

Current Biology

Wave-like Patterns of Plant Phenology Determine Ungulate Movement Tactics

Highlights

- Ungulates moved to track forage in landscapes with wave-like spring green-up
- Patterns of green-up explained where migratory behavior occurred in many ecosystems
- At the species level, migrants and residents received equivalent foraging benefits
- Movement tactics represent behavioral adaptations to specific landscapes

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In Brief

Using GPS-tracking from 61 populations of four ungulate species, Aikens et al. provide evidence that the dynamic nature of forage resources generates the diversity of movement tactics used by animals. Specifically, patterns of spring green-up shaped how closely animals tracked resources and where migration occurred across temperate ecosystems.

Report

Wave-like Patterns of Plant Phenology Determine Ungulate Movement Tactics

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SUMMARY

Animals exhibit a diversity of movement tactics [1]. Tracking resources that change across space and time is predicted to be a fundamental driver of animal movement [2]. For example, some migratory ungulates (i.e., hooved mammals) closely track the progression of highly nutritious plant green-up, a phenomenon called “green-wave surfing” [3–5]. Yet general principles describing how the dynamic nature of resources determine movement tactics are lacking [6]. We tested an emerging theory that predicts surfing and the existence of migratory behavior will be favored in environments where green-up is fleeting and moves sequentially across large landscapes (i.e., wave-like green-up) [7]. Landscapes exhibiting wave-like patterns of green-up facilitated surfing and explained the existence of migratory behavior across 61 populations of four ungulate species on two continents ($n = 1,696$ individuals). At the species level, foraging benefits were equivalent between tactics, suggesting that each movement tactic is fine-tuned to local patterns of plant phenology. For decades, ecologists have sought to understand how animals move to select habitat, commonly defining habitat as a set of static patches [8, 9]. Our findings indicate that animal movement tactics emerge as a function of the flux of resources across space and time, underscoring the need to redefine habitat to include its dynamic attributes. As global habitats continue to be modified by anthropogenic disturbance and climate change [10], our synthesis provides a generalizable framework to understand how animal movement will be influenced by altered patterns of resource phenology.

RESULTS AND DISCUSSION

Animals exhibit a wide diversity of movement behaviors. Some animals live year-round within a restricted area, whereas others traverse the entire planet [1]. Although animals move to find

resources, general principles describing how movement tactics are shaped by the dynamic nature of resources have yet to be clearly defined and tested. For ungulates, newly emergent plants (hereafter green-up) provide the highest-quality forage, but green-up is only available at any one location for a narrow

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window of time [11]. “Green-wave surfing,” or tracking plant green-up that sweeps across the landscape, is thought to be a key driver of ungulate migration [3, 12] and a precursor to the development of migratory behavior [12]. Not all migratory ungulates surf the green wave [13], however, highlighting a key gap in our understanding of how resource dynamics shape migratory movements.

According to the Greenscape Hypothesis, the way green-up propagates across a landscape should determine where surfing is adaptive [7]. Although there are many ways to conceptualize resource dynamics across space and time, the Greenscape Hypothesis characterizes the wave-like nature of resources using the rate, order, and duration of green-up [7]. Accordingly, surfing is predicted to be favored in wave-like environments, where green-up is fleeting locally but progresses sequentially across large areas (i.e., rapid rate, sequential order, and long duration of green-up [7]). By contrast, the need to move and seek out resources should be diminished in landscapes where green-up is prolonged (i.e., a gradual rate of green-up). We tested the predictions of the Greenscape Hypothesis to examine how global variation in patterns of plant phenology (i.e., greenscapes) shape surfing. We compiled a cross-continental dataset of 1,696 GPS-collared individuals from 61 populations (with various proportions of migrants and residents) across four ungulate species (roe deer [*Capreolus capreolus*] and red deer [*Cervus elaphus*] in Europe, and mule deer [*Odocoileus hemionus*] and elk [*Cervus canadensis*] in North America; Figure 1). We quantified green-wave surfing behavior as the absolute difference in days between the date of peak green-up and the date the animal used a location (hereafter Days-From-Peak, 0 = perfect surfing [7]). In support of the Greenscape Hypothesis, animals surfed closer

to the date of peak green-up when green-up occurred in a wave-like pattern, characterized as rapid green-up rate, consecutive green-up order, and long green-up duration (Figure 2). The robust and general support for the Greenscape Hypothesis indicates that surfing the green wave is an adaptation to enhance foraging in environments with fleeting green-up that moves like a wave across northern temperate regions of the globe.

