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Large herbivores surf waves of green-up during spring

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The green wave hypothesis (GWH) states that migrating animals should track or ‘surf’ high-quality forage at the leading edge of spring green-up. To index such high-quality forage, recent work proposed the instantaneous rate of green-up (IRG), i.e. rate of change in the normalized difference vegetation index over time. Despite this important advancement, no study has tested the assumption that herbivores select habitat patches at peak IRG. We evaluated this assumption using step selection functions parametrized with movement data during the green-up period from two populations each of bighorn sheep, mule deer, elk, moose and bison, totalling 463 individuals monitored 1–3 years from 2004 to 2014. Accounting for variables that typically influence habitat selection for each species, we found seven of 10 populations selected patches exhibiting high IRG—supporting the GWH. Nonetheless, large herbivores selected for the leading edge, trailing edge and crest of the IRG wave, indicating that other mechanisms (e.g. ruminant physiology) or measurement error inherent with satellite data affect selection for IRG. Our evaluation indicates that IRG is a useful tool for linking herbivore movement with plant phenology, paving the way for significant advancements in understanding how animals track resource quality that varies both spatially and temporally.

1. Introduction

The green wave hypothesis (GWH) states that migrating herbivores should track or ‘surf’ the leading edge of spring green-up, where forage quality is the highest [1]. Although originally proposed more than 35 years ago to explain the northerly migration of waterfowl in temperate latitudes [2], the GWH is re-emerging as a lens to understand the foraging benefit of migration in ungulate taxa [3,4]. Additionally, Fryxell [5] conceptualized the forage maturation hypothesis, which posits that herbivores should consume vegetation at an intermediate state of phenological growth, because as biomass increases, rate of energy intake by herbivores becomes limited by increasing fibre content [6]. The forage maturation hypothesis has helped frame studies of foraging by large herbivores for over a quarter of a century. As high-resolution spatial data and analyses are allowing more rigorous tests of the GWH [3,7], it is becoming increasingly important to more fully integrate these two hypotheses. In a sense, the GWH, when applied to large herbivores, is the spatial manifestation of the forage maturation hypothesis. As green-up is propagated across large landscapes during spring, animals that forage in habitats according to the forage maturation hypothesis are predicted to surf green waves of high-quality forage in accordance with the GWH. Indeed, the distribution of

intermediate plant biomass has predicted the habitat use and distribution of herbivores such as barnacle geese (*Branta leucopsis*), wildebeest (*Connochaetus taurinus*), Mongolian gazelles (*Procapra gutturosa*), Thomson's gazelles (*Eudorcas thomsonii*) and Rocky Mountain elk (*Cervus elaphus canadensis*) [6,8–11].

Field efforts to identify when forage quality peaks annually across large landscapes are time consuming and sometimes impractical [1,12]. In response, researchers have increasingly used remotely sensed metrics—particularly the Normalized Difference Vegetation Index (NDVI; or greenness)—as a proxy for vegetation phenology and net primary production [13,14]. NDVI correlates with vegetation biomass in arid and semi-arid landscapes [15–17]. More importantly, a slow rate of spring green-up, calculated as the slope between successive data points of NDVI, can enhance juvenile survival in large herbivores [18,19]. Recent work by Bischof *et al.* [3] has proposed the instantaneous rate of green-up (IRG) to index high-quality forage at intermediate biomass from time-series NDVI data. The IRG is calculated as the first derivative of a fitted curve to annual NDVI time series, and represents an objective method to quantify how rate of spring green-up varies across time and space during the growing season [3]. Given a time series of NDVI values in habitats where vegetation growth occurs primarily during a single growing season, the IRG will peak at approximately half of the maximum NDVI value, where biomass levels are intermediate (see the electronic supplementary material, appendix A for a conceptualization). Therefore, according to the forage maturation hypothesis, herbivores should forage in areas at peak IRG to maximize intake of high-quality forage. Estimation of IRG allows testing the GWH within an explicit, spatial context across multiple taxa and ecosystems. Accordingly, migrating animals exposed to gradients of plant phenology (e.g. altitudinal or latitudinal) should surf waves of peak IRG across the landscape [3]. Even within one seasonal range, herbivores should exploit gradients of plant phenology—caused by vegetation community, topography or snow melt—by selecting habitat patches at peak IRG [20].

Using IRG to evaluate the GWH across large landscapes and diverse phenological gradients appears promising [3]. Coupling IRG with animal movement creates avenues for identifying environmental and anthropogenic factors that alter plant phenology and consequently facilitate or constrain optimal tracking of high-quality forage. The value of coupling remotely sensed data with animal movement is increasing as climate change and human development alter plant phenology across the globe [21,22], modifying the ability of individuals to track changes in forage quality. The global decline of migratory animals [23,24] further amplifies the need for new, integrative approaches to understanding the behavioural ecology of migration [25] as these taxa are likely dependent on the foraging benefits of green wave surfing.

Nevertheless, the development of IRG as a tool for understanding how a variety of herbivore species exploit high-quality forage in time and space remains incomplete. It is still unclear whether the IRG and GWH are applicable across multiple species of large herbivores residing in a variety of landscapes. Further, the critical assumption of the green wave and forage maturation hypotheses that highly mobile herbivores select habitat patches at peak IRG has yet to be verified. It is unclear whether highly mobile herbivores across diverse taxa have the behavioural perception to select habitat patches at peak IRG. According to theory [3,18,26,27], animals

should use the most profitable habitat patches available, which assumes an ability to assess spatial and temporal variability in habitat quality and then select superior habitat patches. Understanding how multiple species of large herbivorous perceive and select habitat patches that change in quality over time provides insight into the behavioural capacity or flexibility of animals to minimize foraging losses caused by, for example, alterations in plant phenology driven by climatic change [21].

In this study, we provide a cross-taxa evaluation of the assumption that large herbivores surf waves of spring green-up by selecting habitat patches at peak IRG. Using a movement modelling framework and relocation data collected during the green-up period from two populations each of bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), elk, moose (*Alces alces*) and bison (*Bison bison*) in western Wyoming and eastern Utah, USA, we tested whether individuals select habitat patches when they are at peak IRG. Our mechanistic approach to test this assumption involved three steps. First, for each species we parametrized a base movement model, which included habitat attributes known to influence habitat selection for each species (e.g. cover type, elevation, slope, aspect, distance to escape terrain, integrated NDVI). Second, we evaluated empirical support for the notion that individuals select habitat patches with relatively high IRG values compared with the base model. Third, we quantified whether animals select habitat patches at the leading edge, trailing edge or crest of the IRG wave (see the electronic supplementary material, appendix A for a conceptualization) by examining selection for a quadratic form of NDVI, which represents a flexible form of intermediate NDVI values. Evaluating selection for varying degrees of intermediate biomass is important for assessing whether there are other constraints to optimal surfing not captured by remotely sensed IRG. Our multi-species analysis provides novel insight into the appropriateness of IRG as a phenological cue for large herbivores that forage across a variety of habitats.

