Migrating bison engineer the green wave

Chris Geremia[a,1], Jerod A. Merkle[b], Daniel R. Eacker[c], Rick L. Wallen[a], P. J. White[a], Mark Hebblewhite[c], and Matthew J. Kauffman[b,d]

[a]Yellowstone Center for Resources, Yellowstone National Park, Mammoth Hot Springs, WY 82190; [b]Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071; [c]Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812; and [d]Wyoming Cooperative Fish and Wildlife Research Unit, US Geological Survey, Laramie, WY 82071

Edited by James A. Estes, University of California, Santa Cruz, CA, and approved October 25, 2019 (received for review August 9, 2019)

Newly emerging plants provide the best forage for herbivores. To exploit this fleeting resource, migrating herbivores align their movements to surf the wave of spring green-up. With new technology to track migrating animals, the Green Wave Hypothesis has steadily gained empirical support across a diversity of migratory taxa. This hypothesis assumes the green wave is controlled by variation in climate, weather, and topography, and its progression dictates the timing, pace, and extent of migrations. However, aggregate grazers that are also capable of engineering grassland ecosystems make some of the world's most impressive migrations, and it is unclear how the green wave determines their movements. Here we show that Yellowstone's bison (*Bison bison*) do not choreograph their migratory movements to the wave of spring green-up. Instead, bison modify the green wave as they migrate and graze. While most bison surfed during early spring, they eventually slowed and let the green wave pass them by. However, small-scale experiments indicated that feedback from grazing sustained forage quality. Most importantly, a 6-fold decadal shift in bison density revealed that intense grazing caused grasslands to green up faster, more intensely, and for a longer duration. Our finding broadens our understanding of the ways in which animal movements underpin the foraging benefit of migration. The widely accepted Green Wave Hypothesis needs to be revised to include large aggregate grazers that not only move to find forage, but also engineer plant phenology through grazing, thereby shaping their own migratory movements.

bison | grazing lawn | green wave | migration | surfing

Many animals make elaborate seasonal migrations across vast landscapes in search of food (1–7). Detailed animal tracking and remote sensing indicate a wide range of migratory taxa choreograph their movements with resource waves of ephemeral, high-quality foods that propagate along phenological gradients (8). Large herbivores surf green waves of forage during migration by closely timing their movements in concert with the progression of new plant growth that propagates from low to high elevations or latitudes (9–11). The Green Wave Hypothesis (GWH) has gained empirical support as the best explanation of the timing, pace, and extent of migratory movements. Over 10 species of terrestrial and aquatic mammals and 7 species of birds appear to surf the green wave (7, 12–22). These studies make clear that, for herbivores, following the green wave is a key foraging benefit of migration.

The GWH assumes that grazing by migrating herbivores does not influence the progress of the green wave itself, and thus moving in concert with the wave is the optimal movement tactic. In other words, animals must move to find the highest-quality forage. However, aggregate grazers like bison (*Bison bison*) and wildebeest (*Connochaetes taurinus*) are ecosystem engineers, capable of modifying grasslands through their intense herbivory (23, 24). For example, as bison and wildebeest move and graze their way across grasslands, they enhance plant productivity by as much as 40% (25) and 100% (23), respectively. Large groups of animals migrating and foraging en masse may also be able to extend forage maturation along their migration corridors. If grazing is concentrated and sufficiently intense, it may alter the progress of the green wave itself, releasing aggregate grazers from the need to surf during migration.

Prior to European settlement, 28–30 million plains bison roamed North America, migrating in vast groups across immense latitudinal and elevational gradients. Overhunting virtually eliminated North American bison such that by 1900 only a few hundred remained (26). Today, bison occupy less than 1% of their historic range (26). A remnant population of up to 5,500 animals in Yellowstone National Park which still migrate up to 100 km (27) is the last truly migratory herd. We tested if Yellowstone bison could engineer the green wave through their grazing and migratory movements.

Results

We quantified surfing by tracking female bison (n = 64), instrumented with Global Positioning System (GPS) collars from 2005 to 2015. We estimated the greenness of the migratory landscape using Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery (Fig. 1*A*), from which we calculated the instantaneous rate of green-up (IRG) or rate that each pixel greens up (10) (Fig. 1*A*, green line). Forage quality for bison was highest at peak IRG and declined consistently as the wave passed (i.e., increasing day-from-peak; n = 161, R^2 = 0.58; Fig. 1*D*).

Across their migratory paths, bison (n = 209 animal-years) surfed by matching their date of use with the date of peak

Significance

The Green Wave Hypothesis (GWH) says the green wave—the progression of spring green-up from low to high elevations or latitudes—dictates the pace of herbivore migrations worldwide. Animals move in sync with the wave because young vegetation provides the best forage. We show the GWH needs to be revised to include group-forming grazers that not only move to find forage, but create forage by how they move. Bison, by moving and grazing en masse, release themselves from the need to "surf the wave." Their movements and grazing stimulate plant growth and delay plant maturation, which allows them to eat high-quality foods despite falling behind the wave while also modifying the progression of the green wave itself.

