DRIVERS OF ALTITUDINAL MIGRATION IN UNGULATE SPECIES

By

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Abstract

Migration is extremely important both at the species and ecosystem level, however most research has focused on long-distance migrations. Without an understanding of short-distance migrations, like altitudinal migration, it can be hard to predict how species will be affected by rapid changes in the environment. Migratory ungulates are of special conservation importance as many are keystone species, having significant effects on ecosystem processes. In this study, I provide an overview of the drivers of altitudinal migration in ungulates and discuss its importance in ecology and conservation. Through a review of case studies of various ungulate species, I found four drivers of altitudinal migration: forage quality and quantity, predator avoidance, weather, and pest avoidance. While a pattern of forage quality and quantity emerged as one of the main mechanisms underlying altitudinal migration, most migrations were driven by a combination of the four factors. This knowledge helps better our understanding of altitudinal migration in ungulates, however more research is needed on how climate change, habitat fragmentation, and other environmental factors influence these species. I conclude by discussing future research directions for the study of altitudinal migration in ungulates and how these can be conducted.

Keywords: ungulates, altitudinal migration, driver, forage, environment

Introduction

Migratory species can be found across all major vertebrates and many invertebrate species, in terrestrial, aquatic, and aerial environments (Dingle 2014). Migration is beneficial to species as it allows populations to reach larger numbers than if they were residents and enables them to persist in areas they otherwise could not (Fryxell et al. 1988, Kauffman et al. 2021). Migratory animals are also of vital importance to the ecosystems they inhabit because they serve as vectors of nutrients, spores, seeds, pathogens, and parasites along their migration routes, thereby linking habitats that would otherwise be separated (Bauer and Hoye 2014, Abraham et al. 2022). Loss of migratory behavior would therefore not only affect migrant species, but other species within their ecosystems as well (Shaw 2016).

Migratory species are highly susceptible to changes in their environment (Shaw 2016). Shifts in climate and destruction of habitat could adversely affect migratory species (Wilcove and Wikelski 2008). While species can shift migration timing and frequency to adapt to subtle changes in climate or habitat, more rapid environmental change can lead to failed migrations, or in a worst-case scenario, a loss of migration altogether (Shaw 2016). Understanding the drivers of migration is key to predicting how migratory species may be affected by climate change and anthropogenic habitat changes in the future, thus helping managers make informed decisions on how to best protect these species and their habitats.

Although long distance migration–occurring over hundreds of kilometers, often through rough terrain (Kauffman et al. 2021)–has been well-studied (Hughes et al. 1998, Fox et al. 2003, Luschi et al. 2003, Thirgood et al. 2004, Block et al. 2005, Stutchbury et al. 2009, Horton et al. 2011, Alves et al. 2013, Trierweiler et al. 2014), migrations of shorter distances have been studied far less (Hsiung et al. 2018). Altitudinal migration, a type of short-distance migration where individuals migrate seasonally between discrete elevational ranges (Rappole 2013, Kauffman et al. 2021), is of special conservation importance as these migrants may be more susceptible to harm from rapid changes in their environments caused by climate change or anthropogenic habitat disruption (Hsiung et al. 2018). Since altitudinal migrants have smaller ranges than long-distance migrants, alterations in climate, such as temperature shifts, may impact a larger portion, or the entirety, of their year-round habitat. Habitat fragmentation may also negatively impact altitudinal migrants relying on those fragments for resources (Hsiung et al. 2018). If they are unable to rapidly adapt, these species could undergo significant range reductions, a phenomenon observed in various non-migratory species like the alpine chipmunk (*Tamias alpinus*), Belding's ground squirrel (*Spermophilus beldingi*), and the water shrew (*Sorex palustris*) (Moritz et al. 2008).

In this paper, I provide an overview of the drivers of altitudinal migration in ungulates and discuss its importance in ecology and conservation, ecological theory underlying the study of migration, case studies of specific migratory ungulates, and future directions for the study of altitudinal migration in ungulates. Forty-five percent of extant ungulate species are at least partially migratory (Abraham et al. 2022) and many are keystone species, having significant effects on vegetation composition and ecosystem processes such as transport and nutrient cycling (Kie et al. 2003). Specifically, large herbivores exercise crucial top-down control on plant demography, species composition, and biomass, resulting in fire suppression and a healthy decrease in the abundance of smaller animals (Pringle et al. 2023). The importance of ungulates as a keystone species, in combination with the likely susceptibility of altitudinal migrants to environmental shifts, makes migratory ungulates essential to study.