2. Material and methods

(a) Study area

Western Wyoming and eastern Utah are semi-arid mountainous regions with elevations ranging from approximately 1300 to 4100 m. Major plant communities include shrub (dominated by sagebrush (*Artemisia* spp.)), coniferous forest (dominated by lodgepole pine (*Pinus contorta*)), pinyon-juniper woodland (dominated by singleleaf pinyon (*Pinus monophylla*) and Juniper (*Juniperus* spp.)), and herbaceous meadows. Cover types based on the 2011 National Land Cover Database in the study area included shrub (47%), coniferous forest (30%), herbaceous grassland (13%), woody and herbaceous wetlands (5%), hay fields (2%), deciduous forest (2%) and all others constituted less than 1% of the landscape. Mean annual precipitation ranged from 10–20 cm in the lowest elevations to 150–250 cm in the highest elevations (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>). The regional climate is characterized by long cold winters and relatively short warm summers. Mean daily temperatures ranged from 13 to 21°C in July and –9 to –3°C in December, based on weather stations northeast of Pinedale, WY (Gunsight Pass SNOTEL site; elevation 3000 m; National Water and Climate Center, US Department of Agriculture) and in Cody, WY (elevation 1500 m; NOAA Online Weather Data, National Oceanic and Atmospheric Administration).

(b) GPS collar data

We used spatial relocation data from previous studies of GPS-collared female ungulates. We collated GPS data on individuals collared over 1–3 years from 10 populations representing five species: bighorn sheep in the Teton Range ($n = 20$; years 2008–2010) and Whiskey Basin ($n = 8$; years 2002, 2004, 2012) areas, mule deer in the Upper Green River Basin (UGRB; $n = 29$; year 2012) and southern and eastern Wyoming Range ($n = 46$; years 2013–2014) areas, elk in the Southern Greater Yellowstone Ecosystem ($n = 119$; years 2006–2014) and Absaroka Mountain ($n = 88$; years 2007–2010) areas, moose in the Buffalo Valley ($n = 39$; years 2005–2010) and the eastern slope of the northern Wyoming Range ($n = 64$; years 2011–2014), and bison in the Henry Mountains ($n = 46$; years 2011–2014) and Book Cliffs ($n = 4$; year 2014) areas (see study area figure in the electronic supplementary material, appendix B). Elk used in the analysis from the Southern Greater Yellowstone Ecosystem never visited feedgrounds that also occur in this region. Elk in the Southern Greater Yellowstone Ecosystem occupied the western slope of the Wind River Range, eastern slope of the Wyoming Range and Buffalo Valley areas. The GPS fix rate varied for each population and included a fix every 0.5, 1, 2, 2.75, 3, 5 or 6 h. Collared individuals across all taxa represented a mix of migratory and resident foraging strategies (see the electronic supplementary material, appendix D for proportion of each population that was migratory). Our intent was to test the ability of animals to track IRG regardless of migratory status. Nonetheless, we subset the data to only migratory individuals and reran the analyses explained below; results were not different.

(c) Movement modelling approach

We used step selection functions [28] to test the assumption that herbivores select habitat patches with vegetation at intermediate biomass as indexed by peak IRG during the spring green-up period. We first identified consecutive steps in the movement data that were between 8 and 12 h apart, keeping the step interval the same within a population. We chose this range of temporal sampling for two reasons: (i) to ensure a similar sampling regime given variable fix rates, and (ii) to match as closely as possible the spatial sampling regime of the NDVI data (250 m resolution) so that all species had a mean probability of more than 0.5 of moving outside of a 250 m cell at each step. For each step, we identified the source and target points, and drew 25 potential target points originating from the known source point by sampling from the individuals step and turning angle distribution simultaneously [28]. These 25 potential target points were identified as available and compared to the used target step.

(d) Explanatory variables

Using surface reflectance bands 1 and 2 (250 m spatial and 8-day temporal resolution) from the MOD09Q1 data product from the MODIS terra satellite, we calculated NDVI [13,14] for the entire study area from 2001 to 2014. Following the protocol of Bischof *et al.* [3], we constructed a smoothed and scaled NDVI time series for each pixel. Briefly, this entailed a processing sequence of: (i) setting values less than 0 and clouded pixels to no data; (ii) flooring the time series to a winter value (November through February) calculated as the 0.025 quantile of each pixel's time series; (iii) applying a moving three-window median filter; and (iv) scaling the time series between 0 and 1 based on the upper 0.975 quantile of each pixel's time series. The higher elevations of our study area accumulate significant snow that lasts as snow pack sometimes into May and June. We found that setting all NDVI values after the end of February to 'no data,' as in Bischof *et al.*'s [3] procedure, led to fitted curves that portrayed

green-up starting when sometimes more than a metre of snow was still on the ground. Thus, we used the snow cover band from the MOD09A1 data product (500 m spatial and 8-day temporal resolution) to determine how long after February (if any) to keep the NDVI time series floored to the winter value. NDVI for a time series of a given pixel was floored until the snow cover flag was absent for two consecutive 8-day data points. We followed Bischof *et al.*'s [3] fitting procedure using the double logistic curve. Once the double logistic curves were fitted for each pixel's time series for each year, we calculated the first derivative of this curve during the green-up portion and scaled it between 0 and 1, resulting in an IRG curve for each pixel [3]. Finally, we identified NDVI and IRG values associated in time and space with each potential and used target point.

The base model for all populations included the Euclidian distance (in kilometres) and elevation change (in kilometres) between the source and target points, as a measure of energetic cost to moving to the potential target point [29,30]. Elevation was calculated for each point using the US Geological Survey National Elevation Dataset (30 m resolution). For mule deer, moose and elk, we included the difference in slope (in degrees) between the source and target points and aspect (ranging from -1 as southerly to 1 as northerly aspects) of the target point. For bighorn sheep, we included distance to escape terrain (in kilometres) of each target point. We defined escape terrain as areas with a slope more than 30° and a terrain ruggedness index more than 75 (*sensu* [31]). Slope, aspect and terrain ruggedness were calculated based on the 30 m elevation dataset. We also identified land cover types that have been shown to be important in the habitat selection of each species [32–34]. Using the 2011 National Land Cover Database (30 m resolution), we calculated a dummy variable (except in the case of per cent canopy cover) for the following cover types for each species: meadow (including grassland herbaceous and herbaceous wetlands) and shrub for bighorn sheep; per cent canopy cover for mule deer, elk and bison; and deciduous (including deciduous and mixed forests) and wetlands (including woody and herbaceous wetlands) for moose. Finally, to account for overall productivity or biomass at a given habitat patch, aside from its current relative phenological state, we calculated the integrated NDVI value for each target point [14].

(e) Data analysis and model selection

To ensure that green-up was available to individuals for the analysis, we reduced the step database to only steps that occurred when more than 50% of the available and used target points were undergoing spring green-up (i.e. the green-up period). We defined this period for each target point's pixel by identifying the Julian day of the start and end of spring in a given year, calculated by identifying the first and second derivatives of the IRG curve, respectively. We then further minimized any potential biases caused by functional responses in habitat selection (i.e. selection that varies by availability) by removing complete strata of target points where the range of IRG values in available pixels was less than 0.75 (i.e. 75% of the range of available IRG values).