Author contributions: C.G., R.L.W., P.J.W., M.H., and M.J.K. designed research; C.G. and R.L.W. performed research; C.G., J.A.M., D.R.E., and M.H. analyzed data; and C.G., J.A.M., R.L.W., P.J.W., M.H., and M.J.K. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Data deposition: The data reported in this article have been deposited in Dryad Digital Repository, https://datadryad.org (DOI: 10.5061/dryad.prr4xgxgz).

[1]To whom correspondence may be addressed. Email: Chris_Geremia@nps.gov.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1913783116/-/DCSupplemental.

First published November 21, 2019.

ECOLOGY

Downloaded by guest on April 14, 2021

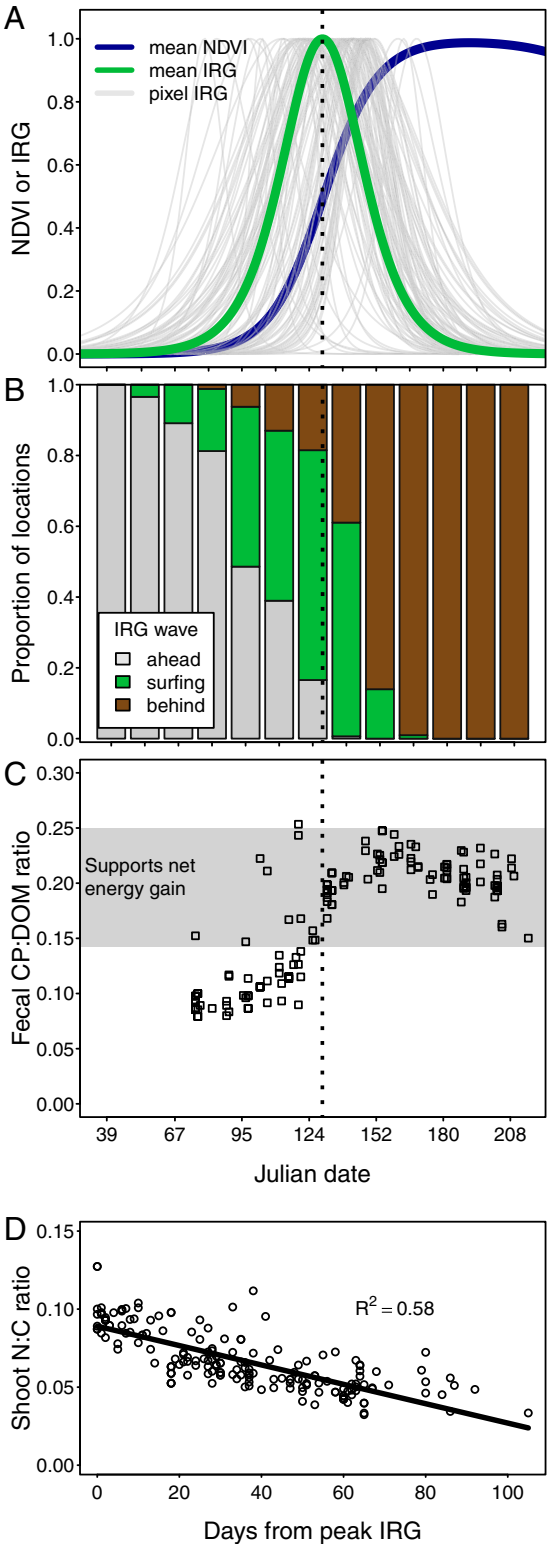

Fig. 1. The relationship between spring green-up, forage quality, and bison diet quality over the growing season. (*A*) The instantaneous rate of green-up (IRG) peaks when the rate of green-up, as indexed from the NDVI curve, is most rapid. (*B*) The daily locations of bison in 2014 (for illustrative purposes) indicate that after peak green-up, most bison fall behind the wave of green-up. (*C*) Despite foraging in habitat patches past peak green-up, bison maintain high-quality diets throughout the growing season. Diets were measured as the ratio of crude protein (CP) to digestible organic matter (DOM) in fecal samples collected in 2014 from migrating bison. (*D*) Plant forage quality measured as the ratio of nitrogen to carbon (N:C) in grasses at key foraging areas, is highest at peak IRG and declines as the green wave passes by.

IRG (11, 18), but mainly in early spring (Figs. 1*B* and 2). Yet, in contrast to other ungulates that surf [e.g., mule deer (*Odocoileus hemionus*) (18); Fig. 2 *B*, *C*, and *E*], bison exhibited a consistent pattern of extended stopover use where they slowed and let the green wave pass them by (Fig. 2 *A* and *D*). Stopping over caused bison to forego approximately 2–3 wk of peak IRG (Fig. 2*F*) as it propagated to higher elevations. Many bison did not reach their highest summer ranges until well after the green wave had passed (Fig. 2*A*).

Remarkably, bison maintained high-quality diets despite falling behind the wave. Diet quality based on (n = 189) fecal samples collected in 2014 increased with the large-scale progression of spring green-up, but remained unexpectedly high for 2–3 mo after the wave had passed (Fig. 1*C*). The migration of bison in Yellowstone, with thousands of animals consuming tons of biomass as they move in unison, is a unique movement and foraging strategy now sustained in only a handful of migratory taxa worldwide. Elsewhere in North America, small, fenced populations of bison have been shown to enhance their diets by grazing intensely, slowing forage maturation and returning to graze previously visited sites (24, 28). These small-scale studies support the possibility that bison maintain high-quality diets through their intense grazing, despite being mismatched to the green wave.

