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Reports of the Taxonomic Sub-Groups: Ungulates[1]

The Cultural Basis of Ungulate Migration

A role for social learning and cultural transmission in the conservation of migratory ungulates:

Ungulates—herbivorous hooved mammals comprising orders Artiodactyla and Perissodactyla—make long, complex seasonal movements that are often choregraphed to match pulses in resource across space and time. For instance, ungulates select forage at an intermediate phenological state (Fryxell and Sinclair 1988, Albon and Langvatn 1992, Esmaeili et al. 2021). When plant phenology progresses across landscapes in a predictable way, 'green waves' of high-quality forage emerge (Aikens et al. 2020). Migratory ungulates track, or 'surf', these waves across the landscape—a behavior known as "green wave surfing" (Merkle et al. 2016, Aikens et al. 2017)—often resulting in increased fitness via greater exposure to and intake of energy and nutrients (Middleton et al. 2018). Ungulate migration can therefore be viewed not only as an adaptive behavior itself, but also as an important foraging behavior. Despite an understanding that conserving migratory behavior is critical for sustaining ungulate populations, our understanding of if and how social learning and cultural transmission maintain this behavior represents an enduring challenge for ecologists and policy makers.

Evidence of social learning in ungulates:

Animal migrations arise through a combination of learned behavior and genetically inherited neurological, morphological, physiological, and behavioral traits (Bolger et al. 2008, Abraham et al. 2022). Ecologists have, however, long hypothesized that the migratory behavior of ungulates stems primarily from social learning and cultural transmission of the spatial knowledge needed to efficiently track green waves (e.g., Nelson 1998, Boone et al. 2006, Fagan et al. 2012). To date, the best available evidence of social learning in ungulates comes from a series of translocations wherein migratory bighorn sheep (*Ovis canadensis*) and moose (*Alces alces*) were moved into areas devoid of conspecifics and where green waves existed (Jesmer et al. 2018). Translocated individuals had no prior knowledge of the spatiotemporal patterns of green waves and did not exhibit migratory behavior, indicating that migratory behavior is not solely based on the ability of ungulates to perceive green waves nor is it under strong genetic control. After decades of opportunity to learn about green waves both socially and asocially, however, the ability of ungulates to track green waves across the landscape increased, resulting in the emergence of migratory behavior. The only plausible explanation for the observed increase in knowledge regarding spatiotemporal patterns of green waves is that information was culturally transmitted vertically or obliquely across generations and improved upon by each generation—a process known as cumulative cultural evolution (Tennie et al. 2009, Jesmer et al. 2018).

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Learning requires information to be stored in memories upon which animals can base their decision making (Shettleworth 2010). With regards to ungulate foraging and migratory behavior, the ability to learn socially or asocially about green waves requires two specific types of memory: spatial memory (i.e., encoding of spatial relationships; Gautestad 2011) and attribute memory (i.e., encoding of locale-specific characteristics; Fagan et al. 2012, Fagan et al. 2013). Indeed, the role of spatial and attribute memory in ungulate foraging ecology has become well established in the literature over the past decade. For example, bison (*Bison bison*) inhabiting a meadow-forest matrix encoded information about the location and quality of meadows into memory and used this information to optimize their patch-to-patch movements in a way that maximized energy and nutrient intake (Merkle et al. 2014, Merkle et al. 2017). Further, the seasonal range and migratory route selection of mule deer (*Odocoileus hemionus*), zebra (*Equus burchelli*), moose and bighorn sheep could not be accurately recreated using simulated animal movements that relied on perception alone (Bracis and Mueller 2017, Jesmer et al. 2018, Merkle et al. 2019). Only when simulated movements are parameterized with memory of migratory routes and seasonal ranges could observed migratory routes and seasonal ranges be recreated (Van Moorter et al. 2009, Bracis and Mueller 2017, Merkle et al. 2019). Thus, when combined with the life history characteristics of ungulates (i.e., prolonged maternal care, natal philopatry of females, site fidelity), evidence that ungulates rely on memory to guide their movement and foraging decisions indicates that social learning likely plays a key role in the development and maintenance of their migratory behavior.