Hypotheses

Animals migrate to gain access to resources not available in their home range and/or to avoid threats (Hebblewhite and Merrill 2009, Shaw 2016). The specific reason(s) behind altitudinal migration in ungulates vary between species and throughout different environments, but forage quality and quantity, predator avoidance, weather, and pest avoidance are four common drivers of altitudinal migration in ungulate species.

I. Forage Quality and Quantity

Forage quality and quantity may explain why some ungulates migrate elevationally. There are often seasonal variations in food production along elevation gradients, influenced by changes in temperature and precipitation patterns throughout the year (Hsiung et al. 2018). In response to these variations, migrating ungulates in temperate and boreal zones move up in elevation in the summer and move down in elevation in the winter (Bischof et al. 2012). This is called 'surfing the green wave' (Bischof et al. 2012), a pattern of following seasonal plant quality and quantity across space and time to maximize energy intake (Abraham et al. 2022). By making small-scale adjustments to habitat use coinciding with the timing of spring plant growth (Bischof et al. 2012), ungulates gain longer access to high quality forage allowing migrants to gain more weight than residents (Albon and Langvatn 1992). Since good body condition is linked with high fitness in ungulates (White 1983), this ultimately results in larger migrant populations than residents (Fryxell et al. 1988, Kauffman et al. 2021).

II. Predator Avoidance

Predation risk may also cause ungulates to migrate. The needs of ungulates vary between breeding and non-breeding seasons. When predation risk differs along an elevational gradient, ungulates often migrate to areas with lower predation risk to maximize fitness (Hsiung et al. 2018). This is especially true for pregnant females and females with young, as areas with low predator density are important to the survival of their offspring (Festa-Bianchet 1988).

III. Weather

Another driver of altitudinal migration in ungulates may be associated with changes in weather. The endothermic costs of maintaining optimal body temperature increases with temperature extremes, increased wind speed, and/or increased exposure to precipitation. To combat this, ungulates migrate to elevations providing more manageable temperatures and more desirable weather conditions, thereby lowering their energetic costs (Hsiung et al. 2018). Weather may also cause indirect effects on the migration of ungulates by affecting food supply, as in the form of decreased access to vegetation due to snow. Above-ground vegetation is dependent upon the initiation and duration of the growing season, so changes in temperature and precipitation affect the availability of vegetation (Hsiung et al. 2018).

IV. Pest Avoidance

Pest avoidance is another possible factor driving altitudinal migration in ungulates. Blood from large mammals, like ungulates, provides a good source of protein for biting and sucking insects (Keiper and Berger 1982) like bot flies (Oestridae), mosquitos (Culicidae), horse and deer flies (Tabanidae) and black flies (Simuliidae) (Skarin et al. 2004). Insect harassment can result in blood loss, disease transmission, infection, and ecto- or endoparasitism (Keiper and Berger 1982). When insect harassment is severe enough, it can influence ungulate habitat selection. On warm, summer days when insect harassment is higher, ungulates are driven to higher altitudes in an effort to avoid pests (Skarin et al. 2004).

Case Studies

A. *Bighorn Sheep (Ovis canadensis)*

Bighorn sheep are partial migrants, migrating seasonally to live at high elevations in the summer and lower elevations in the winter (Spitz et al. 2018). Living at high elevations in the summer allows sheep access to high nutritional value forage. This especially benefits ewes and their lambs, as small differences in the quality of summer forage eaten alter reproductive success and growth of yearling sheep (Martin and Festa-Bianchet 2010). When temperatures drop and snow falls in the winter, the growing season at high altitudes ends and forage availability is limited. This causes sheep to migrate down to lower elevations to find snow-free areas, but they are most susceptible to mountain lions, their main predators, at these lower elevations. Mountain lions are the leading cause of mortality for some bighorn populations, as they limit population growth or even drive extirpation in small populations. (Jones et al. 2022). Thus, sheep residing in higher elevations throughout the year face a reduced threat of predation but an increased risk of starvation. Conversely, those wintering at lower elevations experience a lower risk of starvation but a higher risk of predation (Denryter et al. 2021). A combination of the forage quality and quantity, predator avoidance, and weather hypotheses explain bighorn sheep migration patterns.