To test if bison grazing was capable of altering forage quality, we conducted a grazing experiment during 2012 to 2017 in 1-ha field sites (n = 30) located along migration corridors. Using 0.5 m^2 plots protected within exclosures paired with grazed plots (n = 271), we found that bison grazing removed more than 50% of available plant tissue in the most intensely used areas (Fig. 3*A*). Intense grazing kept plants in low, dense stature, which enhanced forage quality (shoot N:C; Fig. 3 *B*–*D*). Notably, during mid and late summer (i.e., Julian days 200–289), grazing improved forage quality by 50–90% in plots with high bison use (Fig. 3*B*). In plots where bison grazed intensely, they maintained forage in a high-quality state beyond the spring green-up period.

The removal of large amounts of plant material produced each year (Fig. 3*A*) accelerates early plant growth during the following year by improving sunlight availability (23). Moreover, enhanced leaf tissue nitrogen during the growing season (Fig. 3*B*) increases photosynthetic activity, which prolongs plant growth (23, 29). If bison grazing can both accelerate and extend plant green-up at large scale, it may alter the progression of the green wave itself across the landscape.

A decadal shift in bison density set up a natural experiment that we used to test if grazing intensity changed phenology of the same grasslands over time. Bison in northern areas of the park increased from 590 to 3,628 during 2000 to 2015, while in central areas they declined from 3,531–1,282 (2005 to 2015). We used functional regression analysis (30) to estimate annual differences in the shape of Normalized Difference Vegetation Index (NDVI) curves in 25- to 30-ha areas encompassing each grazing experiment site. Intensity of bison grazing strongly influenced the shape of the NDVI curve. In fact, grazing had a stronger influence on plant phenology than environmental or weather variables (5, 31) during the period when bison fell behind the green wave (*SI Appendix*, Fig. S1). Increased grazing of the same grasslands over time caused them to green up faster, more intensely, and for a longer duration (Fig. 4 *C* and *D*). Thus as bison migrate and graze, they modify the very resource wave that their movements track, altering the timing, pace, and extent of their migrations.

Discussion

Our findings broaden the conceptual underpinning of the foraging benefit of migration by large herbivores. The GWH maintains that animals maximize energy intake by aligning their movements with waves of forage created and propagated by environmental gradients. For many herbivores, surfing is so