Ungulates tend to return to or maintain distinct seasonal ranges and migratory paths year after year (Sweanor and Sandegren 1989, Nelson and Mech 1999, Morrison et al. 2021). Because it is only beneficial to exhibit such 'site fidelity' (Piper 2011) if high quality resources are present at a given time and place, the degree to which individuals should exhibit such site fidelity depends on the spatiotemporal predictability of resources (Morrison et al. 2021). It is assumed that spatial and attribute memory underlies the ability of individuals to act on information regarding the spatiotemporal predictability of resources and hence continuously return to profitable areas (for example, see Merkle et al. 2014). For example, 60 years of migratory caribou (*Rangifer tarandus*) data indicated that cows chose calving areas that did not necessarily possess optimal foraging conditions in a given year, but rather chose areas that over decades had predictably above average forage conditions compared to the landscape as a whole (Cameron et al. 2020). The only logical explanation for this result is that caribou had encoded information about the forage attributes of specific locations on the landscape, used spatial memory to navigate back historic calving grounds, and transmitted this information vertically or obliquely over generations such that calving grounds remained unchanged for at least six decades (Cameron et al. 2020).

The interface between social learning, intra and interpopulation phenotypic diversity, vital rates, and the conservation of migratory ungulates:

Species of migratory ungulates exhibit phenotypic variation in their movement behavior along a gradient from resident to migratory behavior. While many ungulate populations exhibit obligate resident or obligate migrant behavior (e.g., Sweanor and Sandegren 1988, Merkle et al. 2016, Sawyer et al. 2019), some populations exhibit partially migratory behavior wherein part of the population migrates and part of the population does not (Chapman et al. 2011). Although some populations of ungulates may switch between migratory and resident strategies using a win stay-loose switch decision making (Martin et al. 2022)—a notion referred to as facultative migration—most ungulate species are obligate migrators (e.g., Sweanor and Sandegren 1988, Merkle et al. 2016, Sawyer et al. 2019). The ability of individuals to employ the win stay-loose switch strategy that allows them to switch between two or more alternative seasonal ranges or migratory routes likely stems from social learning and memory (Morrison et al. 2021). Further, among individual variation in migratory strategy exists within both obligate and partially migratory populations. For instance, groups of individuals within populations of mule deer and bighorn sheep use different migration corridors that end at either shared or distinct seasonal ranges (Monteith et al. 2014, Sawyer et al. 2016, Spitz et al. 2018, Lowrey et al. 2020). Thus, if inter and intrapopulation diversity in migratory strategies stem from cultural transmission, each strategy may represent a 'culturally significant unit' deserving of conservation efforts in a similar fashion as to how conservation biology has focused on genetically significant units over the past ~4 decades (Moritz 1994, Crandall et al. 2000, Silva et al. 2017).

Recently, intrapopulation diversity in migratory strategies has led ecologists to begin testing two key hypotheses regarding the development and maintenance of such phenotypic variation; specifically, the notions of the ideal free distribution and the portfolio effect. The ideal-free distribution hypothesis states that at high population densities some individuals will move to lower quality habitat in an effort to reduce competition for resources. By distributing themselves in a density-dependent manner, among-group fitness will both increase and equalize (Fretwell and Lucas 1969, Holt 1996). This is conceptually similar to the niche variation hypothesis (Van Valen 1965) wherein individuals specialize on different resources via behavioral or morphological specialization in an attempt to reduce intraspecific competition and increase population-level fitness (Roughgarden 1974, Bolnick 2001, Tinker et al. 2008, Jesmer et al. 2020). Correspondingly, the portfolio effect states that intraspecific trait variation should be maintained across environmental contexts in a way that buffers populations from environmental variability via selection for and against specific phenotypes over time and space (Markowitz 1952, Schindler et al. 2015).

