MOVEMENT AND SELECTION BY MIGRATORY UNGULATES IN DYNAMIC LANDSCAPES: PLASTICITY AND INDIVIDUAL DIFFERENCES IN A CHANGING WORLD

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Abstract

A fundamental aspect of many ecological systems is that they fluctuate in habitat quality through time. A common strategy among species is therefore to time reproduction, which is energetically expensive, to when resources are most abundant. A challenge for animals in adopting such a strategy is dealing with environmental change at intra- and inter-annual scales. Within years, migrating individuals can track areas of resource abundance throughout the season to increase energy intake. Alternatively, individuals may time reproduction to coincide with when resources are most abundant, at the cost of being able to track those resources spatially due to young that reduce movement capacity. For either strategy to be successful, individuals must deal with interannual changes in the timing of resource abundance, which threatens to decouple resources and consumers via trophic asynchrony. This is especially important in light of climate change which continues to advance the timing of spring events. Animals or populations can cope with this change in the timing of spring in two ways: individuals can be plastic to change and acclimate their behaviour to annual conditions, and/or populations can adapt if there are consistent differences among individuals in the timing of life-history behaviours that are transmissible across generations, resulting in selective pressures that result in an adaptive response. I tested these ideas in caribou (*Rangifer tarandus*) in Newfoundland and in migratory herbivores in Wyoming, USA. I demonstrate that caribou follow a gradient of melting snow to time their migrations, and as such give birth during the peak of resource availability (green-up). I then demonstrate that timing of migration and timing of parturition are plastic to timing of melting snow and are correlated. I tested for an effect of forage, conspecific density, and predation risk on calf mortality in two populations of caribou and found that avoidance of predators predicted calf survival in one of the two populations. Finally, I found that migratory ungulates in Wyoming had high repeatability in migration timing and were plastic to the timing of annual green-up. The results of my thesis are overall positive news for the conservation of migratory herbivores faced with changing environmental conditions in the Anthropocene.

Summary

Climate change represents a significant threat to migratory species, as important events such as timing of migration and birth are being decoupled from important resources upon which animals depend. Individuals can, however, develop strategies to mitigate these consequences by developing plasticity in their behaviour to changing environmental contexts or across generations via evolutionary adaptation as individuals better adapted to novel conditions gain reproductive advantages. My research incorporates contemporary hypotheses regarding the behavioural ecology of individual differences and applies them to testing drivers of herbivore migration and birth timing. Many herbivores track the flush of vegetation as it greens up along their migratory routes. Conversely, others opt to migrate prior to this green-up to take advantage of high-quality vegetation after migration when young represent an additional energetic burden. Annual reproductive success is maximized when individuals time important life events to take advantage of ephemeral resources. The timing of spring green-up is variable among years and advancing due to climate change. Within its lifetime, an individual may be plastic in the timing of migration and birth to acclimate to inter-annual variation. Across generations within a population, differences among individuals may have the potential to drive changes in mean dates of life history events to allow for adaptation to novel conditions in the Anthropocene. My thesis elucidates how migratory ungulates acclimate the timing of migration and parturition to changes in the timing of spring, and how consistent differences among individuals could allow populations to adapt to climate change.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF BOXES

CHAPTER 1: INTRODUCTION AND OVERVIEW

1.1 Overall introduction

Living in seasonal environments presents many challenges for animal species. Individuals must be able to cope with a range of environmental conditions, from finding food and staying warm in frigid winter months to alleviating heat stress and dealing with insect harassment in the summer, all while avoiding being eaten. Spring is a time that represents both opportunity and challenge for many animal species. As Earth's orbit brings higher angles of incident sunlight to higher latitudes, energy flow into seasonal ecosystems increases, from photosynthetic primary producers and up the food web. This influx of energy and resources has resulted in a common evolutionary strategy across numerous taxa that have evolved to time annual reproduction, the most energetically expensive part of the life cycle, to occur during this boom in seasonal resources (Sadleir 1969, Thomas et al. 2001). To successfully reproduce, animals must not only time reproduction to *when* resources are most abundant, but they must also move to *where* resources are most highly abundant, which in many cases varies throughout the productive season (Schindler et al. 2013). The challenge of matching resource needs to when abundance is highest is exacerbated for migratory species that must migrate at the correct time to exploit resources on winter and summer range and on migratory routes (Armstrong et al. 2016, Aikens et al. 2017). Compounding these challenges is dealing with variability in the timing of spring (e.g., the relative timing of environmental events such as snowmelt, green-up, or insect abundance). Variability in the timing of spring requires animals to either acclimate their behaviours to inter-annual variability and/or adapt to new conditions brought about by climate change. The ability of individuals or populations to acclimate or adapt to changing resource phenologies is key to their persistence in a changing world.