Downloaded by guest on April 14, 2021

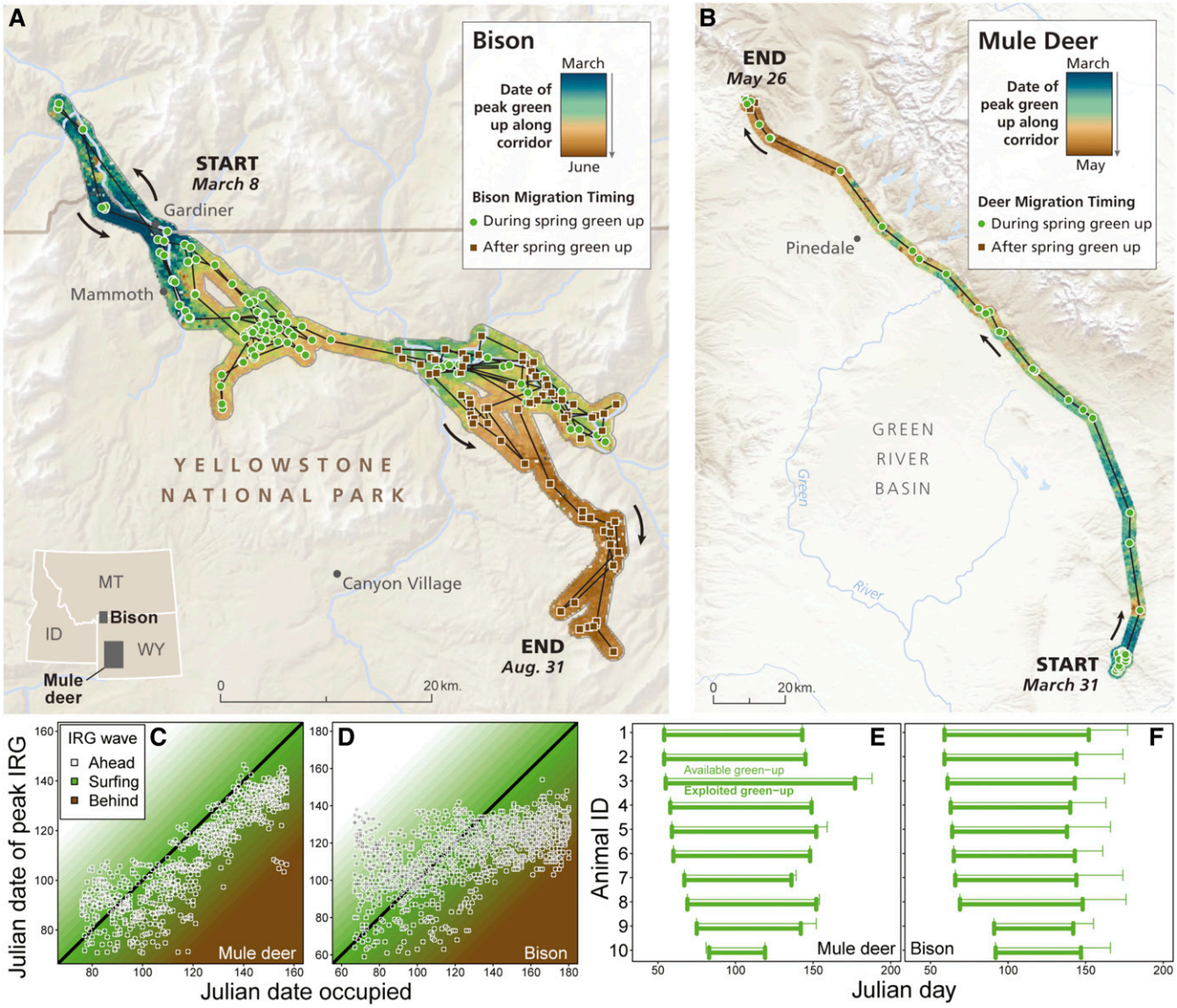

Fig. 2. Comparison of green-wave surfing by migrating bison and mule deer. Typical green-wave surfing by a representative bison (*A*) and mule deer (*B*) in the Greater Yellowstone Ecosystem (United States), 2014. (*C*) A perfect surfer would use each location along its migratory path on the date of peak IRG (black 1:1 line). Mule deer ($n = 12$) move with the wave of green-up that progresses from low to high elevations during spring, extending their exposure to peak green-up (*E*). (*D*) Green-wave surfing in bison ($n = 12$) is mixed, however, with individuals slowing down and letting the green wave pass them by, thereby missing out on the full availability of green-up (*F*). Green-up is indexed by IRG (Fig. 1*A*). Bars in *E* and *F* represent the range of dates that peak IRG is available (thin bars) and used (thick bars). All data were collected in 2014. Cartography by the University of Oregon InfoGraphics Lab.

important that reestablished migratory populations learn to surf as they build knowledge of new landscapes (20). Rather than align their migrations to follow the spring wave of green forage, migratory bison—through their intense grazing in large aggregations—modify the green wave as they move across the landscape. Although foundational studies have established how aggregate grazers track (3, 6) and alter (24, 28) intake rate of nutritious foods, our work connects such grazing dynamics to modification of the green wave, which in turn alters the timing, pace, and extent of bison migrations.

Our findings suggest that the theoretical basis of the GWH needs to be revised to include migrating herbivores that not only track, but also alter the green-up of forage as they move. Migratory ungulates and other migrating herbivores such as insects and birds thus likely fall on a continuum of green-wave surfing. Some migrants (e.g., mule deer, barnacle goose [*Branta leucopsis*], and greater white-fronted goose [*Anser albifrons*]) must carefully time their movements as they passively seek out the green wave, whereas aggregate grazers (e.g., bison) can manipulate the way the green wave propagates across the landscape. In fact, migrants exhibit a wide range of strategies [e.g., jumping (10) or trailing (11) the green wave], and such variability may be created by grazing feedbacks on diet quality, with aggregation playing a key role permitting animals to control vegetation.

The migrations of large herbivores are dwindling across the globe (32), and their absence has likely caused significant alterations to ecosystems. A century and a half ago, the American West was occupied by tens of millions of bison moving seasonally across its big landscapes. With their aggregated grazing across vast areas, phenological patterns would have been radically different from what they are today. Currently, only 20,000 bison remain protected in conservation herds, and only 8,000 of those

