

Research

Green-wave surfing increases fat gain in a migratory ungulate

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Each spring, migratory herbivores around the world track or ‘surf’ green waves of newly emergent vegetation to distant summer or wet-season ranges. This foraging tactic may help explain the great abundance of migratory herbivores on many seasonal landscapes. However, the underlying fitness benefits of this life-history strategy remain poorly understood. A fundamental prediction of the green-wave hypothesis is that migratory herbivores obtain fitness benefits from surfing waves of newly emergent vegetation more closely than their resident counterparts. Here we evaluate whether this behavior increases body-fat levels – a critically important correlate of reproduction and survival for most ungulates – in elk *Cervus elaphus* of the Greater Yellowstone Ecosystem. Using satellite imagery and GPS tracking data, we found evidence that migrants ($n = 23$) indeed surfed the green wave, occupying sites 12.7 days closer to peak green-up than residents ($n = 16$). Importantly, individual variation in surfing may help account for up to 6 kg of variation in autumn body-fat levels. Our findings point to a pathway for anthropogenic changes to the green wave (e.g. climate change) or migrants’ ability to surf it (e.g. development) to impact migratory populations. To explore this possibility, we evaluated potential population-level consequences of constrained surfing with a heuristic model. If green-wave surfing deteriorates by 5–15 days from observed, our model predicts up to a 20% decrease in pregnancy rates, a 2.5% decrease in population growth, and a 30% decrease in abundance over 50 years. By linking green-wave surfing to fitness and illustrating potential effects on population growth, our study provides new insights into the evolution of migratory behavior and the prospects for the persistence of migratory ungulate populations in a changing world.

Keywords: *Cervus elaphus*, elk, instantaneous rate of green-up (IRG), migration, movement ecology, ungulate nutrition, phenology, Rocky Mountains, Yellowstone National Park.



Introduction

Animal movements are an integral part of the fabric of life on Earth, sustaining the reproduction and survival of diverse species and coupling distinct habitats and ecosystems (Bauer and Hoyer 2014). Yet studies identifying how animal movements influence individual fitness are rare (Nathan et al. 2008). Quantifying the fitness consequences of animal movement is important to understanding how they evolve, how they underpin foraging strategies, and how they may enable or constrain the ability of animals to respond to environmental changes.

Mass ungulate migrations are among the most dramatic and important of animal movements, supporting carnivore and scavenger diversity and altering large-scale patterns of plant growth and nutrient cycling (Bauer and Hoyer 2014). Seminal studies have proposed that the primary driver of ungulate migration is the fitness benefit associated with feeding on emerging vegetation (Fryxell et al. 1988, Fryxell and Sinclair 1988), conceptualized as the “forage maturation hypothesis” (FMH). The FMH predicts that ungulates should consume plants of intermediate growth, because before this growth stage, overall biomass is low, whereas after this growth stage, the prevalence of structural tissue reduces digestibility (McNaughton 1985, Fryxell 1991, Hebblewhite et al. 2008). The FMH has received substantial empirical support (Albon and Langvatn 1992, Hebblewhite et al. 2008). Though migrating ungulates may also benefit from reduced predation risk (Fryxell and Sinclair 1988), we focus here on the FMH as the proposed primary driver of ungulate migration behavior in temperate landscapes.

The “green wave hypothesis” (GWH) (Drent et al. 1978) can be viewed as the spatial formulation of the FMH (Merkle et al. 2016), predicting that migrating herbivores closely track intermediate plant biomass along latitudinal and elevational gradients during spring (i.e. they “surf” green waves of forage) (Sawyer and Kauffman 2011, Bischof et al. 2012). The advent of satellite imagery and GPS tracking have greatly advanced our ability to test the GWH by evaluating linkages between the green wave and animal movements. Several recent studies of mountain ungulates have developed indices of overall spring and summer greenness using the satellite-derived normalized difference vegetation index (NDVI), then demonstrated associations of those indices with proxies of nutrition and fitness (Pettorelli et al. 2007, Hamel et al. 2009). Other studies have examined the influence of the green wave on the progression of spring migrations at much finer scales, showing that some birds (van der Graaf et al. 2006) and North American ungulates (Sawyer and Kauffman 2011, Merkle et al. 2016, Aikens et al. 2017) closely surf the green wave through spring, whereas others ‘jump’ to summer range (Bischof et al. 2012, Lendrum et al. 2014, Si et al. 2015). This growing body of work shows that some taxa closely track intermediate plant growth and supports the GWH, yet the expected benefits of fine-scale surfing to individual fitness have not been quantified. Testing the effect of green-wave

surfing on fitness is important to building a robust theory for the evolution and persistence of migration.