Because green-wave surfing leads to migration [12], wave-like greenscapes may predict the landscapes where migration should be a common movement tactic. Thus, we extended the Greenscape Hypothesis to evaluate whether green-up dynamics determine if animals exhibit a migratory or resident tactic. We classified movement tactics of individuals as migratory, resident, or other [14] and compared the greenscapes available to individuals across populations with different proportions of migrants and residents. At the individual level, migrants occupied landscapes with an average of 21%–27% more rapid rates of green-up (range represents species-specific averages; Figures S1A–S1D) and 21%–35% more consecutive green-up order than residents (Figures S1E–S1H). At the population level, as the phenology of a landscape became more wave-like (i.e., green-up was more rapid and ordered), the proportion of individuals exhibiting a migratory strategy increased (Figure 3). Additionally, the proportion of migrants and residents within a population was strongly controlled by the wave-like pattern of plant phenology, with partial migration (i.e., when individuals from the same population exhibit different movement tactics) being favored in landscapes with intermediate greenscape attributes (Figure 3). Although movement is shaped by a myriad of factors (e.g., conspecific density and environmental variability [15]), our results indicate that a composite attribute of habitat—the wave-

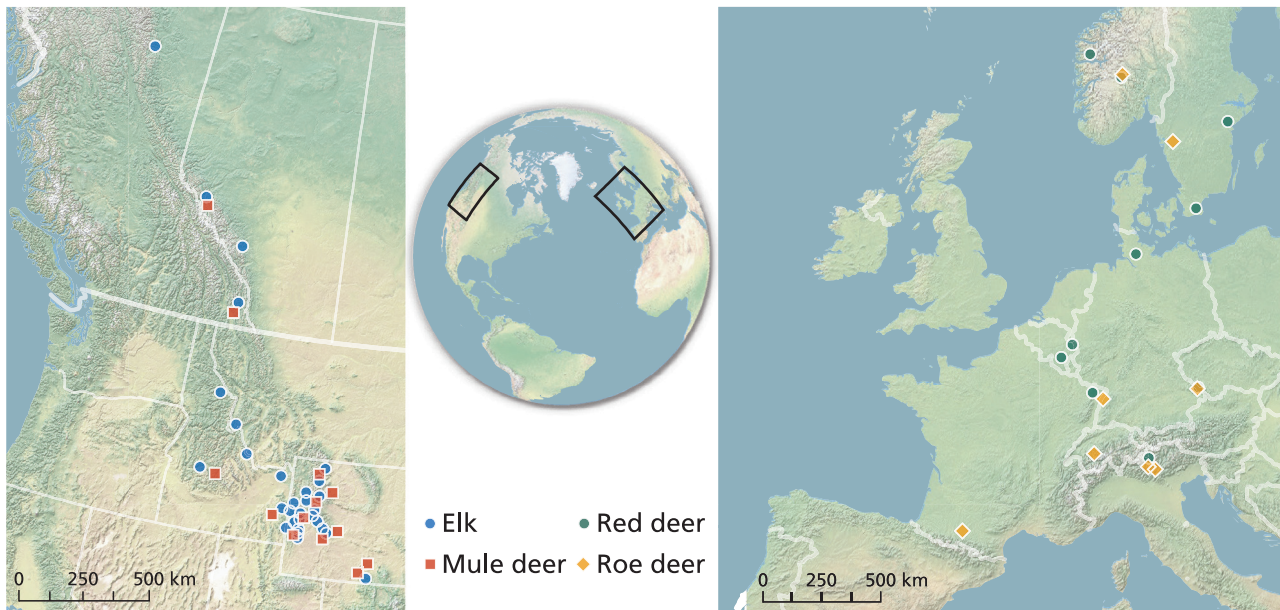


Figure 1. Geographic Location of Study Populations

Each dot represents the centroid of the GPS locations for a population. North American elk are represented as blue circles ($n = 903$ individuals, 30 populations), mule deer as orange squares ($n = 422$ individuals, 13 populations), red deer as green circles ($n = 176$ individuals, 10 populations), and roe deer as yellow diamonds ($n = 195$ individuals, 8 populations). Cartography by University of Oregon InfoGraphics Lab. See also [Table S1](#).

like nature of foraging resources—determines whether migration or residency is favored for ungulates in northern temperate ecosystems. These findings provide support for a general principle whereby animal movement tactics are fine-tuned to the pace and pattern of ephemeral foraging resources.

Animals are expected to derive foraging benefits from the movement tactics they employ. If movement tactics are adaptive, the resulting foraging benefits of different tactics should be broadly comparable across different populations and ecosystems [15]. To examine the consequences of different movement tactics, we compared how well animals aligned their movements with the green wave (i.e., surfing behavior, Days-From-Peak) and the

resulting foraging benefit of surfing between migrants and residents within each species. To characterize the potential foraging benefit of surfing, we calculated the Instantaneous Rate of Green-up (IRG), which incorporates both the rate of green-up and date of peak green-up, to estimate exposure to green-up [13]. At the species level, migrants consistently surfed closer to the date of peak green-up than residents ([Figure 4A](#)). However, moving in sync with the green wave did not translate to greater exposure to spring green-up compared with residents, a pattern that was consistent across all four species ([Figure 4B](#)). Despite differences in surfing, migrants and residents had equivalent exposure to spring green-up, presumably because residents inhabited