Downloaded by guest on April 14, 2021

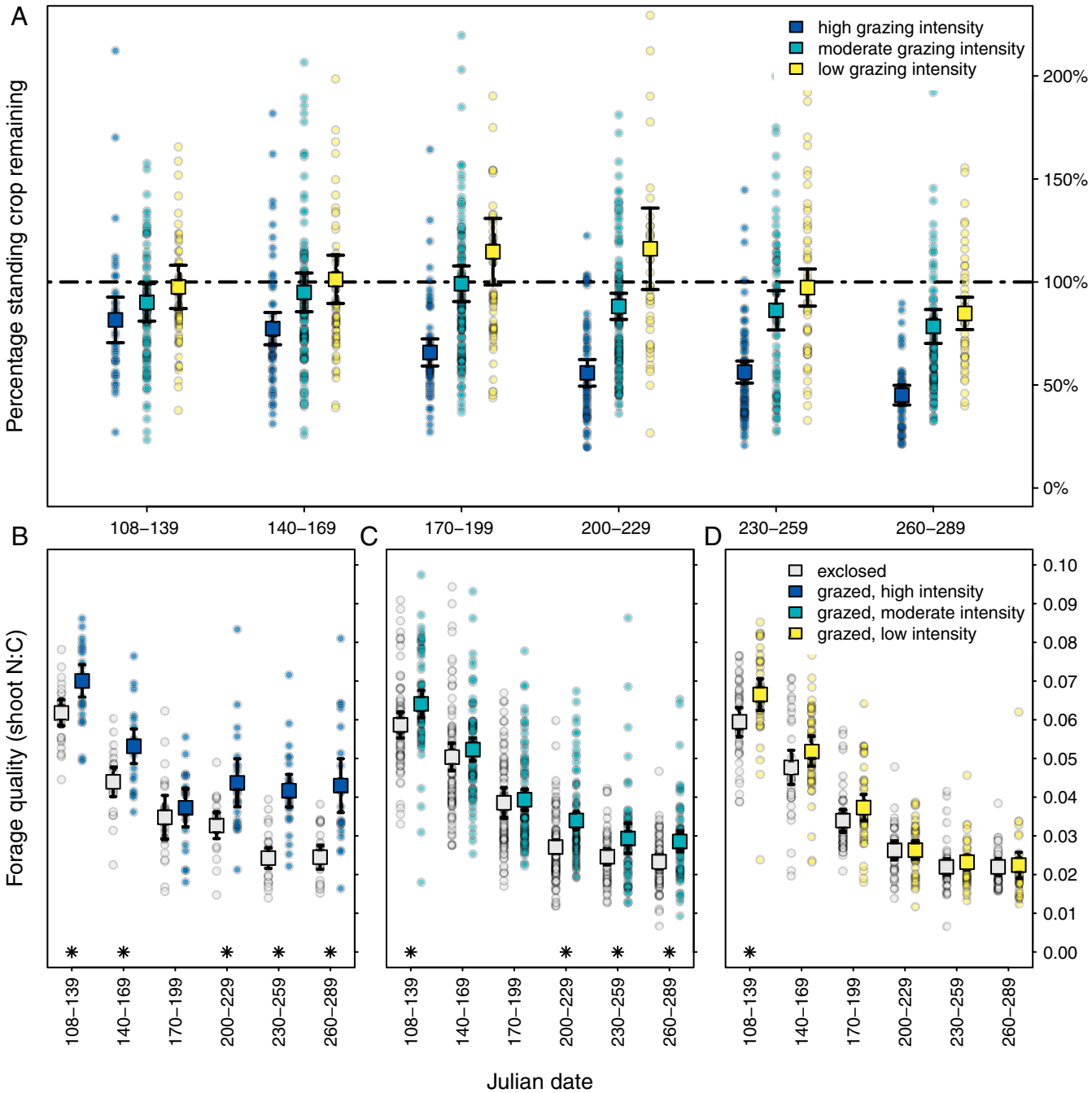

Fig. 3. The effect of bison grazing on plant-forage quality. (*A*) Small-scale exclosure experiments found that bison, particularly in areas of high grazing intensity, can consume more than 50% of available plant biomass. (*B*) High-intensity grazing increased plant-forage quality, measured as the ratio of nitrogen to carbon (N:C) in shoot tissue, with smaller effects in plots receiving moderate (*C*) or low-intensity (*D*) grazing. Asterisks depict significant differences among grazed and exclosed plots. Plant and grazing metrics were derived from a field experiment of $n = 30$ sites with grazed (treatment) and exclosed (control) plots maintained from 2012 to 2017.

are allowed to freely move across large landscapes (33). Moreover, today's model of bison conservation involves maintaining small bison populations within fenced areas and actively managing their abundance for light to moderate grazing. The massive bison migrations that existed before European settlement are gone. Conserving North American ecosystems as a semblance of what they were prior to the loss of bison will involve the restoration and protection of large herds. Restoring lost bison migrations will require that these animals be allowed to freely aggregate, intensely graze, and move in sync with landscape-level patterns of plant phenology.

Materials and Methods

Green Wave Surfing Analysis. We tested whether bison matched their spring movements with peaks in the instantaneous rate of green-up (IRG) (10, 18). We calculated the Julian date of peak IRG across the study area from 2001 to 2016 following the methods of Bischof et al. (10) and Merkle et al. (11). IRG was calculated as the first derivative of annual time series of NDVI, determined from surface reflectance bands 1 and 2 (250-m spatial and 8-d