We used a three-step approach to test the assumption that herbivores select habitat patches at peak IRG during the spring green-up period. First, we parametrized a base model for each population, which included distance, elevation, slope, aspect, escape terrain (for bighorn sheep), land cover and integrated NDVI. We then parametrized a second model that included the variables of the base model plus IRG, and assessed the empirical support for adding IRG. Finally, we compared the empirical support of the base and IRG models with a model containing variables from the base model and NDVI, and the base model and NDVI plus NDVI². By calculating the local maximum of the quadratic relationship between relative probability of selection and NDVI,

Table 1. Relative empirical support for selection of habitat patches when at peak IRG during the green-up season. Step selection functions were parametrized by data from two populations each of bighorn sheep, mule deer, elk, moose and bison in western Wyoming and eastern Utah (totalling 463 individuals) between 2004 and 2014. The base model included variables representing habitat attributes known to influence habitat selection of each species (e.g. cover type, elevation, slope, aspect, distance to escape terrain). The model including IRG also contained all variables in the base models. Support was assessed using the QIC, n refers to the number of individuals in a population, n event refers to the number of movement steps used to fit the model and K is the number of model parameters.

pop model	QIC	Δ QIC	n event	K	pop model	QIC	Δ QIC	n event	K
Teton Range bighorn sheep ($n = 20$)					Whiskey Basin bighorn sheep ($n = 8$)				
IRG	9762.6	0.0	1584	7	IRG	1336.1	0.0	211	7
base	9793.4	30.8	1584	6	base	1339.5	3.4	211	6
Green River Basin mule deer ($n = 29$)					SE Wyoming Range mule deer ($n = 46$)				
IRG	8580.6	0.0	1366	7	IRG	12709.5	0.0	2046	7
base	8646.2	65.6	1366	6	base	12716.9	7.4	2046	6
S Greater Yellowstone elk ($n = 119$)					Absaroka mountains elk ($n = 88$)				
base	65747.1	0.0	10 345	6	base	14727.5	0.0	2371	6
IRG	65750.2	3.1	10 345	7	IRG	14727.5	0.0	2371	7
Buffalo Valley moose ($n = 39$)					NE Wyoming Range moose ($n = 64$)				
IRG	7998.6	0.0	1243	8	IRG	8034.3	0.0	1259	8
base	7999.6	1.0	1243	7	base	8120.4	86.1	1259	7
Henry Mountains bison ($n = 46$)					Book Cliffs bison ($n = 4$)				
IRG	15302.9	0.0	2669	7	base	854.7	0.0	156	6
base	15314.3	11.4	2669	6	IRG	855.5	0.8	156	7

we could determine whether animals select the leading or trailing edge of the IRG curve.

Models were parametrized using conditional logistic regression, with each stratum identified as a used point and its paired 25 available target points. We calculated robust SE and 95% CI of parameters using generalized estimating equations, because of temporal autocorrelation and a lack of independence within an individual's movements [35]. All strata for a given individual and year were assigned a unique cluster. We assessed the level of relative empirical support received for each model by calculating the quasi-likelihood under independence criterion (QIC), which accounts for non-independence among observations within a cluster [35]. The level of collinearity among variables within fitted models was assessed by calculating variance inflation factors (VIFs) for all variables (except for NDVI and NDVI² when they were in the same model). VIFs were always less than 2. We validated models for each species with the most empirical support using five-folds cross-validation repeated 100 times, following the framework developed by Fortin *et al.* [36] for step selection functions.

3. Results

For all populations, we established base models that quantified the effect of static habitat attributes on discrete movement steps, while taking into account the distance and elevation change between source and target points. Bighorn sheep generally selected habitat patches that were closer to escape terrain, had higher integrated NDVI values, and were covered by meadow and shrub. Mule deer, elk and bison generally selected less steep habitat patches with lower tree cover, higher integrated NDVI values and a southerly aspect. Moose generally selected flatter habitat patches that were on southerly aspects, and they used patches classified as deciduous or wetland

areas in accordance with their availability (see coefficient tables for models with most empirical support in the electronic supplementary material, appendix C).

The annual green-up period that all populations were exposed to lasted for a mean of 90 days, starting on a mean date of 5 April (electronic supplementary material, appendix D). In all populations, except for both elk populations and Book Cliffs bison, adding IRG to the base model improved model fit by more than 1 QIC unit (mean decrease in QIC = 29.4; table 1). Thus, populations of bighorn sheep, mule deer, moose and Henry Mountains bison selected habitat patches with higher IRG values than available patches (β_{IRG} ranged from 0.02 to 1.40; all lower 95% CI for β_{IRG} did not overlap zero, except for Buffalo Valley moose; figure 1).

Our flexible analysis to evaluate the position on the IRG curve that animals select for revealed that Teton Range bighorn sheep and SE Wyoming Range mule deer selected habitat patches at the trailing edge of the IRG curve (figure 2; electronic supplementary material, appendix E). Except for Book Cliffs bison, which selected habitat patches at the leading edge of the IRG curve, all other populations (Whiskey Basin bighorn sheep, UGRB mule deer, both populations of moose and Henry Mountains bison) selected for patches at the crest of the IRG curve (figure 2; electronic supplementary material, appendix E). The IRG, however, was not always the best variable to explain habitat selection (electronic supplementary material, appendix F). For Teton Range bighorn sheep, SE Wyoming Range mule deer and bison, a model containing NDVI and NDVI² received more empirical support than a comparable model containing IRG (mean of 54.9 QIC units better than a model containing IRG). For both elk populations, a model including NDVI alone best predicted selection of habitat patches (electronic supplementary material, appendix F).

