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Industrial Energy Development Decouples Ungulate Migration from the Green Wave

Ellen O. Aikens

Teal B. Wyckoff

Hall Sawyer

Matthew J. Kauffman

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Ellen O. Aikens[1,2], Teal B. Wyckoff[2,3], Hall Sawyer[4] and Matthew J. Kauffman[5]

The ability to freely move across the landscape to track the emergence of nutritious spring green-up (termed 'green-wave surfing') is key to the foraging strategy of migratory ungulates. Across the vast landscapes traversed by many migratory herds, habitats are being altered by development with unknown consequences for surfing. Using a unique long-term tracking dataset, we found that when energy development occurs within mule deer (*Odocoileus hemionus*) migration corridors, migrating animals become decoupled from the green wave. During the early phases of a coalbed natural gas development, deer synchronized their movements with peak green-up. But faced with increasing disturbance as development expanded, deer altered their movements by holding up at the edge of the gas field and letting the green wave pass them by. Development often modified only a small portion of the migration corridor but had far-reaching effects on behaviour before and after migrating deer encountered it, thus reducing surfing along the entire route by 38.65% over the 14-year study period. Our study suggests that industrial development within migratory corridors can change the behaviour of migrating ungulates and diminish the benefits of migration. Such disruptions to migratory behaviour present a common mechanism whereby corridors become unprofitable and could ultimately be lost on highly developed landscapes.

Across the globe, ungulates migrate to access seasonally available forage and avoid harsh weather[1]. As a result, migration represents a key strategy that allows herbivores to survive in seasonal landscapes, bolstering population sizes that often exceed those of residents by an order of magnitude[2]. Large aggregations of migratory ungulates influence community dynamics[3], play a key role in ecosystem processes through herbivory and nutrient transfer[4] and sustain rural livelihoods both culturally and economically[5]. Despite the importance of ungulate migration for many ecosystems, the traditional migration corridors used by populations around the world face unprecedented change from the expanding footprint of human development.

The flux of forage resources across space and time is a key factor shaping how animals benefit from seasonal migration[6,7]. Fleeting spring green-up, when plants are both rich in protein and highly digestible, provides the highest quality forage for ungulates[8]. The Green Wave Hypothesis conceptualizes the notion that migratory herbivores should benefit by following the emergence of young and nutritious plant green-up along elevational or latitudinal gradients[9,10]. Growing evidence shows that many migrants synchronize their movements with the progression of the green wave[6], a behaviour referred to as 'surfing the green wave'. Surfing is key to the foraging and fitness benefit of migrants[11–13] and a likely precursor to the cultural evolution of migratory behaviour in ungulates[14]. The burgeoning evidence of

[1]U.S. Geological Survey, South Dakota Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Management, South Dakota State University, Brookings, SD, USA. [2]Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA. [3]The Nature Conservancy, Arlington, VA, USA. [4]Western Ecosystems Technology, Inc., Laramie, WY, USA. [5]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA.
e-mail: eaikens@usgs.gov

green-wave surfing in migratory herbivores underscores the notion that the migration corridor itself is critical habitat that requires conservation attention[12]. Indeed, maintaining freedom of movement for migrating animals, as the working lands they traverse become more developed, is a critical conservation concern[15].

The loss of long-distance movements and migrations is becoming commonplace[16,17]. Disrupted migrations often result in population decline or local extinction[18,19]; however, the mechanisms underlying such outcomes often remain unclear[1,20]. In the American West, energy development in areas rich in natural resources overlaps with landscapes that support some of the region's most iconic migrations[21]. Development can act as a barrier and sever migrations when it impedes the ability of animals to move between seasonal ranges[1]. More commonly, however, anthropogenic disturbances act as semipermeable barriers, which migrating animals can still traverse despite their behaviours being altered[15]. For example, migrating mule deer in Wyoming and Colorado modified their movement behaviour when they encountered energy development; they detoured around development (although this was rare)[22], stopped over less and sped up when moving through developed areas[15,23–25]. Despite a clear influence of energy development on migratory movements, it is unclear how these altered behaviours influence green-wave surfing and thus the foraging benefit of migration. If development disrupts movement behaviour and diminishes surfing, this would provide a mechanism by which the benefits of migration are reduced. As a result, heavily impacted corridors may become unprofitable habitats (sensu ref. [26]), where local populations are no longer viable, threatening the persistence of existing corridors.

Understanding the impact of energy development on green-wave surfing requires long-term movement data collected at various stages of development[20], which have been lacking. There are still very few studies that record fine-scale movement data over decade-long time scales. This is especially true for studies that monitor the movements of animals before, during and after major disturbances along their migration corridors[20]. Using a 14-year movement dataset of migratory mule deer in south-central Wyoming, USA, we evaluated how energy development along the migration corridor altered movement behaviour and green-wave surfing during low, medium, high and sustained high stages of coalbed natural gas development (Fig. 1). In addition to a temporal change in the intensity of development, the impacted segments of the migration corridors also varied in the spatial extent of development, including small and large footprints of disturbance (Fig. 1). This unique time series also allowed us to evaluate how expanding energy development influences the ability of animals to surf during migration.

Results

Holding up at the edge of energy development

Previous work in this system indicated that deer migrating through development stopped over in areas immediately preceding development and that animals moved quickly through development[22]. We assessed how energy development along the migration corridor impacted movement patterns by quantifying movement speed and the proportion of time animals spent along segments of their routes before and after energy development. Across all levels of development, migrants spent more time in the 1 km segment of the route directly before development in comparison to the 1 km segment of the route after development ($P < 0.05$ for all paired *t*-tests; Fig. 2, Supplementary Fig. 1 and Supplementary Table 1). The intensity of this 'holding-up' behaviour (measured as the difference in the proportion of points before and after encountering development) was more pronounced in animals migrating through the large energy development footprint, yet there was a decline in the intensity of holding up between the high and sustained high energy development phases in the large footprint (Fig. 2 and Supplementary Fig. 1i,j). Although our sample size of tracked individuals varied across the intensity and size of energy development ($n = 13–40$), the holding-up pattern was consistent across various spatial scales of analysis (Supplementary Text (SM1) and Supplementary Figs. 2 and 3). The movement speeds of deer accelerated after encountering energy development (Fig. 2 and Supplementary Table 2). In the large energy development footprint, this pattern became more evident as energy development intensified from low to high development, but in the small energy development footprint this pattern was consistent across all energy development intensities (Fig. 2).