1.2 Resource tracking and "the green wave"

The availability of resources often varies in space and through time, and animals exploit this heterogeneity by moving to where resources are locally abundant for short periods of time (Schindler et al. 2010). Following resources allows consumers to take advantage of resources that may be abundant for longer periods over regional spatial scales, but locally ephemeral. Exploiting resource waves is a common phenomenon used by many taxa. For example, gazelles (*Eudorcas thomsonii*) on the Serengeti Plains move to exploit local patches of high-quality vegetation driven by local rainfall (Fryxell et al. 2005), and brown bear (*Ursus arctos*) and glaucous-winged gull (*Larus glaucescens*) activity was correlated with the location of spawning salmon (*Oncorhynchus nerka*) in Alaska (Schindler et al. 2013). Other examples include blue whales (*Balaenoptera musculus*) tracking prey associated with phytoplankton blooms (Abrahms et al. 2019) and herbivores such as geese (Shariatinajafabadi et al. 2014, Kölzsch et al. 2015) and ungulates (Merkle et al. 2016, Aikens et al. 2017) tracking high-quality vegetation; see review by Armstrong et al (2016).

Resource tracking in herbivores involves following the flush of high-quality emergent vegetation as it grows in the spring. The Forage Maturation Hypothesis (see Table S1.1 for a glossary of terms) posits that the quality of vegetation as a resource for herbivores is a trade-off between biomass and digestibility (Fryxell 1991, Hebblewhite et al. 2008). As plants begin to mature, their overall biomass increases to where cropping and bite rates become less limiting for herbivores; however, changes in cell wall structure and an increase in secondary chemicals as plants further mature results in a decline in digestibility and passage rates (Spalinger and Hobbs 1992). As such, vegetation quality for herbivores is maximized at an intermediate stage of plant growth where the trade-off between handling time and digestibility is maximized. For remotely sensed studies, forage maturation is typically quantified using the normalized difference vegetation index (NDVI). NDVI quantifies the “green-ness” of a given location as a measure of photosynthetic activity. A time series of NDVI values during spring green-up are fit to a logistic curve and the first derivative is taken to represent the instantaneous rate of green-up, IRG (Hamel et al. 2009, Bischof et al. 2012). IRG therefore represents the rate of plant green-up through time and is used as a proxy for vegetation quality.

Vegetation resources mature along elevational and latitudinal gradients, creating a “green wave” of vegetation that herbivores surf. By migrating concurrently with the green wave, herbivores can maximize the duration of time over which they are able to exploit this high-quality vegetation. For example, migratory barnacle geese (*Branta leucopsis*) track vegetation green-up along migratory routes (Shariatinajafabadi et al. 2014). Green wave surfing occurs in multiple ungulate taxa including bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and bison (*Bison bison*; Merkle et al. 2016). A more linear progression of green-up along migration routes has been shown to improve the ability of mule deer to track these vegetation resources (Aikens et al. 2017), and across partially migratory populations of multiple cervid species, the proportion of individuals that are migrants increases when migratory routes have a clearer green wave in their green-up pattern (Aikens et al. 2020). Selecting for areas associated with high values of IRG has been shown to increase faecal nitrogen content (Hamel et al. 2009), and surfing the green wave has been shown to increase fat gain in elk and presumably increase fitness (Middleton et al. 2018).