Downloaded by guest on April 14, 2021

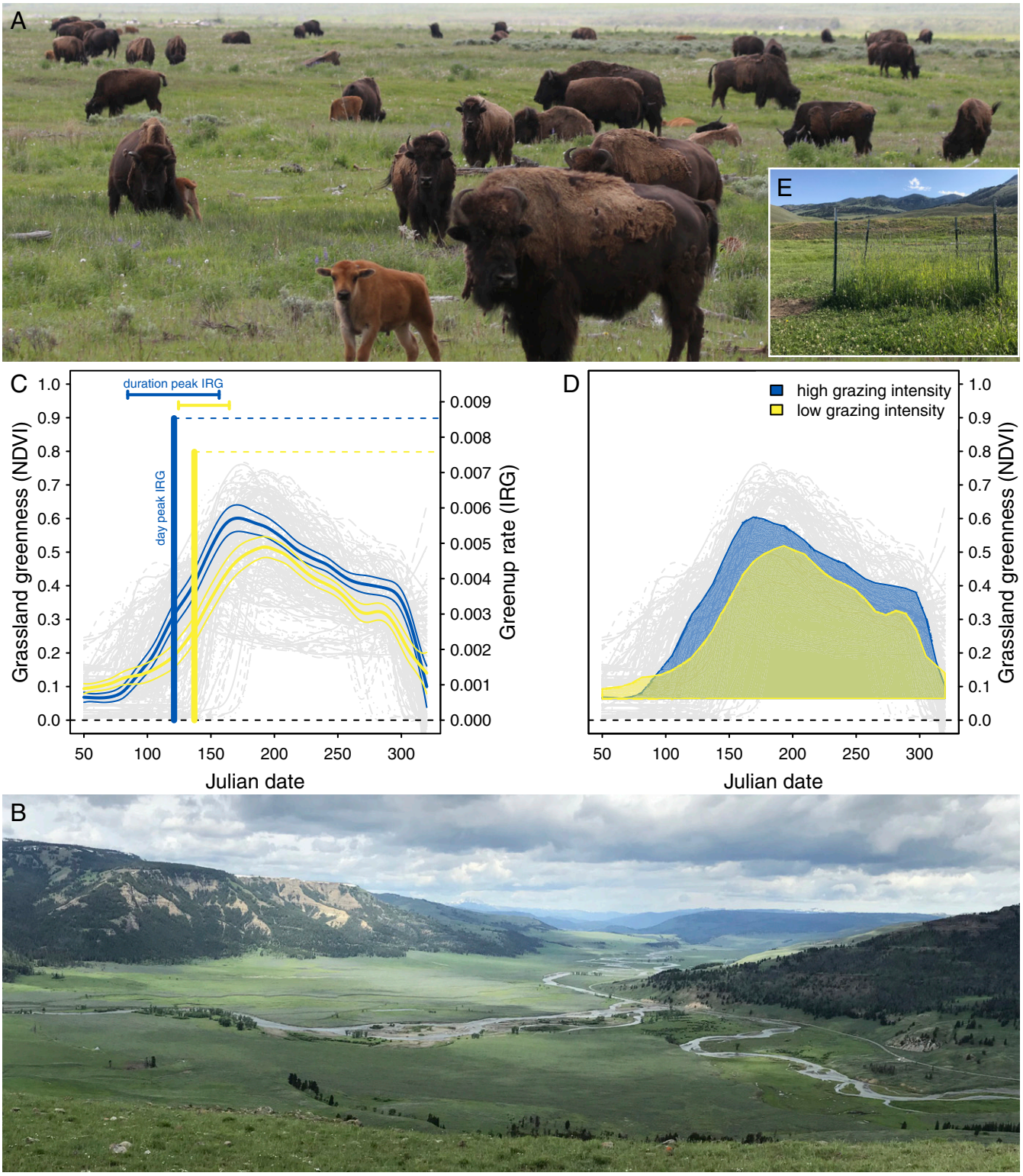

Fig. 4. Grazing effects on broad-scale patterns of the green wave. (*A*) Bison created massive grazing lawns, which are larger than most fenced bison preserves in North America, as they migrated across the (*B*) extensive Yellowstone grasslands. Greenness of 25- to 30-ha grasslands encompassing grazing experiment sites changed with decadal shifts in bison grazing intensity. (*C*) When bison grazing was more intense, vegetation greened up earlier, more intensely, and for a longer duration, as measured by NDVI and IRG. (*D*) More intense grazing also elevated net aboveground production. In *C* and *D*, blue and yellow lines show model predicted NDVI for the same grassland under high and low bison grazing. Gray lines show spline-fitted NDVI curves for grazing experiment sites during 2005 to 2015. (*E*) At small scale, vegetation conditions outside exclosures were kept in an early phenological stage even late in the growing season.

Downloaded by guest on April 14, 2021

temporal resolution) from the MOD09Q1 data product from the MODIS terra satellite (*SI Appendix*, Text S1). Global positioning (GPS) data were collected from radio-collared adult female bison during 2005 to 2015. For each GPS location collected in each year (n = 209 animal-years from 64 individuals), we extracted the Julian date of peak IRG (*SI Appendix*, Text S2). Following similar methods of Bischof et al. (10), we broke each spring period into 4 equal periods (~3–4 wk each) and used piecewise regression to test for surfing. For each period, we identified surfing when the piecewise linear model coefficient term relating Julian day of peak IRG and the Julian day of occupation was positive and the 95% confidence interval did not overlap zero.

Diet Quality of Migrating Bison. We collected fecal (n = 189) and plant (n = 161) samples from radio-collared bison (n = 21) as they migrated from winter to summer ranges during March 18 to August 4, 2014. We homogenized 15 g of wet material from 5 separate, fresh dung piles deposited by any individual in groups associated with radio-collared animals. Homogenates were analyzed for crude protein and digestible organic matter using near-infrared spectroscopy (34, 35) at the Texas A&M Grazing Animal Nutrition Lab. We collected plant tissue by locating the center of foraging areas, randomly selecting four 300 cm^2 circular areas that were 10 m from the center and collecting all aboveground plant matter rooted within each area. Plant material was rinsed with deionized water, dried, and ground to a powder using a Wiley Mill. We determined shoot nitrogen and carbon concentrations using a Costech NA 2100 elemental analyzer.