Development decoupled migration from the green wave

To investigate if development influenced green-wave surfing behaviour, we calculated how closely animals surfed the green wave along 1 km segments of the route. We used remotely sensed data to calculate the date of peak green-up[11,27] and took the difference in days between the date of peak green-up and the date the animals occupied a given location (0, perfect surfing; <0, early, ahead of the green wave; >0, late, behind the green wave[12]). We used the coefficient estimates from linear regressions of the relationship between distance from development and green-wave surfing to quantify if migrating individuals were early or late when they first encountered development and whether animals tracked, reduced mismatch (that is, catching up if late or letting the wave catch up if early), or became further mismatched from the green wave as they migrated to summer range (Supplementary Table 3).

As energy development increased beyond low levels of development, migrants became mismatched from the green wave (Fig. 3). At low levels of development, animals tended to be ahead of the green wave (that is, early; mean intercept = −13.1 (large footprint), −7.6 (small footprint); $P < 0.05$ for both footprint sizes, two-sided *t*-tests; Supplementary Table 4). During this period, in the large energy development footprint deer let the wave catch up to them (mean slope = 0.0008, $P = 0.02$), but for the small energy development footprint this mismatch did not change over the course of migration (mean slope did not differ from 0; two-sided *t*-tests). At medium, high and sustained high levels of development, animals were on average 8.5–22.4 days behind the green wave (i.e., late; $P < 0.05$ for all development levels and footprint sizes, except for $P = 0.06$ in the high development, large footprint; two-sided *t*-test). Migrating animals were only able to reduce mismatch with the green wave after moving through development in both study areas during medium development (slope = −0.001 (large footprint), −0.0004 (small footprint); $P < 0.0001$) and during sustained high development in the large footprint (slope = −0.001; $P < 0.001$; two-sided *t*-tests; Fig. 3 and Supplementary Table 4).

No evidence of acclimation to development

We evaluated if there was a temporal change in the ability of migrating mule deer to surf the green wave. Annual environmental variability strongly mediates green-wave surfing, by changing the pace and pattern of plant phenology along the route[6,12]. To test for a temporal reduction in surfing, while accounting for potential differences in the green wave across years, we examined if there was a temporal trend in the duration, order and rate of spring green-up along migration routes and if these phenology metrics explained variability in green-wave surfing. Across the 14-year study duration, tracking data were not collected in 2007 and 2011–2014.

Mule deer did not acclimate to energy development. Although the number of individuals tracked each year varied ($n = 12–31$), these data indicate that movements became increasingly mismatched from the green wave as development increased along their migration corridor. Specifically, days-from-peak, or the absolute difference in days between the date of peak green-up and the date of deer use, increased with time (representing poorer surfing as development increased; $\beta = 0.369$, standard error = 0.126, $P = 0.0217$). A model including year accounted for ~50% of the variance in annual average days-from-peak (adjusted coefficient of determination (R^2) = 0.4885, multiple $R^2 = 0.5524$; Fig. 4). Over the 14-year study duration, days-from-peak increased 38.65%,

