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# LETTER

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# The greenscape shapes surfing of resource waves in a large migratory herbivore

# Abstract

The Green Wave Hypothesis posits that herbivore migration manifests in response to waves of spring green-up (i.e. green-wave surfing). Nonetheless, empirical support for the Green Wave Hypothesis is mixed, and a framework for understanding variation in surfing is lacking. In a population of migratory mule deer (*Odocoileus hemionus*), 31% surfed plant phenology in spring as well as a theoretically perfect surfer, and 98% surfed better than random. Green-wave surfing varied among individuals and was unrelated to age or energetic state. Instead, the greenscape, which we define as the order, rate and duration of green-up along migratory routes, was the primary factor influencing surfing. Our results indicate that migratory routes are more than a link between seasonal ranges, and they provide an important, but often overlooked, foraging habitat. In addition, the spatiotemporal configuration of forage resources that propagate along migratory routes shape animal movement and presumably, energy gains during migration.

#### Keywords

Forage maturation hypothesis, green wave hypothesis, migration, mule deer, normalised difference vegetation index, *Odocoileus hemionus*, phenology, resource landscape, ungulate, Wyoming.

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# INTRODUCTION

The resource landscape - i.e. the spatiotemporal configuration of resources - strongly influences behavioural strategies of mobile organisms. Resource landscapes where resources are temporally predictable and spatially homogeneous favour resident (i.e. home range) movement strategies (Mueller & Fagan 2008). Resource landscapes also can be characterised by resource waves, where natural gradients (e.g. elevation) create pulses of resources that propagate across space and time. Classic examples of resource waves include the onset of spring green-up and emergence of insects across latitudinal gradients (Hodkinson 2005; Moser et al. 2010). Resource waves should favour movement strategies where animals match their movements with resources as they propagate across the landscape (Armstrong et al. 2016). From grizzly bears (Ursus arctos) pursuing sockeye salmon (Oncorhynchus nerka) across spawning sites (Schindler et al. 2013), to surf scoters (Melanitta perspicillata) pursuing waves of spawning herring (Clupea pallasii; Lok et al. 2011), consumers enhance foraging by tracking resource waves.

For herbivores, plant phenology is a key factor that shapes the resource landscape. Herbivores balance forage quality and quantity by selecting for vegetation at intermediate biomass (hereafter green-up) because net energy intake is mediated by a trade-off between intake rate and digestibility (i.e. The Forage Maturation Hypothesis; Fryxell 1991). Because plant growth is delayed at high elevations and latitudes in spring, green-up moves as a resource wave, often across vast areas.

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Viewing migration as a movement strategy that is in part driven by resource waves challenges traditional conceptualisations of migration. Migration is commonly viewed as the movement between two distinct seasonal ranges, which allows migrants to exploit resource abundances in one seasonal range while avoiding resource deficits in the other (Alerstam *et al.* 2003). Although this view of migration is generally supported (e.g. Shaffer *et al.* 2006), it ignores how resources acquired *en route* influence movement and energy gain during migration (Avgar *et al.* 2013). Migration has even been defined as movement that is 'undistracted' by surrounding resources (Dingle 2014). The GWH suggests an alternative view, where migratory movements themselves prolong exposure to high-quality resources and serve to enhance energy gain.

Accumulating evidence supports the notion that some migratory ungulates surf green waves of forage during migration (Avgar *et al.* 2013). The migration of wildebeest (*Connochaetes taurinus*) in the Serengeti appears to result from individuals seeking habitat patches flush with new vegetation

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(Boone *et al.* 2006). During spring migration, mule deer (*Odocoileus hemionus*) in the Rocky Mountains spend prolonged amounts of time (95% of the migratory period) at stopover sites, and use of stopover sites is synchronised with green-up (Sawyer & Kauffman 2011). Moreover, red deer (*Cervus elaphus*) that experienced more heterogeneous plant phenology (akin to experiencing a longer green wave) grow larger than those that experience less variable phenology (Albon & Langvatn 1992; Mysterud *et al.* 2001), which suggests a fitness benefit associated with green-wave surfing.

