








CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecology, 102(4), 2021, e03293
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The plasticity of ungulate migration in a changing world

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Citation: Xu, W., K. Barker, A. Shawler, A. Van Scoyoc, J. A. Smith, T. Mueller, H. Sawyer, C. Andreozzi, O. R. Bidder, H. Karandikar, S. Mumme, E. Templin, and A. D. Middleton. 2021. The plasticity of ungulate migration in a changing world. *Ecology* 102(4):e03293. 10.1002/ecy.3293

Abstract. Migratory ungulates are thought to be declining globally because their dependence on large landscapes renders them highly vulnerable to environmental change. Yet recent studies reveal that many ungulate species can adjust their migration propensity in response to changing environmental conditions to potentially improve population persistence. In addition to the question of *whether* to migrate, decisions of *where* and *when* to migrate appear equally fundamental to individual migration tactics, but these three dimensions of plasticity have rarely been explored together. Here, we expand the concept of migratory plasticity beyond individual switches in migration propensity to also include spatial and temporal adjustments to migration patterns. We develop a novel typological framework that delineates every potential change type within the three dimensions, then use this framework to guide a literature review. We discuss broad patterns in migratory plasticity, potential drivers of migration change, and research gaps in the current understanding of this trait. Our result reveals 127 migration change events in direct response to natural and human-induced environmental changes across 27 ungulate species. Species that appeared in multiple studies showed multiple types of change, with some exhibiting the full spectrum of migratory plasticity. This result highlights that multidimensional migratory plasticity is pervasive in ungulates, even as the manifestation of plasticity varies case by case. However, studies thus far have rarely been able to determine the fitness outcomes of different types of migration change, likely due to the scarcity of long-term individual-based demographic monitoring as well as measurements encompassing a full behavioral continuum and environmental gradient for any given species. Recognizing and documenting the full spectrum of migratory plasticity marks the first step for the field of migration ecology to employ quantitative methods, such as reaction norms, to predict migration change along environmental gradients. Closer monitoring for changes in migratory propensity, routes, and timing may improve the efficacy of conservation strategies and management actions in a rapidly changing world.

Key words: animal behavior; conservation; environmental change; migration; movement ecology; phenotypic plasticity; reaction norm; resilience; ungulate.

INTRODUCTION

Manuscript received 13 March 2020; revised 24 August 2020; accepted 12 November 2020. final version received 21 January 2021. Corresponding Editor: Madan K. Oli.

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Ungulate migrations spanning global grasslands and forests have long fascinated humans and are increasingly recognized for their impacts on ecosystem structure and

function (Bauer and Hoyer 2014, Middleton et al. 2020). Because these migrations span large landscapes and steep environmental gradients, they are often considered particularly vulnerable to global environmental change (Bolger et al. 2008, Harris et al. 2009, Teitelbaum et al. 2015). Compounding this perceived vulnerability is the common assumption that migration patterns are static traits in large mammals (Gaillard 2013, Eggeman et al. 2016). As a result, altered ungulate migration patterns are considered an alarming harbinger of declining population viability (e.g., Berger 2004, Wilcove and Wikelski 2008).

At the same time, a number of recent studies have suggested that changes in migratory behavior within an individual's lifetime might be relatively common in ungulates. Importantly, for example, accumulating observations of individuals switching between resident and migrant status marked the first applications of the term "plasticity" to ungulate migration behavior (Eggeman et al. 2016, Berg et al. 2019, Peters et al. 2019). Besides their propensity to migrate, ungulates can also alter their migratory behavior in space and time. For example, ungulates can adopt new ranges and migration corridors (e.g., Skarin et al. 2015, Xu et al. 2019) or modify the timing and duration of migratory movements (e.g., Le Corre et al. 2016, Rickbeil et al. 2019). Despite the widespread acknowledgment that *where* and *when* to migrate are as fundamental as *whether* to migrate in describing migration tactics (Gurarie et al. 2017), these spatial and temporal migration changes appear as idiosyncratic observations and have not yet been fully integrated into our conception of behavioral plasticity. The emerging recognition of migratory plasticity in ungulates carries important implications for ecology and conservation, yet we still lack an understanding of its extent and mechanisms.

Animals alter behavior in response to environmental change via two pathways: contemporary evolution and phenotypic plasticity (Box 1; Van Buskirk 2012, Winkler et al. 2014). Avian studies of migration change have supported both mechanisms (Hairston et al. 2005, Knudsen et al. 2011). For migratory ungulates, however, phenotypic plasticity is likely the dominant mechanism for three reasons. First, theory suggests migration evolved in ungulates to cope with variable environments (Avgar et al. 2013) and is maintained by learning and cultural transmission, one dominant mechanism of behavioral plasticity (Brown 2012, Jesmer et al. 2018). Phenotypic plasticity in individual migration behavior (sometimes deemed migratory flexibility; Eggeman et al. 2016) appears fundamental to an ungulate's ability to respond to rapid environmental change. Second, unlike in many birds, migration in ungulates is not a direct mapping of genotype or phenotype, making it flexible by nature (Bolger et al. 2008, Hebblewhite and Merrill 2011, Berg et al. 2019). Finally, long generation time among ungulates reduces the likelihood that contemporary evolution occurs quickly enough to respond to rapid environmental change (Chevin et al. 2010, Winkler et al. 2014).

Box 1. Glossary

Contemporary evolution: Heritable trait evolution observed in contemporary time (i.e., less than a few hundred generations).

Phenotypic plasticity: Includes the ability of a single genotype to create multiple phenotypes through developmental responses to environmental cue, or the ability of an individual organism to alter its phenotype (behavior) in response to changes in environmental conditions. In migratory plasticity, the second ability is more commonly studied in ungulates. Note that changed behavior can be adaptive or maladaptive. The latter includes disruptive changes leading to a decline or cessation of migration.

Migration change vs. migration variation: Migration variation refers to coexistence of different migration patterns in one population (i.e., mixed migrants and residents in one population). Migration change refers to dynamic transitions among the variations (i.e., individual switch from migratory to resident).

Reaction norm: The set of phenotypes (i.e., behaviors) that can be produced by an individual genotype over an environmental gradient.