1.3 Resource tracking, or resource matching?

Reproduction is costly for most species, and as such has often evolved to occur when resource abundance is highest to allow individuals to energetically support the increased cost of reproduction (Sadleir 1969, Thomas et al. 2001). In ungulates such as caribou (*Rangifer tarandus*), energetic requirements increase to ~1.5 times base energetic needs during late pregnancy and more than double during the peak of lactation, which occurs approximately 2–3 weeks post-parturition (Oftedal 1985, Robbins 1993, Pekins et al. 1998, Parker et al. 2009). That energy requirements peak several weeks after parturition presents a challenge for migratory herbivores who give birth after migration. Surfing the green wave increases exposure to high-quality vegetation (hereafter "green-up") allowing animals to exploit spatial variation in green-up; however, this results in animals nursing young after the peak in green-up as individuals arrive on summer range concurrently with the green wave.

The idea that individuals should match their phenology to synchronize the cost-intensive time of offspring rearing to the peak phenology of their resource seems to be at odds with animals' ability to track resource waves. Most animals must stop to give birth, and young are not able to move as fast as adults for several days to several months. Birds are restricted to a single location from egg laying until their young fledge, and ungulates such as caribou must stop moving to give birth and must reduce average movement speed for the first weeks of their offspring's lives (DeMars et al. 2013, Bonar et al. 2018). Individuals who surf resource waves will in theory arrive on summer range concurrently with their resource, the result being that this resource will therefore be in decline as offspring provisioning needs increase. Given this restraint on reproduction and resource tracking, it would seem that these two strategies—reproductive matching and wave surfing—are mutually exclusive tactics, or at least tactics that exist on two ends of a continuum.

The potential disconnect between resource needs and abundance during the reproductive season may be the impetus for “jumping” the green wave (Bischof et al. 2012)—instead of surfing the green wave, individuals may instead time their migrations to arrive on summer range and give birth such that the peak of green-up occurs during the critical weeks post-parturition where the energetic burden of provisioning young is at its peak. Green wave jumping suggests a potential alternative approach for individuals to time migration, and that is to follow a gradient of receding snow as it melts across the landscape in a manner analogous to the green wave. Indeed, the timing of snowmelt has been shown to influence the timing of migration in caribou (Gurarie et al. 2019) and elk (Rickbeil et al. 2019). Migrating concurrently with snowmelt also likely facilitates movement, as moving through deep snow is energetically expensive (Parker et al. 1984, Fancy and White 1987), but frozen ground and lakes may facilitate travel (Leblond et al. 2016a).

Whether surfing the green wave or timing reproduction to occur with peak resource quality results in the highest fitness may depend on several factors. One important factor may be growing season length. Shorter summers at higher latitudes may force migratory herbivores to give birth earlier in the season during green-up for young to have sufficient time to mature prior to the onset of winter. By contrast, herbivores in more temperate regions may surf the green wave, give birth after the peak of green-up, and still allow young sufficient time to mature before winter. These strategies are also closely related to the concept of capital versus income breeding. Capital breeding species are better adapted to acquiring resources earlier and using stored energy reserves to finance reproduction, as opposed to income breeders who depend on resources during the important reproductive period (Jönsson 1997, Stephens et al. 2009). Indeed, strategies for birth timing are variable among ungulate species. For example, timing of birth in pronghorn (*Antilocapra americana*) was more synchronized with environmental optima than in bighorn sheep, reflecting differences in capital-income breeding strategies (Hogg et al. 2017). Intermediate tactics do exist, however. For example, barnacle geese appear to initially track the green wave early in migration before overtaking it to arrive on breeding range before it arrives there (Kölzsch et al. 2015, Si et al. 2015).

1.4 Climate change and phenological mismatch

Global climate change is significantly impacting the life history of many species. Ranges have shifted poleward (Parmesan 1996, Hughes 2000, McCarty 2001) at an average rate of 16.9 km per decade and upwards in elevation by 11.0 m per decade (Chen et al. 2011). However, responses to changing climate are inconsistent among taxa, the outcome of which is a change in community assemblages and a potential decoupling of trophic interactions (Fromentin and Planque 1996, Saetre et al. 1999, Walther et al. 2002). In addition to changes in range and distribution, climate change has also resulted in changes in phenology in many taxa, including woody (Ahas 1999) and herbaceous (Bradley et al. 1999) plants, birds (Crick and Sparks 1999), insects (Roy and Sparks 2000), amphibians (Beebee 1995), and fish (Ahas 1999; reviewed by Parmesan and Yohe 2003). As with differential responses in range shifts, different responses in phenology induced by climate change can result in phenological asynchrony, a decoupling of predator-prey interactions. If this asynchrony results in reduced fitness, the result is a phenological mismatch (Visser et al. 1998, Samplonius et al. 2021).