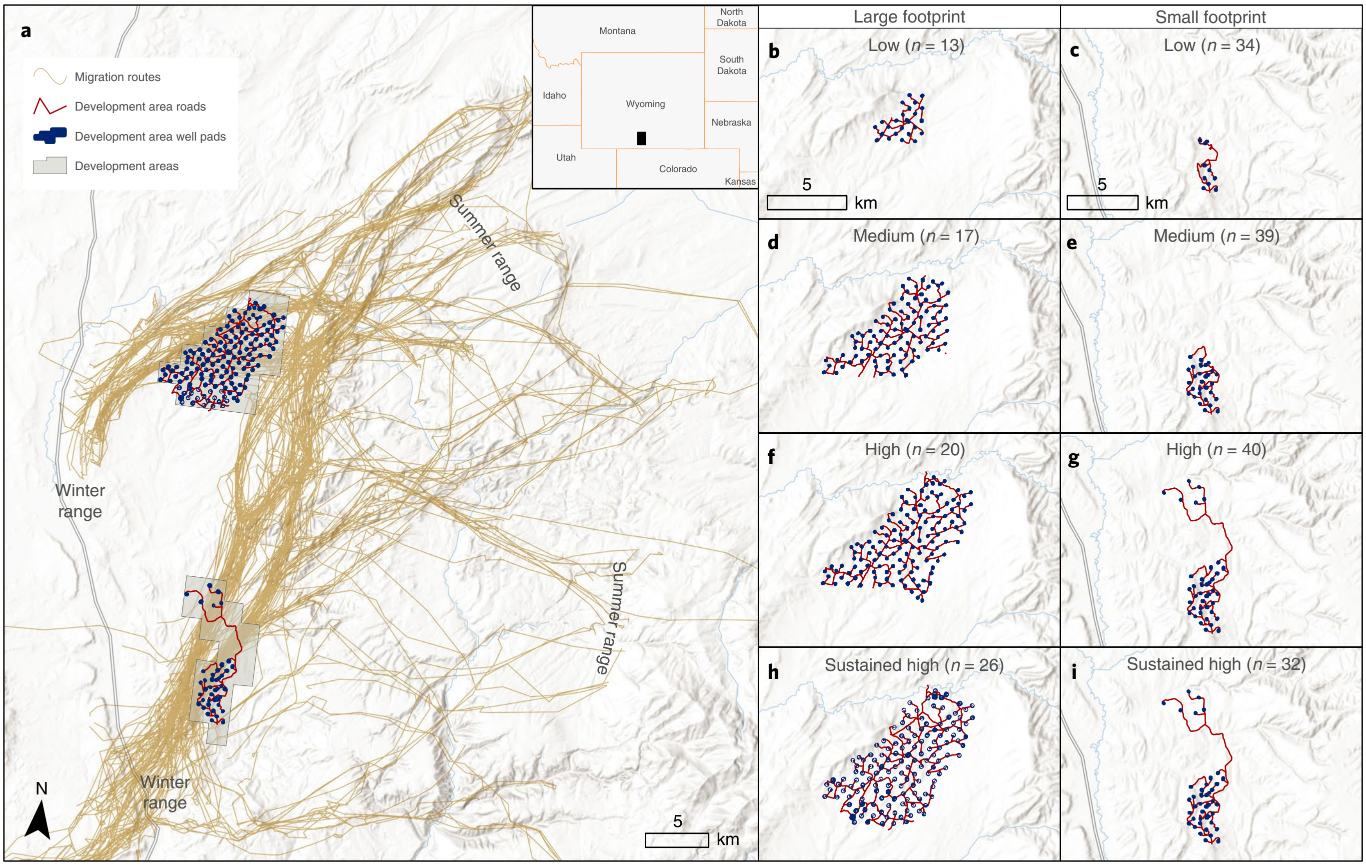

Fig. 1 | Study area map. a, Study area map showing spring migration routes (brown lines) for mule deer that move through an energy development area (well pads in blue and well pad roads in red) in south-central Wyoming, USA. Development increased through time with low levels of development in 2005–2006 (**b**,**c**), medium levels in 2008–2010 (**d**,**e**), high levels in 2015–2016 (**f**,**g**) and sustained high levels in 2017–2018 (**h**,**i**). Additionally, some migration corridors intersected with energy development that had a large footprint of disturbance (**b**,**d**,**f**,**h**), while other corridors intersected with a smaller footprint of disturbance (**c**,**e**,**g**,**i**). Sample sizes for the number of animals tracked at each development level (*n*) and footprint size are shown in **b**–**i**.

indicating that deer became more decoupled from the green wave over time. Importantly, there was no temporal trend in the phenology metrics of rate, duration or order of green-up ($P > 0.05$; Supplementary Table 5), which suggests that directional changes in the phenological landscape could not explain the temporal decline in surfing. Furthermore, these phenology metrics did not explain variability in green-wave surfing (Supplementary Table 6). A continued decline in green-wave surfing over time indicates that deer were unable to acclimate to energy development.

Discussion

We documented a reduction in the ability of mule deer to surf the green wave due to energy development which took place within their migration corridor over a 14-year period. Although previous work has provided clear evidence of changes in migratory behaviour due to energy development[22,23,28], these studies took place over shorter time periods and did not link changes in behaviour to the functional benefit of migration (surfing). Green-wave surfing is a key foraging behaviour that allows animals to put on fat over the growing season[13,29], a behaviour that is thought to underlie the cultural basis of migration in ungulates[14]. We found a link between holding up at the edge of development and diminished green-wave surfing. The clearest changes in green-wave surfing behaviour occurred during the transition from low to medium levels of energy development (Fig. 3a–d), yet disrupted migratory behaviour persisted throughout our 14-year study period (Figs. 3 and 4). These documented changes in migration provide new evidence that behavioural responses to energy development probably come at the cost of a reduction in the foraging benefit of migration. Thus, this work clarifies that the growing list of anthropogenic disruptions to migratory behaviour are probably associated with a loss in the foraging benefits of migration, with potential population-level consequences[1,30,31].

This work highlights the importance of considering not only landscape connectivity (the ability of animals to move through development) but also the functional attributes of movement corridors, such as the foraging benefit they provide. To maintain viable migrations, animals must be able to move freely along their migration corridors to optimally track resources and meet key life-history requirements for survival and reproduction[15]. Despite increases in semipermeable barriers to movement, most deer in our study area continued to migrate through areas of energy development[22]. Increased disturbance along the migration corridor, however, has the potential to alter or curtail migratory behaviour because mule deer avoid migratory habitat when surface disturbance exceeds 3% (ref. [32]). Here, green-wave surfing appeared especially sensitive to disturbance, as effects were detected with both small and large development footprints. Critically, despite still being able to move along their corridors, migrating deer received less of a foraging benefit from doing so because their movements were mismatched with green-up (Figs. 1 and 4). Thus, connectivity was maintained but a key function of migration—green-wave surfing—was not. We suggest that the definition of functional connectivity[33,34] be updated to include the ability of animals to synchronize their movements with spatial fluxes of resources to meet key life-history requirements such as foraging, avoiding predators and optimally timing birth[35,36].