Migration propensity: Whether an individual adopts a migratory or residency tactic.

Nomadism: A movement type in which individuals or populations of animals move frequently between locations with irregular timing and/or direction, producing both within-year and between-year variability in location and movement patterns.

Partial migration: Populations of animals that are composed of a mixture of resident and migratory individuals.

Locomotion capacity: The set of traits (e.g., biomechanical or morphological machineries) that enables the focal individual to execute or facilitate movement.

Site fidelity: The tendency to return to the same sites and ranges each year.

Navigation mechanism: The set of traits (e.g., cognitive or sensory machineries that obtain and use information) that enables the focal individual to orient its movement in space and/or time.

A comprehensive understanding of the scope and degree of migration change will bring predictive and mechanistic insights to migration ecology. Clearly described phenotypic dynamics over an environmental gradient link external selection pressures to phenotypic outcomes (i.e., the maintenance of migratory variations in evolutionary processes; Dingemanse et al. 2010, Fusco and Minelli 2010). Understanding the interface between environment and behavior will also help to predict behavioral change in modified environments and

conditions (Palkovacs et al. 2012). Furthermore, understanding migration change can be crucial for conservation. Evidence across taxa has shown that behavioral plasticity can maintain or improve population persistence under environmental change (Møller et al. 2008, Beever et al. 2017). In this sense, changes in ungulate migration may not always indicate decline, but rather resilience. Knowledge of the prevalence, extent, mechanisms, and ultimately, the outcomes of migration change can significantly inform effective conservation efforts. A prerequisite to achieve these advances in migration ecology and conservation is to establish a common framework to unify idiosyncratic observations of changes in migration behaviors and to clearly classify types of changes (Berg et al. 2019).

Here we argue that the concept of migratory plasticity should be expanded beyond migratory propensity (*whether to migrate*) to include the spatial and temporal patterns of migration (*when and where to migrate*). We introduce a novel framework to conceptualize and identify the full spectrum of migratory plasticity (Fig. 1). To demonstrate the utility of our framework and assess current evidence of migratory plasticity, we conducted a literature review to classify documented migration change events, and their inferred causes, within the framework. This classification of migration change offers novel insights into the fine-scale behavioral variations of

migratory ungulate populations in context with a spectrum of environmental changes. We discuss current knowledge gaps, including the almost complete absence of studies that link migration changes to demographic consequences. Finally, we suggest future research avenues to understand the mechanisms of migratory plasticity, and we emphasize the importance of considering plasticity within the management and conservation of migratory ungulates.

EVALUATING MIGRATORY PLASTICITY WITH A TYPOLOGICAL FRAMEWORK

Our framework classifies migration change into three interconnected dimensions to describe the extent and diversity of migration change (Fig. 1). These dimensions include migration propensity (*whether to migrate*), spatial change (*where to migrate and along which route*), and temporal change (*when to migrate and for how long*). Migration propensity describes whether an individual migrates. Spatial change can manifest in four ways: (1) animals move from the original start range along a historic migration route but stop before or after the original end range, (2) animals move from the original start range but along a new migration route to reach to the original end range, (3) animals move from the original start range along a new migration route to reach a new

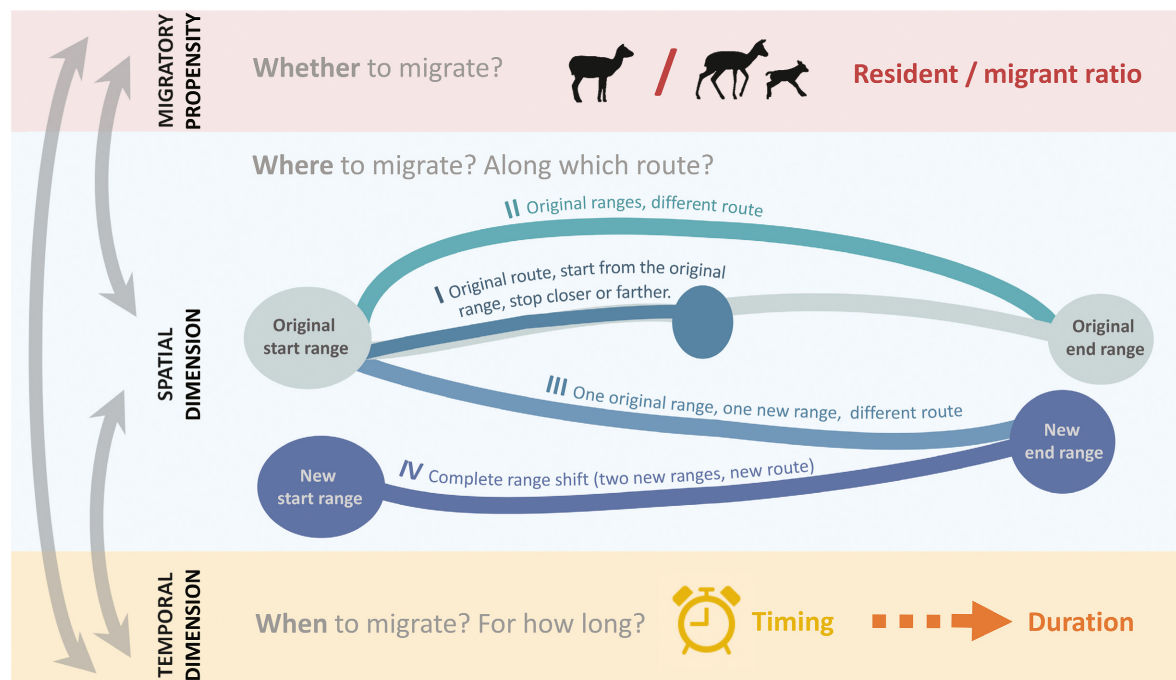


Fig. 1. Typological framework for migratory plasticity. Migratory plasticity can manifest as changes in three dimensions: migration propensity, spatial migration patterns, and temporal migration patterns. Migration propensity focuses on whether an individual migrates. Spatial change focuses on where animals migrate and can be classified as one of four types based on alterations to the starting range, ending range, and/or migration route. Temporal change is measured via migration timing and duration. These three dimensions are interdependent, and changes in one dimension can lead to alterations in other dimension(s). Hence, multiple types of migration change within and across dimensions can, and often do, co-occur.