Paired Design Grazing Experiment. During 2012 to 2017 we established 30 1-ha sites to measure net aboveground production, standing crop, consumption, and shoot nutrient concentration. We did not monitor each site every year (2012 to 2014, n = 2; 2015 to 2016, n = 22; and 2017, n = 15). Sites were located in areas where bison concentrated their use during spring migrations, based on clusters of GPS locations.

At each site, we used a paired design of naturally grazed grassland (treatment) and exclosed grassland (control) to measure net aboveground production, grazing intensity, standing crop, and plant nutrients. We made measurements using established methods (29, 36–38). For controls, we placed 3 semipermanent 9-m^2 fenced exclosures at each site. We set up semipermanent exclosures as snow receded during the first year each site was monitored. Semipermanent exclosures were in place for between 1 and 3 y. Each semipermanent exclosure included two 0.5-m^2 plots that were used to measure vegetation conditions. For treatments, we set up 6 temporary exclosures paired with one or two 0.5-m^2 plots as snow melted. We randomly relocated these exclosures and plots monthly through the growing season. Temporary exclosures were 2.25 m^2 and protected a 0.5-m^2 plot. Shoot biomass was measured in all plots (semipermanent exclosure, temporary exclosure, and unprotected) at the beginning and end of each monthly monitoring period using the canopy intercept method (39). We collected plant tissue samples from all plots throughout the year by randomly selecting a 300-cm^2 circular area and collecting all aboveground plant matter rooted within the area. Plant material was rinsed with deionized water, dried, and ground to a powder using a Wiley Mill. Shoot nitrogen and carbon concentrations were determined using a Costech NA 2100 elemental analyzer. We calculated net aboveground production, consumption, and grazing intensity from monthly shoot biomass measurements (*SI Appendix*, Text S3). We compared standing crop and shoot nutrients across 3 levels of grazing intensity: low (e.g., lower quartile: grazing intensity ≤11%), moderate (inner quartile: grazing intensity 12–40%), and high (upper quartile: grazing intensity ≥41%); and 6 equally spaced Julian date intervals: 108–139, 140–169, 170–199, 200–229, 230–259, and 260–289. We used pairwise, 2-sided t tests to identify significant differences between grazed and ungrazed conditions at the 0.05 significance level. Across sites and years, we compared n = 63 (low), n = 130 (moderate), and n = 78 (high) paired plots.

Functional Regression Analysis of NDVI. We used functional data analysis (30, 40) to test if bison grazing was capable of modifying broad-scale patterns of the green wave. Functional analysis is a multivariate statistical approach that allows one to describe how the NDVI curve varies across the entire growing season rather than evaluating single growing-season parameters that are often highly correlated. We generated NDVI curves for 25- to 30-ha areas encompassing each 1-ha grazing experiment site (grazing exclosures occupied <0.01% of total analysis area) each year, which served as our functional response variable (*SI Appendix*, Text S4). We related variation in the topology of NDVI curves to bison grazing intensity (*SI Appendix*, Text S5) and other factors known to be important climatic and landscape (*SI Appendix*, Text S6) controls of plant phenology.

All analyses were natively programmed in Program R. We complied with all relevant ethical regulations, including animal capture and handling protocols reviewed by the National Park Service IACUC Committee.

Data Availability Statement. The data reported in this article have been deposited in Dryad Digital Repository (DOI: 10.5061/dryad.prr4xgxgz) (41).

ACKNOWLEDGMENTS. The National Park Service and NSF Long Term Research in Environmental Biology Grant 1556248 provided funding. We thank Eugene William Hamilton III for completing plant assays, Stephen Prince for completing fecal assays, and Douglas Alan Frank for reviewing this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government.