Despite indirect support for the GWH and its strong conceptual underpinnings, the first explicit test of the GWH in an ungulate revealed that red deer do not surf (Bischof et al. 2012). Instead, red deer 'jump' the green wave, moving rapidly from winter range to summer range, without regard to the progression of the green wave across the landscape. Nevertheless, ungulates should have the capability to surf because several species select habitat patches at peak green-up (Merkle et al. 2016), and African ungulates appear to track gradients of plant growth and precipitation during their seasonal movements (Fryxell et al. 2004; Holdo et al. 2009; Bartlam-Brooks et al. 2013; Bohrer et al. 2014). These findings highlight an important, yet unresolved, question of whether green-wave surfing is a common behaviour among migrating ungulates. Answering this question will help shape our ecological understanding of migration in ungulates, especially as to whether the key benefit of migration is simply access to seasonal ranges, or if the migratory route itself also provides a foraging benefit.

Despite ongoing debate regarding the existence of greenwave surfing, factors that facilitate or constrain surfing are almost completely unexplored. The way that the green wave progresses across the landscape - a concept we refer to as the 'greenscape' - could be an important factor influencing surfing. For example, rapid green-up is thought to influence demography by reducing the amount of time that high-quality forage is available (Middleton et al. 2013). Furthermore, rapid green-up has been linked to declines in recruitment of young for several ungulate species (Pettorelli et al. 2007; Monteith et al. 2015). Such demographic consequences of rapid greenup may manifest, in part, by constraining the ability of herbivores to optimally surf phenological gradients. To conceptualise this idea, we propose the Greenscape Hypothesis, wherein the speed, duration and order of green-up along a migratory route influence the ability of animals to surf green waves of forage. Accordingly, we predicted that migratory routes with resource waves that green-up gradually, last for a long time, and progress consecutively from one seasonal range to the other, should enhance surfing.

Several other factors could affect green-wave surfing. First, surfing may involve behavioural trade-offs (e.g. parental care, socialisation, risk avoidance) such that the reproductive or nutritional state of an animal influences behaviour during migration. State-dependent foraging exists in a wide range of animal taxa (e.g. Hutchings *et al.* 2001; Heithaus *et al.* 2007), where animals in poor condition prioritise foraging to enhance energy gain over other behaviours (e.g. vigilance; Mcnamara & Houston 1992). Green-wave surfing is fundamentally a foraging behaviour and thus, we extend the State-Dependent Hypothesis, and predict that individuals in poor condition, or those that

anticipate high energetic costs (e.g. lactation), should prioritise green-wave surfing to maximise energy gains.

Memory and learning also may influence green-wave surfing. Resource waves in natural environments are inherently noisy (Guttal & Couzin 2010), and taxis along noisy environmental gradients is inefficient (Grunbaum 1998). Efficient surfing should be contingent upon knowing when and where to move to access high-quality forage, which can be enhanced by social interactions (Berdahl et al. 2013; Merkle et al. 2015), learning (Mueller et al. 2013) and memory (Merkle et al. 2014). Spatial memory influences foraging efficiency across a wide range of taxa (Fagan et al. 2013), including ungulates (Merkle et al. 2014), and older animals have been shown to migrate more efficiently than inexperienced individuals (Mueller et al. 2013). We propose the Learning Hypothesis, and posit that efficient green-wave surfing must be learned and thus surfing should improve with experience. We predict that older, more experienced individuals should be more proficient at surfing than young, inexperienced individuals.

We tested the GWH and assessed empirical support for hypotheses that explain individual variability in green-wave surfing using GPS collar data from migratory mule deer in Wyoming, USA. We first tested the prediction that deer should use foraging patches along their migratory route when they are at peak green-up, providing a quantitative test of the GWH. Second, we quantified how surfing differed among 3 years (with variable precipitation) and across short-, moderate- and long-duration migrations. Third, we examined empirical support for the Greenscape and State-Dependent Hypotheses, and a modified version of the Learning Hypothesis to explain individual variation in surfing. Our findings provide empirical support for the GWH and the Greenscape Hypothesis – suggesting that access to plant green-up along the migratory route is a key foraging benefit of migration, and that certain phenological characteristics of migratory routes promote green-wave surfing.