Evaluation of the fitness components of different mule deer and elk phenotypes (e.g., resident, short and long-distance migrators) provides support for the ideal free distribution and the portfolio effect hypotheses. For example, phenotypic variation was linked to short-term (e.g., 5-30 years) variation in the survival and reproduction of these species and resulted in shifting proportions of phenotypes over time (Monteith et al. 2014, Cole et al. 2015, Sawyer et al. 2016, Ortega et al. *In Review*). Further, the ways in which climate change will alter phenological patterns across landscapes are unpredictable, suggesting a diversity of movement strategies will allow populations to adapt (Schindler et al. 2015, Zuckerman et al. 2023). For these reasons and because the movement strategies of ungulates are thought to be inherited via social learning and cultural transmission (Sweanor and Sandegren 1988, Nelson 1998, Nelson and Mech 1999, Jesmer et al. 2018, Jakopak et al. 2019), efforts to conserve or promote phenotypic diversity (i.e., subcultures of movement behavior) in the face of unprecedented rates of climate and land-use change is likely to promote the long-term stability of ungulate populations.

Incidence and distribution of migratory behavior in ungulates:

If the migratory behaviors of ungulates stem from cultural transmission of information regarding the spatiotemporal patterns of green waves, then any threat to their ability to track green waves and access seasonal ranges (e.g., reduced landscape connectivity or loss of migratory diversity) threatens both maintenance of their traditional knowledge and population viability. Hence, important first steps in conserving migratory ungulates at the global scale are to (1) understand which of the 205 species of ungulates are migratory, (2) which species exhibit transboundary migrations, and (3) which parties to the CMS are stewards of which species. We therefore quantified the incidence of migratory behavior across all ungulate taxa, identified parties with possible transboundary migrations, mapped the global distribution of migratory ungulates, and cross-referenced each species with the International Union for Conservation of Nature's (IUCN) threat status (Fig. 1; see appendix for tabular representations of these data and additional species information).

To determine whether or not a species was migratory, we searched the literature for reports of at least one population of the species exhibiting migratory or partially migratory behavior (for further detail, see the supplemental material of Abraham et al. 2022). We then used the Mammal Diversity Database (2022) to append IUCN status to each species. To map the general distribution of migratory species we downloaded geographical range boundaries for each species from the IUCN (2022) spatial data server and intersected these range boundaries with the political boundaries of each party to the CMS as defined by the World Bank (2022).

We discovered evidence of migratory behavior for 90 ungulates species and evidence of resident behavior for 89 ungulate species. For the remaining 26 species where reports confirming or denying the presence of migratory behavior were absent in the literature, we used the predictive model of Abraham et al. (2022) to impute migratory status. Ultimately, we found evidence of migratory behavior in 45% (93 of 205) of ungulate species. After intersecting the ranges of migratory ungulates to the political boundaries of parties to the CMS, we found that the parties are stewards of 81 species of migratory ungulates and 68 potential transboundary migratory species (see appendix). By integrated these published, peer reviewed data we were able to create a species by party matrix containing all the above information (see appendix) and map the ranges of each migratory species (Fig. 1A) and the total number of migratory species present within each parties' political boundary (Fig. 1B). Parties to the CMS can use the appendix as a tool for reviewing which migratory ungulate species are present within their political boundaries, potentially migrate across political boundaries, and their IUCN Red List status, which are the three criteria needed to consider adding a species to CMS appendices I and II.

Recommendations for conserving the cultural capacity in migratory ungulates:

In accordance with the CMS Appendix II, we provide the following recommendations for advancing conservation capacity for migratory ungulates:

Recommendation 1. Fill gaps in knowledge about the presence and absence of transboundary migrations by using both in country and resources derived from the Global Initiative on Ungulate Migration (GIUM; https://www.cms.int/en/gium), such as local knowledge and GPS tracking data, to identify and map migrations.

Recommendation 2. Make concerted efforts to maintain landscape connectivity in way that provides ungulates access to green waves across political boundaries as well as within party boundaries.

