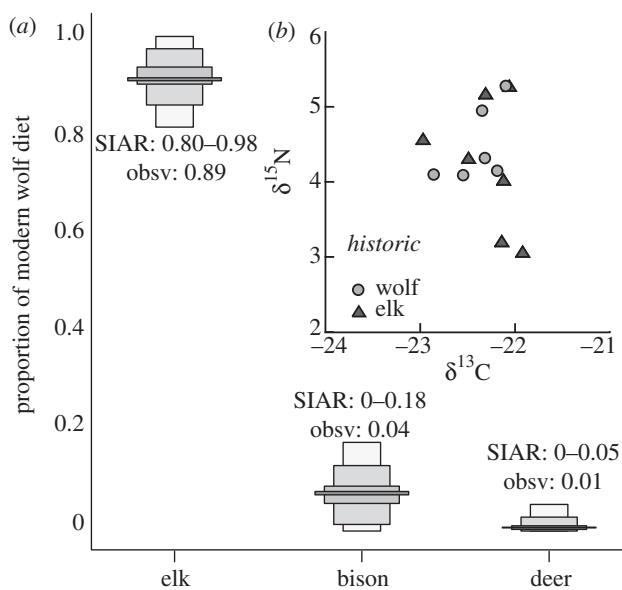

Figure 2. Contributions of the potential prey to *modern* YNP wolf diet (a), as determined by a SIAR mixing model. Box-plots show the relative proportions of each prey with 95% (darkest grey), 75%, 25% and 5% (lightest grey) credibility intervals. Above/below each boxplot are estimates of prey contribution to wolf diet determined by SIAR model (5% credibility intervals) and observational records of winter wolf kills (1995–2004 average) [5]. Plot of *historic* YNP wolf and elk δ^{13}C and δ^{15}N values (‰) (b). Wolf isotopic values are shifted to account for trophic differences between wolf and prey collagen values [8].

consumer diet composition, and it suggests that soil and plant δ^{13}C values were not strongly regulated by the mechanism(s) responsible for the shift in faunal δ^{15}N values.

The SIAR analysis of modern YNP wolves suggested an average diet based primarily on elk (5% credibility interval of the posterior distribution = 80–98%, mean = 90%; figure 2a), as observed in winter wolf kill records [5]. Scat analyses suggest that summer wolf diet is more variable than winter diet, including a greater proportion of mule deer, and smaller mammals [12]. The same pattern of a primarily elk-based diet was deduced for the

historic wolf population, because the distributions of isotopic values were indistinguishable between the two species (MANOVA, $F_{2,18} = 0.72$, $p = 0.50$; figure 2b). While we can be certain that bison were not part of wolf diet during the historic time period, we cannot rule out some contribution of mule deer. But based on a modern understanding of mule deer abundances and movement patterns, as well as their isotope values, mule deer were probably not a major fraction of historic wolf diet. Our data suggest that reintroduced wolves fill the same ecological niche as the historic wolves.

4. DISCUSSION

Recent work highlights the importance and role of the geohistorical perspective in modern ecology and conservation biology [13]. Yet, historical datasets are often bounded by taphonomic factors (natural and anthropogenic), and generally cannot be held to the same standards of evidence as neoecological datasets. Our approach is to catalogue dynamics that are well understood in comparable modern ecosystems, and use the principle of parsimony to suggest the most plausible mechanisms to explain historical data.

Because the overlap in habitat between YNP bison and elk occurs in grasslands, it is most likely that the shift in faunal δ^{15}N values reflects changes in this habitat over the nineteenth century. Climatic factors, such as changes in temperature and precipitation in YNP over the last century [14], are less likely explanations for the shift in faunal δ^{15}N values because they should also be recorded in plant, and thus grazer, δ^{13}C values [15]. Furthermore, because bison and elk have seasonally different habitat preferences [16], it is doubtful that well-documented environmental changes in the greater YNP ecosystem (e.g. expansion of forests, reduction in riparian vegetation, occurrence of wildfires and introduced plant species; [3]), would be recorded similarly by both species' δ^{15}N values.

We focus on three anthropogenic factors that potentially affected YNP grassland δ^{15}N values over the past century. First, sediment cores from regional lakes record the isotopic fingerprint (low δ^{15}N values) of

increased atmospheric deposition of anthropogenic N [17]. The isotopic signal of this change is less coherent in terrestrial ecosystems, and reported plant $\delta^{15}N$ chronologies can increase or decrease over the same time period [18,19]. Second, rising atmospheric CO_2 concentrations have been correlated to a decline in North American prairie foliar $\delta^{15}N$ values, owing to an increase in ecosystem N storage (and decrease in plant available N) [20]. However, experimental data from YNP grasslands suggest that plant N and soil N cycling increase in plots where plant $\delta^{15}N$ values decrease [1,2,21], all in response to higher grazer abundance. The third factor is the dramatic growth of native YNP grazer populations since 1900 (the winter number of bison has increased greater than or equal to 10 times, and elk greater than or equal to 2 times; [3]).

Plant and soil biogeochemical datasets collected from fenced exclosure plots suggest that grazers strongly affect N processes in YNP grasslands, and the temporal shift in faunal $\delta^{15}N$ values we report is similar to plant $\delta^{15}N$ values after several decades of grazer absence/presence [1]. Urine and dung deposition are a mechanisms by which grazers impact N processes, and urine addition in grazed plots results in lower grass $\delta^{15}N$ values than in ungrazed plots at local and regional scales (mechanisms presented in earlier studies [1,22]). While our faunal data may serve as a proxy for changes in grazer–grassland interactions, it is difficult to fully disentangle the relative influences of grazer densities from baseline shifts driven by atmospheric conditions, because these factors have changed over the same timescale in YNP. Additional insight may be derived from similar datasets in the future, because YNP grazer population sizes are stabilized in part by the presence of reintroduced wolves, thus constraining this important variable.

Molecular work has documented the significant loss of genetic heritage in western North American large mammal populations owing to grazer overharvest and predator control over the past 150 years [23]. Our biogeochemical results now show that recent human activity may have permeated the ecosystem far beyond the large mammals. Because grazer populations were decimated across their historical range, this probably represents a widespread phenomenon. Our observation that reintroduced wolves rapidly filled the same dietary niche as historic wolves illustrate that reconstitution of ecological roles is possible within large mammal communities.

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