# METHODS

#### Study area

Western Wyoming, USA ( $42^{\circ}25'N$ ,  $110^{\circ}42'W$ ), is a semi-arid region in the Rocky Mountains characterised by long, cold winters and warm summers (see Appendix S1 in Supporting Information). Low elevations receive approximately 18 cm of precipitation per year (Big Piney, WY weather station, 2080 m), and high elevations receive approximately 5 times that amount (Spring Creek Divide SNOTEL site, 2750 m). Low elevations (~ 1800–2300 m) are dominated by sagebrush (*Artemesia* spp.), with sparse mountain shrub communities and willow complexes. Middle elevations (~ 2300–2750 m) include aspen (*Populus tremuloides*), sagebrush, mixed-mountain shrubs and conifers, and high elevations (> 2750 m) contain pine and fir species and tall forb communities.

#### Animal capture

In March and December 2013–2015, we captured and fit GPS collars on 99 adult (> 1-year-old; age range = 2-12) female

mule deer from two winter ranges via helicopter netgun (Barrett *et al.* 1982). We extracted one incisiform canine to estimate age by cementum annuli (Bleich *et al.* 2003). Each March, we recaptured individuals to quantify nutritional condition (ingesta-free body fat), pregnancy, and foetal number (Appendix S2). All animal capture and handling protocols were approved by an independent Institutional Animal Care and Use Committee at the University of Wyoming (Protocol #20151204KM00135–01).

#### GPS telemetry data

We programmed GPS collars (Advanced Telemetry Systems Inc, Isanti, MN, USA and Telonics Inc, Mesa, AZ, USA) to collect fixes every 1-5 h. We quantified surfing during two time periods: the period of migration (defined by the start and end of spring migration using GPS data) and the period of spring green-up (defined as the time when green-up was available across the study area). We used Net Squared Displacement (NSD) to delineate the start and end of spring migration for each deer annually (Fig. S3; Appendix S3; Bunnefeld et al. 2011). To delineate the physical pathway that individuals used during migration, hereafter the migratory route, we first interpolated points between fixes, using a correlated random walk model (Johnson et al. 2008). We then applied the Visvalingam line simplification algorithm (Harrower & Bloch 2006) to the interpolated paths, which removed tortuosity (Appendix S4). We simplified the interpolated path so that areas heavily used by deer (i.e. stopovers) were not oversampled in our calculation of the greenscape, because the greenscape is intended to quantify patterns of plant phenology irrespective of the movement of individuals. We used the simplified paths representing migratory routes solely to calculate the greenscape, whereas we calculated green-wave surfing scores using GPS locations from deer.

#### Metrics of green-wave surfing

We indexed vegetation quality across space and time by estimating the Instantaneous Rate of Green-up (IRG), a metric derived from a time series of the Normalised Difference Vegetation Index (NDVI; MOD09Q1; 250-m spatial resolution, 8-day temporal resolution; Appendix S5). The NDVI was correlated with vegetation biomass in a similar study area (Garroutte et al. 2016). To calculate IRG, we pre-processed NDVI data and fit double-logistic curves to time series following Bischof et al. (2012) and Merkle et al. (2016; Fig. 1a; Appendix S5). The IRG is the first derivative of the fitted NDVI curve, which results in a curve that peaks when vegetation growth is most rapid (i.e. intermediate biomass), hereafter peak green-up (Fig. 1a). We defined the period of spring green-up as the date range when IRG peaked across our study area. We defined our study area as the 95% minimum convex polygon of all GPS locations of deer, and defined the start and end of spring greenup as the 0.02 and 0.98 quantiles of peak IRG dates within the study area (Appendix S6).