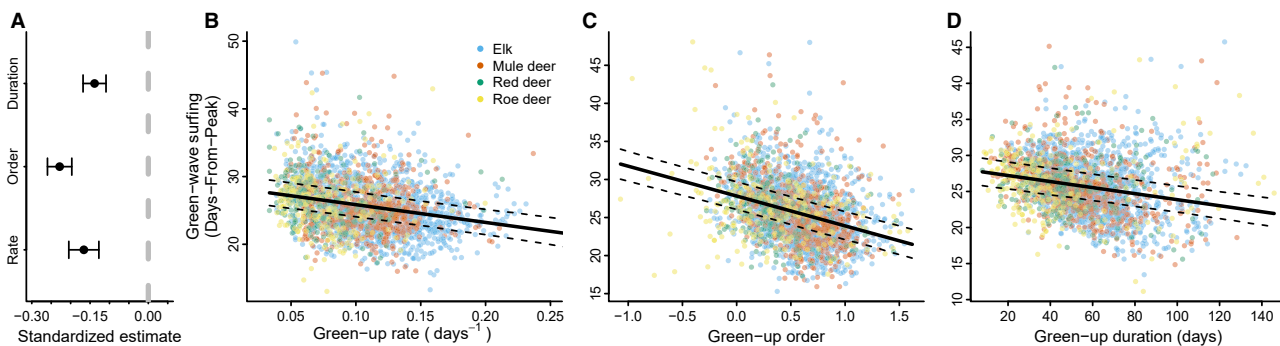


Figure 2. Relationship between the Greenscape and Green-Wave Surfing

The greenscape is conceptualized using three metrics of green-up: rate (how long green-up lasts locally), duration (how long green-up lasts across the landscape), and order (the progression of green-up across the landscape).

(A) Patterns of plant phenology influenced surfing (standardized coefficients \pm 95% CI shown) across 61 populations of northern temperate ungulates.

(B–D) Animals surfed better (fewer Days-From-Peak) when spring green-up was rapid (B), more consecutive (C), and of longer duration (D).

Days-From-Peak is a behavioral metric of surfing, where a value of zero represents perfect surfing (i.e., a perfect match between the date of peak green-up and the date that the animal used locations; averaged over a 120-day spring period). See also [Figures S2](#) and [S4](#) and [Table S2](#).

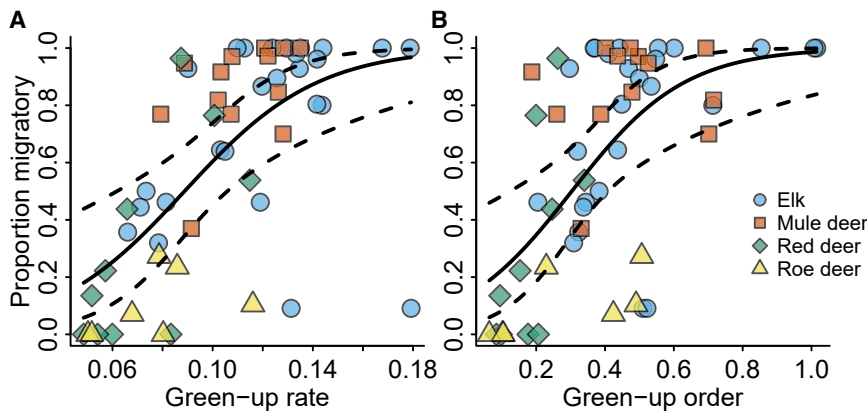


Figure 3. The Influence of the Greenscape on Migration Propensity

The proportion of migratory individuals in a population increases as green-up rate becomes more fleeting (A) and as green-up becomes more ordered (B). Specifically, odds of having a completely migratory herd increased 330-fold from an environment with no wave (i.e., order = 0) to an environment with an idealized wave (order = 1). Likewise, odds of the herd being completely migratory decreased 137-fold when comparing environments with the most ephemeral green-up to the most prolonged green-up. Green-up rate was measured as the mean green-up rate available to all individuals in a population. Green-up order was estimated from a semivariogram measuring the shape of semivariance in the date of peak green-up at increasing distance lags (larger values = more consecutive green-up order). See also [Figures S1](#) and [S2](#).

landscapes with less wave-like green-up ([Figure 3](#)). The equivalent exposure to spring green-up between migrants and residents indicates that individuals exhibit movement tactics that are adapted to the underlying resource dynamics they experience, allowing them to derive similar foraging benefits across different landscapes.

For nearly a century, ecologists have sought to understand how animals select habitat [16]. In early work, habitat was often viewed as a set of static resource patches (e.g., [8, 17]), with relatively little attention paid to how animals cope with resources that change across space and time (but see [18, 19]). Nevertheless, phenological diversity is intrinsic to natural food webs and controls the temporal availability of key food resources for consumers as diverse as blue whales (*Balaenoptera musculus*) and fig wasps (superfamily Chalcidoidea [2, 20, 21]). The technological revolution in animal tracking and remote sensing [22] has resulted in a proliferation of case studies quantifying how animals move in response to dynamic environments (e.g., [2, 23]). While movement ecology has developed increasingly powerful means to quantify and reconstruct the movement paths of animals [6, 24], our study advances the field by connecting animal movement paths explicitly to the underlying resource dynamics that animals experience (also see [25, 26]). We find that green-wave surfing leads to the emergence of migratory behavior, with both behaviors being most adaptive in environments with wave-like spring green-up. Importantly, migration is not always superior to residency in terms of forage acquisition [27], but rather the way forage resources progress (or not) across the landscape determines the movement tactics that are adaptive on a given landscape.