The link between green-wave surfing and individual fitness may also have implications for the conservation and management of migratory populations. Climate and land-use change have the potential to alter landscapes such that herbivores cannot surf green waves of forage effectively. Drought and climate change may alter phenological events such as spring snowmelt and green-up (Badeck et al. 2004), which are drivers of ungulate migration (White et al. 2010, Monteith et al. 2011, Singh et al. 2012). Meanwhile, human development, especially physical barriers, may constrain the ability of migrants to track waves of green-up optimally (Sawyer et al. 2013, Lendrum et al. 2014). Thus, exploring the link between green-wave surfing and fitness may help us understand why migratory ungulates are declining in some altered climate regimes and landscapes (Bolger et al. 2008, Harris et al. 2009), and inform future mitigation and restoration efforts.

We tested two predictions of the GWH: that ungulates surf the green wave, and that surfing increases individual fitness. In a partially migratory elk population of the Greater Yellowstone Ecosystem (GYE; Fig. 1), we evaluated the link between individual movements during the growing season and body-fat levels at the end of the growing season (i.e. in September; $n=39$). Body-fat levels in autumn are known to influence conception, pregnancy, and overwinter survival in elk and other ungulates (Cook et al. 2004, Parker et al. 2009). To estimate how well individuals surfed, we calculated the number of days either ahead or behind the date of peak rate of green-up that an individual occupied a given site. First, we evaluated whether migratory individuals, which should be able to access a longer green wave, surfed the wave more closely than their resident counterparts. Second, we evaluated whether individuals that surfed more successfully gained more fat. Finally, we used a heuristic model to explore whether hypothetical constraints on green-wave surfing might influence population performance via alterations in the reproductive rate, mediated by autumn fat. This integrative approach provides new insight into the drivers of migratory behavior – and the potential impacts of human activity on migratory populations.

Methods

Study area

Our sample focused on the Clarks Fork elk herd, a partially migratory population of approximately 4500 individuals in the Absaroka Mountains of Wyoming, USA. Migratory and resident elk in this herd winter in the foothills and valleys (mean = 1769 m in elevation) northwest of Cody, WY, an area characterized by sagebrush-steppe and spruce-fir forests. In spring, individuals migrate 40–60 km to high-elevation (mean = 2588 m) summer ranges inside Yellowstone National