The match/mismatch hypothesis is founded on the idea that the most energetically expensive part of a species annual phenology, e.g., rearing young, should have evolved to correspond with the phenology of the trophic level upon which they depend such that food abundance is highest when energy needs are greatest (Sadleir 1969, Thomas et al. 2001, Durant et al. 2007). For example, birds time their nesting phenology to match when nestlings require the most provisioning to the timing of peak insect prey abundance (Lack 1968). The match/mismatch hypothesis suggests that individuals that do a better job of matching the phenology of their resource will have higher fitness. While the concept was initially formulated in the context of fisheries biology to describe the importance of fish survival in early stages of development (Hjort 1914), its importance has recently become an issue in conservation ecology. The differential effect of climate change across trophic levels drives these key trophic interactions into a state of mismatch. For example, mean egg-laying date in great tits (*Parus major*) did not advance significantly between 1973–1995, whereas date of peak caterpillar abundance (their main food source) advanced by nine days (Visser et al., 1998). Phenological mismatches have been described in numerous consumer taxa, including fish (Cushing 1990, Beaugrand et al. 2003), insects (Visser and Holleman 2001), birds (Visser et al. 1998, 2003, Both and Visser 2001), and potentially ungulates (Post and Forchhammer 2008, Kerby and Post 2013).

Phenological matching for herbivores involves matching the timing of peak reproductive needs to when IRG is highest (Hebblewhite et al. 2008, Bischof et al. 2012). Ungulates should give birth just prior to peak green-up to take advantage of green-up when needs are highest (Post and Forchhammer 2008). Current evidence of mismatch in cervids is unclear. Roe deer (*Capreolus capreolus*) in France failed to advance the timing of parturition to advancing spring green-up dates (Plard et al. 2014). In Greenland, the onset of plant growth advanced more than the mean date of calving in reindeer (also *R. tarandus*), which was correlated with a population-level decline in annual reproductive success (Post and Forchhammer 2008). Other studies in caribou however have shown that some populations may be acclimating or adapting to advancing plant phenology. Parturition dates for caribou in Alaska did not advance despite changing plant phenology; however, vegetation quality (nitrogen content) remained consistent and no reduction in annual reproductive success was detected (Gustine et al. 2017). Other caribou populations appear to be more plastic or have adapted in response to changing plant phenology. The peak of calving in the Qamanirjuaq caribou herd that summers in Nunavut advanced by 9.42 days from 2004–2016, outpacing the 7.25 days that plant phenology had advanced (Mallory et al. 2020). Indeed, advanced parturition date has been observed in many caribou populations in Canada and Alaska (Davidson et al. 2020), suggesting that caribou populations have the capacity to either adapt or acclimate to changing environmental conditions; however, the mechanism itself remains unclear.

1.5 Behavioural reaction norms—plasticity and individual differences

Behavioural plasticity describes the ability of individuals or single genotypes to produce different phenotypes as a function of different environments/contexts (Komers 1997), and is important for understanding how individuals acclimate their behaviours to changing circumstances over their lifetime (Piersma and Drent 2003, Dingemanse et al. 2010). For example, elk can alter the timing of their migration to changes in environmental condition such as timing of snowmelt and green up (Rickbeil et al. 2019). Other aspects of ungulate migration however appear to not be plastic—whether to migrate and migratory route in mule deer (Sawyer et al. 2018), for example. To successfully track resources across years in variable environments, individuals should be plastic in the timing of their migration as a function of the timing of spring to maximize their exposure to profitable foraging resources on an inter-annual scale.