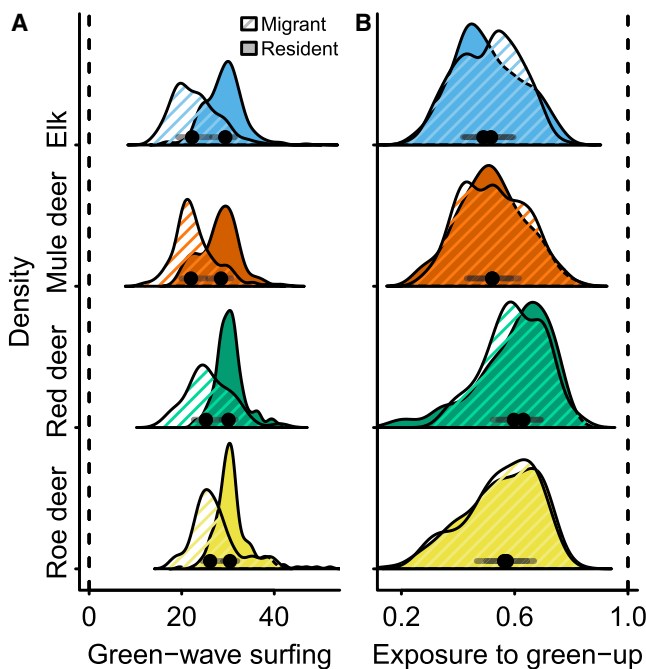


Figure 4. A Comparison of Green-Wave Surfing and Exposure to Spring Green-Up between Migrants and Residents

(A) Migrants surfed better across all four species, as measured by Days-From-Peak, where zero (black dashed line) represents a perfect match between the date of peak green-up and the date of animal use.

(B) Despite not surfing as well, residents obtained equivalent exposure to spring green-up, as measured by the Instantaneous Rate of Green-up (IRG). An IRG value of one (black dashed line) represents the maximum possible exposure to spring green-up and the greatest foraging benefit. Black dots represent the median and transparent gray lines represent the interquartile range. See also [Figure S3](#) and [Table S3](#).

Long-distance animal movements are being lost or truncated across the globe [10]. Loss of migratory behavior can result from barriers that prevent migrants from freely moving across large landscapes [28]. Our results indicate that migrations can also be lost when changes in the underlying resource landscape eliminate the need to migrate over long distances. For example, shortened migrations or increased residency have been caused by food subsidies (e.g., agriculture, landfills [29]) and climate-induced shifts in phenology or resource distribution [30], which can alter or eliminate the progression of green waves across the landscape. Thus, some shifts in movement may be adaptive in a changing world, whereas others—those caused by barriers to movement—might be an early warning signal of future population decline. Indeed, we found that greater exposure to anthropogenic disturbance resulted in poorer surfing, even after taking into account differences in the greenscape ([Figure S4A](#)), suggesting that green-wave surfing is already threatened or altered

in many systems. Characterizing wave-like greenscapes where migration is required will allow ecologists to identify landscapes where migration must be conserved. Such movement behaviors often must be socially learned, and thus population declines represent not only the loss of individuals, but also the loss of fine-tuned behaviors that have developed over generations through cultural evolution [12]. As landscapes become increasingly altered by climate change and anthropogenic development, identifying movement tactics that should be profitable but have been lost or altered will be critical to the conservation of animal movement and the ecological processes it sustains.

STARMETHODS

Detailed methods are provided in the online version of this paper and include the following:

- **KEY RESOURCES TABLE**
- **RESOURCE AVAILABILITY**
 - Lead Contact
 - Materials Availability
 - Data and Code Availability
- **EXPERIMENTAL MODEL AND SUBJECT DETAILS**
- **METHOD DETAILS**
 - The greenscape and green-wave surfing
 - Validating Days-From-Peak to quantify green-wave surfing
 - Classifying movement behavior
- **QUANTIFICATION AND STATISTICAL ANALYSIS**
 - Testing the Greenscape Hypothesis
 - Comparing greenscapes across movement tactics

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.06.032>.

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AUTHOR CONTRIBUTIONS

E.O.A., M.J.K., A.M., I.M.R., J.A.M., F.C., M. Hebblewhite, M.A.H., W.P., and K.L.M. conceived of the research. All authors contributed data and J.D.G. and E.O.A. managed the data. E.O.A., J.A.M., and I.M.R. analyzed the data. E.O.A. and M.J.K. wrote the manuscript and all authors contributed to revisions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Hansson, L.-A., Akesson, S., and Åkesson, S. (2014). *Animal Movement across Scales* (Oxford University Press).