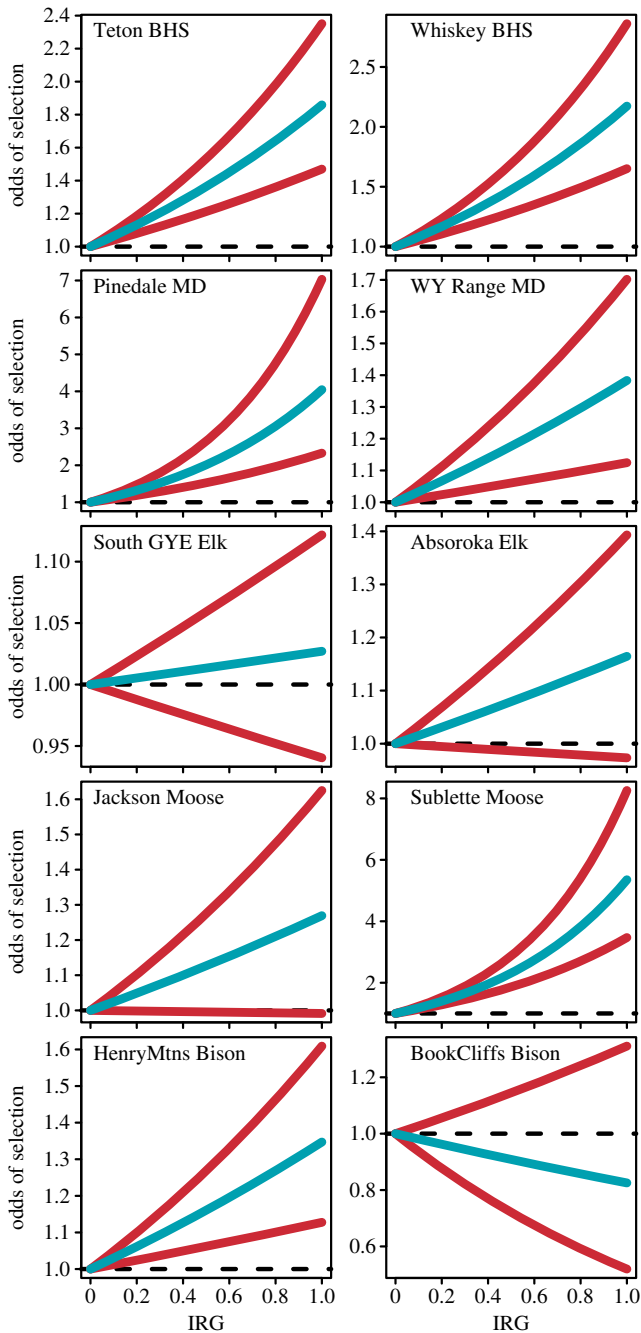


Figure 1. Relationship between odds of selection (with 95% CI in red, reported as odds ratio or exponent of the beta coefficient for IRG) of a habitat patch and its IRG value for two populations each of elk, mule deer (MD), bighorn sheep (BHS), moose and bison in western Wyoming and eastern Utah between 2004 and 2014. Probability of selection based on predicted values of a Step Selection Function parametrized with GPS collar data in each population. (Online version in colour.)

Top models for each population had satisfactory to excellent robustness based on *k*-fold cross-validation: mean observed Spearman rank correlation across all populations was 0.60 (s.d. = 0.24), and mean expected under random selection patterns was -0.18 (s.d. = 0.21; see the electronic supplementary material, appendix G for details).

4. Discussion

We evaluated whether multiple large herbivore species residing in different study areas select habitat patches at peak IRG

in spring and thus track forage at intermediate biomass—a critical assumption of the green wave and forage maturation hypotheses [3]. In support of the GWH, seven of the 10 populations we examined surfed an IRG-indexed green wave by selecting habitat patches with relatively high IRG values (table 1). Nevertheless, five of the seven populations surfed the crest of the IRG wave, whereas the other two surfed the trailing edge of the wave (figure 2). Three populations did not surf the IRG wave at all; both elk populations selected habitat patches at peak NDVI values (far later than peak IRG), and Book Cliffs bison neither selected nor avoided habitat patches when at peak IRG or NDVI. Although variability existed across taxa, our results indicated that habitat selection of temperate large herbivores in spring is indeed influenced by temporal dynamics in habitat quality and patterns of plant phenology that are mainly captured by IRG, thereby helping to enhance our understanding of, and power to predict, animal movement and migration [3].

The IRG metric provides a much-needed tool for researchers and managers seeking to understand how animals track forage resources that change as the growing season progresses across large landscapes. First, assessing change in selection strength for IRG over time may provide insights into how well animals are surfing waves of high-quality forage. Detecting changes in surfing ability can alert researchers and managers to when tracking abilities (i.e. movement) of individuals are threatened by, for example, environmental (e.g. climate change, drought) or land-use (e.g. land development or disturbance) change. Second, from a management and conservation perspective, understanding how large herbivores track waves of forage may help guide habitat improvement projects. For example, after observing a decrease in successful green wave surfing, managers may be able to alter habitat (e.g. remove fencing, or restrict human access) at specific times (i.e. during the green-up season) so that high-quality forage again becomes accessible. Third, assessing how individuals across species and ecosystems select IRG incorporates a key temporal dimension of habitat quality that, heretofore, has been more of a static view and will no doubt inform investigations of optimal foraging, movement and migration [3,20]. Finally, monitoring changes in IRG over the growing season can provide insight into how climate change is affecting the timing and rate of spring green-up, which is emerging as a key component of annual habitat quality, and ultimately, fitness and population performance (e.g. [18,19,37,38]). Incorporating IRG into such analyses will prove useful for quantifying the loss in forage availability—because of climate change or land development—that animals might experience in the future.

The forage maturation and green wave hypotheses have their roots in foraging theory, where individuals who seek to maximize their intake rate of forage will enjoy higher fitness than those who do not [27]. Our results support the notion that movement decisions and spatial distribution of animals are related to energy intake [11], where selecting for sites at peak IRG likely corresponds to a balance between forage biomass and quality. During spring, such a foraging strategy is essential as animals departing winter ranges are often experiencing a net energy deficit [39], and female ungulates that are pregnant will soon face lactation, their highest energy burden of the year. Tracking and selecting habitat patches with high-quality forage is imperative for replenishing fat reserves and acquiring the energy needed to provision young during lactation [39]. We would therefore expect that tracking

ability would be correlated with herbivore fitness. To date, however, we are not aware of a study that has linked the ability of individuals to surf IRG with any fitness correlates. Nevertheless, Searle *et al.* [38] related body condition with the synchrony of NDVI-based rate of green-up within home ranges of mule deer in Colorado, and Hurley *et al.* [40] reviewed relationships between other NDVI metrics and life-history characteristics linked to performance and population abundance. Connecting phenology tracking to forage quality, diet, nutrition and demography is the next step in integrating the forage maturation and green wave hypotheses.

Three of the 10 populations we examined did not select habitat patches at peak IRG, and two others did not select the crest of the IRG wave but selected habitat patches that lagged behind the IRG wave. We propose the following four hypotheses that might explain variation in selection for IRG that we observed. First, species-specific differences may be a function of body size and ruminant physiology, resulting in adaptations in behaviour to exploit forage at phenological states to enhance energy intake. For instance, ruminant herbivores vary along a gradient in morphophysiological feeding types from concentrate selectors (e.g. deer and moose) to grass and roughage eaters (e.g. elk and bison), where concentrate selectors seek out plants with less cell wall and fibre than roughage eaters [41]. Relative to the forage maturation and green wave hypotheses, grass/roughage eaters should select habitat patches at higher biomass, i.e. after peak IRG, than smaller-bodied ungulates. Our results only partially support this hypothesis. Selection of habitat patches by elk, moose and bighorn sheep generally follows such ruminant physiological predictions. Yet, bison should select habitat patches at the highest biomass values, whereas mule deer should be selecting at the most intermediate biomass values—neither appears to do so.

Second, variation in selection for IRG could be explained by measurement error where there is a mismatch between the scale of NDVI data used to quantify forage quality and the scale of habitat selection. NDVI is satellite-derived and quantifies a mean of all photosynthetic activity occurring at a given pixel [14]. In our instance, NDVI is indexing an average greenness or biomass of millions of individual plants that grow within a 250 m patch. Each species (and potentially each population) of large herbivores we examined presumably forages on different plant species and functional groups. If a given herbivore targets a plant species with a phenology different from the mean of all plants in a community or NDVI pixel, then NDVI will not correctly index the phenology of the plant species sought by a given herbivore. Indeed, the relationship between NDVI and biomass can differ (including varying degrees of correlation) among plant communities [42]. Furthermore, the relationship between NDVI and biomass in some vegetation types can be nonlinear [43], complicating coarse indices of vegetation phenology. A comprehensive, species-specific test of whether IRG correctly indexes digestible energy and growth of forage plants—including evaluating the ability of herbivores to mediate patch-based NDVI through diet selection—would complement our study and help determine the ability of large herbivores to surf waves of high-quality food. Nonetheless, individuals of most populations we investigated selected for high IRG, suggesting that until further studies provide refinements, the IRG is a useful tool.