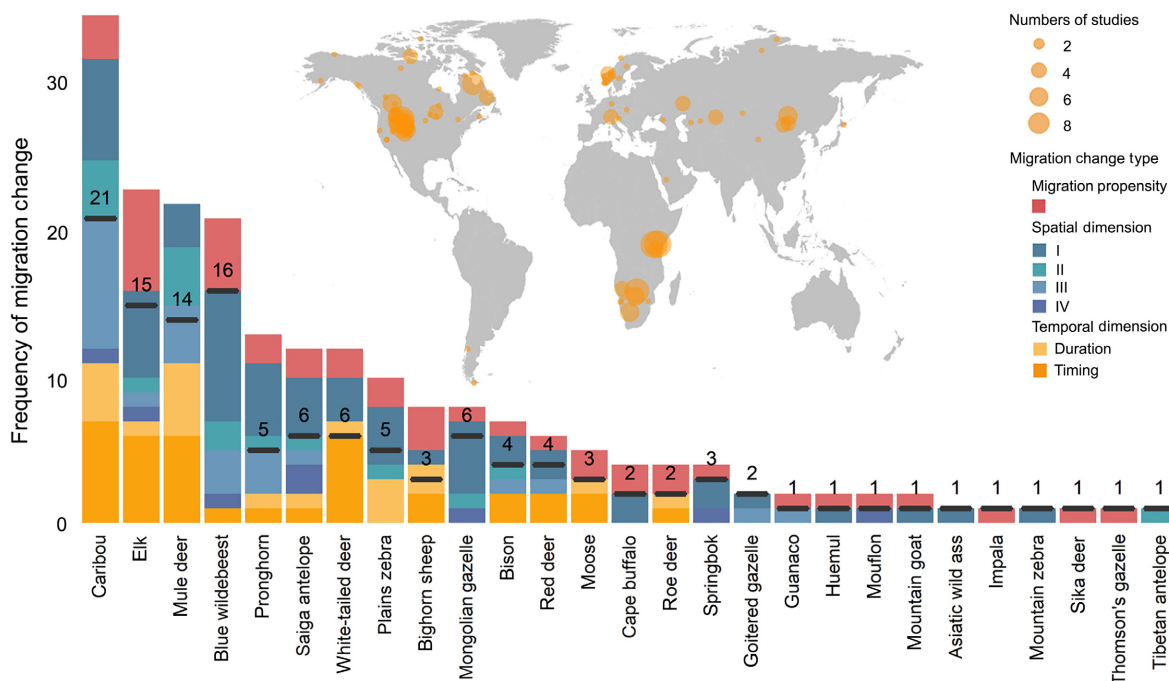


FIG. 2. Frequency and type of migration change events reviewed. Black number labels are the number of studies for each species, and the map shows the geographic distribution of these studies. Most individual studies only focus on a narrow aspect of migration when examining changes. Considering multiple studies together, however, reveals that most species can modify multiple aspects of their migration patterns in response to environmental changes.

end range, or (4) animals move from a new start range along a new migration route to reach a new end range. Finally, temporal change can occur in both migration timing (departure and/or arrival date) and duration (time spent on a migration route).

To examine the prevalence of these three dimensions of migration change in ungulates and their potential relationships with different types of environmental change, we conducted a comprehensive literature review based on a combination of a snowball search, whereby we reviewed papers cited by pre-identified key studies, and a systematic search of Web of Science using the query "TS = (Ungulate AND (migration OR "migrat* behavior")) AND (change OR shift OR decrease OR loss)." We classified each migration change event reported in relevant studies based on our framework (detailed review method in Appendix S1).

We found that migratory plasticity is widespread and can include simultaneous behavioral changes in multiple dimensions. We recorded 127 migration change events documented in 116 studies for 27 ungulate species worldwide, covering all types of migration change proposed by our framework (Fig. 2, Data S1). Of the 127 change events, 33.9% involved a change in migration propensity, 86.8% involved spatial change, and 35.4% involved temporal change. Species that appeared in multiple studies often exhibited multiple changes, with some species exhibiting every type of migration change (e.g., elk [*Cervus canadensis*], Box 2).

We also found that changes in migration were associated with 12 different types of environmental change, including biotic interactions (density dependence, intraspecific interaction, and predation), anthropogenic interferences (human disturbance, harvest, habitat fragmentation, habitat loss, translocation management, and supplementary feeding), and climate and weather (climate change, extreme weather, and interannual climatic variations). Habitat loss (29 events, 28.7%), interannual climatic variations (27 events, 26.7%), and habitat fragmentation (27 events, 26.7%) were the most frequent correlates of migration change.

To investigate potential relationships between types of environmental changes and migration changes, we evaluated migration change events derived from primary studies (101 out of the 127 migration change events). We found no consistent relationship between types of environmental change and specific migration changes (Fig. 3). This lack of relationship may indicate that ungulates can respond to multiple environmental changes simultaneously, in multiple dimensions. This complexity of response may have complicated researchers' abilities to disentangle the external causes of migration change and link these causes to fitness consequences. In addition, interdependence in the three dimensions of migratory plasticity can obfuscate causal relationships between the environment and migratory patterns. For example, a change in migratory duration could be the result of an animal adjusting its migration

Box 2. Elk: a case study in migratory plasticity

Elk (*Cervus canadensis*) exhibit particularly plastic migratory behavior. Most populations of elk are partially migratory, with some individuals migrating seasonally and others residing on a shared range year-round (Barker et al. 2019a). Despite past belief that migratory behavior is fixed at the individual level, recent long-term studies reveal that some elk switch between migratory and resident behaviors (Eggeman et al. 2016). Elk that do migrate display a range of behavioral adaptations including migrating to or from a different seasonal range, migrating along a different route, and beginning or ending migration earlier or later.