To evaluate variation in green-wave surfing among individuals, we used two metrics of surfing: (1) the IRG experienced during spring green-up (Bischof *et al.* 2012); and (2) the daysfrom-peak IRG, hereafter Days-From-Peak, which was calculated as the absolute difference (in days) between the date a deer used a given location and date of peak IRG at that same location. We calculated both metrics for each GPS location, and then averaged by day to reduce potential bias from inconsistent fix rates and, thus, unbalanced sample size. We calculated surfing scores, using both IRG and Days-From-Peak, for each animal (n = 99) during spring green-up in 2013, 2014 and 2015 (total deer-years = 191).

Although large values of IRG and small values of Days-From-Peak indicate that an animal matches its movements with peaks in IRG, there is an important but subtle difference between the two metrics. The IRG is comprised of two parameters, one that describes when peak green-up is reached, and another that controls the speed at which that peak is reached (the spring scale which corresponds to the reciprocal of the green-up rate; Bischof *et al.* 2012). Two locations on the landscape can have the same date of peak green-up, but different rates at which green-up occurred, which influences the shape of the IRG curve. If a deer visited these two locations 5 days before peak green-up, it would receive different IRG scores solely because of different rates of green-up (Fig. 1b–c). Therefore, we view IRG as a metric that reflects both animal behaviour and the environment, whereas Days-



**Figure 1** Hypothetical illustration of annual change in forage biomass (grey dashed line) estimated by a double-logistic curve fit to a scaled time series of NDVI data, and forage quality (solid black line) represented as the Instantaneous Rate of Green-up (IRG) or first derivative of the NDVI curve for one patch along a migratory route (a). We quantified green-wave surfing using mean IRG and Days-From-Peak (DFP) IRG, which measures the absolute difference in days between deer use of a patch and the date of peak IRG. An IRG value of 1 or a DFP value of 0 represents perfect tracking of green-up. Because IRG is a measure of both environment and behaviour, equivalent tracking (e.g. DFP = 5) can dramatically reduce IRG when green-up occurs rapidly (b) compared to patches with more gradual green-up (c).

From-Peak reflects only behaviour. We explored how duration of migration influenced green-wave surfing by examining annual patterns in Days-From-Peak and IRG for migrations that were classified as short (< 0.33 quantile), mid (0.33-0.66 quantile) and long (> 0.66 quantile) duration migrations.

#### Metrics of the greenscape

We calculated three metrics to characterise the greenscape: green-up rate, green-up order and green-up duration. We estimated the date of peak green-up and rate of green-up at 1-km intervals along the migratory route. We used the reciprocal of the rate of green-up – the spring scale, which can be interpreted as an index of the time to reach peak green-up - to avoid subsequent issues associated with skewed distributions in green-up rate. We calculated average spring scale of the 1km intervals, as our metric of green-up rate. To quantify green-up order, we calculated Spearman's rank correlation between the physical order of each location along the migratory route (1-km interval) and the chronological order in which those locations reached peak green-up. A rank correlation of one represents a migratory route that greens up consecutively from winter to summer range, whereas a rank correlation of 0 indicates random green-up order. We determined the duration of green-up of a route by calculating the difference between the mean Julian date of peak green-up at the first and last location (buffered by 500 m) along the migratory route. We buffered the locations to avoid erroneous endpoints that may not be representative of the NDVI signatures around them.

# Statistical analysis

We tested the key prediction of the GWH by comparing the date that a deer occupied a habitat patch to the date of peak green-up of that habitat patch. If deer surf according to the GWH, we expect a strong, positive relationship with a slope of one and an intercept of zero. We used linear regression to estimate the intercept and slope of the relationship between date of peak green-up and date of deer use, for each individual during both the year's spring green-up period and migration period. We classified each regression as: (1) theoretically perfect surfing (i.e. 95% confidence intervals [CIs] of the slope overlapped one and 95% CIs of the intercept overlapped with zero); (2) surfing that was better than random (i.e. slope was positive and 95% CIs did not overlap zero) or (3) not surfing (i.e. a negative slope or a slope with 95% CIs overlapping zero).