Third, variation in selection for IRG may be caused by a mismatch between movement and optimal plant phenology

driven by site fidelity. All of the animals we monitored portrayed varying levels of fidelity to annual or seasonal ranges, and migration routes. Site fidelity, by means of remembering past experience [44], plays an important role in movement and habitat selection of mobile animals [45]. In some instances, site fidelity can be such a strong adaptive force that animals will use familiar, but poorer-quality habitat patches over ones of higher quality [46]. The ability of animals to track IRG is likely constrained by past experience and knowledge repertoire. A mismatch between the true, current locations of high-quality food and locations of high-quality food in memory is likely exacerbated in areas where weather patterns are rapidly changing, because of climate and land-use change. For example, previous work on the Absaroka elk population in our analysis indicates that rate of spring green-up has increased, leading to shorter spring periods [37]. Shorter springs likely make it difficult for individuals with strong site fidelity to adapt to new environmental conditions. Further, accelerated spring green-up should be a strong factor limiting the ability to assess habitat quality at a given time and successfully surf the green wave. Indeed, the Absaroka elk population did not select habitat patches when at peak IRG, but selected habitat patches when at their peak greenness or highest NDVI values (figure 2).

Finally, variation in selection for IRG may be attributable to inter- and intraspecific interactions (including predation risk) that affect optimal habitat selection [47,48]. For example, female red deer (*C. elaphus*) on the Isle of Rum, Scotland trade-off selecting high-quality resources with diminished lifetime reproductive success because of relatively high density at high-quality sites [49]. Similar density-dependent trade-offs may limit the ability of individuals in some of the populations we examined to select habitat patches when at peak IRG. For animals foraging at the trailing edge of IRG or at peak NDVI, it may be beneficial to forage on vegetation with relatively high biomass to attain rumen fill quickly (i.e. a time-minimizing foraging objective), resulting in extra time to, for example, be more vigilant or maintain social status [50]. Further, anthropogenic land-use change or other disturbance could result in the cessation of the link between foraging cues and their foraging benefits for animals, causing a miscue in timing of movements (e.g. [51]). For example, mule deer within our study area increase movement rate, detour from established migration routes and reduce stopover use in areas of intense human development [52]—all observations that could lead to poor tracking or surfing ability.

In conclusion, remotely sensed measures of vegetation biomass and phenology, such as the NDVI and its derivatives, have proven useful in connecting animal movement to phenological changes in vegetation across large landscapes [3,4,13,20]. Earlier work by Bischof *et al.* [3] made a key step forward by identifying IRG as an index to quantify the spatial and temporal distribution of high-quality forage, and using it to mechanistically link the green wave and forage maturation hypotheses, plant phenology and animal movement. Our multi-species examination largely supports the critical assumption of the green wave and forage maturation hypotheses: herbivores track plants at intermediate biomass by selecting habitat patches at peak IRG. Consistent with the findings of Bischof *et al.* [3], IRG appears to capture broad-scale variation in forage quality that multiple large herbivores can perceive and respond to while foraging. Further, our work highlights species- and population-specific

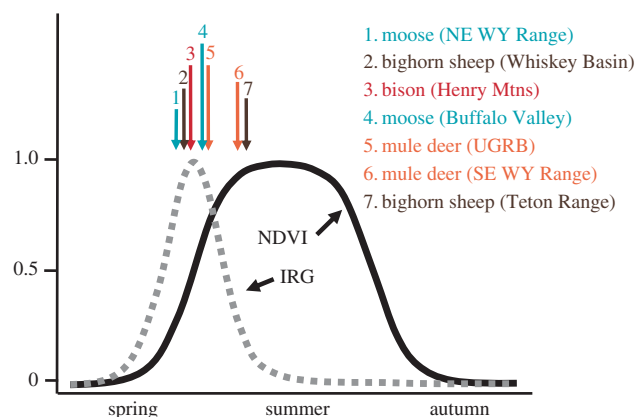


Figure 2. Selection for the leading edge, trailing edge or crest of the IRG wave by mule deer, bighorn sheep and moose in western Wyoming, and bison in eastern Utah between 2004 and 2014. The location on the wave was determined by calculating the local maximum of the quadratic relationship between relative probability of selection and NDVI. Probability of selection was based on a step selection function parametrized with GPS collar data in each population. (Online version in colour.)

variation in the position on the IRG wave that individuals and populations select. We hypothesize that variation in phenology tracking is related to differences in foraging strategies among taxa, phenological mismatches and other factors that constrain individuals from optimally tracking plant phenology. Unravelling differences in selection for IRG among species, populations and individuals should prove fruitful in understanding how landscape- and climate-related changes affect gradients in plant phenology that animals rely on, and for identifying when habitat

manipulation will benefit herbivores that move across large landscapes.

Data accessibility. Raw GPS collar data used in this analysis can be accessed via the Wyoming Migration Database and Viewer located at migrationinitiative.org.

Authors' contributions. J.A.M. and M.J.K. conceived the idea. J.A.M., M.J.K., K.L.M., E.O.A. and M.M.H. designed the study. J.A.M. conducted all analyses and wrote the manuscript. Datasets were collected and managed by all authors and cooperators. All authors contributed to revisions and gave final approval for publication.