Migratory elk are remarkably flexible in their spatial use of the landscape. For example, elk in Colorado forged a new migration route to avoid pressure from human hunters (Type II; Conner et al. 2001), and elk in Yellowstone found a new migration route to a new seasonal range in response to high risk of mortality from both human hunters and natural predators (Type III; White and Garrott 2005). Elk also change the distance migrated along traditional routes in response to changes in land use and forage availability (Type I; Craighead et al. 1972, Jones et al. 2014). Transplanted elk in Canada and the northern United States have established entirely new migrations (Type IV; Allred 1950, Fryxell et al. 2008), albeit sometimes over historical migration routes, indicating a strong propensity for learning and flexibility.

Alternatively, or in addition, to changing where they migrate, elk also change when they migrate. Elk have been noted to alter both the timing (Jones et al. 2014, Rickbeil et al. 2019) and the duration of migration (Middleton et al. 2018), often to align movements with forage phenology. Elk also alter the timing of migration in response to other factors including changing precipitation regimes (Rickbeil et al. 2019), human hunting activities (Conner et al. 2001), and risk of predation (White and Garrott 2005).

However, a highly plastic migration strategy does not promise an optimal fitness outcome. In some cases, elk have retained historic migratory patterns despite decreased survival (White and Garrott 2005), reproduction (Middleton et al. 2013), or recruitment (Cole et al. 2015). Thus, behavioral plasticity may, but does not always, allow migrants to compensate for unfavorable environmental conditions.

route rather than a direct response to environmental dynamics. In other cases, an individual's migratory propensity change from resident to migratory could be followed by high variability in timing or routes. Furthermore, internal factors, such as genetics, personality,

learning, and physiological condition, can play a significant role in the type and degree of migratory plasticity manifested by individuals (Berg et al. 2019). However, much of the work on how internal factors contribute to migration patterns and behavioral plasticity remains theoretical rather than empirical, limiting our ability to explore this in the review.

Below, we synthesize the 101 migration change events by change type and discuss potential environmental and non-environmental causes driving each of the three dimensions of migration change. This synthetic evaluation for each dimension of behavioral change provides a foundation on which to build future knowledge of the demographic and conservation-related consequences of migration changes. It is worth noting that our results reflect the existing scope of current literature, which is influenced by research methodology, data availability, and funding, and thus may not yet reflect the full suite of ecological processes in play.

Migration propensity

Partial migration describes the variation among individual migration propensity (i.e., migrant vs. resident) within a population and is recognized as the rule rather than the exception in ungulates (Dingle and Drake 2007, Cagnacci et al. 2016); hence, *whether* an individual migrates is a fundamental starting point for studies of migration ecology and evolution. Recent evidence that migratory propensity can switch within an individual's lifetime adds another layer of complexity to "*whether* to migrate" (Eggeman et al. 2016). Consequently, it is important to consider both the migration tactic individuals employ and whether that tactic changes over time. Among the 101 empirical migration change events, 34 events (33.7%) of migration propensity change were documented in 22 of the 27 (81.5%) species studied.

Altered migration propensity has been speculated to improve fitness by decreasing risk (e.g., predation risk avoidance hypothesis) or by increasing nutrition (e.g., forage maturation hypothesis; Middleton et al. 2013, Eggeman et al. 2016). Changes to the distribution of high-quality forage can also affect migration propensity (Barker et al. 2019a). Among the 34 propensity change events documented in the literature we reviewed, 5 were influenced by predation (14.7%; e.g., Hebblewhite and Merrill 2011, White et al. 2014) and 11 by interannual climate conditions (32.4%; e.g., Fieberg et al. 2008, Cagnacci et al. 2011).

Still, not all changes in migration propensity are voluntary decisions. Habitat fragmentation and loss (11, or 32.4% and 10, or 29.4%, of the 34 propensity change events) often led to forced residence of migrants, possibly increasing intraspecific competition and reducing population fitness (e.g., Said et al. 2016). Forced-resident populations can sometimes persist at a low population density if individuals develop alternative foraging

