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Spatial Ecology: Herbivores and Green Waves — To Surf or Hang Loose?

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A classic distinction in spatial ecology is between range-residency and migration. A new study — on dozens of ungulate populations worldwide — demonstrates how the dynamics of food resources help determine which movement pattern animals will exhibit.

Across the globe, many species of ungulate (hoofed animals, including members of the deer, horse, and cow families) migrate seasonally as they seek out food resources, shelter from predation, or suitable areas for reproduction. Some of the most recognizable terrestrial migrations occur in remote environments — think Arctic caribou or the great Serengeti wildebeest migrations — but ungulate migrations are also surprisingly common in temperate zones of North America and even densely populated western Europe. In fact, major new migratory routes are still being discovered [1]. Unlike caribou or wildebeest, where essentially all individuals in a particular herd migrate, temperate ungulates exhibit a wide variety of strategies: some populations within a generally migratory species may be range-resident (living year-round in a home range), some individuals within an otherwise cohesive population may not migrate, and individual animals may even choose to migrate or not in a given year [2]. Collectively, these phenomena are known as 'partial migration'. Understanding the costs, benefits, timing and mechanisms of terrestrial migration is a long-standing ecological challenge; understanding whether and why certain individuals within a partially migratory population migrate adds an additional layer of mystery.

A recent conceptual contribution to the study of migration is the 'green wave surfing' hypothesis [3,4]. This hypothesis posits that migrating ungulates follow a progressive spatial pulse of the earliest, most digestible and most nutritious plant growth in spring as that pulse moves across the landscape in a wave-like fashion — either poleward across latitudes or upward in elevation. Where present, these green waves follow a clearly discernible pattern that can be observed using time series of satellite imagery of NDVI (normalized difference vegetation index), a useful measure of vegetative greenness and productivity on large scales [3,5]. But spring green-up progresses across landscapes in very different ways in different places. In some landscapes, spring arrives in a 'surfable', wave-like fashion. In others, spring might creep up slowly, suddenly appearing over a large area. Or spring may arrive unpredictably and patchily, depending on highly localized characteristics of the dominant vegetation. A study in this issue of *Current Biology* by Ellen Aikens,

Figure 1. Roe deer fawns.
Whether these fawns will grow up to migrate seasonally or remain range-resident will be determined in large part by the vegetative dynamics of the landscape in which they live, with coherent, wave-like seasonal vegetative dynamics favoring a migratory lifestyle (photo: Ophélie Couriot).

Matthew Kauffman and colleagues [6] demonstrates that — just as surfing an ocean wave with a board relies on particular kinds of wave for success — green-wave surfing by ungulates occurs under particular green-up conditions.

Drawing on NDVI imagery, the authors identify three features of spring vegetation dynamics that determine whether a wave is surfable: the duration of a vegetation pulse, the rate of growth of that pulse and the spatiotemporal ordering of that pulse. Their 'greenscape hypothesis' suggests that a surfable green wave must be not too broad, not too rapid and clearly progressive in space and time — a kind of Goldilocks green wave where everything is just right. The authors compiled a dataset that includes ungulate populations across two species in western North America — mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) — and an analogous pair of species in western Europe — roe deer (*Capreolus capreolus;* Figure 1) and red deer (*Cervus elaphus*). The study populations range over many degrees of latitude: from southern Wyoming to northern British Columbia, and from northern Italy to Norway. These regions feature different degrees of extreme weather, topographic complexity, human impacts, and — most relevantly — spring green-up dynamics. The authors tested to see if the greenscape hypothesis accurately predicted the prevalence and timing of migration.

In accordance with the hypothesis, green-wave surfing, which was defined as a close tracking of the spatio-temporal shifts in new vegetative growth [4], was most prominent in landscapes with rapid, narrow and well-ordered green-up trajectories. In contrast, in less surfable landscapes, populations were less likely to be migratory. This work shows how migration — including some rather long-distance migrations — can emerge as a localized response to spring resource dynamics.