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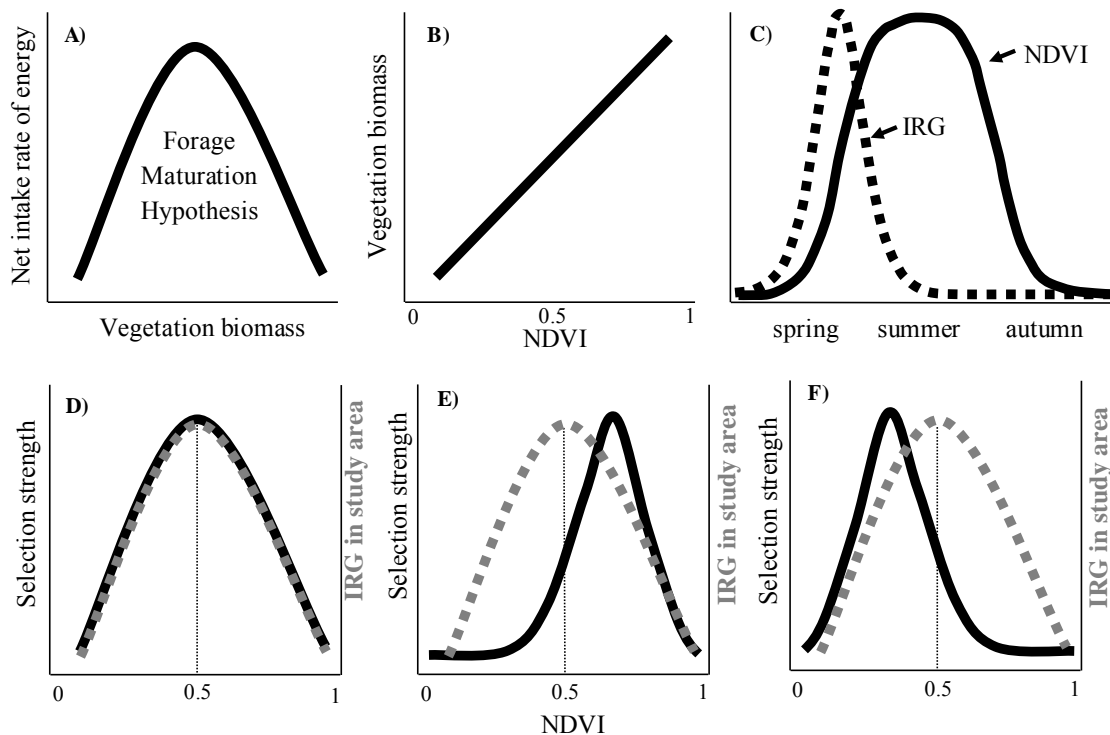
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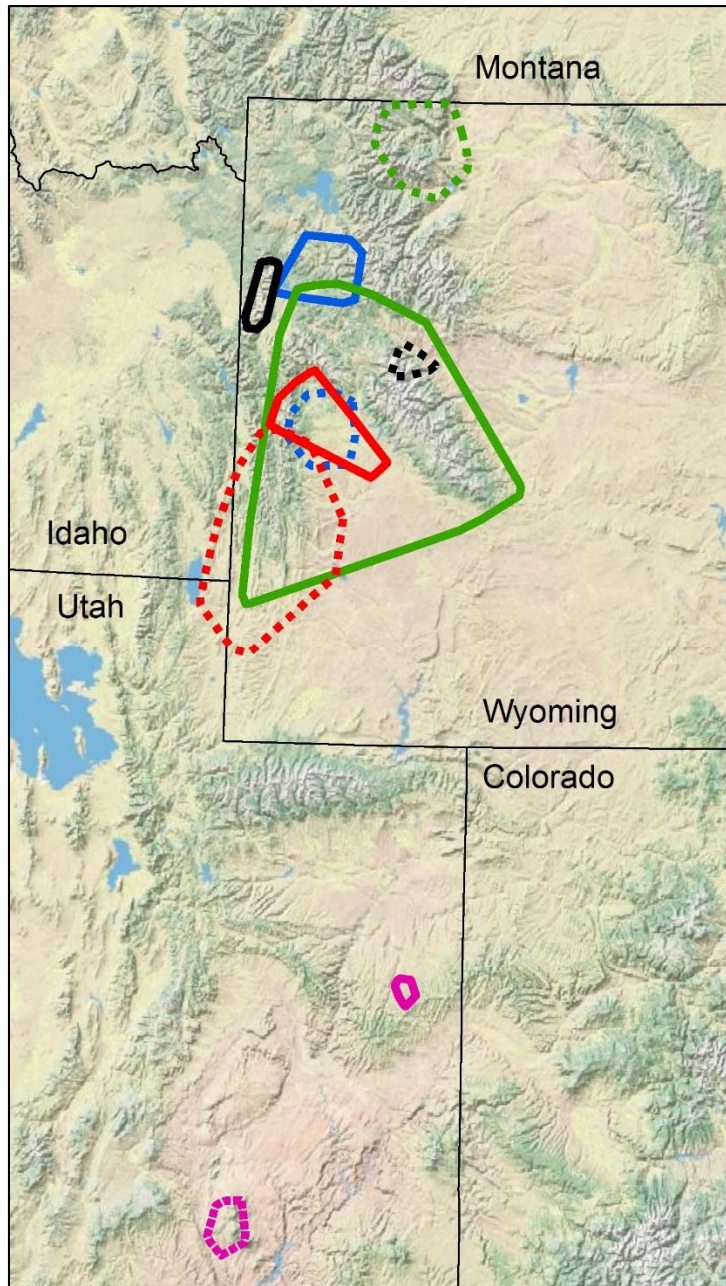
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Appendix A. Conceptual chart depicting relationships between the forage maturation hypothesis, vegetation biomass, the Normalized Difference Vegetation Index (NDVI), the Instantaneous Rate of Green-up (IRG), and selection for intermediate values of NDVI. The forage maturation hypothesis (A) purports that herbivores will maximize their net rate of energy intake by eating vegetation at intermediate biomass, because as biomass increases, plants become fibrous and limit the intake rate of energy. NDVI can be a reliable correlate of vegetation biomass (B), and is often used as an index of available green biomass. In most temperate ecosystems, NDVI increases during the spring growing season, then decreases in late summer and autumn (C). The relationship between time (a calendar year) and NDVI can be quantified using a double logistic curve (NDVI in C) fit to a pixel-level, time series of NDVI data. The first derivative of this curve during spring generates the IRG curve (C), which tracks the rate of change of NDVI, reaching its peak during the rapid green-up of vegetation in spring when vegetation is assumed to be at intermediate biomass. The relationship between the strength of selection for a certain habitat patch and NDVI (D, E, F; black lines) is currently unknown. Herbivores that strongly select for IRG will inherently select habitat patches with NDVI values that are half their maximum NDVI (D). Deviations from strong selection for IRG might exist for different taxa or habitats, constituting animals that select the trailing (E, black line) or leading (F, black line) edge of the IRG curve.



Appendix B. Map of study area in western U.S.A. indicating a 95% MCP around each of the 10 study populations: bighorn sheep (black), mule deer (red), elk (green), moose (blue), and bison (pink). State boundaries demarcated by black lines.



Appendix C. Coefficient tables for movement models with most empirical support in each population. Movement models were parameterized by data from two populations each of bighorn sheep, mule deer, elk, moose, and bison in western Wyoming and eastern Utah (totaling 463 individuals) between 2004 and 2014. The movement model was a Step Selection Function, parameterized using conditional logistic regression and general estimating equations. Empirical support was assessed using the Quasi-likelihood under independence criterion (QIC).

Bighorn sheep (Teton range)

Variable	β	SE	z	P
Meadow	0.885	0.104	8.473	< 0.001
Shrub	0.582	0.104	5.575	< 0.001
Distance	0.328	0.028	11.842	< 0.001
Elevation	3.149	0.205	15.358	< 0.001
Distance to escape terrain	-0.087	0.027	-3.231	0.001
Integrated NDVI	0.014	0.012	1.113	0.266
NDVI	5.698	0.667	8.545	< 0.001
NDVI ²	-3.353	0.576	-5.820	< 0.001

Bighorn sheep (Whiskey Basin)

Variable	β	SE	z	P
Meadow	0.589	0.345	1.706	0.088
Shrub	0.483	0.367	1.317	0.188
Distance	-0.195	0.067	-2.930	0.003
Elevation	1.670	0.532	3.140	0.002
Distance to escape terrain	-0.076	0.128	-0.597	0.550
Integrated NDVI	0.028	0.022	1.255	0.209
IRG	0.776	0.167	4.643	< 0.001

Mule deer (Upper Green River Basin)

Variable	β	SE	z	P
% tree cover	-0.013	0.006	-2.287	0.022
Distance	0.015	0.034	0.459	0.646
Elevation	0.003	0.460	0.007	0.994
Slope	0.012	0.007	1.867	0.062
Aspect	-0.085	0.087	-0.976	0.329
Integrated NDVI	0.084	0.020	4.251	< 0.001
IRG	1.398	0.336	4.160	< 0.001

Mule deer (SE Wyoming Range)