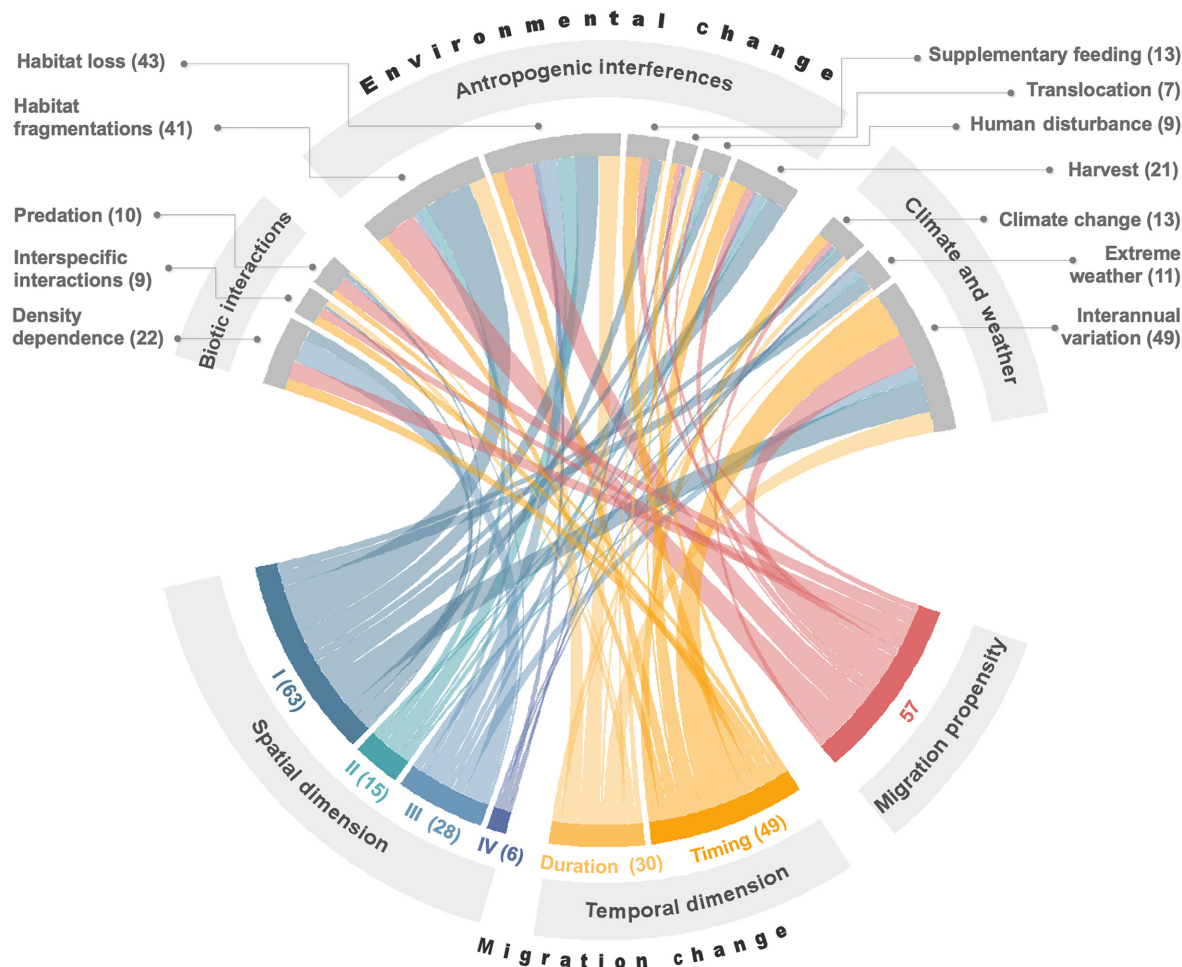


FIG. 3. The interrelations between type of environmental change and migration change based on literature with primary data. Labels represent the number of migration change events that are associated with the corresponding type of migration or environmental change. Width of the links is proportional to the number of events that show connections between the two types of change. One migration change can be correlated with multiple types of environmental change, and one environmental change can cause changes in multiple aspects of ungulate migration. Types of environmental change are not the sole determinant of types of migration change.

strategies during residence, as observed in formerly migratory bighorn sheep in northwest Wyoming (Courtemanch et al. 2017).

Although propensity changes have been documented in 22 ungulate species, this dimension of migratory plasticity is not ubiquitous, even within populations that exhibit partial migration. For example, over seven years of monitoring 36 individuals from a partially migratory moose population (*Alces alces*), Sweaner and Sandegren (1988) found that no individuals altered migration propensity. Similarly, mule deer (*Odocoileus hemionus*) exhibit some spatial and temporal changes in migration pattern (Fig. 2) while displaying high fidelity to their migrant-resident status (Sawyer et al. 2019b). The reason for interspecies variation in migration propensity plasticity remains unknown, but spatial memory (Merkle et al. 2019), mating strategies (Peters et al. 2019), and the

range species experience across environmental gradients (Mueller et al. 2011) may be important factors.

Spatial changes

Conservation planning for migratory species often relies on identifying critical spatial components of animal ranges, such as stopover sites, high-use corridors, and bottlenecks (Sawyer et al. 2009, Sawyer and Kauffman 2011). Understanding spatial change in migratory plasticity will therefore prove particularly relevant to current conservation measures (Allen and Singh 2016). In our review, spatial change was observed in 81 of the 101 (80.2%) migration change events in 22 ungulate species. Type I change, in which the migration route was shortened or lengthened, was the most frequently observed type of spatial change (44, or 43.6% of the 81

change events), followed by Type III (19 events, 18.8%) in which an altered migration route led to a new end range.

The most common environmental changes reported to correlate with migratory spatial change were habitat fragmentation and habitat loss (both 19, or 54.3%, of the 81 spatial change events), and harvest by humans (14 events, 17.3%). Accordingly, these categories of environmental change often have strong spatial characteristics (e.g., clumped or distributed along linear infrastructure) and directly alter the accessibility or quality of migratory routes and seasonal ranges, thereby altering spatial preference of migratory ungulates. Density-dependent factors (8 events, 9.9%) also influenced space use by ungulates. Dramatic population growth, for example, in a barren-ground caribou (*Rangifer tarandus granti*) population in southwest Alaska led to an erratic migratory pattern in some individuals, shifting traditional seasonal ranges into novel areas to create new subpopulations (Hinkes et al. 2005).

Generally, the four types of spatial change in migration can be explained by three factors: (1) locomotion capacity, (2) site fidelity, and (3) navigation mechanism. The importance of locomotion capacity can be illuminated by ungulate response to fencing; fences can affect species differently based on the animals' inclination or capacity to jump. For example, mule deer are more likely to jump fences than pronghorn (*Antilocapra americana*, Scott 1992). Thus, mule deer may more readily cross fences without significant spatial change, whereas pronghorn may alter behavior significantly to circumvent barriers (Type II or Type III), if they are able to do so at all (Type I; Sheldon and Lindzey 2006, Kauffman et al. 2018).

Site fidelity can also influence spatial change. For example, Tibetan antelope (*Pantholops hodgsonii*) have high site fidelity to summer ranges, which serve as shared calving sites and locations for gene exchange across subpopulations (Schaller 1998, Xu et al. 2019). When a railway bisected a key migration route, animals still attempted to reach the same summer site by modifying migration routes to cross the railway (Type II; Xu et al. 2019). In contrast, barren-ground caribou display low site fidelity and more readily migrated to different summer calving site locations (Type III; Hinkes et al. 2005). Species with particularly low site fidelity are often considered nomadic and are believed more capable of maintaining population viability when faced with various external changes than species with high site fidelity (Mueller et al. 2011, Teitelbaum and Mueller 2019).

Last, navigation can influence the types of spatial changes exhibited. Migratory ungulates appear to be guided by both sensory perception and memory (Bracis and Mueller 2017). Animals relying predominantly on perception can more quickly adjust behaviors in response to immediate conditions. For example, zebras (*Equus burchelli*) perceive and respond to precipitation rapidly and can reorient and even reverse migration to

avoid adverse conditions (Type III; Bartlam-Brooks et al. 2013). This ability may partially explain the rapid recovery of zebra migration in Botswana after fence removal (Type I; Bartlam-Brooks et al. 2011). Alternatively, memory-dominated navigation may result in more rigid migratory behavior (Bracis and Mueller 2017, Merkle et al. 2017, Sawyer et al. 2019b). As demonstrated by translocated moose and bighorn sheep, restoring lost knowledge of optimal migration paths can take decades (Jesmer et al. 2018). In such cases, protecting existing migration habitats and social structure to maintain spatial memory and cultural transmission of the population appears paramount for conservation (Brakes et al. 2019).