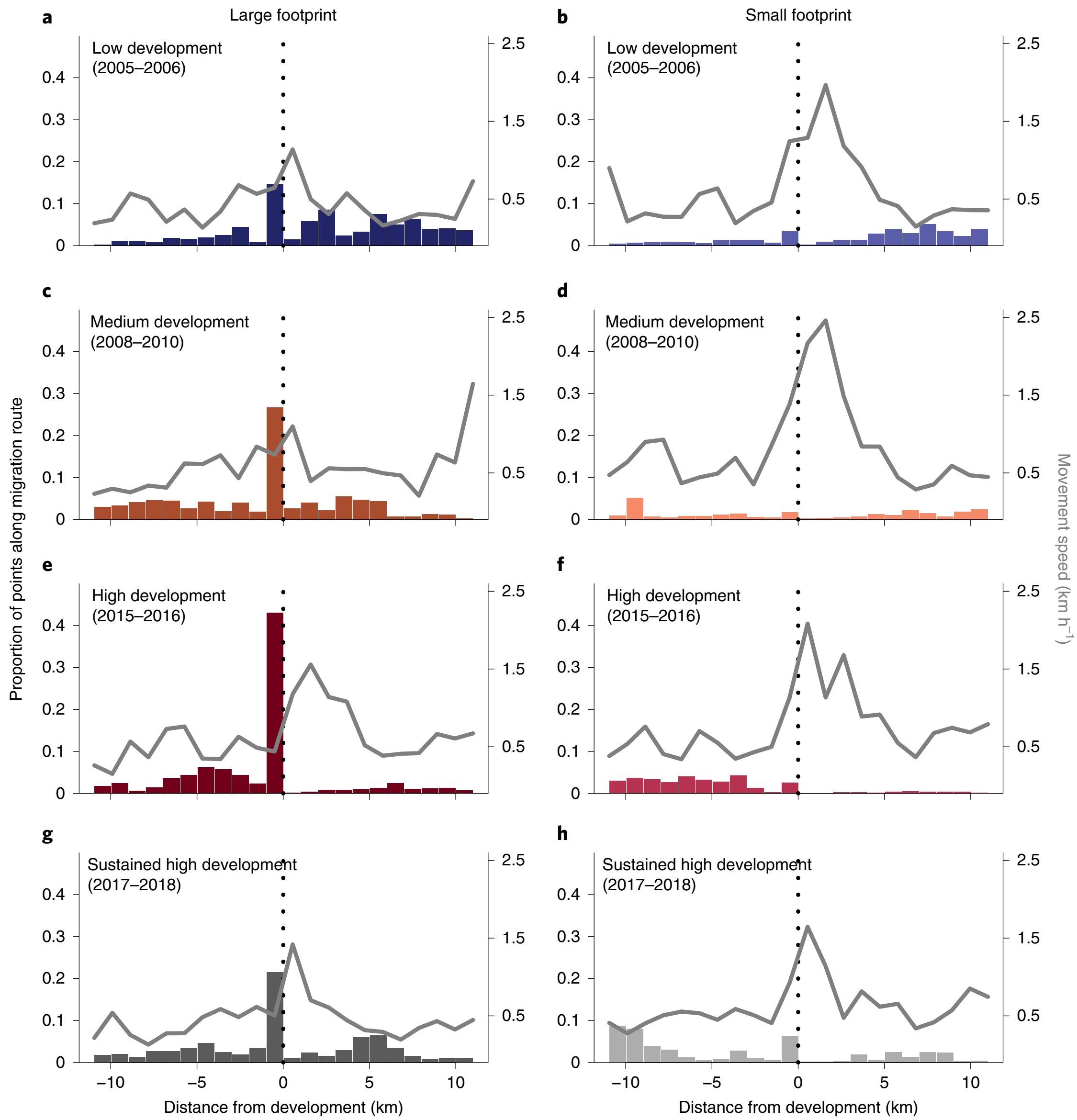

Fig. 2 | The influence of development on time spent along segments of the migration route of mule deer in south-central Wyoming, USA. Mule deer held up at the edge of development (vertical dotted lines in **a**–**h**), as shown by the peak in the proportion of points in the 1 km segment of the route before development. **a**–**h**, Holding-up behaviour was more pronounced for deer migrating through the large energy development footprint (**a**,**c**,**e**,**g**) in comparison to the small energy development footprint (**b**,**d**,**f**,**h**). The light grey line shows the average movement speed (km h^{-1}) along the migration route, which was elevated during and just after deer encountered development. Negative and positive distances on the *x* axis represent movements before and after encountering development, respectively.

In comparison to the myriad studies documenting the loss of migration due to impermeable barriers (reviewed in ref. [1]), the ubiquity of semipermeable barriers and their effect on the functional benefit of migration due to worldwide increases in human development are not well understood[15]. Over 14 years, we found that energy development reduced the foraging benefit of migration, as measured by days-from-peak, by more than 30% (Fig. 4). Similar reductions in green-wave surfing resulted in poorer nutritional condition of elk in the Greater Yellowstone ecosystem, which was predicted to reduce individual fitness and population growth[13]. Furthermore, the negative consequences of decoupling movement from the green wave due to energy development and other semipermeable barriers are likely to be further exacerbated by drought and climate change. Drought alters the pattern and progression of the green wave, resulting in a shorter time window when high-quality food is available on the landscape[37]. Thus, migratory ungulates are doubly challenged by climate change and anthropogenic disturbance[16]. The likely result of ignoring the effects of semipermeable barriers on the foraging benefits of migration is that heavily impacted corridors will become sink habitats that function as ecological traps for migrants with high fidelity to their migration routes[38–40]. When use of impacted corridors by migrating animals is no longer demographically viable across the full annual cycle, such movements—and the accumulated knowledge needed to make them—will probably be lost[14].

To conserve ungulate migration in the face of rapid environmental change and anthropogenic disturbance, an important first step is mapping the migration corridors[16]. Such detailed maps are proving invaluable in planning future energy development projects and mitigating the negative effects of development[16]. Although the exact cognitive mechanisms are unclear (for example, memory and long-range visual