To examine the factors influencing green-wave surfing among individuals, we modelled IRG and Days-From-Peak as a function of predictor variables that corresponded to the Learning (age), Greenscape (rate, duration and order of green-up) and State-Dependent (nutritional condition and foetal number) Hypotheses. Although learning is critical during early life stages (Wunderle 1991), we were unable to obtain fine-scale movement data for young-of-the-year deer. We therefore reframed this hypothesis as the Adult Learning Hypothesis and evaluated the effect of increased experience on surfing proficiency for adults. We transformed Days-FromPeak using the natural log, and arcsine transformed green-up order, because their distributions were skewed. We used an information-theoretic approach to assess the relative support for hypotheses (Burnham & Anderson 2002). We modelled IRG and Days-From-Peak using a linear mixed-effects model that included a random intercept to account for variability across years. Using a two-step modelling procedure, we first developed a global model based on predictor variables that corresponded to each hypothesis and subsequently evaluated all possible combinations of the predictor variables, without allowing collinear variables to enter the same model (Doherty et al. 2012). Then, to improve the precision of coefficient estimates, we reparametrised top models (those within two  $\Delta AIC_{c}$ units from the best model) with random slopes, so that each variable in the model could vary by year (Bolker 2015). We considered predictor variables within top models as significant if the 95% CIs of the coefficient estimate did not overlap zero.

To visualise the effect of the greenscape across our study area, we mapped predicted IRG from deer monitored across the 3-year study period (n = 32). We derived predicted IRG based on fixed-effect coefficients estimated from the top ranking IRG model based solely on greenscape metrics. Using a permutation test, we compared the greenscape across years and across routes to determine: (1) if the greenscape was different from the null hypothesis of no difference in the greenscape among years; and (2) if individual routes maintained consistently high- or low-quality greenscapes (i.e. routes with greenscapes that were easier or more difficult to surf) against the null hypothesis that there was no difference in quality among routes. We calculated P-values for the permutation test as the total number of permutations more extreme (both higher or lower) than the average greenscape (for a given year or a given route) divided by the total number of permutations  $(n = 100\ 000)$  for each year (n = 3) or for each route (n = 32).

#### RESULTS

Across the entire study area, the period of spring green-up ranged from 14 April to 20 June in 2013 (a drought year), from 2 April to 30 June in 2014 (heavy snowpack year) and from 14 February to 14 June in 2015 (a low snowpack year with a wet spring). Mule deer generally matched their movements with peaks in green-up (Fig. 2), with surfing that was nearly twice that of simulated migrations based on the daily rate of displacement from winter to summer range along the same elevational gradient (Appendix S7). The vast majority (98.4%) of individual regressions between the date of peak IRG and the date of deer use were classified as surfing that was better than random, and 31.7% of those regressions were consistent with theoretically perfect surfing during the migration or spring period.

On average, deer received IRG values above 0.8 for fewer days in 2013 (28.87  $\pm$  1.13, mean  $\pm$  SE) than in 2014 (43.96  $\pm$  1.86) and 2015 (57.35  $\pm$  2.70). In 2013, long-duration migrants had IRG values above 0.8 for a shorter amount of time than short- or mid-duration migrants (short = 31.63  $\pm$  1.64, mid = 31.43  $\pm$  1.64 and long = 21.80  $\pm$  1.85 days; mean  $\pm$  SE), whereas the opposite was true in 2014



Figure 2 Date of use relative to date of peak IRG for migratory mule deer in western Wyoming, USA, in 2013 (a), 2014 (b) and 2015 (c). A perfect match between the date of peak IRG and the date of deer use is represented with a grey 1:1 line. Individual regressions indicate that 31% of deer surfed no different than that of a theoretically perfect surfer, whereas the vast majority of deer (98%) surfed better than random. Black points represent days during the period of spring green-up across the study area, whereas coloured points correspond to days during the spring migration period.

(short =  $39.65 \pm 2.57$ , mid =  $41.38 \pm 3.40$  and long =  $49.43 \pm 3.18$  days; mean  $\pm$  SE) and 2015 (short =  $46.33 \pm 5.37$ , mid =  $60.77 \pm 4.41$  and long =  $64.06 \pm 3.14$  days; mean  $\pm$  SE; Fig. 3). Days-From-Peak varied similarly across the 3 years (Appendix S8).