Ecologists have realized the importance of behavioural differences among individuals as meaningful variation with important ecological consequences (Dingemanse et al. 2010). Consistent differences among individuals, or animal personality, is defined as differences in behaviour among individuals that remain consistent across time and contexts (Réale et al. 2007). Animal personality results in a diversity of behavioural phenotypes within a population, which may allow populations to adapt to changing environmental conditions. One of the most well-studied aspects of animal personality is boldness, which is known to affect behaviours such as migration tendencies (Chapman et al. 2011). Consistent differences have also been shown in movement and habitat selection behaviours. For example, habitat selection in brown bears has been shown to vary consistently among individuals across time (Leclerc et al. 2016). The differentiation among different phenotypes can be measured by quantifying repeatability, which is the proportion of phenotypic variance that can be explained by differences among individuals (Bell et al. 2009). Higher values of repeatability suggest greater differences among individuals and lower differences within individuals through time. Repeatability provides an upper threshold for heritability (Dochtermann et al. 2015), as behaviours must be repeatable to be heritable. Behaviours can also be transmitted through non-genetic means, either via maternal environment or via cultural learning from conspecifics (Jesmer et al. 2018). High repeatability in the timing of migration will result in populations that are better buffered against environmental change, with different individuals being adapted to different spring conditions. Likewise, high repeatability in behaviours related to green wave surfing such as selection for green-up would suggest that tracking and selecting foraging resources is transmissible and that this behaviour is one upon which sufficient variation exists for selection to occur. Climate change is resulting in many populations having to adapt to changing climates or face population declines and potential extirpation (Visser 2008, Hoffmann and Sgró 2011), and animal personalities provide key intraspecific variation vital to eco-evolutionary dynamics (Wolf and Weissing 2012) and the potential for ecological rescue (Vander Wal et al. 2013).

Behavioural reaction norms (BRNs) are powerful tools that allow for the integration of plasticity and personality into a single analytical framework (Dingemanse et al. 2010). BRNs plot the behavioural response of individuals against an environmental gradient. Here, intercepts quantify personality (the predicted behaviour of an animal in an average environment), and slopes represent plasticity (how the behaviour changes as a function of the environmental gradient). By correlating slopes and intercepts across two behaviours, it is possible to define a behavioural syndrome—a suite of correlated behaviours. This analytical framework allows ecologists to examine questions on how related behaviours covary and link to fitness outcomes. Typically, syndromes compare plasticity and personality within a single trait, for example, do individuals that are more aggressive also have higher plasticity in their level of aggression across contexts. Syndromes also compare intercepts or slopes across two behaviours, e.g., are more aggressive individuals also more exploratory or are individuals that are more plastic in their level of aggression across contexts also more plastic in their exploratory tendency.

1.6 Acclimating or adapting to climate change

There are two potential explanations for how populations are advancing their phenology in response to climate change-induced changes at lower trophic levels (Boutin and Lane 2014, Charmantier and Gienapp 2014). First, changing resource phenologies may change selective pressures on the optimal timing of life history events, resulting in an evolutionary change in phenology across generations as individuals with better-matched phenologies gain higher fitness. Alternatively, individuals may display behavioural plasticity and be able to acclimate the timing of life history events to match inter-annual variation in environmental conditions. In the former case, there must be heritable variation in these life history traits that confer a fitness advantage. In the latter, individuals must have evolved the capacity to be plastic to change (Nussey et al. 2005), something that may only arise if there is sufficient short-term (within generation) inter-annual variability in the environment to allow for the evolution of such plastic responses.