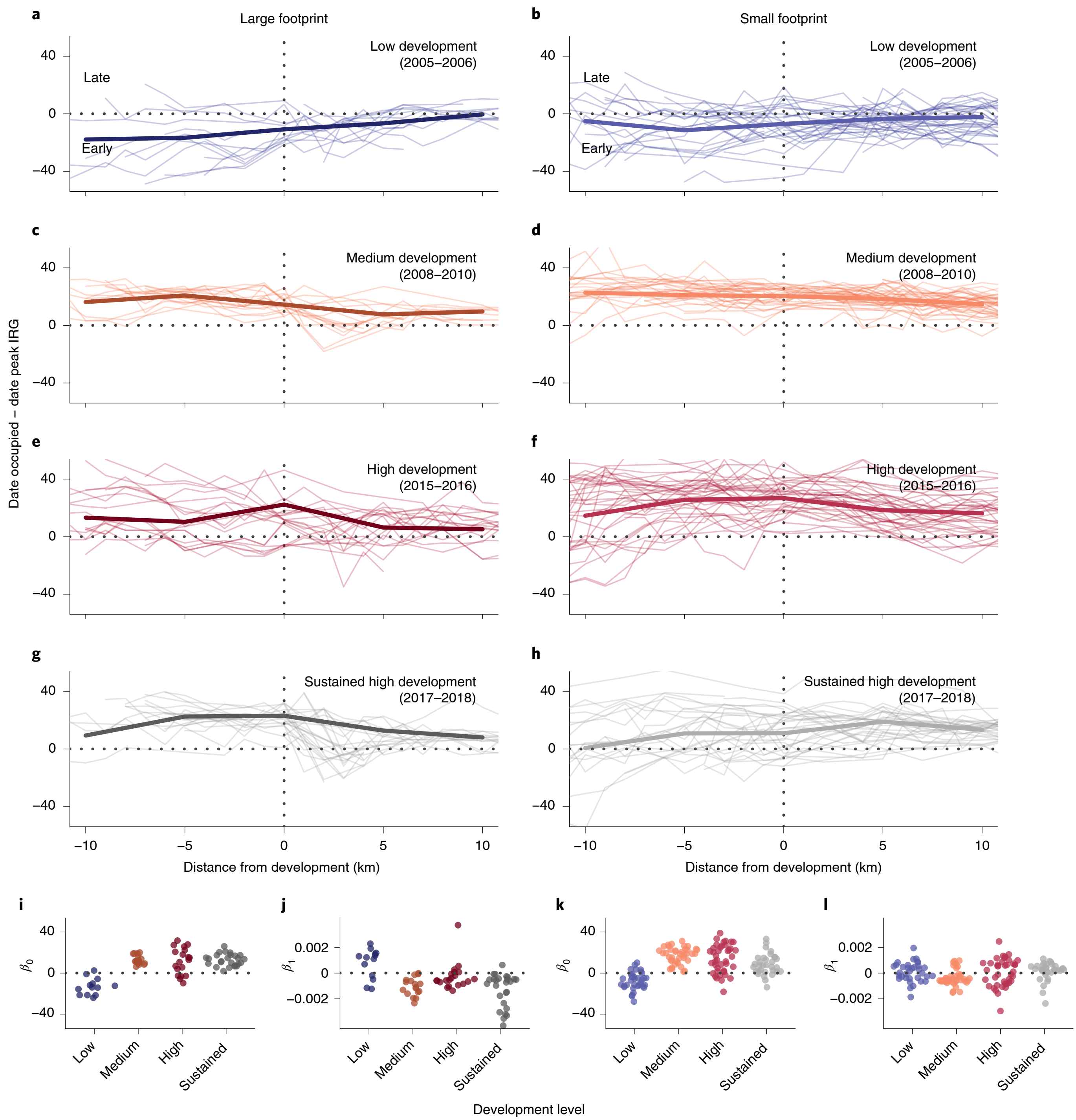

Fig. 3 | Route-level influence of energy development on green-wave surfing by mule deer in south-central Wyoming, USA. Green-wave surfing is measured as the difference in days, between the date a deer occupied a location and the date of peak Instantaneous Rate of Green-up (IRG). At low levels of development, deer were slightly ahead of the green wave when they encountered development. As energy development increased in intensity, deer let the green wave pass by (perfect surfing is indicated by the horizontal dotted line in **a**–**h**). **a**–**h**, Each semitransparent line in **a**–**h** represents a single individual and the thicker solid line represents the sample mean at 5 km intervals along the route. Intercept coefficients (β_0; **i** and **k**) from the linear relationship between distance from development and green-wave surfing indicate that most individuals were late during the three phases of increased development. The slope coefficients (β_1; **j** and **l**) quantify the ability of individuals to catch up with the green wave, which only occurred at medium levels of development for both footprint sizes and sustained high levels of development for the large footprint.

perception), development within a small proportion of the migration corridor elicited strong effects on space-use patterns and green-wave surfing behaviour both upstream and downstream of development. At the same time, many high-use corridors and critical bottlenecks are relatively narrow, so it may be possible to balance energy or other development demands with wildlife conservation by placing new energy development projects outside of high-use corridors and stopover habitats[25,41–43]. Without detailed information on key migratory habitats, it will be difficult to design development projects in ways that retain landscape connectivity and functional migratory routes for wide-ranging

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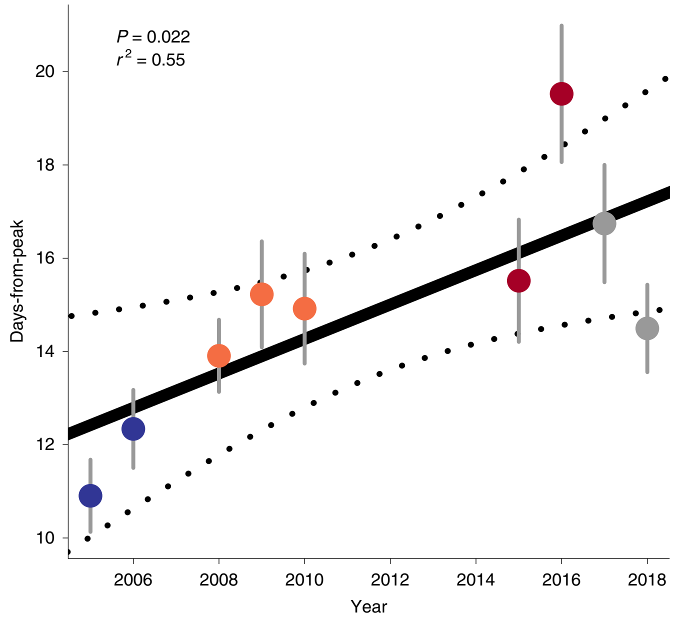

Fig. 4 | Migratory movements of mule deer became increasingly mismatched with the green wave over time. Energy development was low in 2005–2006 (blue points), medium in 2008–2010 (orange points), high in 2015–2016 (red points) and remained at a sustained high level of development in 2017–2018 (grey points). Annual variability in the pattern of the green wave did not account for the reduction in surfing over time. The solid black line represents the fitted relationship of a linear regression and the black dotted lines represent the 95% confidence intervals. Grey lines represent standard errors for each annual mean (sample sizes for each annual mean: 2005 n = 14, 2006 n = 23, 2008 n = 19, 2009 n = 25, 2010 n = 12, 2015 n = 31, 2016 n = 29, 2017 n = 28, 2018 n = 30).

ungulates. Thus, detailed planning for migration at the landscape scale will be necessary to assure that corridors remain intact, barriers are minimized and migrations remain viable over the long term.