1. J. M. Fryxell, A. R. Sinclair, Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.* **3**, 237–241 (1988).
2. S. Albon, R. Langvatn, Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* **65**, 502–513 (1992).
3. J. M. Fryxell, J. F. Wilmshurst, A. R. Sinclair, Predictive models of movement by Serengeti grazers. *Ecology* **85**, 2429–2435 (2004).
4. R. B. Boone, S. J. Thirgood, J. G. C. Hopcraft, Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology* **87**, 1987–1994 (2006).
5. M. Hebblewhite, E. Merrill, G. McDermid, A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* **78**, 141–166 (2008).
6. R. M. Holdo, R. D. Holt, J. M. Fryxell, Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am. Nat.* **173**, 431–445 (2009).
7. T. Mueller *et al*., In search of forage: Predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J. Appl. Ecol.* **45**, 649–658 (2008).
8. J. B. Armstrong, G. Takimoto, D. E. Schindler, M. M. Hayes, M. J. Kauffman, Resource waves: Phenological diversity enhances foraging opportunities for mobile consumers. *Ecology* **97**, 1099–1112 (2016).
9. A. Van der Graaf, J. Stahl, A. Klimkowska, J. P. Bakker, R. H. Drent, Surfing on a green wave—how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea* **94**, 567–577 (2006).
10. R. Bischof *et al*., A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *Am. Nat.* **180**, 407–424 (2012).
11. J. A. Merkle *et al*., Large herbivores surf waves of green-up during spring. *Proc. Biol. Sci.* **283**, 20160456 (2016).
12. M. Shariatinajafabadi *et al*., Migratory herbivorous waterfowl track satellite-derived green wave index. *PLoS One* **9**, e108331 (2014).
13. B. Abrahms *et al*., Memory and resource tracking drive blue whale migrations. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 5582–5587 (2019).
14. P. Beck, T. Wang, A. Skidmore, X. Liu, Displaying remotely sensed vegetation dynamics along natural gradients for ecological studies. *Int. J. Remote Sens.* **29**, 4277–4283 (2008).
15. G. Bohrer, P. S. Beck, S. M. Ngene, A. K. Skidmore, I. Douglas-Hamilton, Elephant movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape. *Mov. Ecol.* **2**, 2 (2014).
16. Y. Si *et al*., Do Arctic breeding geese track or overtake a green wave during spring migration? *Sci. Rep.* **5**, 8749 (2015).
17. I. M. Rivrud, M. Heurich, P. Krupczynski, J. Müller, A. Mysterud, Green wave tracking by large herbivores: An experimental approach. *Ecology* **97**, 3547–3553 (2016).
18. E. O. Aikens *et al*., The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.* **20**, 741–750 (2017).
19. K. Thorup *et al*., Resource tracking within and across continents in long-distance bird migrants. *Sci. Adv.* **3**, e1601360 (2017).
20. B. R. Jesmer *et al*., Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* **361**, 1023–1025 (2018).
21. X. Wang *et al*., Stochastic simulations reveal few green wave surfing populations among spring migrating herbivorous waterfowl. *Nat. Commun.* **10**, 2187 (2019).
22. H. L. Bartlam-Brooks, P. S. Beck, G. Bohrer, S. Harris, In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *J. Geophys. Res. Biogeosci.* **118**, 1427–1437 (2013).
23. D. A. Frank, S. J. McNaughton, B. F. Tracy, The ecology of the Earth's grazing ecosystems. *Bioscience* **48**, 513–521 (1998).
24. A. K. Knapp *et al*., The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience* **49**, 39–50 (1999).
25. D. A. Frank, R. L. Wallen, P. J. White, Ungulate control of grassland production: Grazing intensity and ungulate species composition in Yellowstone Park. *Ecosphere* **7**, e01603 (2016).
26. A. C. Isenberg, *The Destruction of the Bison: An Environmental History, 1750-1920* (Cambridge University Press, 2001).
27. C. Geremia *et al*., Integrating population- and individual-level information in a movement model of Yellowstone bison. *Ecol. Appl.* **24**, 346–362 (2014).
28. E. J. Raynor, A. Joern, J. B. Nippert, J. M. Briggs, Foraging decisions underlying restricted space use: Effects of fire and forage maturation on large herbivore nutrient uptake. *Ecol. Evol.* **6**, 5843–5853 (2016).

Downloaded by guest on April 14, 2021

29. D. A. Frank, R. L. Wallen, E. W. Hamilton, P. J. White, J. D. Fridley, Manipulating the system: How large herbivores control bottom-up regulation of grasslands. *J. Ecol.* **106**, 434–443 (2018).
30. M. A. Hurley *et al*., Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **369**, 20130196 (2014).
31. E. L. Garroutte, A. J. Hansen, R. L. Lawrence, Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. *Remote Sens.* **8**, 404 (2016).
32. D. S. Wilcove, M. Wikelski, Going, going, gone: Is animal migration disappearing. *PLoS Biol.* **6**, e188 (2008).
33. C. C. Gates, C. H. Freese, P. J. Gogan, M. Kotzman, *American Bison: Status Survey and Conservation Guidelines 2010* (IUCN, 2010).
34. R. K. Lyons, J. W. Stuth, Fecal NIRS equations for predicting diet quality of free-ranging cattle. *J. Range Manage.* **45**, 238–244 (1992).
35. J. Stuth, A. Jama, D. Tolleson, Direct and indirect means of predicting forage quality through near infrared reflectance spectroscopy. *Field Crops Res.* **84**, 45–56 (2003).
36. S. J. McNaughton, Grazing lawns: Animals in herds, plant form, and coevolution. *Am. Nat.* **124**, 863–886 (1984).
37. S. McNaughton, Ecology of a grazing ecosystem: The Serengeti. *Ecol. Monogr.* **55**, 259–294 (1985).
38. D. A. Frank, S. J. McNaughton, The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* **73**, 2043–2058 (1992).
39. D. A. Frank, S. J. McNaughton, Aboveground biomass estimation with the canopy intercept method: A plant growth form caveat. *Oikos* **57**, 57–60 (1990).
40. J. Ramsay, G. Hooker, S. Graves, *Functional Data Analysis with R and MATLAB* (Springer Science & Business Media, 2009).
41. C. Geremia *et al*., Data from "Migrating bison engineer the green wave." Dryad Digital Repository. https://doi.org/10.5061/dryad.prr4xgxgz. Deposited 7 November 2019.

Downloaded by guest on April 14, 2021