B. *Reindeer (Rangifer tarandus)*

Reindeer are another example of altitudinal migrants forced to balance the trade-offs between high forage availability and quality and low predation risk. Brown bears prey on reindeer calves and can kill up to 30% of juveniles during calving (Sivertsen 2017). Calf predation primarily occurs in the first few weeks after birth (Sivertsen 2017), coinciding with the beginning of spring plant growth. Calving is energetically expensive for female reindeer, making it necessary for them to use the short growing season in the spring and summer to refuel their bodies after depletion in the winter (McEwan and Whitehead 1972). The presence of brown bears, however, affects reindeer migration. In areas with high brown bear densities, reindeer select movement paths with lower quality forage, deviating from the green wave, likely in an effort to reduce predation risk (Rivrud et al. 2018). Reindeer may also move to higher elevations with more snow cover and less access to forage in order to reduce predation risk (Bergerud and Page 1987, Barten et al. 2001, Gustine et al. 2006, Pinard et al. 2012).

Reindeer were also found to increase movement speed and reduce stopover time in places with higher bear densities throughout the growing season (Rivrud et al. 2018). Stopover areas are important for resting and refueling during migration, so reduction in stopover time can lead to less optimal foraging during the migration route (Rivrud et al. 2018). High movement speeds can also lead to phenological mismatch at the seasonal site (Rivrud et al. 2018). Attempting to surf the green wave while also avoiding predators coincides with the forage quality and quantity and predator hypotheses.

Insect harassment is also known to drive reindeer to higher altitudes where pests are less prevalent (Skarin et al. 2004), the pest avoidance hypothesis, but forage quality is lower, possibly creating a mismatch with spring plant growth (Mörschel and Klein 1997, Hagemoen and

Reimers 2002, Skarin et al. 2010). Once again, reindeer are faced with the tradeoff between high quality forage and avoiding threats. However, while pest avoidance is more important in the summer, predation risk is the driving factor behind female movement patterns (Bergerud and Luttich 2003).

C. Alpine Ibex (Capra ibex)

Weather is a driver of altitudinal migration in Alpine ibex. While snow cover can force them to lower elevations (Parrini et al. 2003), increased temperatures can cause ibex to migrate to higher elevations in an effort to avoid the heat (Aublet et al. 2009). Temperate ungulates, like the Alpine ibex, are more prone to experiencing heat stress at lower temperatures than species adapted to warmer environments (Schwab and Pitt 1991, Owen-Smith 1998). A study on Alpine ibex in Italy found that on hot, sunny days, ibex migrated to higher elevations and rarely fed. On cooler, cloudy days, ibex stayed at lower elevations and spent four to five times more time feeding (Aublet et al. 2009). Frequent migrations of up to 800 m in elevation induce significant energy costs, so ibex must have a reason for inducing these costs. It is not likely attributed to difference in vegetation quality as the difference was found to be trivial and ibex fed very little at high altitudes, instead migrating back down to feed in the evenings when temperatures dropped (Aublet et al. 2009). This indicates altitudinal migration in these Alpine ibex is driven by thermoregulation, the weather hypothesis

D. Mule Deer (Odocoileus hemionus)

A long-term study of a population of mule deer in the Sierra Nevada, California concluded that altitudinal migration was driven by weather and forage quality and quantity, with some variation due to individual life-history characteristics. Autumn migration was mainly driven by changes in the severity of winter weather in the form of snow depth and low temperatures (Monteith et al. 2011). Increased snow depth and decreased temperatures result in increased energetic costs associated with thermoregulation and locomotion in ungulates like mule deer (Telfer and Kelsall 1979, Parker et al. 1984). Snow depth also affects availability of forage which in turn affects nutritional condition and overall survival of mule deer (Garroway and Broders 2005). In order to avoid being trapped by severe winter weather, thus incurring greater energetic costs (Parker et al. 1984) and becoming more susceptible to predators (Berger 1986, Patterson and Messier 2000, Bleich and Pierce 2001), the majority of mule deer migrated to lower elevations before the onset of winter weather (Monteith et al. 2011). While this allows them more predictable access to forage, mule deer that left their winter range early missed out on taking full advantage of high quantity and quality of summer range forage (Monteith et al. 2011). This could end up affecting them later on as even small diet changes over time can negatively affect growth and reproduction (White 1983, Parker et al. 2009).