Methods

Study area

This study took place in south-central Wyoming, USA, a region characterized by high elevation (1,700–2,100 m) basins dominated by sagebrush (*Artemisia* spp.) steppe shrublands interspersed with occasional greasewood (*Sarcobatus vermiculatus*) flats, Gardner saltbush (*Atriplex gardneri*) and a variety of forbs and grasses. The basins are surrounded by mountains to the east (2,100–3,354 m) dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and interspersed with aspen (*Populus tremuloides*). Precipitation ranges from 15–38 cm in the basins to 53–150 cm in the surrounding mountains where winter snow is the dominant precipitation regime. Elevation of seasonal ranges used by deer varied from 1,762 m in winter to 2,719 m in summer. Deer migrated 11–119 km between seasonal ranges and were exposed to variable levels of energy development (coalbed natural gas) as they moved through a mix of public (79%) and private (21%) lands.

Movement data

We used GPS-collar data from female mule deer (n = 120) that moved through energy development during their spring migrations (n = 221) between 2005 and 2018[15,25,41]. All data were collected using store-on-board GPS-collars (TGW 3500; Telonics) programmed to record a location every 2 or 2.5 h. We used helicopter net-gunning to capture and collar adult (>1-year-old) female mule deer when they were concentrated on winter ranges. We captured all deer following protocols consistent with the University of Wyoming Institutional Animal Care and Use Committee and recommendations of the American Society of Mammalogists[44].

Measuring development

Development phases were defined as low (2005–2006), medium (increased development above baseline; 2008–2010), high (largest well-installation phase; 2015–2016) and sustained high (some additional development; 2017–2018; Fig. 1)[15]. Tracking data were not collected during 2007 or from 2011–2014. In the large and small energy development footprints, respectively, well pad densities (wells per km^2) were 0.44 and 0.22 during the low development phase, 1.62 and 0.64 at medium development, 2.18 and 0.90 at high development and 2.43 and 1.27 at sustained high development. We used polygons of the energy development footprints to quantify distance to development for each animal-year. The energy development footprint was defined as the parcels of land leased for development. The start of energy development (distance from development = 0) was defined as the first point where the animal's spring migratory movements (or the linear interpolation of those movements) intersected the energy development footprint. The end of energy development was defined as the last point (or the linear interpolation of those movements) that intersected the development footprint. If points occurred before development, the start of energy development was used as the reference point and if the points occurred after encountering development, the end of energy development was used as the reference point. From these reference points, the distances between all other locations during spring migration were calculated and placed into 1 km bins (Supplementary Fig. 4). Hereafter, we refer to these bins as the 1 km segments of the migration route. If an individual's movements did not intersect with the energy development footprint, they were excluded from the analysis, which resulted in 221 out of 253 animal-years (87%) being retained for analysis. Of those individuals that did not migrate directly through energy development, 39% moved within 1 km of the energy development footprint and may have also been influenced by energy development. Because of their close proximity to development and relatively low sample size (only two or three animals in most years), we could not use these animals as a control group. We examined the proportion of time spent, movement speed and how well migrants matched their movements with the progression of the green wave along the 1 km segments of the route. Unless otherwise stated, these analyses were performed on the 1 km segments along the entire migration route. For visualization purposes, only 10 km segments before and after encountering development are shown; however, all analysis was performed on the entire migration.

Holding-up behaviour

To examine the effects of energy development on space-use patterns during migration, we used the density of points within each 1 km segment to quantify the amount of time spent in different segments of the route. We used proportions of points rather than simple frequency counts (frequency count in a distance bin divided by the total number of points) because the number of animals collared during each year varied. To quantify change in time spent along various segments of the route, we examined the cumulative proportion of points that occurred along various distances, ranging from 1 to 10 km, before and after deer encountered energy development (Supplementary Information). We also calculated movement speed (km h^{-1}) as displacement distance divided by change in time between subsequent relocations and then calculated the average value for each animal-year along each 1 km segment of the migration route. If space-use patterns were unaltered by increasing energy development, we expected the proportion of time spent in each segment of the route and movement speed to remain constant over time.

Green-wave surfing

To quantify green-up, we used the Instantaneous Rate of Green-up (IRG), which calculates the change in Normalized Difference Vegetation

Index (NDVI) through time (MOD09Q1, 250 m spatial resolution, 8 d temporal resolution)[27,45]. The NDVI is often used as an index of biomass in temperate and montane ecosystems[46,47] and has been correlated with forage quality for ungulates across a range of systems[48], including in the nearby Greater Yellowstone ecosystem[49]. To calculate IRG, we first fit a double logistic curve to a time series of NDVI data for each pixel in our study area, following refs. [11,27]. There is some uncertainty associated with fitting the double logistic curve to the time series of NDVI data. We did not incorporate this uncertainty into further analysis because we assumed that the degree of uncertainty was randomly distributed across space and time and therefore unlikely to bias our results. We estimated IRG by taking the first derivative of the annual fitted NDVI curve, which results in a curve that peaks when vegetation growth is most rapid, hereafter peak green-up. For additional details, refer to refs. [11,12].