The Greenscape Hypothesis best described individual variability in green-wave surfing. Green-up duration was the strongest predictor of IRG across individuals ( $\Delta AIC_c$  of second best supported model > 6; AIC<sub>c</sub> Weight = 0.92; Appendix S9). As the duration of green-up increased, IRG also increased ( $\beta = 0.0034$ ; 95% CI = 0.0022–0.0045; Fig. 4). Days-From-Peak was best explained by three models, containing a combination of green-up duration, spring scale (reciprocal of the green-up rate) and green-up order (cumulative AIC<sub>c</sub> weight > 0.5; Appendix S9). Days-From-Peak decreased as spring scale decreased, green-up order became more consecutive and green-up duration increased (Fig. 4).

The greenscape was most difficult to surf in 2013 (P = 0.0013) and easiest to surf in 2014 (P < 0.0001), according to predicted IRG (Fig. 5 and Fig. S10). Despite annual fluctuations in the greenscape, 4 of 32 routes (12.5%) were consistently of higher quality and were predicted to result in deer receiving 9% higher average IRG than other routes. Two routes were consistently of lower quality and were predicted to result in deer receiving 7.5% less average IRG (Appendix S10).

#### DISCUSSION

Approximately a third of mule deer surfed the green wave as well as a theoretically perfect surfer, and the vast majority of deer surfed the green wave better than random, providing empirical support for the GWH in a migratory ungulate. Nonetheless, surfing varied among individuals and years (Figs 3 and 4). Variation in surfing was unrelated to animal experience or physiological state, but instead was determined by the way the green wave progressed along the migratory route (i.e. the 'greenscape'). In support of the Greenscape Hypothesis, migratory routes with longer and more consecutive green-up allowed deer to more closely synchronise movement with peaks in green-up. Our findings provide strong evidence that green-wave surfing plays an important role in the foraging strategy of mule deer, and that spatial variability in plant phenology structures the presumed foraging benefits acquired during migration.

In contrast to the first explicit test of the GWH in a migratory ungulate wherein only a few (5.2%) animals surfed the green wave (i.e. red deer; Bischof et al. 2012), mule deer synchronised their movements during spring migration with plant green-up (Fig. 2). We suspect that different movement strategies employed by mule deer and red deer may be a function of physiological differences between the two species that manifest in specialised foraging behaviours (Bell 1971; Jarman 1974). Larger species such as red deer require greater forage intake and can tolerate lower quality forage, and thus may be limited more by forage quantity than smaller-bodied ruminants like mule deer that may be limited more by forage quality (Muller et al. 2013). In addition, the distance and duration of migration varied substantially between our study (mean duration = 34.4 days; mean distance = 67 km) and that of Bischof et al. (2012; mean duration = 7.4 days; mean distance = 23 km). Migration strategies of red deer and mule deer could result from different resource landscapes in Norway and Wyoming. Red deer in Norway might have jumped the green wave because parts of their migratory routes were low-quality habitat, or had poor greenscape characteristics. Despite these differences, our work provides strong evidence that green-wave surfing is a behaviour that is fundamental to the foraging benefit of migration for mule deer in our study area.

In accordance with the Adult Learning Hypothesis, we predicted that older, more experienced individuals would better surf the green wave. Nevertheless, age had no influence on surfing in adults. Numerous behaviours, from foraging efficiency (Gillingham & Bunnell 1989) to fawn rearing (Ozoga & Verme 1986), are learned in ungulates. Mule deer in western Wyoming have high fidelity to their migratory routes (Sawyer & Kauffman 2011), and the geographic



Figure 3 Instantaneous Rate of Green-up (IRG) experienced by mule deer in western Wyoming, USA, in 2013 (a–c), 2014 (d–f) and 2015 (g–i), by short-(a, d, g), mid- (b, e, h) and long-duration (c, f, i) migrants. Annual IRG experienced by individual deer are shown with orange (2013), green (2014) or purple (2015) lines; average IRG is shown in black with 95% CIs (grey lines). The light grey area represents the spring green-up period for a given year and the dark grey area represents the mean migration period.

location of migratory routes is thought to be learned within the first year of life (Nelson 1998). Therefore, learning to efficiently surf a given route might occur in the first year of life. As we only monitored adults, we had inadequate data to examine the effect of learning in fawns or yearlings. Future work that evaluates green-wave surfing across all life stages will provide important insights into the effects of learning early in life, when it is often most critical (Wunderle 1991; Rotics *et al.* 2016).