While autumn migration was mostly driven by the avoidance of severe winter weather, differences in the timing of autumn migration in female mule deer were due to various life-history characteristics including location of summer residency, age, and nutritional condition (Monteith et al. 2011). Females summering on the west side of the Sierra Nevada crest delayed autumn migration compared to east-side females, thus further exhibiting how the local environment influences migration timing (Monteith et al. 2011). Older female mule deer and those in good nutritional condition were more likely to delay autumn migration and risk encountering severe winter weather. Therefore, with respect to the potential loss of foraging opportunities due to deep snow, they were more risk-prone than young females and those in poor nutritional condition. Older females' more risk-prone migration tendencies were likely due their advanced knowledge of weather and forage patterns. In large herbivores, an increase in age and experience is often associated with greater reproductive performance (Cameron et al. 2000, Gaillard et al. 2000, Weladji et al. 2006, 2010) and advanced knowledge of forage distribution and availability patterns (Mirza and Provenza 1992, Ortega-Reyes and Provenza 1993). Consequently, older females' greater knowledge of weather and forage patterns likely led them to delay autumn migration in order to maximize nutritional gain and improve likelihood of reproductive success (Monteith et al. 2011).

On the other hand, spring migration of female mule deer did not vary based on individual life-history characteristics and was consequently nearly twice as synchronous as autumn migration. This was likely due to pregnant females' nutritional demands making it advantageous for them to depart from wintering grounds as soon as snow cover and foraging conditions allowed (Monteith et al. 2011). Spring migration was instead driven by both duration in snow cover and timing of spring plant growth (Monteith et al. 2011). Female mule deer migrated to higher elevations in the spring to consume plants at an earlier phenological stage (Klein 1965, Morgantini and Hudson 1989) when they are more protein-packed and digestible (Soest 1994, Barboza et al. 2009, Parker et al. 2009). Autumn migration is thus explained by the weather hypothesis whereas spring migration is explained by both the forage quality and quantity and weather hypotheses.

Future Directions

There is a need to study how environmental factors influence altitudinal migration in ungulates. In the face of a rapidly changing climate, altitudinal migrating ungulates are under extreme threat. Ungulates rely on the timing of the growing season to migrate. Phenological mismatch is already occurring, like in the case of the reindeer, but with global warming changing the distribution and phenology of plants and animals, phenological mismatch is likely to worsen (McCarty 2001, Walther et al. 2002). Not only does climate change affect plant phenology, but the warming climate may cause temperate ungulates to migrate to higher altitudes more frequently, even when there is less abundance of food, like in the case of the Alpine ibex (Aublet et al. 2009). By missing the growing season and being forced to higher altitudes with less food, forage quality and availability are significantly reduced. This could lead to weight loss and reduced growth in ungulates, thus affecting the fitness of these populations, and ultimately species as a whole (Aublet et al. 2009). Further research on how climate change is affecting these migrants is necessary to ensure the protection of these species in the future.

Population estimates, habitat modeling, climate data, and individual movement data are needed to conduct these studies. In the past, population estimates were determined by trapping ungulates, marking them with ear tags, and then completing a series of ground and aerial censuses over a defined period of time (Lentfer 1955). While these methods are still used today, combining or replacing them with new methods using more recent technological advancements can yield more accurate results with less expensive, invasive, and safer methods (Taylor et al. 2022). For example, the use of motion activated trail cameras is less invasive, less expensive and safer than aerial surveys, and often produces more precise, consistent estimates of abundance (Taylor et al. 2022). These methods are then used to determine population estimates and gain demographic data to use in a population viability analysis. This, in combination with habitat modeling, the collection of climate data from regional weather stations, and individual movement data, can then be compared to assess the impacts of climate change on ungulates and their migration patterns (White et al. 2018).