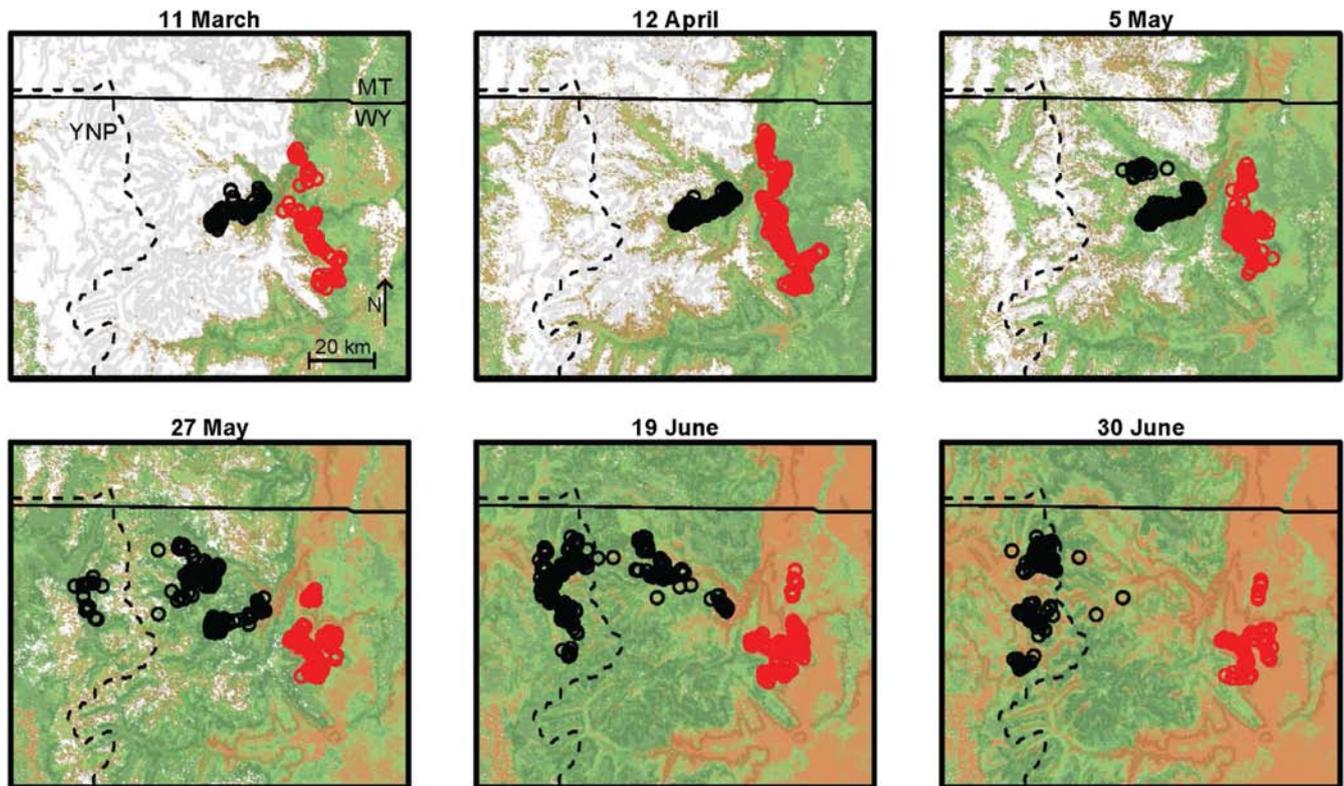


Figure 1. A chronosequence of maps depicting snow, green-up, and the daily locations of resident (red circles) and migratory (black circles) elk from 2008 in the study area in northwestern Wyoming, USA. Black line represents the border between Wyoming (WY) and Montana (MT), while the dotted black line represents the northeastern boundary of Yellowstone National Park (YNP). White coloration represents snow cover (or pre-green-up), while dark green represents high rate of green-up (i.e. high IRG values) and brown represents slow rate of green-up or vegetation senescence. There is an elevation gradient from right (low elevation) to left (high elevation), and the grey lines in the background represent elevation contours.

Park (YNP), an area characterized by open grasslands and conifer forests (Fig. 1).

Capture and animal characteristics

We captured adult female elk via helicopter net-gunning in January 2007 and 2008 and fitted them with GPS collars. We recaptured a subset of GPS-collared individuals via helicopter darting to estimate body fat just before the growing season (March 2008 and 2009) and body fat and lactation status after the growing season (early September 2008 and 2009). We classified females as lactating if milk could be extracted from the udder. During initial captures, a vestigial canine was extracted for ageing via cementum annuli. Percent ingesta-free body fat was estimated using an arithmetic combination of body condition score and rump-fat thickness allometrically scaled using nonpregnant body mass (Cook et al. 2010). Further details on capture and handling protocols are provided in Middleton et al. (2013a). Our analysis was based on 22 individuals in 2008 and 17 individuals in 2009 that had complete GPS collar data during the growing season and corresponding autumn body fat and lactation estimates. We manually defined each individual's annual movements as 'migratory' ($n=23$) or 'resident' ($n=16$) based on whether

the individual had discrete seasonal ranges in a given year (Fryxell and Sinclair 1988).

Quantifying surfing by individual elk

We quantified green-wave surfing based on an index of how well individuals matched their movements to intermediate biomass levels (i.e. peak forage quality). Intermediate biomass was indexed by the instantaneous rate of green-up (IRG). We first calculated NDVI for the entire study area using surface reflectance bands 1 and 2 (250m spatial and 8-day temporal resolution) from the MOD09Q1 data product from the MODIS terra satellite. We then followed the methods of Bischof et al. (2012) and Merkle et al. (2016) to smooth and scale the NDVI data and calculate IRG for each cell in each year. The IRG is calculated as the first derivative of a fitted curve to a time series of NDVI data for a given cell, and provides a modest to robust index of high-quality forage at intermediate biomass (Bischof et al. 2012), including in the GYE (Garrouette et al. 2016). We estimated the date (in Julian days) of peak IRG for each cell in each year of the study. Then for each observed elk GPS location, we identified the IRG cell it was located in and calculated the number of days from peak IRG as the absolute value of the

difference between the date occupied and the date of peak IRG in Julian days.

This index of green-wave surfing was calculated following the methods of Aikens et al. (2017). First, we sampled one GPS location per day to minimize pseudoreplication and to minimize the effects of temporal autocorrelation within an individual's GPS locations. We then identified the period of time in which spring green-up was 'available' to the population each year. This period was defined, for each year, as the 0.05 quantile of the date spring began, and the 0.95 quantile of the date spring ended for the IRG pixels containing GPS locations of all individuals monitored in a given year. Julian days of the start and end of spring were calculated as the minimum and maximum of the first and second derivatives of the fitted IRG curve, respectively. Spring green-up for the landscape used by our elk population lasted from 24 March to 18 July in 2008, and from 21 March to 11 July in 2009. Our surfing index was estimated for each individual in each year as the absolute value of mean days from peak IRG during the period when green-up was available.