A wide range of behaviours across numerous animal taxa are affected by the nutritional or reproductive state of an individual (Martin & Lopez 1999; Heithaus *et al.* 2007). Nutritional condition has been linked to the timing of migration in mule deer (Monteith *et al.* 2011) and habitat selection in elk

(Long *et al.* 2014). Nevertheless, reproductive status and nutritional condition were unrelated to surfing. Ungulates living in seasonal environments should maximise energy intake during spring green-up because winter often is associated with a nutritional bottleneck (Parker *et al.* 2009). Therefore, it is possible that all animals, regardless of their energetic state in late winter, seek to maximise net energy gain via green-wave surfing in spring to bolster somatic gain, and subsequently, reproductive success. Nevertheless, state-dependent foraging also may occur at scales finer than our landscape-level evaluation.

In support of the Greenscape Hypothesis, animals using routes with longer durations of green-up had more time (up to 73 days) to access heterogeneity in resources than



**Figure 4** Green-wave surfing of migratory mule deer in western Wyoming, USA, measured by IRG (a) and Days-From-Peak IRG (b–d) was largely explained by characteristics of a route's greenscape. Greenscape metrics included green-up duration (a–b), spring scale (c; the inverse of green-up rate, interpreted as the time to reach peak green-up) and green-up order (d). Surfing metrics were calculated during the period of spring green-up in 2013–2015. An IRG value of 1 or Days-From-Peak value of 0 represent perfect surfing. Fitted values (black line) and 95% CIs (grey polygon) were calculated using parametric bootstrapping of a univariate linear mixed-effects model that included both a random intercept and a random slope for year, allowing the effect of the greenscape to vary by year.

individuals using routes with shorter durations of green-up. Deer using routes with consecutive green-up did not have to revisit areas along their route (a behaviour that we did not observe in our data) to track the green wave. Long green-up durations and gradual green-up rates have been linked to



**Figure 5** Predictive maps of green-wave surfing by mule deer along their migratory routes in 2013 (a; drought year), 2014 (b; heavy snowpack year) and 2015 (c; low snowpack year with a wet spring) illustrate considerable spatial and temporal variability caused by variation in the greenscape. Map predictions depict the relationship between average IRG and the duration of green-up along each route based upon the best fit model across all candidate models (see Table S9a). An IRG value of 1 represents perfect surfing.

improved fitness in a diverse range of ungulates (Pettorelli *et al.* 2005, 2007; Middleton *et al.* 2013; Monteith *et al.* 2015; Searle *et al.* 2015). Although we did not quantify fitness benefits, we hypothesise that deer migrating along profitable greenscapes will receive better forage and have higher fitness than deer using migratory routes with poor greenscapes. Because the greenscape was a strong predictor of green-wave surfing, we suggest that the greenscape largely dictates the habitat quality of a given migratory route. The importance of the greenscape highlights the value of incorporating both the spatial structure of resources and the temporal dynamics of resources into the definition and quantification of habitat (Armstrong *et al.* 2016).

In contrast to our prediction, deer deviated less from the date of peak IRG when green-up occurred rapidly. Rapid green-up has been correlated with negative demographic effects for ungulates (e.g. Middleton *et al.* 2013), and could be considered a negative attribute of the greenscape because there is less time when high-quality forage is available. Nonetheless, closer tracking of peaks in IRG when green-up was rapid indicates that animals can adjust behaviourally to compensate for rapid rates of green-up (Fig. 4). Behavioural buffering – in which animals adjust behaviours in response to environmental stochasticity – has been attributed to effective thermoregulation (Ortega *et al.* 2016) and improved demographic rates (Loe *et al.* 2016). Unlike previous studies, the behavioural buffering of mule deer in our study was not based upon changes in habitat use (mule deer have high fidelity to

migratory routes; Fig 5), but rather based upon when they use habitat along their migratory route. Combining both IRG (reflecting the phenological environment and animal behaviour) and Days-From-Peak (reflecting the behavioural component of surfing) presents great utility in unravelling how behaviour and the environment interact to shape migration.