Variable	β	SE	z	P
% tree cover	-0.013	0.003	-4.369	< 0.001
Distance	0.082	0.013	6.365	< 0.001
Elevation	-0.235	0.453	-0.519	0.604
Slope	0.031	0.006	5.525	< 0.001
Aspect	-0.641	0.077	-8.297	< 0.001
Integrated NDVI	0.020	0.016	1.310	0.190
NDVI	2.003	0.548	3.656	< 0.001
NDVI ²	-1.250	0.497	-2.516	0.012

Elk (S greater Yellowstone ecosystem)

Variable	β	SE	z	P
% tree cover	-0.012	0.001	-10.229	< 0.001
Distance	0.061	0.018	3.439	< 0.001
Elevation	0.150	0.190	0.792	0.428
Slope	-0.021	0.002	-8.557	< 0.001
Aspect	-0.368	0.026	-14.051	< 0.001
Integrated NDVI	-0.006	0.006	-0.979	0.328
NDVI	0.794	0.119	6.693	< 0.001

Elk (Absaroka)

Variable	β	SE	z	P
% tree cover	-0.023	0.003	-7.734	< 0.001
Distance	0.068	0.024	2.901	0.004
Elevation	-0.456	0.230	-1.987	0.047
Slope	-0.039	0.003	-11.429	< 0.001
Aspect	-0.089	0.077	-1.155	0.248
Integrated NDVI	0.026	0.016	1.654	0.098
NDVI	0.494	0.241	2.054	0.040

Moose (Buffalo valley)

Variable	β	SE	z	P
Deciduous forest	0.056	0.234	0.242	0.809
Wetlands	0.167	0.183	0.911	0.362
Distance	0.070	0.030	2.299	0.022
Elevation	-2.444	0.524	-4.660	< 0.001
Slope	-0.027	0.008	-3.202	0.001
Aspect	-0.340	0.080	-4.268	< 0.001
Integrated NDVI	0.018	0.013	1.381	0.167
IRG	0.238	0.150	1.587	0.113

Moose (NE Wyoming Range)

Variable	β	SE	z	P
Deciduous forest	0.219	0.362	0.605	0.546
Wetlands	0.100	0.111	0.897	0.370
Distance	0.283	0.068	4.158	< 0.001
Elevation	-5.996	1.354	-4.429	< 0.001
Slope	-0.033	0.016	-2.008	0.045
Aspect	-0.075	0.073	-1.022	0.307
Integrated NDVI	0.027	0.024	1.116	0.264
IRG	1.678	0.264	6.366	< 0.001

Bison (Henry mountains)

Variable	β	SE	z	P
% tree cover	-0.002	0.002	-1.080	0.280
Distance	-0.053	0.023	-2.262	0.024
Elevation	0.424	0.182	2.327	0.020
Slope	-0.085	0.006	-15.052	< 0.001
Aspect	-0.219	0.049	-4.519	< 0.001
Integrated NDVI	0.036	0.010	3.505	< 0.001
NDVI	1.687	0.443	3.808	< 0.001
NDVI ²	-1.657	0.487	-3.400	< 0.001

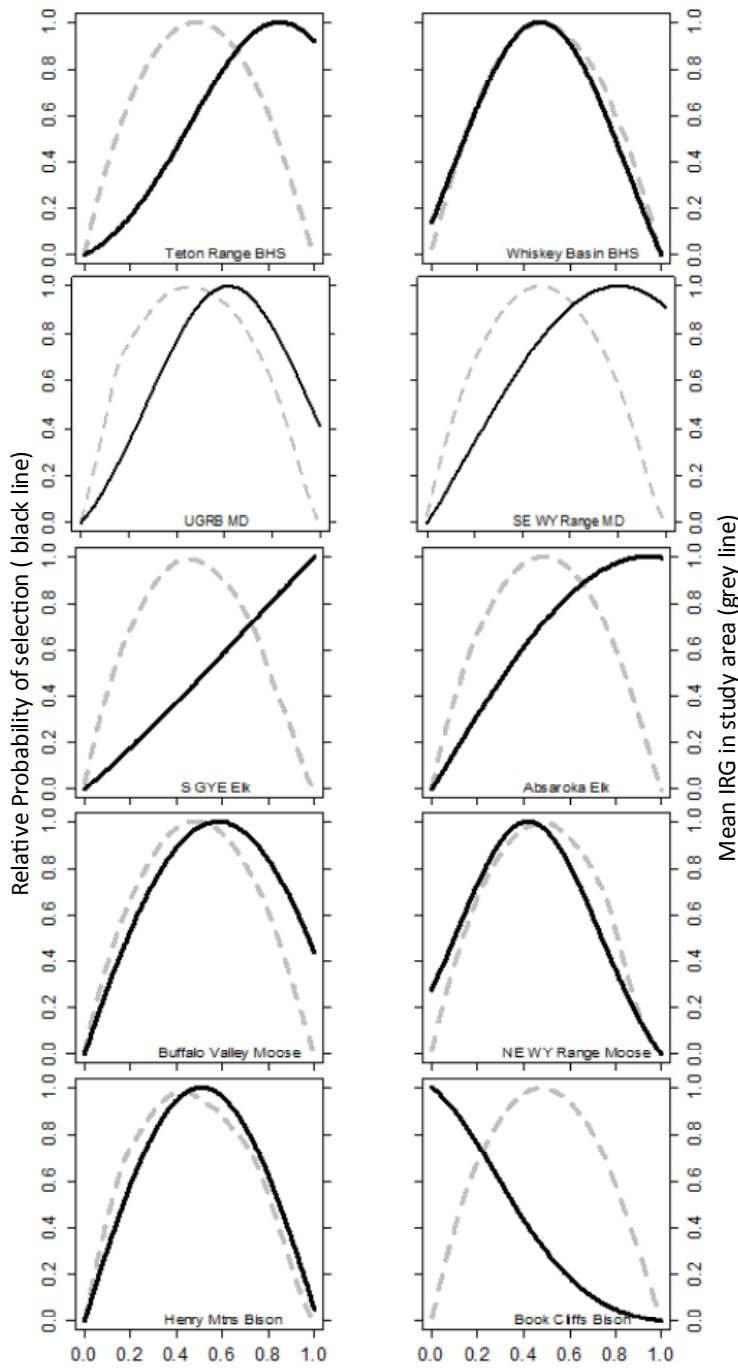
Bison (Book cliffs)

Variable	β	SE	z	P
% tree cover	-0.074	0.021	-3.538	< 0.001
Distance	0.167	0.030	5.644	< 0.001
Elevation	-0.718	0.254	-2.822	0.005
Slope	-0.113	0.016	-7.256	< 0.001
Aspect	-0.224	0.246	-0.912	0.362
Integrated NDVI	0.270	0.044	6.087	< 0.001
NDVI	-0.711	1.635	-0.435	0.664
NDVI ²	-3.255	0.540	-6.027	< 0.001

Appendix D. Mean annual green-up period that individuals were exposed to for two populations each of bighorn sheep, mule deer, elk, moose, and bison in western Wyoming and eastern Utah (totaling 463 individuals) between 2004 and 2014. We defined the green-up period for each used pixel in each year of investigation by identifying the Julian day of the start and end of spring, calculated as the minimum and maximum of the first and second, second derivatives, respectively, of a fitted double logistic curve to the NDVI time series. We calculated the proportion of each population that was migratory by plotting each individual-year movement trajectories and net squared displacement over time, and manually identifying whether there was distinct summer and winter ranges [1, 2].