Statistical analyses

To test whether migratory elk were more successful surfers than residents, we conducted an analysis of variance of the surfing index based on whether each individual was classified as resident or migratory. We used multivariate linear regression to test whether increased surfing results in higher percent body fat at the end of the growing season, while taking into account other variables expected to influence fat dynamics. We modeled September percent body fat as a function of green-wave surfing during the growing season, lactation status, a quadratic form of age ($\text{Age} + \text{Age}^2$) to account for senescence, and migration status (i.e. migrant or resident). We assessed the empirical support for the influence of surfing on September fat by comparing Akaike information criterion (AIC; Burnham and Anderson 2002) of parameterized models with and without the surfing index, and by investigating whether the 95% confidence intervals of the surfing coefficient overlapped zero. Prior to parameterizing the model, we examined univariate relationships between body fat and each variable, and found that all variables were significant predictors at the 0.05 alpha level. We then screened for correlation, and found that migratory status and the surfing index were correlated (Pearson correlation of -0.81). Therefore, we calculated variance inflation factors (VIFs) for our multivariate model (without the quadratic term for age), and found that all variables had VIFs < 3.6 . Finally, we verified that the sign of each coefficient in the multivariate model was in the same direction as each univariate relationship, and that removing any individual variable from the multivariate model did not change the direction of the remaining relationships. To verify that September percent fat was indicative of fat gain during the growing season, not body condition being carried over from prior to the growing season, we regressed September body fat estimates on the previous March body fat estimates for 22 of the 39 individual-years where data were available, accounting for lactation status.

We found no statistically significant relationship between the two values ($t_{22} = 1.41$, $p = 0.17$. $R^2 = 0.08$).

The effect of surfing on population performance

We developed a heuristic model based on a matrix modeling framework (Caswell 2001) to explore how hypothetical changes in surfing might influence population performance by altering pregnancy rates. We simulated elk population dynamics based on two age classes – yearlings (1 year old) and adults (> 1 year old) – by constructing a female-based, pre-birth pulse, age structured matrix with a one-year projection interval. We assumed that the sex ratio at birth was 50:50, calf survival did not differ between the sexes, there was no intrauterine mortality, and females only gave birth to a single calf (Johnson 1951, Kittams 1953, Raithel et al. 2007). At each iteration of the simulation, the number of adults in the population at time t was calculated as

$$Na_t = Na_{t-1} \times \hat{S}_a + Nyr_{t-1} \times \hat{S}_{yr}$$

and the number of yearlings in the population at time t was calculated as

$$Nyr_t = Na_{t-1} \times \hat{S}_a \times Preg_t \times \hat{S}_c \times 0.5$$

We calculated adult annual survival as $\hat{S}_a = (0.72 \times \hat{S}_{pa}) + (0.10 \times \hat{S}_{oa}) + (0.05 \times \hat{S}_{sa})$, using prime age (pa), old age (oa), and senescent (sa) survival and age structure data reported in Raithel et al. (2007). Calf \hat{S}_c and yearling \hat{S}_{yr} survival rates were also specified as reported in Raithel et al. (2007). Probability of being pregnant in September was calculated based on a relationship with September percent body fat Fat using the logistic equation reported in (Cook et al. 2004),

$$Preg_t = \frac{\exp(-4.715 + 0.594 \times Fat_t)}{1 + \exp(-4.715 + 0.594 \times Fat_t)}$$

where Fat_t was derived from predicted values of our multivariate linear model of September percent body fat.

We simulated populations for 50 years, with starting number of adults $Na_0 = 2520$ and yearlings $Nyr_0 = 542$ derived from mean population size, male:female ratios, and calf:cow ratios estimated in winter between 2007 and 2011 for our study area (Wyoming Game and Fish Dept, unpubl.). We simulated four different populations. The first was based on predicted September percent body fat values derived from our multivariate model with mean and SE (23.61 ± 1.25) of the observed surfing index, and observed mean values of age, proportion lactating, and proportion migratory in our population. The second through fourth were based on adding 5, 10 and 15 days to the average days from peak green up (based on approximately half the mean observed surfing index), while holding all other variables constant. Because of the threshold (logistic) relationship between body fat and pregnancy, whereby there are no associated increases in probability of

pregnancy as body fat increases above $\sim 12\%$ (Cook et al. 2004), we took a conservative approach to incorporating predicted body fat values and also included uncertainty in the predicted relationship between surfing ability and September body fat. For each iteration of each simulation, we identified a random bootstrapped variate of predicted September body fat based on error identified in coefficient estimates of the multivariate model. Each population was simulated 1000 times.