Although the development of IRG has advanced our understanding of green-wave surfing and ungulate migration (e.g. Bischof et al. 2012; Rivrud et al. 2016), several analytical hurdles remain. First, the Forage Maturation Hypothesis predicts an asymmetrical relationship between forage quality (i.e. energy intake rate) and plant biomass (Fryxell 1991), whereas IRG assumes a symmetrical relationship (see Fig. 1). Thus, IRG does not capture the differences in forage quality between phenological stages pre- and post-peak IRG. Second, because IRG is scaled (0-1), IRG cannot differentiate between habitat patches that differ in overall plant biomass. Consequently, IRG only quantifies timing of peak forage quality for a given location, and thus, does not necessarily reflect differences in absolute forage quality between locations. Refining this approach in future studies will help improve our ability to quantify the spatiotemporal dynamics in forage quality for herbivores.

Maps of predicted IRG depicted remarkable variability in the greenscape across our 3-year study (Fig. 5). For instance, the drought in 2013 diminished the quality of the greenscape for all routes, however, some routes were less affected. Nevertheless, 12.5% of routes were consistently of higher quality across years and weather conditions. This result highlights the importance of answering questions such as why some routes are consistently better than others, and what are the demographic implications for individuals with fidelity to high- or low-quality routes. Foraging theory predicts that animals experiencing higher rates of energy intake from forage will have higher fitness than animals experiencing lower rates of energy intake (Stephens & Krebs 1986). For migratory ungulates, routes with high-quality greenscapes may lead to higher fitness, resulting in a larger proportion of the population using them. Increased use of high-quality migratory routes could manifest simply because of maternal inheritance of routes (Nelson 1998) or strong fidelity to routes (Sawyer & Kauffman 2011). Consequently, future work should (1) investigate the mechanism underlying selection of migratory routes with variable greenscapes, especially via cultural transmission, and (2) test how variability in greenscapes underpin eco-evolutionary processes such as density-habitat relationships, genetic structuring across landscapes and vulnerability to environmental stochasticity.

Our findings indicate that a migratory ungulate surfs the green wave and in so doing, extends the amount of time exposed to high-quality forage. Although migratory routes function as corridors between distinct seasonal ranges that are critical to the persistence of migratory taxa, they also are themselves foraging habitat that likely yield substantial nutritional benefits to individuals that exploit them. Researchers and conservationists must expand their view of migration to not only consider the importance of animal movement or temporal resource dynamics but also how these two processes meld together in space and time to influence fitness and population dynamics of consumers. Indeed, building upon the GWH (Drent *et al.* 1978) and the notion that migration

should emerge in environments that are seasonal and predictable (Mueller & Fagan 2008), we demonstrate that the structure of a resource wave (i.e. the greenscape) shapes the benefit of migration. We also showed how annual variation in weather can affect resource waves, and in turn, the ability of animals to enhance resource gain via synchronised movement with resources. Such a linkage has implications for how climate change will affect the persistence of migratory taxa, and highlights the need to incorporate temporal variability into our conceptualisation and quantification of habitat.

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#### STATEMENT OF AUTHORSHIP

EOA, MJK and KLM developed the research idea. KLM, MJK, GLF and EOA secured funding. All authors collected the data and SPHD managed the data. EOA and JAM analysed the data. EOA wrote the first draft of the manuscript and all co-authors contributed to revisions.

#### DATA ACCESSIBILITY STATEMENT

Data are available in the Dryad Digital Repository: doi:10. 5061/dryad.7kc09.

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#### SUPPORTING INFORMATION

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