However, perception and memory are not mutually exclusive and may both contribute to a decision to migrate. Roe deer (*Capreolus capreolus*) and mule deer can use "scouting behavior" to explore immediate environmental conditions, leading to high interannual variability in migration propensity (Gurarie et al. 2017, Jakopak et al. 2019). After beginning migration, however, roe deer show a high degree of site fidelity, suggesting that the "whether to migrate" decision is based on perception of the immediate environment, whereas "where to migrate" is more likely influenced by their previous experience (Gurarie et al. 2017).

Temporal changes

Temporal change was documented in 54 of the 101 (53.5%) empirical migration change events (Fig. 2). Migration timing was more frequently examined than migration duration (15 events, or 34.7% of the 101 events vs. 19 events, or 18.8%). Migrants often adjust migration phenology to accommodate interannual variations in weather, forage availability, and predation risk (e.g., Bischof et al. 2012, Middleton et al. 2018). However, migratory timing may shift outside the interannual range if triggered by one of two pathways: (1) the local environmental gradient exceeds its interannual normal range or (2) environmental changes obstruct ungulates' ability to track the natural gradient.

Abnormal environmental gradients often result from climate change or extreme weather events (29.6% of the 54 temporal change events). Across all migratory taxa, the most common responses to climate change involve changes to the timing or duration of migration (Beever et al. 2017). However, temporal behavioral change may not always keep pace with climate change. When climate change affects an area where migration is cued by emerging vegetation, vegetation may respond to climate faster than ungulates respond. This could lead to a phenological (or trophic) mismatch, in which migrants arrive at a site before or after peak vegetation nutrition, reducing nutrient intake and influencing fitness (Post and Forchhammer 2008, Gustine et al. 2017).

In addition to climate change, land use practices can create an abnormal environmental gradient by altering

the nutritional landscape. For example, elk in Wyoming that were provided supplementary feed during winter spent less time migrating during spring, arrived on summer range later, and departed for winter range earlier than unfed elk (Jones et al. 2014). Although fed elk gained an immediate benefit of obtaining easy food, such temporal change may ultimately be maladaptive if it causes elk to miss peak green-up, resulting in decreased access to quality forage throughout the year (Jones et al. 2014). Additionally, unintentional supplementary feeding areas such as irrigated agricultural land can alter traditional nutritional benefits of migration and may lead to year-long residency, increasing the potential for human–wildlife conflict (Krausman et al. 2014, Barker et al. 2019b).

The second pathway causing temporal change in migration occurs when ungulates' abilities to track an existing natural environmental gradient are obstructed, for example, by habitat fragmentation and loss (35.6% of temporal change events; Middleton et al. 2018). Certainly ungulates may lose access to migration routes or seasonal ranges when movement is obstructed by impermeable physical barriers, but even semipermeable features can alter migration phenology without causing conspicuous spatial change (Sawyer et al. 2013). For instance, mule deer in Wyoming sped up when crossing energy development areas without changing their direction or route, creating short-term phenological mismatches between vegetation green-up and migration (Sawyer et al. 2013). Notably, animals attempted to correct for these mismatches by slowing down after moving through the development areas. Although the demographic consequences of changes in migration speed or reduced stopover use are unknown, these mule deer clearly modify their migratory behavior in response to energy development through relatively flexible en route scheduling.

Exceptions to migratory plasticity

Despite the prevalence of migratory plasticity, we observed important exceptions whereby ungulate populations were unable to adapt their migratory strategy to environmental changes. We found substantial differences in the capacity for plasticity among well-studied species, between populations of a single species, and even among individuals in the same population. For example, some elk frequently alter their migration propensity, whereas mule deer have not been observed to alter their migration propensity (Fig. 2; Sawyer et al. 2019b). Even among elk, some individuals appear more likely to alter migration propensity than others (Eggeman et al. 2016). Similarly, a recent review revealed a wide range of plasticity in the migration propensity of white-tailed deer, with the range of switch rates fluctuating between 7% and 39% across six studies (Berg et al. 2019). Understanding variation within the degree of plasticity is critical for accurately predicting population trajectories and

estimating the capacity of species or populations to withstand disturbance (Chevin et al. 2010).

Additionally, some highly plastic species experience strong limitations imposed by the physical landscape. For instance, although pronghorn have been observed to employ six types of migration change across all three dimensions (Fig. 2), one well-known population in the Greater Yellowstone Ecosystem can only access winter range through a narrow bottleneck, restricting the population's ability to adjust its migratory path (Berger et al. 2006). Unfortunately, empirical evidence on migrations that *do not* change is extremely limited in current literature (but see Sawyer et al. 2019a). To better recognize the extent and limits of migratory plasticity, reporting non-plastic migration (including due to physical environmental barriers) is at least as important as, if not more important than, reporting migration change.

Importantly, our results reveal strong species and geographic biases within existing migration ecology literature, and we caution against generalizing our findings to understudied species and areas. More than half (52.0%) of all migration change events were observed in the top four most-studied species, and only a few studies were conducted in North Africa, Central Asia, and Latin America despite their known ungulate diversity. Given that the development of migration plasticity is likely highly dependent on local historical dynamics (David et al. 2004, Fusco and Minelli 2010), and that modern global environmental change exhibits high spatial heterogeneity (Walther et al. 2002), it is necessary to expand research of ungulate migratory plasticity beyond current “model” species and geographic locations. Due to the high variability of migratory plasticity across individuals, populations, and species, applying any overly general prediction of how migrations change may be a detriment to species that are less understood.

TOWARD MECHANISTIC UNDERSTANDING OF MIGRATORY PLASTICITY

Migratory plasticity appears much more prevalent among ungulates than previously appreciated, indicating that multidimensional migratory plasticity likely comprises a fundamental component of ungulate behavioral ecology. At least 27 ungulate species in habitats ranging across tropical, temperate, and arctic regions have been observed to exhibit some (and often more than one) forms of migratory plasticity (Fig. 2) in response to various types of environmental change (Fig. 3). Collectively, the studies we reviewed indicate that responses of migratory ungulates to environmental change vary across species, space, and time. Notably, different types and dimensions of migration change often occur simultaneously. Hence, properly capturing behavioral dynamics requires measuring full aspects of migration change. For example, it is unknown whether animals with less-plastic migration propensities compensate for environmental change via higher plasticity in migration timing or route

setting. Expanding the concept of migratory plasticity to also include spatial and temporal dimensions will achieve a more holistic understanding of the extent of plasticity across species and populations.