Results

Elk generally surfed the green wave, as measured by how well they tracked the peak IRG during the green-up period. On average, elk lagged behind the IRG curve as they often occupied habitat patches just after peak IRG (Fig. 2a). In comparison to resident individuals, migratory elk were able to prolong exposure to habitat patches at peak forage quality (Fig. 2a). During the period when spring green-up was available to the population, migratory elk used sites on average 12.7 days closer to peak IRG than did their resident counterparts (Fig. 2b).

Elk body-fat levels in September (i.e. after the growing season) varied widely (from 8 to 22%) among individual female elk. Based on a multivariate linear model, female elk were fatter in September when they were not lactating, when at an intermediate age, and when they were migratory as opposed to resident. Adding an index of green-wave surfing to the model had empirical support as AIC decreased by 2.75 units, and the model including the index had 0.8 of the AIC weight. When female elk better timed their movements with

peak IRG during the growing season, they were fatter the following September (Table 1, Fig. 2c). Our model explained approximately 62% of the observed variation in percent body fat in September. Importantly, this result was largely driven by non-lactating elk; for elk that carried the cost of lactation, we did not detect an influence of surfing on autumn fat levels.

Our population simulations, based on a heuristic model of the relationship between surfing, fat and pregnancy, suggested that the potential effects of green-wave surfing on fat gain and pregnancy were large enough to influence population growth (Fig. 3). With average elk vital rates, along with mean age, proportion lactating, proportion migratory (held constant), and the observed distribution of green-wave surfing from our study population, the model predicted a slowly increasing population (mean $\lambda = 1.01$), with mean September percent body fat at 15.2% and pregnancy rate at 98.6%. However, when surfing success deteriorated by 5 to 15 days, the model predicted up to a mean 15% decrease in September percent body fat, and up to a mean 6% reduction in pregnancy rate, which led to a 0 to 2.5% decrease in λ and a 0 to 27% reduction in population size over 50 years (Fig. 3).

Discussion

Our findings suggest an important fitness benefit of green-wave surfing in a migratory ungulate. Migratory elk surfed green waves of high-quality forage more successfully than their resident counterparts, occupying habitat patches on average almost two weeks closer to peak green-up (Fig. 2b). In turn, elk that were more successful at green-wave surfing during the growing season had higher levels of autumn fat