More research on the effects of other environmental factors, like habitat fragmentation and human encroachment on the ranges of altitudinally migrating ungulates, is also required (Shaw 2016). Altitudinal migrants traveling longer distances between their breeding and non-breeding sites often make stops along the way (Sawyer et al. 2009, Sawyer and Kauffman 2011, Leopold and Hess 2014). Connectivity between these sites is therefore crucial to the survival of these migrants (Powell and Bjork 1994, 2004, Chaves-Campos 2003). Researching the effects of environmental factors and conservation strategies to protect these corridors is essential to the persistence of altitudinally migrating ungulates.

Collecting individual movement data is the first step to studying the effects of habitat fragmentation on altitudinally migrating ungulates. Once again, aerial surveys were used in the past to observe ungulate migration (Pruitt 1959), but the advancement of tracking devices has made migration studies increasingly more efficient. Radio-telemetry and Global Positioning System (GPS) tracking collars are now commonly used to track ungulate movements (Zweifel-Schielly et al. 2009, Qviller et al. 2013, Collins 2016) and can be used across elevational gradients. New spatial and statistical modeling tools can also help analyze the potential effects of changes in landscape composition and configuration, like habitat fragmentation, on populations of altitudinal migrants (Royle et al. 2013, Graves et al. 2014, Fuller et al. 2016).

Additionally, ongoing advancements in technology and methods for quantifying movement continue to provide us with an increasing array of tools at our disposal for use in these studies. GPS and accelerometer devices are becoming cheaper, smaller, and more efficient (Joo et al. 2022). Magnetometers and gyroscopes are even newer devices becoming increasingly more popular in movement ecology studies (Joo et al. 2022). The use of R has also increased in popularity, leading to the development of more R packages which in turn makes quantitative methods more accessible (Joo et al. 2022). While only ~10% of movement ecology papers used R in the late 2000s, the majority of published studies in the last few years report using R (Joo et al. 2022).

Conclusion

Understanding the drivers of altitudinal migration in ungulate species is the first step to helping ecologists determine the effects of environmental changes on migratory species and conservation strategies that can most effectively be employed to mitigate them. The case studies presented here support four drivers of altitudinal migration in ungulate species: forage quality and quantity, predator avoidance, weather, and pest avoidance. Many of these hypotheses influence one another, but the forage quality and quantity hypothesis is especially interconnected to all others. Ungulates are often forced to weigh the tradeoffs between quantity and quality of forage and the avoidance of predators, pests, and extreme weather. Ultimately, there is no single driver of altitudinal migration in all ungulates. Instead, a combination of these factors drives altitudinal migration, varying across species and environments.

In this paper, I reviewed current understanding of the drivers of altitudinal migration in ungulate species. The case studies discussed support four mechanisms underlying altitudinal migration in ungulates, but given the magnitude of ungulate species not covered, there could be additional factors driving altitudinal migration not included in this review. Forage quality and quantity was at least one of the drivers in three out of the four species discussed. This seems to show a general pattern of ungulates migrating altitudinally to follow forage quality and quantity, or surf the green wave. The pest avoidance hypothesis, on the other hand, was only one of the driving factors in the reindeer case study. While this is the least common factor driving the ungulate species reviewed, there may be other species' migrations also driven by insect avoidance that were not covered in this review. It is also important to note that the timing of autumn migration in female mule deer varied due to life-history characteristics. While this may not have been the driver underlying their migration, it is still interesting to consider as this variation was not documented in the other species reviewed. These results help provide a better understanding of the drivers underlying altitudinal migration in ungulates.

Increasingly more studies are being conducted on altitudinal migration. A search on Google Scholar shows that within the last ten years, 1,600 studies have been published on altitudinal migration. Almost two-thirds (64%) of those results are just from the last five years. Clearly, altitudinal migration studies are gaining more traction, but it is not happening fast enough. Human-induced global warming has been increasing at an unprecedented rate of over 0.2° C in the last decade, with warming averaging 1.14° C from 2013-2022 and 1.26° C in 2022 alone (Forster et al. 2023). Altitudinally migrating species are at increased risk to climate change and other human-induced changes to the environment. As such, there is a need to better understand how these changes influence migratory species, specifically ungulates, so managers can incorporate this knowledge into conservation plans and better protect these species. If we continue to study altitudinal migration and the effects of rapid environmental change, migratory species may just have a chance.

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