2. Armstrong, J.B., Takimoto, G., Schindler, D.E., Hayes, M.M., and Kauffman, M.J. (2016). Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. *Ecology* *97*, 1099–1112.
3. Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., Oates, B.A., Sawyer, H., Scurlock, B.M., and Kauffman, M.J. (2016). Large herbivores surf waves of green-up during spring. *Proc. Biol. Sci.* *283*, 20160456.
4. van der Graaf, S.A.J., Stahl, J., Klimkowska, A., Bakker, J.P., and Drent, R.H. (2006). Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea* *94*, 567–577.
5. Drent, R., Ebbinge, B., and Weijand, B. (1978). Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. *Verhandlungen der Ornithologischen Gesellschaft in Bayern* *23*, 239–264.
6. Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. USA* *105*, 19052–19059.
7. Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinell, S.P.H., Fralick, G.L., and Monteith, K.L. (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.* *20*, 741–750.
8. MacArthur, R., and Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. *Proc. Natl. Acad. Sci. USA* *51*, 1207–1210.
9. Elton, C. (1927). *Animal Ecology*, 1927 (Sidgwick and Jackson), p. 10.
10. Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., et al. (2018). Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* *359*, 466–469.
11. Fryxell, J.M. (1991). Forage quality and aggregation by large herbivores. *Am. Nat.* *138*, 478–498.
12. Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L., and Kauffman, M.J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* *367*, 1023–1025.
13. Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., Van Moorter, B., and Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *Am. Nat.* *180*, 407–424.
14. Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J., and Ericsson, G. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J. Anim. Ecol.* *80*, 466–476.
15. Lundberg, P. (1988). The evolution of partial migration in Birds. *Trends Ecol. Evol.* *3*, 172–175.
16. Grinnell, J. (1917). Field tests of theories concerning distributional control. *Am. Nat.* *51*, 115–128.
17. MacArthur, R.H., and Pianka, E.R. (1966). On optimal use of a patchy environment. *Am. Nat.* *100*, 603–609.
18. Bell, W.J. (1990). Searching behavior patterns in insects. *Annu. Rev. Entomol.* *35*, 447–467.
19. Wiens, J.A. (1976). Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* *7*, 81–120.
20. Abrahms, B., Hazen, E.L., Aikens, E.O., Savoca, M.S., Goldbogen, J.A., Bograd, S.J., Jacox, M.G., Irvine, L.M., Palacios, D.M., and Mate, B.R. (2019). Memory and resource tracking drive blue whale migrations. *Proc. Natl. Acad. Sci. USA* *116*, 5582–5587.
21. Bronstein, J.L., Gouyon, P.-H., Gliddon, C., Kjellberg, F., and Michaloud, G. (1990). The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology* *71*, 2145–2156.
22. Kays, R., Crofoot, M.C., Jetz, W., and Wikelski, M. (2015). *ECOLOGY*. Terrestrial animal tracking as an eye on life and planet. *Science* *348*, aaa2478.
23. Oudman, T., Piersma, T., Ahmedou Salem, M.V., Feis, M.E., Dekinga, A., Holthuijsen, S., Ten Horn, J., van Gils, J.A., and Bijlvelde, A.I. (2018). Resource landscapes explain contrasting patterns of aggregation and site fidelity by red knots at two wintering sites. *Mov. Ecol.* *6*, 24.
24. Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., and Calabrese, J.M. (2016). Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data. *Ecology* *97*, 576–582.
25. Mueller, T., and Fagan, W.F. (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* *117*, 654–664.
26. Bartlam-Brooks, H.L.A., Beck, P.S.A., Bohrer, G., and Harris, S. (2013). In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *J. Geophys. Res. Biogeosci.* *118*, 1427–1437.
27. Fryxell, J.M., Greever, J., and Sinclair, A.R.E. (1988). Why are migratory ungulates so abundant. *Am. Nat.* *131*, 781–798.
28. Sawyer, H., Kauffman, M.J., Middleton, A.D., Morrison, T.A., Nielson, R.M., and Wyckoff, T.B. (2013). A framework for understanding semi-permeable barrier effects on migratory ungulates. *J. Appl. Ecol.* *50*, 68–78.
29. Satterfield, D.A., Marra, P.P., Sillett, T.S., and Altizer, S. (2018). Responses of migratory species and their pathogens to supplemental feeding. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *373*, 20170094.
30. Stepanian, P.M., and Wainwright, C.E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Glob. Change Biol.* *24*, 3266–3275.
31. Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., et al. (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Sci. Data* *3*, 160067.
32. Vermote, E. (2015). MOD09A1 MODIS/Terra Surface Reflectance 8-Day L3 Global 500m SIN Grid V006 (NASA EOSDIS Land Processes DAAC). <https://doi.org/10.5067/MODIS/MOD09A1.006>.
33. R Core Team (2014). R: A language and environment for statistical computing (R Foundation for Statistical Computing).
34. Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., and Stenseth, N.C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* *20*, 503–510.
35. Pinero, J., and Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS (Statistics and Computing)* (Springer).
36. Clark, I. (1979). *Practical Geostatistics Volume 3 (Applied Science Publishers London)*.
37. Wang, X., Cao, L., Fox, A.D., Fuller, R., Griffin, L., Mitchell, C., Zhao, Y., Moon, O.-K., Cabot, D., Xu, Z., et al. (2019). Stochastic simulations reveal few green wave surfing populations among spring migrating herbivorous waterfowl. *Nat. Commun.* *10*, 2187.
38. Berdahl, A., Torney, C.J., Ioannou, C.C., Faria, J.J., and Couzin, I.D. (2013). Emergent sensing of complex environments by mobile animal groups. *Science* *339*, 574–576.
39. Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A.J.M., Morellet, N., Kjellander, P., Linnell, J.D.C., Mysterud, A., Neteler, M., et al. (2011). Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos* *120*, 1790–1802.
40. Fox, G.A., Negrete-Yankelevich, S., and Sosa, V.J. (2015). *Ecological Statistics: Contemporary Theory and Application (Oxford University Press)*.
41. Davison, A.C., and Hinkley, D.V. (1997). *Bootstrap Methods and Their Application Volume 1 (Cambridge University Press)*.

STARMETHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
2009 Human Footprint Index	[31]	https://doi.org/10.5061/dryad.052q5
MOD09Q1 v006 surface reflectance data	[32]	https://doi.org/10.5067/MODIS/MOD09Q1.006
Experimental Models: Organisms/Strains		
Elk (<i>Cervus canadensis</i>)	See Table S1	See Table S1
Mule deer (<i>Odocoileus hemionus</i>)	See Table S1	See Table S1
Red deer (<i>Cervus elaphus</i>)	See Table S1	See Table S1
Roe deer (<i>Capreolus capreolus</i>)	See Table S1	See Table S1
Software and Algorithms		
R 3.6.3	[33]	http://www.r-project.org/

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Ellen Aikens (ellen.aikens@gmail.com).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

The gps-collar data supporting the current study have not been deposited in a public repository because these are part of further investigation, but data and code is available from the corresponding author on request. MODIS data is publicly available through the NASA Earthdata database (<https://earthdata.nasa.gov/>). The Human Footprint Index data is available at <https://doi.org/10.5061/dryad.052q5>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We compiled relocation data from GPS collared mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) in North America, and roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) in Europe. We only included adult (> 1-year-old) individuals within a given year with at least one relocation per day over the 120-day spring period (see below for details). Populations were only included in the analysis if there was a minimum of ten individuals in the population. These criteria resulted in a total of 2,446 animal-years derived from 1,696 unique individuals and 61 populations. Details of each population can be found in Table S1.

METHOD DETAILS

The greenscape and green-wave surfing

We quantified forage quality using remotely sensed data. We calculated the Normalized Difference Vegetation Index (NDVI [34]) from bands 1 and 2 of MOD09Q1 v006 surface reflectance data (250-m spatial resolution, 8-day temporal resolution). We cleaned and filtered the NDVI data as described by Bischof et al. [13], except that we used the snow flag for the MOD09Q1 data to floor values during winter rather than using a fixed window [3]. For each pixel in each of the 61 study areas, we fit a double logistic curve to the annual time series of the processed NDVI data. To pinpoint the date of peak green-up, we took the first derivative of the double logistic curve, resulting in a curve of the Instantaneous Rate of Green-up (IRG [13]) that peaks on the day when NDVI increases most rapidly. Furthermore, we also used the spring scale parameter, which is estimated when fitting the double logistic curve to the annual time series of NDVI [13]. Specifically, the spring scale measures the time it takes (in days) for the logistic curve to change from the midpoint (date of peak IRG) to $\frac{3}{4}$ of the asymptote ([35], p 274). We used the date of peak green-up and the spring scale parameters to calculate greenscape metrics, green-wave surfing, and exposure to spring green-up.

To characterize the greenscape, we quantified the key components of the green wave (i.e., duration, order, and rate of green-up) for each animal-year. To convert the spring scale parameter to a rate, we took the inverse. Then, we calculated the mean green-up rate of all used points during an animal-year as our metric of green-up rate. To calculate green-up duration, we took the difference between the 0.975 and 0.025 quantiles of the date of peak green-up extracted from all used points for each animal-year. This estimates the amount of heterogeneity in peak green-up across the landscape used by the animal. To calculate order, we used semi-variograms to measure half of the squared difference in the date of peak green-up across pairs of locations at different spatial scales (i.e., the semivariance [12, 36]). A perfect resource wave exhibits progressively later dates of peak green-up at increasingly larger distance lags, resulting in an increasing steepness in semivariance at greater distance lags (Figures S2A and S2B). In most landscapes, however, the resource wave truncates and the steepness in the corresponding semivariogram either decreases (Figures S2C and S2D) or reaches an asymptote. Thus, the shape of the semivariogram quantifies the wave-like nature of green-up, with a concave up increase representing an idealized resource wave and a concave down curve representing a truncated resource wave. For the year-round range of each animal, we modeled semivariance as a function of the distance lag raised to an estimated power. A power greater than one represents an increasing steepness in semivariance, or an idealized wave, whereas a power less than one represents a decreasing steepness in semivariance at larger distance lags (Figure S2). We used the estimated power as our measure of green-up order, with values above one indicating more consecutive green-up order and values below one representing less consecutive green-up order.