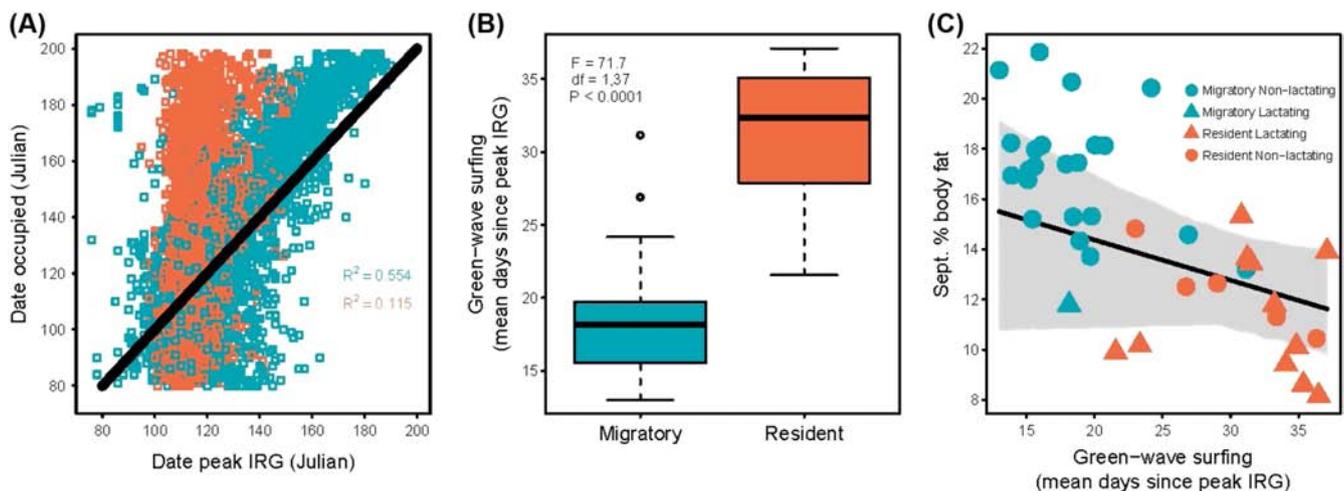


Figure 2. (A) Relationship between Julian date of daily patch occupation and the date of peak instantaneous rate of green-up (IRG) for that patch based on migration status, (B) box and whiskers plot of green-wave surfing as a function of migration status, and (C) observed data and predicted percent body fat in September (black line plus 95% CI in gray) based on individual green-wave surfing while accounting for age, lactation status, and migration status in the Clarks Fork elk herd of the Greater Yellowstone Ecosystem 2008–2009 ($n = 39$ elk-years). In (A), the black line represents a theoretical perfect surfer (i.e. matching movement to occupy habitat patches when at peak IRG). Green-wave surfing was calculated as the mean difference between the Julian date when an elk occupied a patch and the Julian date of peak IRG for that same patch (i.e. the smaller the number, the better the surfer).

Table 1. Parameter estimates (including SEs and 95% CIs) of a multivariate linear model of percent body fat in September for 29 elk on the eastern slopes of the Greater Yellowstone Ecosystem 2008–2009 ($n = 39$ elk-years). Green-wave surfing represents the mean number of days that the Julian date an elk occupied a habitat patch was different from the Julian date that peak instantaneous rate of green-up (IRG) occurred (i.e. smaller the number the better the surfer).

Variable	Estimate	SE	LCI	UCI	t	p
Intercept	19.02	2.84	10.04	23.58	6.69	0.000
Lactating	-1.34	1.08	-3.55	0.87	-1.24	0.225
Age	0.50	0.56	-0.64	1.65	0.90	0.376
Age ²	-0.04	0.03	-0.10	0.02	-1.25	0.219
Green-wave surfing	-0.16	0.08	-0.33	0.00	-2.07	0.047
Migratory	2.21	1.39	-0.62	5.03	-1.59	0.122

Adj $R^2 = 0.619$.

(Fig. 2c). Our heuristic simulations of elk demography suggested that constraints on successful green-wave surfing could have population-level consequences (Fig. 3). Altogether, these findings provide support for the predicted link between finely tuned migration behavior and fitness that is central to the ‘green wave’ hypothesis.

Foraging theory, which underpins many behavioral studies, hinges on a single, important link – that successful foraging behavior increases individual fitness (Stephens and Krebs 1986, Houston and McNamara 2014). Yet connecting the dots from movement, to a foraging currency, to fitness, and on to demography is challenging, especially across the vast landscapes exploited by large mammals (Nathan et al. 2008, Gaillard et al. 2010). Recent studies have begun to build a picture of the suite of movement tactics that are likely to increase the energy intake and fitness of large ungulates at broad scales. For example, in elk, selection for habitats with high-quality forage can accelerate fat accumulation (Long et al. 2016), and in roe deer, the establishment of home ranges in areas with variable food, cover, and edge (meadows,

thickets, and increased road density) relates to lifetime reproductive success (McCloughlin et al. 2007). Our findings provide new evidence that a large-scale, seasonal movement tactic – surfing the green-wave – may increase fat gain. This finding is especially important given that fat gain can influence key vital rates in temperate ungulate populations, from reproduction to juvenile and adult survival (Parker et al. 2009). Indeed, our simulation shows one potential pathway by which the effects of green-wave surfing on fat accumulation could have important, population-level consequences.

One weakness of our dataset introduces uncertainty about the magnitude of the effect of surfing on body-fat levels: a low sample size of lactating, migratory females with both GPS and body-fat data. This means that the relationship we describe between surfing and body-fat levels, though strong, was driven largely by non-lactating females. Non-lactating females can be a nutritionally heterogeneous group by autumn, having lost calves and been freed of the associated energetic costs of lactation at different times during the growing season (Cook et al. 2013). Since migratory elk