Species	Population	Proportion migratory	Start date of green-up	Duration of green-up
Bighorn sheep				
	Teton Range	0.02	1 June	64
	Whiskey Basin	0.25	28 April	55
Mule deer				
	Upper Green River Basin	1.00	15 March	110
	SE Wyoming Range	0.96	12 March	112
Elk				
	S Greater Yellowstone	0.72	29 March	91
	Absaroka mountains	0.49	11 March	127
Moose				
	Buffalo Valley	0.81	29 April	48
	NE Wyoming Range	0.30	23 April	64
Bison				
	Henry Mountains	0.52	22 March	143
	Book Cliffs	0.50	8 March	84

Appendix E. Relationship between mean Normalized Difference Vegetation Index (NDVI) and mean Instantaneous Rate of Green-up (IRG) within each study area (grey dashed lines), and relationship between mean predicted relative probability of selection (black lines, based on model with NDVI and $NDVI^2$) of a habitat patch and its NDVI value for two populations each of elk, mule deer (MD), bighorn sheep (BHS), moose, and bison in western Wyoming and eastern Utah between 2004 and 2014. Probability of selection was based on predicted values of a Step Selection Function parameterized with GPS collar data in each population.



Appendix F. Relative empirical support for four movement models of selection for habitat patches by large herbivores during the green-up season. Movement models were parameterized by data from two populations each of bighorn sheep, mule deer, elk, moose, and bison in western Wyoming and eastern Utah (totaling 463 individuals) between 2004 and 2014. The Base model included variables representing habitat attributes known to influence habitat selection of each species (e.g., cover type, elevation, slope, aspect, distance to escape terrain). All other models included variables from the base model. The models were specified follows: NDVI - included a variable that contains spatially and temporally explicit values of fitted (and scaled) Normalized Difference Vegetation Index (NDVI) curves over time; NDVI² – included a quadratic form of the NDVI values, where NDVI and NDVI² was included in the model; and IRG – included the Instantaneous Rate of Green-up calculated as the first derivative of the fitted NDVI curve over time. The movement model was a Step Selection Function parametrized using conditional logistic regression. We calculated robust SE and 95% CI of parameters using generalized estimating equations, because of temporal autocorrelation and a lack of independence within an individual's movements. Support was assessed using the Quasi-likelihood under independence criterion (QIC), and n refers to the number of individuals in a population, n event refers to the number of movement steps used to fit the model, and K is the number of model parameters.

Pop	Model	QIC	Δ QIC	<i>n</i> event	K	Pop	Model	QIC	Δ QIC	<i>n</i> event	K
Teton Range bighorn sheep (<i>n</i> = 20)						Whiskey Basin bighorn sheep (<i>n</i> = 8)					
	NDVI ²	9615.3	0.0	1584	8		IRG	1336.1	0.0	211	7
	NDVI	9669.5	54.2	1584	7		NDVI ²	1336.8	0.7	211	8
	IRG	9762.6	147.3	1584	7		NDVI	1339.4	3.3	211	7
	Base	9793.4	178.1	1584	6		Base	1339.5	3.4	211	6
Green River Basin mule deer (<i>n</i> = 29)						SE Wyoming Range mule deer (<i>n</i> = 46)					
	IRG	8580.6	0.0	1366	7		NDVI ²	12700.8	0.0	2046	8
	NDVI ²	8587.2	6.6	1366	8		NDVI	12707.0	6.2	2046	7
	NDVI	8618.0	37.4	1366	7		IRG	12709.5	8.7	2046	7
	Base	8646.2	65.6	1366	6		Base	12716.9	16.1	2046	6
S Greater Yellowstone elk (<i>n</i> = 119)						Absaroka mountains elk (<i>n</i> = 88)					
	NDVI	65654.8	0.0	10345	7		NDVI	14724.1	0.0	2371	7
	NDVI ²	65656.1	1.3	10345	8		NDVI ²	14724.2	0.1	2371	8
	Base	65747.1	92.3	10345	6		Base	14727.5	3.4	2371	6
	IRG	65750.2	95.4	10345	7		IRG	14727.5	3.4	2371	7
Buffalo Valley moose (<i>n</i> = 39)						NE Wyoming Range moose (<i>n</i> = 64)					
	IRG	7998.6	0.0	1243	8		IRG	8034.3	0.0	1259	8
	Base	7999.6	1.0	1243	7		NDVI ²	8067.2	33.0	1259	9
	NDVI ²	8001.2	2.6	1243	9		NDVI	8089.7	55.5	1259	8
	NDVI	8002.3	3.7	1243	8		Base	8120.4	86.1	1259	7
Henry Mountains bison (<i>n</i> = 46)						Book Cliff bison (<i>n</i> = 4)					
	NDVI ²	15294.3	0.0	2669	8		NDVI ²	848.5	0.0	156	8
	IRG	15302.9	8.6	2669	7		NDVI	851.2	2.7	156	7
	Base	15314.3	20.1	2669	6		Base	854.7	6.1	156	6
	NDVI	15314.6	20.3	2669	7		IRG	855.5	7.0	156	7

Appendix G. Mean (and SD) Spearman rank correlation coefficients of the match between predicted versus withheld observed data based on a 5-folds cross-validation repeated 100 times for the Step Selection Function in each population with the most empirical support. Step Selection Functions were parameterized with data from two populations each of bighorn sheep, mule deer, elk, moose, and bison in western Wyoming and eastern Utah (totaling 463 individuals) between 2004 and 2014. n refers to the number of GPS collared individuals in the population. We conducted cross-validation following the methods outlined in Fortin et al. [3] for the use of conditional logistic regression to parametrize Step Selection Functions.

Species	Population	Observed		Random	
		Mean	SD	Mean	SD
Bighorn sheep					
	Teton Range ($n = 20$)	0.88	0.04	-0.05	0.76
	Whiskey Basin ($n = 8$)	0.28	0.15	-0.11	0.46
Mule deer					
	Upper Green River Basin ($n = 29$)	0.33	0.15	-0.18	0.24
	SE Wyoming Range ($n = 46$)	0.78	0.07	-0.22	0.43
Elk					
	S Greater Yellowstone ($n = 119$)	0.93	0.02	-0.11	0.82
	Absaroka mountains ($n = 88$)	0.85	0.05	-0.08	0.61
Moose					
	Buffalo Valley ($n = 39$)	0.53	0.13	-0.03	0.26
	NE Wyoming Range ($n = 64$)	0.60	0.12	-0.02	0.57
Bison					
	Henry Mountains ($n = 46$)	0.36	0.07	-0.75	0.13
	Book Cliffs ($n = 4$)	0.49	0.10	-0.21	0.40

[1] Fryxell, J.M., Greever, J. & Sinclair, A. 1988 Why are migratory ungulates so abundant? *Am. Nat.*, 781-798.

[2] Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. & Ericsson, G. 2011 A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* **80**, 466-476.

[3] Fortin, D., Fortin, M.E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. 2009 Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology* **90**, 2480-2490.