Gaining predictive insights of migration change

A clearer delineation of migration change types sets the stage for applying ecological theories and techniques to better predict migration behavior in altered environments. For instance, the reaction norm concept in behavioral ecology (David et al. 2004, Charmantier et al. 2008, Spiegel et al. 2017) offers a valuable and intuitive measure of phenotypic plasticity of migration. Reaction norms are quantified by estimating individual variability in relation to environmental change to examine causes and selective consequences of phenotypic plasticity and diversification across species and taxa (Charmantier et al. 2008, Dingemanse et al. 2010, Pfennig et al. 2010). When the behavior–environment relationship is nonlinear, specified behavioral reaction norms can illustrate the thresholds at which migration change may be expected or exacerbated. The potential of reaction norms to predict thresholds has been supported by recent work showing that migrating mule deer exhibit much stronger avoidance of energy development above a threshold level of surface disturbance (Sawyer et al. 2020).

Currently, applications of reaction norms remain rare in ungulate migration work, largely limited by study designs (Chapman et al. 2011). With the assumption that migration characteristics are fixed, most studies were not designed to examine the dynamics of the migration pattern. Rather, migrations are mostly characterized by a snapshot of propensity, temporal attributes, or spatial characteristics averaged over time, potentially neglecting the change process among variations. Even when migration changes are acknowledged, characterization of the states between which changes occur is often oversimplified. For example, in early studies of partial migration, migratory propensity was often treated as a dichotomy of resident vs. migratory (Berg et al. 2019). More recent work in which partial migration was observed along a behavioral continuum marked a step toward applying reaction norms to understand variation in migration propensity (Cagnacci et al. 2011, Gurarie et al. 2017, Barker et al. 2019a). Given the interdependence of multiple dimensions of migratory plasticity, the concept of behavioral continuum could also be applied to the temporal and spatial dimensions. The types of migration change defined in our framework can serve as baselines along which behavioral continua can be measured. For example, Spatial Type II can be measured as the largest distance between the old and new routes, and Spatial Type III can be quantified as the percentage of overlap between the old and new ranges.

It is critical, yet difficult, to determine proper metrics for environmental gradients and the spatiotemporal

scale at which these metrics are measured to match the behavioral continuum (Martin et al. 2011, Murren et al. 2014). Most of the papers we reviewed documented environmental change categories, but not the severity of such changes. Partially due to the difficulty of teasing apart confounding environmental variables, causal relationships between environment and migration changes are sometimes inferred but not empirically examined. The lack of a consistent correlation between types of migration change and environmental change (Fig. 3) demonstrates that more nuanced environmental measures are required for predicting migration changes. For example, instead of using a binary measurement of presence and absence, habitat loss can be measured as percent land use change (e.g., Sawyer et al. 2020), and predation risk can be calculated as relative probability of predator–prey encounters (e.g., Prugh et al. 2019). Advances in technologies such as remote sensing and on-animal environmental sensors will play an increasingly important role in accurate quantification of environmental changes (Pettorelli et al. 2014, Kays et al. 2015).

Consequences of migratory plasticity

Currently, ungulates with more plastic migration behavior are considered more resilient to environmental change (Teitelbaum and Mueller 2019, Sawyer et al. 2019b). However, phenotypic plasticity can still be associated with costs at the individual and the population level (Ghalambor et al. 2007). The uncertainty of whether migratory plasticity is beneficial is further complicated by varying levels of plasticity across different populations and individuals. Species with more flexible migratory behavior may indeed react to the changing environment more readily, but whether the behavioral response is strong or fast enough to compensate for the impacts of environmental change remains unknown (Hendry et al. 2008, Van Buskirk 2012). For example, the same behavioral adaptation may have disparate demographic impacts on ungulates with different navigation mechanisms. A change of migration route may allow perception-driven animals to continue tracking high-quality forage but cause reduced foraging efficiency if they rely on spatial memory to learn migration behaviors. For animals in the latter case, corridors maintained through cumulative herd knowledge may not be readily re-learned once lost (Bracis and Mueller 2017, Jesmer et al. 2018). Moreover, adaptive behavioral change itself can lead to a population decline (Kokko 2011).

Furthermore, the population consequences of migration change may not remain consistent over time. Even a migration change that relieves the immediate negative impacts of environmental change may ultimately prove maladaptive (Fahrig 2007, Wong and Candolin 2015). For example, animals attracted to agriculture fields or supplementary feeding sites might be engaged in maladaptive behavioral responses due to growing mortality associated with increasing contact with humans or predators (Sigaud

et al. 2017, Simon and Fortin 2020). Increasingly swift and severe environmental change may leave little time for migratory plasticity to manifest and may irreversibly impact population viability. Indeed, rapid environmental change is already a reality for many ungulate populations (e.g., Said et al. 2016, Pei et al. 2019).

To better understand the consequences of migratory plasticity, future studies should prioritize long-term, individual-based migration monitoring paired with demographic or fitness information and environmental gradients. Such studies are of paramount importance to record and classify types of migratory plasticity, differentiate decreases in population viability from baseline population dynamics, examine causes and consequences of migration change, reveal interspecific differences in plasticity, and bridge the gap between migration ecology and evolution (Gaillard 2013, Eggeman et al. 2016). Improved tracking technology has brought long-term migration monitoring at a finer spatiotemporal scale within reach for ungulates of all sizes (Kays et al. 2015). On the other hand, very few studies couple ungulate migration change with demographic information or proxies of fitness over the period of behavioral change, and almost all of existing studies come from resource-rich model ecosystems (e.g., Mahoney and Schaefer 2002, Middleton et al. 2013).