To quantify the impact of development on green-wave surfing, we first calculated the difference in days between the date an animal occupied a location and the date of peak green-up at that location for each individual along each 1 km segment of the migration route. Using this metric of surfing, negative values indicate that an animal is early with respect to the green wave, while positive values indicate late surfing. For each individual, we fitted a linear regression between distance to development and green-wave surfing. As described above, the distance from development metric was standardized so that development occurred at zero. Movements that occurred before development had negative distance from development values and movements after encountering development had positive distance from development values. From each linear regression, we used the intercept to quantify if individuals were early or late with respect to the green wave upon encountering development during migration (a negative intercept would indicate being early, while a positive intercept would indicate animals being late). We used the slope of the line to quantify the extent to which animals were able to realign their movements with the green wave (catching up to the green wave if late or letting the green wave catch up to them if early). For animals that start their migration early with respect to the green wave, a positive slope would indicate letting the green wave catch up to them. For animals starting out their migration late, a negative slope would indicate a reduced mismatch with the green wave as the migration progressed (Supplementary Table 3). In these cases, a non-zero slope indicates some degree of compensation for being mismatched from the green wave but does not indicate if this compensation is partial (some mismatch remains) or complete (movements become perfectly matched to green-up). For each level of development intensity (low, medium, high and sustained high), we examined the mean intercepts to estimate the tendency for the sampled population to be early or late. To determine if animals were able to catch up with the green wave, we estimated the sampled population's mean slopes of individual linear regressions between distance to development and green-wave surfing. We used two-sided *t*-tests to determine if the population mean intercepts and slopes across development levels were different from zero.

In addition to calculating green-wave surfing along each segment of the migration route, we also calculated an overall surfing score for each animal-year using days-from-peak, calculated as the absolute difference in days between the date a deer used a location and its date of peak green-up[12]. Following the approach of ref. [12], we first calculated the mean daily value of days-from-peak for all GPS locations during the spring before calculating the overall mean value for each animal-year to reduce potential bias introduced by differences in fix-rate. Days-from-peak was used to calculate an overall surfing score because the absolute value prevents early surfing (negative values) from cancelling out late surfing (positive values), which would result in a false signal of surfing when averaged together to generate an overall surfing score.

Evaluating the impact of expanding development on surfing

We used the year-averaged days-from-peak values to determine if migratory mule deer acclimated to disturbance. Specifically, we examined the temporal trend in days-from-peak for evidence of either: (1) an improvement in surfing at sustained high levels of development which would indicate acclimation or (2) no change in surfing or a greater decoupling between movement and the green wave indicating a lack of acclimation. To calculate change in green-wave surfing over time, we calculated the percentage change in predicted days-from-peak between the last and first year of our study derived from a linear model of days-from-peak over time (Fig. 4).

We also considered the alternative hypothesis that changes in the 'greenscape' or how the green wave progresses along a migration route, could account for changes in green-wave surfing. To characterize the greenscape, which is defined as the duration, order and rate of green-up along migration routes, we first isolated the migration route of each individual following the methods described in ref. [12]. We then calculated duration as the difference in days between the date of peak green-up at the beginning and the end of the route[12]. Order was calculated as Spearman's rank correlation between the physical order of points along the route and the order at which those points greened-up[12]. Finally, green-up rate was calculated as the average spring scale parameter, estimated in the process of fitting the double logistic curve to the annual time series of NDVI[12]. Spring scale is equivalent to the inverse of green-up rate and can be interpreted as the time to reach peak green-up, where larger values indicate more gradual green-up[12]. To determine if differences in the greenscape across years could be a confounder in our analyses, we examined the temporal trend in the greenscape from 2005 to 2018.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

GPS locations and energy development footprints can be found in the following Dryad Data Digital Repository: https://doi.org/10.5061/dryad.7d7wm37z5. MODIS data are available from the U.S. Geological Survey LP DAAC (https://lpdaac.usgs.gov/).

References

1. Bolger, D. T., Newmark, W. D., Morrison, T. A. & Doak, D. F. The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* **11**, 63–77 (2008).
2. Fryxell, J. M., Greever, J. & Sinclair, A. R. E. Why are migratory ungulates so abundant. *Am. Nat.* **131**, 781–798 (1988).
3. Holdo, R. M., Holt, R. D., Sinclair, A. R., Godley, B. J. & Thirgood, S. in *Animal Migration: A Synthesis* (eds Milner-Gulland, E. J. et al.) 131–143 (Oxford Univ. Press, 2011).
4. Bauer, S. & Hoye, B. J. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552 (2014).
5. Middleton, A. D. et al. Conserving transboundary wildlife migrations: recent insights from the Greater Yellowstone Ecosystem. *Front. Ecol. Environ.* **18**, 83–91 (2020).
6. Aikens, E. O. et al. Wave-like patterns of plant phenology determine ungulate movement tactics. *Curr. Biol.* **30**, 3444–3449 (2020).
7. Mueller, T. & Fagan, W. F. Search and navigation in dynamic environments—from individual behaviors to population distributions. *Oikos* **117**, 654–664 (2008).
8. Fryxell, J. M. Forage quality and aggregation by large herbivores. *Am. Nat.* **138**, 478–498 (1991).
9. Drent, R., Ebbinge, B. & Weijand, B. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. *Verh. Ornithol. Ges. Bayern* **23**, 239–264 (1978).
10. van der Graaf, S. A. J., Stahl, J., Klimkowska, A., Bakker, J. P. & Drent, R. H. Surfing on a green wave—how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea* **94**, 567–577 (2006).