We estimated green-wave surfing and exposure to green-up across an equal number of days during the “spring period,” calculated as a 120-day period centered on the median date of peak green-up for all used relocations for a given animal-year. We used a fixed 120-day period to represent a consistent window of time across which we evaluated green-wave surfing each spring. We quantified green-wave surfing using the metric Days-From-Peak (0 = perfect surfing), calculated as the absolute difference in days between the date of peak green-up and the day the animal used a location during the spring period [7]. We used the absolute value to calculate Days-From-Peak to prevent potential bias from early surfing (i.e., positive values) cancelling out late surfing (i.e., negative values) [7]. To evaluate the difference in exposure to spring green-up, we calculated IRG for migrants and residents (see below for details of how this classification was determined). For each relocation during the spring period, we extracted the corresponding IRG value on the day the animal used that location [13]. An IRG value of one represents the maximum exposure to spring green-up because IRG is scaled between zero and one [13]. To correct for unbalanced sample size because of different GPS-collar sampling schedules, we calculated the average Days-From-Peak and IRG values for each day, and then took the average value across the 120-day period for each animal-year [7].

Validating Days-From-Peak to quantify green-wave surfing

Recent work has articulated concern over a potential confounding bias in green-wave surfing analyses [37]. Specifically, there is concern that animals may be moving in sync with a cue that is collinear with spring green-up (e.g., temperature or photoperiod), thus giving a false positive for green-wave surfing [37]. One option to test for the influence of confounding factors is stochastic simulations, in which movement paths of individuals are simulated and used to quantify a baseline in green-wave surfing that the animal might experience if they moved along their migration paths in the absence of a behavioral response to the green wave [7, 20]. If green-wave surfing is identified in both the simulated paths and the actual movement data, then it is concluded that animals are not truly surfing the green wave [37].

Although it is commendable to try to correct for potential confounding factors, there are several drawbacks associated with the stochastic simulation method. First, the simulated paths are parameterized using the movement characteristics of the animals (e.g., directionality, step length, turning angle). Thus, the likelihood of false negatives refuting the existence of true surfing increases as simulated movements more closely reflect an animal’s actual movements. Additionally, under this framework, migratory movements are dichotomized as either surfing or not surfing; dichotomized outcomes are more likely to suffer from type I and type II errors.

Because prior work has revealed considerable individual variability in green-wave surfing [7], we decided not to dichotomize the classification of surfers and non-surfers, but rather to estimate green-wave surfing as Days-From-Peak, which is a continuous metric. To validate that our use of Days-From-Peak was an unbiased measure of surfing, we compared our results to an additional metric called the “gradient tracking performance” [38]. Gradient tracking performance was calculated as the exposure to the resource being tracked (in our case the IRG), divided by a null performance metric [38]. We calculated null performance as the temporal average of IRG for each used location during the spring, which equates to the IRG an animal would experience if it used the same locations but at a different sequence in time. A tracking performance value of one represents surfing no better than random movements, while any value greater than one represents surfing [38].

Days-From-Peak was correlated strongly with gradient tracking performance (Pearson’s correlation coefficient = -0.89), suggesting that Days-From-Peak and gradient tracking performance are nearly redundant metrics. Additionally, we estimated the gradient tracking performance of migrants and residents as a validation of our approach to use Days-From-Peak. Similar to our result comparing Days-From-Peak between migrants and residents, 95% of migrants surfed better than random (i.e., gradient tracking performance > 1), whereas 69% of residents surfed better than random. On average, migrants had a gradient tracking performance that was greater than residents (mean \pm SE; migrants = 1.61 ± 0.0073 ; resident = 1.06 ± 0.0050). There was no relationship, however, between IRG and gradient tracking performance (Pearson’s correlation coefficient = 0.051). Thus, we decided to use only Days-From-Peak in our main analysis because it is an established method used to quantify green-wave surfing [7].

Classifying movement behavior

We used a semi-automated process to classify individual movements as migratory, resident or other [13]. We first calculated the Net-Squared Displacement (NSD) as the squared Euclidian distance between the first GPS location of an animal-year and subsequent locations for the entire year. The NSD plotted through time can be used to identify different patterns in movement [14]. For example, an NSD profile which resembles a double logistic curve is often interpreted as seasonal migration, defined as movement between two distinct seasonal ranges. Next, we used the method of Bunnefeld et al. [14] to classify each animal's movement tactic within a given year as "migratory," "resident" or "other," based on AIC ranking [14]. For each animal-year, we visually inspected the NSD curve, and when necessary refit the logistic functions separately for the spring and fall migration, following the methods of Bischof et al. [13]. This allowed the asymptote of the spring and fall migration to differ, which improved the identification of the start and end of migration events when the summer range shifted throughout the season [13]. All visual inspections and modifications of the automated classifications were performed by a single researcher (EOA) to reduce the potential of introducing bias across different observers.

We dichotomized animals as either migrants or residents to compare the foraging benefit of utilizing different movement behaviors. Dichotomizing animal movement, however, is controversial and often not straight-forward [39]. To explore the impact of dichotomizing movement behaviors, we also compared exposure to spring green-up (IRG) and surfing behavior (Days-From-Peak) across a continuous metric of space-use. We defined space-use as the number of unique NDVI pixels (250 m²) an animal used during the year. We examined differences in green-wave surfing and exposure to spring green-up using a linear mixed-effects model with a random intercept for species, year and population. Before we performed regression analyses that examined the relationship between space-use and green-wave surfing, we used a square root transformation on the space-use metric to meet normality assumptions. Like the dichotomized result (Figure 4), animals that moved across vast landscapes surfed two times closer to the date of peak green-up (Figure S3A) but did not experience greater exposure to spring green-up compared to animals that exhibited restricted space-use (Figure S3B). Thus, the key finding that animal movements are fine-tuned to the resource landscape hold whether movement behavior is dichotomized or quantified across a continuous spectrum.