Without direct fitness measurements corresponding to migration change, consequences of migration changes might be inferred by comparing the fitness of individuals with different migration patterns in the same species or population (e.g., Hebblewhite and Merrill 2011, White et al. 2014). Still, most studies consider a migrant-resident dichotomy, potentially overlooking a multitude of other important differences, such as that of individuals migrating long vs. short distances within a population (Sawyer et al. 2016). Emerging advances in long-term wildlife tracking technologies and methods to measure physiological traits in free-living animals may provide necessary data that can inform physiological mechanisms and evolutionary theory of migratory plasticity (Hegemann et al. 2019).

IMPLICATIONS OF MIGRATORY PLASTICITY FOR CONSERVATION

A better understanding of the causes and consequences of migratory plasticity could significantly inform contemporary conservation and management efforts of ungulate populations. Common conservation strategies involve identifying and protecting key migration habitats, such as wintering areas, parturition ranges, migration corridors, and bottlenecks (Berger et al. 2008, Sawyer et al. 2009). These strategies rely on assumptions that migratory animals move regularly in the identified areas and that changes to movement pattern warrant prevention (Harris et al. 2009, Mueller et al. 2011). Indeed, it has been occasionally documented and widely argued that alterations in migration patterns are often accompanied by dramatic decreases in population size,

overall fitness, or even collapse of the associated ecosystem (Said et al. 2016, Løvschal et al. 2017).

However, as we refine our understanding of migratory plasticity as a default attribute for many migratory ungulates, these assumptions face two challenges. First, not all migration changes reduce population viability. Conversely, migratory plasticity can sometimes facilitate population resilience to external changes. As discussed in the previous section, some migration changes represent tactical strategies to mitigate immediate negative impacts (e.g., Sawyer et al. 2013). Second, the efficiency of conservation approaches hinges on the drivers of migratory plasticity and the type of plasticity manifested. Some environmental factors, such as climate or predator density, fluctuate despite the boundaries of areas protected by conservation or management actions. In response, ungulates might alter migration patterns to cope with these environmental variations outside of the protected habitat. If migration drastically varies in space, a fixed conservation area will become a barrier, limiting migratory plasticity. Given that today's protected areas are often accompanied with fenced boundaries or intense human pressure along their borders, attempted conservation actions might actually fail to support or even constrain a population's resilience to environmental changes (Jones et al. 2018, Veldhuis et al. 2019).

Despite the challenges faced by migratory ungulates, migratory plasticity indicates potential positive outcomes for migration conservation. We suggest that managers identify conservation concerns beyond merely whether migration is changing, but how and why. For anthropogenic disturbances, it could be beneficial for government agencies to conduct before-during-after migration monitoring, which has, to date, yielded some of the only research showing clear causal relationships between environmental and migration changes (e.g., Sawyer et al. 2013, 2017). Management actions aimed at facilitating adaptive behavioral adjustment may prove most beneficial for the conservation of migratory ungulates (Buchholz et al. 2012). For example, a management plan that focuses on maintaining social structure that allows for cultural transmission of optimal migratory strategies would be more effective than a plan aiming only to prevent migration change. In addition, understanding the degree to which migration is flexible makes it possible to project dynamic migration patterns and resultant population vulnerability, and to identify and protect corridors for species that are less responsive to environmental change (Blumstein 2015, Spiegel et al. 2017). With demographic information, researchers and managers can evaluate whether an observed migration change is optimal, beneficial, or maladaptive and identify change thresholds that would result in fitness impacts (Angilletta et al. 2003, Chevin et al. 2010). These predictions can assist prioritization and allocation of resources by determining circumstances where intervention by managers is needed (e.g., Lewison et al. 2015, Allen and Singh 2016). Recognizing the extent of migratory plasticity in ungulates may even unveil new lines of

inquiry and conservation, such as the restoration of migrations previously thought to be lost.

CONCLUSION

Studies of migration changes have proliferated in recent years and comprise an important component of the field of movement ecology, yet our understanding of the implications of migratory plasticity, especially in ungulates, remains in its infancy. Our synthesis of current knowledge reveals that migratory plasticity is common in ungulates worldwide. Distilling dynamic migration patterns into *whether*, *where*, and *when* under the proposed migratory plasticity framework allows us to recast the widely accepted binary narrative that migration is either declining or thriving. Using a common typological framework to describe and compare behavioral change offers a key opportunity to identify environmental disturbance thresholds beyond which populations start to decline. Currently, the lack of concurrent demographic information has restricted us to ask new questions about when plasticity indicates adaptation as opposed to population decline or collapse.

To inform theoretical understanding and contemporary conservation, mechanistic insights regarding causes and consequences of migratory plasticity can be developed via deliberate study designs and data collection emphases. Specifically, where possible, insights would be gained by (1) collecting long-term, individual-based, tracking data; (2) conducting concurrent long-term physiological or demographic monitoring; (3) quantifying behavior to measure behavioral continua of *whether*, *where*, and *when* animals migrate; (4) measuring the type and magnitude of environmental change; (5) linking migratory plasticity to fitness consequences; and (6) expanding studies beyond current model species and geographic ranges.

Importantly, recognizing behavioral plasticity in migratory ungulates does not conflict with efforts to conserve migratory routes or behaviors, nor does it imply that predictable, high-quality resources are unimportant for migratory herds. Indeed, retaining knowledge of multiple, viable migration routes can be important for many ungulate species to take advantage of long-term spatiotemporal variability in resources. The precautionary principle should be employed when wildlife and land managers and developers are uncertain about the plasticity of a species or a population. Fundamentally, conserving populations requires understanding the full breadth of behavioral adaptations they may employ, and perhaps more importantly, recognizing animals as agents responding dynamically to their world.

ACKNOWLEDGMENTS

We thank J. Fryxell, R. Viejou, and an anonymous reviewer for their constructive comments that substantially improved the quality of the manuscript. We are grateful to B. A. Whyte for inspiration and discussions on the topic of behavioral plasticity

and evolution. We thank the 2019 Gordon Research Conference for the opportunity to present the original idea and results. W. Xu thanks D. Tu and K. Lee. This research was supported by National Geographic Society Grant WW-100C-17 and the Knobloch Family Foundation. W. Xu was supported by the Smithsonian Institution Predoctoral Fellowship. Kristin Barker, Avery Shawler, and Amy Van Scoyoc contributed equally to this work.

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