11. Merkle, J. A. et al. Large herbivores surf waves of green-up during spring. *Proc. R. Soc. B*. **283**, 20160456 (2016).
12. Aikens, E. O. et al. The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.* **20**, 741–750 (2017).
13. Middleton, A. D. et al. Green-wave surfing increases fat gain in a migratory ungulate. *Oikos* https://doi.org/10.1111/oik.05227 (2018).
14. Jesmer, B. R. et al. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* **361**, 1023–1025 (2018).
15. Sawyer, H. et al. A framework for understanding semi-permeable barrier effects on migratory ungulates. *J. Appl. Ecol.* **50**, 68–78 (2013).
16. Kauffman, M. J. et al. Mapping out a future for ungulate migrations. *Science* **372**, 566–569 (2021).
17. Doherty, T. S., Hays, G. C. & Driscoll, D. A. Human disturbance causes widespread disruption of animal movement. *Nat. Ecol. Evol.* **5**, 513–519 (2021).
18. Berry, J. Aspects of wildebeest *Connochaetes taurinus* ecology in the Etosha National Park—a synthesis for future management. *Madoqua* **1997**, 137–148 (1997).
19. Williamson, D. & Williamson, J. Botswana's fences and the depletion of Kalahari wildlife. *Oryx* **18**, 218–222 (1984).
20. Northrup, J. M. & Wittemyer, G. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecol. Lett.* **16**, 112–125 (2013).
21. Kauffman, M. J., Meacham, J. E., Sawyer, H., Rudd, W. & Ostlind, E. *Wild Migrations: Atlas of Wyoming's Ungulates* (Oregon State Univ. Press, 2018).
22. Wyckoff, T. B., Sawyer, H., Albeke, S. E., Garman, S. L. & Kauffman, M. J. Evaluating the influence of energy and residential development on the migratory behavior of mule deer. *Ecosphere* **9**, e02113 (2018).
23. Lendrum, P. E., Anderson, C. R. Jr., Monteith, K. L., Jenks, J. A. & Bowyer, R. T. Migrating mule deer: effects of anthropogenically altered landscapes. *PLoS ONE* **8**, e64548 (2013).
24. Lendrum, P. E., Anderson, C. R. Jr, Long, R. A., Kie, J. G. & Bowyer, R. T. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere* **3**, 82 (2012).
25. Sawyer, H. & Kauffman, M. J. Stopover ecology of a migratory ungulate. *J. Anim. Ecol.* **80**, 1078–1087 (2011).
26. Sawyer, H., LeBeau, C. W., McDonald, T. L., Xu, W. & Middleton, A. D. All routes are not created equal: an ungulate's choice of migration route can influence its survival. *J. Appl. Ecol.* **56**, 1860–1869 (2019).
27. Bischof, R. et al. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *Am. Nat.* **180**, 407–424 (2012).
28. Skarin, A., Nellemann, C., Rönnegård, L., Sandström, P. & Lundqvist, H. Wind farm construction impacts reindeer migration and movement corridors. *Landsc. Ecol.* **30**, 1527–1540 (2015).
29. Mysterud, A., Langvatn, R., Yoccoz, N. G. & Stenseth, N. C. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *J. Anim. Ecol.* **70**, 915–923 (2001).
30. Johnson, H. E. et al. Increases in residential and energy development are associated with reductions in recruitment for a large ungulate. *Glob. Change Biol.* **23**, 578–591 (2017).
31. Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L. & Strickland, D. Mule deer and energy development—long-term trends of habituation and abundance. *Glob. Change Biol.* **23**, 4521–4529 (2017).
32. Sawyer, H., Lambert, M. S. & Merkle, J. A. Migratory disturbance thresholds with mule deer and energy development. *J. Wildl. Manag.* **84**, 930–937 (2020).
33. Uezu, A., Metzger, J. P. & Vielliard, J. M. E. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biol. Conserv.* **123**, 507–519 (2005).
34. Keeley, A. T. H., Beier, P. & Jenness, J. S. Connectivity metrics for conservation planning and monitoring. *Biol. Conserv.* **255**, 109008 (2021).
35. Abrahms, B. et al. Emerging perspectives on resource tracking and animal movement ecology. *Trends Ecol. Evol.* **36**, 308–320 (2021).
36. Aikens, E. O. et al. Migration distance and maternal resource allocation determine timing of birth in a large herbivore. *Ecology* **102**, e03334 (2021).
37. Aikens, E. O. et al. Drought reshuffles plant phenology and reduces the foraging benefit of green-wave surfing for a migratory ungulate. *Glob. Change Biol.* **26**, 4215–4225 (2020).
38. Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinnell, S. P. H. & Monteith, K. L. Migratory plasticity is not ubiquitous among large herbivores. *J. Anim. Ecol.* **88**, 450–460 (2019).
39. Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480 (2002).
40. Delibes, M., Gaona, P. & Ferreras, P. Effects of an attractive sink leading into maladaptive habitat selection. *Am. Nat.* **158**, 277–285 (2001).
41. Sawyer, H., Kauffman, M. J., Nielson, R. M. & Horne, J. S. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecol. Appl.* **19**, 2016–2025 (2009).
42. Sawyer, H., Hayes, M., Rudd, B. & Kauffman, M. J. *The Red Desert to Hoback Mule Deer Migration Assessment* (Univ. Wyoming, 2014).
43. Berger, J., Young, J. K. & Berger, K. M. Protecting migration corridors: challenges and optimism for Mongolian saiga. *PLoS Biol.* **6**, e165 (2008).
44. Sikes, R. S. & Gannon, W. L. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**, 235–253 (2011).
45. Vermote, E. *MOD09A1 Surface Reflectance 8-day L3 Global 500m SIN Grid V006* (NASA EOSDIS Land Processes DAAC, 2015).
46. Pettorelli, N., Mysterud, A., Yoccoz, N. G., Langvatn, R. & Stenseth, N. C. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc. R. Soc. B.* **272**, 2357–2364 (2005).
47. Pettorelli, N. et al. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* **20**, 503–510 (2005).
48. Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J. M. & Cote, S. D. Spring normalized difference vegetation index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J. Appl. Ecol.* **46**, 582–589 (2009).
49. Geremia, C. et al. Migrating bison engineer the green wave. *Proc. Natl Acad. Sci. USA* **116**, 25707–25713 (2019).

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Author contributions
E.O.A., T.B.W., H.S. and M.J.K. conceived the work. H.S. collected the data. E.O.A. and T.B.W. analysed the data. E.O.A., T.B.W. and M.J.K. wrote the manuscript and all authors contributed to revisions.

Competing interests
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Correspondence and requests for materials should be addressed to Ellen O. Aikens.

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