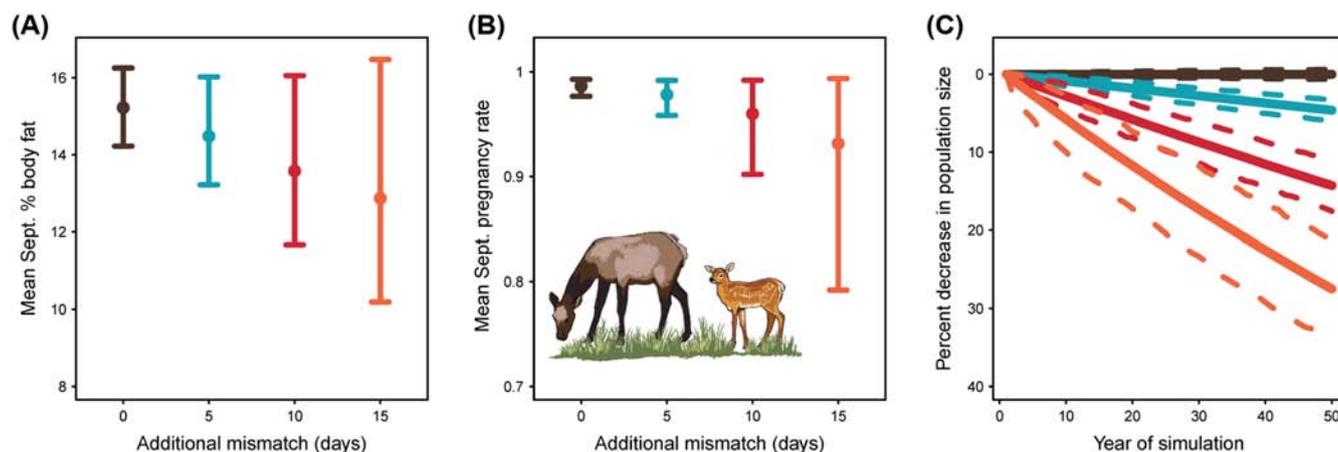


Figure 3. Simulated mean September percent body fat (A) and pregnancy rate (B), and the resulting percent change in population size (C) under four scenarios of variable green-wave surfing simulated 50 years into the future. Mean (and SE) of observed green-wave surfing (i.e. mean difference between the Julian date when an elk occupied a patch and the Julian date of peak IRG for that same patch), derived from 29 elk on the eastern slopes of the greater Yellowstone ecosystem 2008–2009 ($n = 39$ elk-years), was used as the baseline (i.e. observed), with three additional scenarios where the mean observed values were increased by 5, 10 and 15 days (i.e. poorer green-wave surfing). Simulations were based on a two age-class, female-based, pre-birth pulse, age structured matrix population model, where pregnancy rate was determined based on the predicted relationship between spring surfing ability and September percent body fat (from this study), and between September percent body fat and probability of being pregnant in September (from Cook et al. 2004).

experience heavier and earlier neonatal predation than resident elk (Middleton et al. 2013a), a migratory, non-lactating female may be freed from the nutritional costs of lactation earlier in summer than her resident counterparts, allowing her to gain fat quickly regardless of the nutritional environment around her (Cook et al. 2004). Without information on the timing of calf loss, we cannot estimate whether and how much fat gain in our non-lactating sample is attributable to early release from the costs of lactation. Two primary observations support our conclusion that surfing is explaining a portion of the variation in fat gain in migratory animals. First, we have found a relationship between surfing and fat gain across all non-lactators, suggesting an important role of fine-scale movement decisions. Second, though migrants do experience higher levels of predation than residents, the resident elk by no means escape predation – they are hunted by wolves, black bears, mountain lions, and, since the early days of our study, recolonizing grizzly bears (Middleton et al. 2013a). If predation-caused release from lactational costs were the main driver of summer fat gain in this system, we suspect resident, non-lactating female elk would attain much higher fat levels than they do.

More broadly, large-scale differences in predation are proposed as an evolutionary force behind migration in ungulates (Fryxell and Sinclair 1989, Hebblewhite et al. 2008). When migrating ungulates leave winter or dry-season range in search of high-quality food, they may be able to distance themselves from predators that are temporarily tied to den sites and/or relatively immobile offspring. Conventionally, this hypothesis has been restricted to direct predation (particularly on calves), but recent studies have suggested a pathway for so-called non-consumptive effects of predation (NCEs) to reduce prey foraging success and ultimately limit nutritional condition (Christianson and Creel 2010). In the context of this study, then it is reasonable to ask whether a release from NCEs could explain the increases in fat gain that we observed in migrants. However, in this system, where grizzly and black bears emerge onto the landscape in spring and summer, we suspect overall predation risk is not any lower in summer – fundamentally at odds with the notion that migrants obtain a release from predation risk. Second, in testing for NCEs of wolves on winter body-fat levels of elk in our study population (Middleton et al. 2013b), we found no such effects for them to be released from in the first place.