QUANTIFICATION AND STATISTICAL ANALYSIS

Testing the Greenscape Hypothesis

To test the Greenscape Hypothesis, we quantified the influence of greenscape metrics on green-wave surfing (i.e., Days-From-Peak) using a linear mixed-effects model with a random intercept for species, year, and population. We compared the effect size of each greenscape metric using standardized coefficient estimates to control for differences in the range of values across each metric [40]. We calculated 95% confidence intervals for predicted values of the linear mixed-effects models using parametric bootstrapping with 1000 simulations [41]. To compare how well migrants and residents surf and the resulting foraging benefit of each movement tactic, we calculated the median Days-From-Peak and IRG of migrants and residents within each species.

We examined the potential confounding effect of human development and productivity on our test of the Greenscape Hypothesis. We compared the coefficient estimates of the original models and models that included the 2009 Human Footprint Index [31] to account for human development, or integrated NDVI to account for productivity. Human development or productivity had no effect on the test of the Greenscape Hypothesis or the examination of the effect of space-use on green-wave surfing (Figure S4).

We also examined the potentially confounding effect of an overrepresentation of elk in our dataset and found no evidence that this biased our inference. Specifically, our GPS collar dataset contains two potential drawbacks that could bias our inference. First, some animals were collared for more than one year resulting in temporal pseudoreplication for 31% of the animal-years in the dataset. Second, elk were overrepresented in the dataset, composing 62% of the animal-years of data, with data from Wyoming elk composing 55% of all elk animal-years and 30% of all animal-years. To determine the degree to which these drawbacks influenced the inference drawn from our analysis, we subset the dataset by 1) randomly selecting one animal-year for any individual that was monitored for greater than one year, and 2) randomly selecting only three out of the 20 elk populations from Wyoming so that the number of populations for each species was evenly represented. We repeated the subsampling 100 times and conducted the greenscape analysis and the green-wave surfing analysis on each of the subsampled datasets. We compared the mean and 95% CIs for the coefficient estimates derived from the tests of the Greenscape Hypothesis and the influence of space-use on green-wave surfing for the 100 subsampled datasets to the coefficient estimates of the full dataset. In all instances, the 95% CI for the subsampled datasets overlapped with the original estimates of the intercepts or slopes for both the greenscape model and the model examining the impact of space-use on green-wave surfing (Table S2). We compared the median Days-From-Peak and IRG for migrants and residents of each species from the full dataset to that of the subsampled datasets. In all instances, the median of interquartile range of the 100 subsampled datasets always included the median value from the full dataset (Table S3). Together, these findings suggest that temporal pseudoreplication and overrepresentation of elk from Wyoming are an unlikely source of bias in our analysis.

Comparing greenscapes across movement tactics

To examine the impact of the greenscape on individual movement tactics, we quantified the greenscape that was available to each animal instead of the greenscape derived from its used points. We focused on the available greenscape because the movement behavior an individual adopts may influence the greenscape that is observed in the used locations. For example, in an environment with a resource wave (i.e., Figure S2A), the wave would not be reflected in the used points of an animal that remains in a restricted area and does not move to exploit the wave. To quantify the available greenscape, we placed a species-specific buffer (i.e., the

maximum migration distance derived from the NSD classifications; elk = 123 km, mule deer = 235 km, red deer = 76 km and roe deer = 31 km) around the centroid (mean x and y coordinates) of each animal-year's GPS locations to delineate the area that was available to the animal. Across all pixels that fell within the circular buffer, we calculated green-up rate, order, and duration using the methods described above [12]. To determine if differences in productivity influenced movement behavior [10], we also calculated the integrated NDVI [3] across the available landscapes. We compared the available green-up rate, order (exponent estimated from a power model fit to the semivariogram), duration (difference between the 0.975 and 0.025 quantiles of the date of peak green-up), and productivity (mean annual integrated NDVI), between migrant and resident individuals within each species to determine if migrants and residents occupied different phenological landscapes (i.e., green-scapes). To test for differences in the available green-scapes of migratory and resident individuals within the same species, we use two-sided Kolmogorov-Smirnov tests, corrected for multiple comparisons using a Bonferroni correction.

To examine the influence of the green-scape on migratory propensity at the population level, we first subset the data to only include individuals classified as migratory or resident (52% and 27% of animal-years respectively). Before calculating the proportion of migratory individuals in a population (hereafter migratory propensity), we excluded any populations with less than 10 individuals total that were classified as either migratory or resident, which resulted in 56 out of 61 original populations being retained. We calculated the population-level average of the available green-up rate, order and duration to quantify the green-scape for each population. To examine the relationship between the green-scape and migratory propensity, we conducted multiple logistic regressions because green-up order was collinear with green-up rate (Pearson's correlation = 0.53) at the population level.