Because ungulate migration is maintained via social learning and cultural transmission, conserving landscape connectivity will also conserve the capacity for ungulates to continue to learn about green waves and transmit this information to other social conspecifics and across generations.

Recommendation 3. Identify and conserve culturally significant units.

Although the scientific community is only now beginning to develop knowledge about the importance of the presence and maintenance diverse migratory strategies, several long-standing ecological and evolutionary theories (i.e., portfolio effect, ideal-free distribution, niche variation hypothesis) all suggest that maintaining behavioral diversity is a key component of buffering populations and species against environmental change.

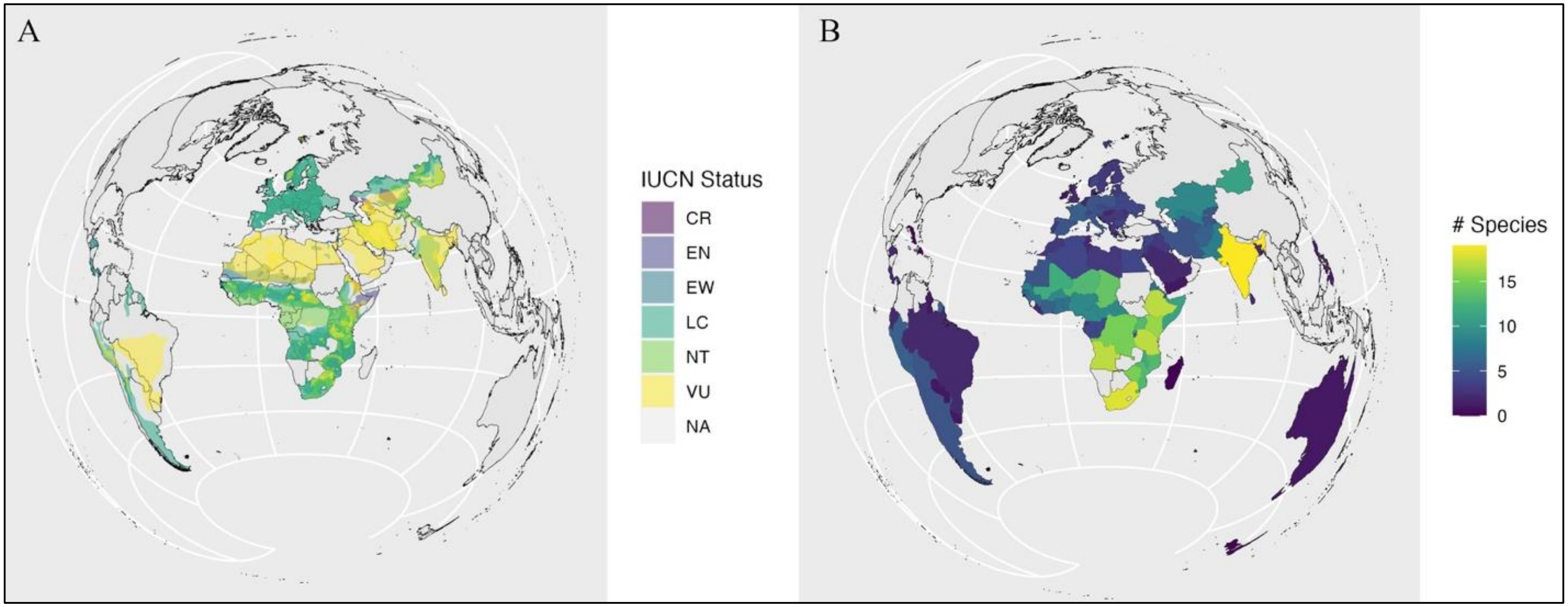

Figure 1. (A) Distribution and IUCN status for all migratory ungulates residing within the political boundaries of parties to the CMS. (B) Total number of migratory ungulate species residing within the political boundaries of parties to the CMS. See appendix for tabular representations of these data and additional species information.

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