Intriguingly, Aikens and colleagues [6] found that both migratory and resident individuals achieved similar exposure to springtime vegetative green-up in their respective landscapes. This broad similarity — in which different movement strategies resulted in comparable resource availability — indicates that neither migration nor range-residency is a universally superior strategy, even in highly seasonal environments (for a modeling study, see [7]). Moreover, this matching between movement strategies and resource dynamics highlights just how important local adaptation and plasticity are to foraging success and, ultimately, reproductive output.

The study of Aikens and colleagues [6] underscores the insights that can be obtained from large, collaborative, international, and cross-taxa datasets and analyses [8,9]. Such large-scale collaborations, which pull in data sets from individual long-term localized monitoring efforts — Aikens *et al*. [6] involves 36 coauthors and dozens of ungulate populations — allow for robust sample sizes and incisive analyses that are simply impossible from single-site, single-species studies.

This work sets the stage for predicting on a global scale where — and how exclusively— we might expect different forms of animal movement to occur [7]. We already know that both the abundance and the spatial structure of food resources determine the distances that migratory ungulates travel during their seasonal search for resources [10]. Likewise, breakdowns in temporally coherent resource availability can cause migrating ungulates to reverse course [11]. With the rate, duration, and order of vegetative waves now clearly linked to the likelihood of migratory movements, it should soon be possible to tell how close individual landscapes are to the boundary zones that differentiate among movement strategies [6,7,12,13], thus identifying the landscapes where climate change, fragmentation and other human-mediated changes are most likely to impinge on animal populations by disrupting their movement strategies [8,14]. To this end, Aikens and colleagues [6] also highlight the importance of large-scale, dynamic concepts of habitat and the corresponding need for integrative thinking about how to best conserve highly mobile species [14]. One of their tucked-away results is that species' ability to surf green waves is lessened in areas of higher human development because the regularity and spatial cohesiveness of the green waves is compromised in such areas. In many places, animal migrations are disappearing [6,14], so understanding the spatial and temporal contexts of migration is critical for strategizing and prioritizing conservation efforts.

In a broader context, gradient-following mechanisms such as green-wave surfing are but one of many mechanisms animals use to maximize their fitness in seasonal environments. For example, migratory Arctic caribou conduct their mass migrations mainly before the emergence of springtime vegetation as they seek to calve in places with lower predation risk [15]. Other species, such as red deer in Scandinavia [3], jump the green wave, traveling through suboptimal environments in anticipation of abundant resources at their destination. Similarly, zebra time their migration to meet the rainy season and newly filled watering holes, relying on memory (rather than gradient following) to determine their migration route and timing [16]. Social learning of migratory routes, developed and passed down through generations, appears critical for reintroduced or translocated foragers to acquire seasonal migratory behavior [17]. Other ungulates eschew both migratory and range-resident strategies, opting instead for nomadic movements, wandering — sometimes across vast landscapes — as they search for patchy and ephemeral food resources [12,13].

Scaling up from individual-level movement decisions to population-level spatial distributions is critical to our understanding of how animals take advantage of the landscapes in which they live [12,18]. Individual-level responses of ungulates to the transient availability of their food resources in space and time underpin both the continuum across migration, range residency and nomadism, and the phenomenon of partial migration. Continuing to explore the roles of inter-individual communication [19], social interactions [18,20], and spatial memory and learning will expand our understanding of large-scale movement patterns.

Terrestrial animal migrations are a unique and astonishing phenomenon that remains poorly understood. Diverse movement strategies have evolved to exploit dynamic, heterogeneous, and complex environments. However, as habitats are disappearing due to human development or are being criss-crossed with barriers, many animals are having an increasingly harder time navigating their landscapes. Ecosystem-level changes due to global warming compound these challenges. Many migrations have already been lost, and, as a multi-generationally learned 'culture', a migration is very difficult or impossible to recover once lost [17]. The research by Aikens and colleagues [6] exemplifies the kind of synthetic, large-scale study that — in shedding light on the mechanisms of migrations — can also point a way toward conserving this vital ecological phenomenon.

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