Though we found evidence for green-wave surfing within our study population, other recent behavioral studies have identified countervailing pressures that may reduce the degree to which migrants surf, or even provided altogether different explanations for migratory behavior. For example, Bischof et al. (2012) found that red deer in Norway “jumped” ahead of the green wave on their spring migration and hypothesized that this tactic could result from predation risk along the migration route, or high pressure to reach summer range before giving birth. In a study of mule deer, Lendrum et al. (2014) suggested that jumping behavior may be a tactic to preempt intraspecific resource competition on summer range. Along these lines, barnacle geese seem to jump

the green wave to arrive on breeding grounds in time for their goslings to benefit from peak foraging (Si et al. 2015). Meanwhile, a recent study of partially migratory moose found that migratory behavior did not increase autumn body fat, but did increase calf survival associated with refuge from predation (White et al. 2014). Together these studies suggest that in some ecological contexts the benefits of tracking the green wave might be of similar importance next to the costs of predation, resource competition, and potentially other factors.

The link between surfing success and fat gain has important implications for the management and conservation of migratory ungulates. There is a growing recognition that migration corridors are themselves important foraging habitat (Aikens et al. 2017). For example, mule deer in western Wyoming forage at stopovers for up to 95% of the migratory period (Sawyer and Kauffman 2011). In disturbed areas, some deer accelerate through corridors or detour outside them, abandoning or spending less time in stopover habitats (Sawyer et al. 2013). Our results suggest that this avoidance behavior may reduce the ability of ungulates to surf the green wave – and if so, reduce fat gain and erode a key fitness benefit of migration. Further, our simulation results point to at least one pathway by which an increase in barriers to migration could operate via constraints on fat gain to limit populations. These accumulating insights may help explain why human activity along migration corridors has been a prominent factor in the decline of migratory populations (Berger 2004, Harris et al. 2009).

Development and human disturbance can alter the ability of migrants to track the green wave, but climate change can alter the progression of the wave itself. Migratory movements are closely timed to patterns of temperature, snowmelt and green-up (White et al. 2010), all of which are changing in the Rocky Mountains (Westerling et al. 2006, Shuman 2011, Pederson et al. 2011). One relevant study found that even a small amount of experimental warming decreased spatial variability in plant emergence within caribou habitat (Post et al. 2008). Another study showed that mule deer in home ranges with more synchronous vegetation green-up had lower winter body fat (Searle et al. 2015). Given these findings, if climate warming reduces the spatial variability of green-up at large scales – which surfing behavior is meant to exploit – our work suggests potential reductions in the fat gain of migratory ungulates.

In a previous study of the same elk herd, we documented a lower rate of pregnancy among migratory elk compared with residents (Middleton et al. 2013a). If migrants are better surfers and surfing increases fat, why would we see comparatively low pregnancy rates among migrants? We suspect several factors may together answer this question. We have observed a long-term decline in the duration of green-up in our study area, coupled with an older age structure of the migratory subpopulation (Middleton et al. 2013a), both of which may limit the pregnancy rates of migrants. Meanwhile, and importantly, in July and August many resident elk use irrigated hay and alfalfa (likely inaccurately indexed by

IRG) that could insulate them from long-term changes in the green-up (Middleton et al. 2013a). The biomass of high-quality forage in irrigated fields of the GYE was up to 200% greater at peak green-up than on native elk summer range, and remained high through the growing season (Garrouette et al. 2016). We strongly suspect resident elk in our study population obtained a nutritional subsidy from these fields before and during conception that boosted pregnancy rates (Cook et al. 2013). Although not well recognized, nutrition around the time of breeding can have a major influence on ovulation independently of the body-fat level (Bronson and Manning 1991, Gerhart et al. 1997). Unfortunately, we did not have body-fat estimates from a sufficient number of the elk that used agricultural fields to evaluate the effect of irrigated agricultural lands on the performance of resident elk. Given the prevalence of agriculture on the frontiers of the GYE and other ecosystems, it will be important for future studies to explore whether and how agricultural subsidies affect performance of these animals as well as surfing behavior and its benefits.

For decades, ecologists and wildlife biologists have sought to understand migration in terms of the characteristics of the seasonal ranges that bookend these movements. We found that green-wave surfing – how elk moved along corridors in the months of the growing season – can influence fat gain. Further, since body fat is a key currency of fitness in temperate ungulates, partly determining who breeds and who survives winter, our work suggests that variation in green-wave surfing may have population-level consequences. These linkages imply that freedom to move within migration corridors, matching movements to the flux of high-quality, emergent forage, may be critically important to migratory populations. Further research is needed to determine how major environmental changes affect green-wave surfing and the foraging benefits of migration across large spatial and temporal scales – especially as the climate changes.

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