Current evidence suggests that most observed phenological shifts are likely due to plasticity as opposed to evolution in mammals (Boutin and Lane 2014), birds (Charmantier and Gienapp 2014) and amphibians (Phillimore et al. 2010). For example, a long-term study of great tits concluded that based on current selection and heritability acting on egg-laying dates, selection differentials would be required to be around four times higher than observed to explain levels of advancement observed over 47 years of study (Charmantier et al. 2008). Plasticity as a mechanism to deal with phenological change has the advantage of being relatively fast, as it does not rely on change across generations (Charmantier and Gienapp 2014); however, it does have two major limitations. First, plasticity depends on animals using reliable cues that are consistent indicators of environmental changes linked to fitness. For example, differential warming between early and late spring in the Netherlands negatively affected reproductive success in great tits, as breeding timing was plastic to early spring temperatures, whereas the timing of peak caterpillar abundance was correlated with late spring temperatures (Visser et al. 2006, Visser 2008). Second, there are often natural limits to the extent to which behaviours can be plastic, and if conditions change beyond the annual variation upon which plasticity has evolved then populations may begin to decline in the absence of evolution (Lande and Shannon 1996). For example, a study of common frogs (*Rana temporaria*) in Britain suggests that while frogs do respond plasticly to changing temperatures, this plasticity is likely to be insufficient to allow populations to remain locally adapted and would require a stronger evolutionary response, which remains uncertain (Phillimore et al. 2010). There is therefore concern that plasticity alone may only provide a temporary buffer against changing conditions and be insufficient to prevent population declines longer term without evolutionary change (Simmonds et al. 2020).

1.7 Juvenile mortality and predation risk

In addition to finding foraging resources, animals must also develop strategies to avoid predation, especially when accompanied by vulnerable young. Predation risk influences many behaviours, including fine-scale habitat selection (Creel et al. 2005, Mao et al. 2005) and home range placement (Perry et al. 2020). The presence of predators forces individuals to develop strategies to effectively trade-off predation risk and forage acquisition (Festa-Bianchet 1988, Fryxell et al. 1988). For example, female caribou with calves were found to select habitat with lower predation risk than females without calves (Leblond et al. 2016b, Viejou et al. 2018). Animals can also dilute their per capita risk of predation by associating with conspecifics. While detection by predators may increase, the individual probability of being depredated decreases in larger groups (Hamilton 1971, Foster and Treherne 1981, Bonar et al. 2020). Elucidating the relative impact of predation risk, foraging resources, and grouping behaviour on calf mortality will highlight direct mechanisms relating to annual reproductive success in caribou.

1.8 Study area and species

1.8.1 Caribou in Newfoundland

Newfoundland is an island off the east coast of Canada (47°44’ N, 52°38’ W to 51°44’ N, 59°28’ W). Most of the island is a matrix of forests dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), along with white birch (*Betula papyrifera*). Forests are interspersed with lakes, bogs, open heath and rocky barrens. Newfoundland has a highly variable climate driven by changes in the North Atlantic Oscillation (Finnis et al. 2015), resulting in species being adapted to living in a highly variable environment. While anthropogenic disturbance and human activities are a major source of concern for caribou in much of their range, development and logging remain a relatively low threat to caribou in Newfoundland (COSEWIC 2014).

Caribou and reindeer are a medium-sized member of the deer family and have a circumpolar distribution and occur in northern North America, Greenland, Fennoscandia, and northern Asia. They have large hooves adapted for digging through deep snow for forage. They are the only deer species in which females grow antlers, though they are smaller than they are in males. Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recognizes 11 extant caribou designatable units (COSEWIC 2011), including the Newfoundland designatable unit.

Caribou are endemic and widespread throughout the island of Newfoundland. Prior to the 1960s there were a total of 12 sub-populations. Relocations of caribou in the 1960s and 1970s resulted in a total of 36 sub-populations having existed (Mercer et al. 1985); however, as of 2014 there were only around 14 recognized sub-populations (COSEWIC 2014). My thesis includes data from five of these populations: Buchans, Grey River, La Poile, Middle Ridge, and Topsails. Chapter 4 only uses data from Lapoile and Middle Ridge, as we only had predator data available for these two populations.

Caribou typically select for old growth coniferous forests throughout the year (Festa-Bianchet et al. 2011). These areas are not typically used by other ungulates and notably tend to have lower densities of predators such as wolves (*Canis lupus*). In winter, these forests may provide increased access to terrestrial lichens as snow depth here is more limited (Mayor et al. 2009). During snow-free seasons, caribou tend to select for wetlands, barren lands and shrub lands (Mahoney and Virgl 2003). In much of their range, habitat selection by caribou is strongly driven by avoiding predation risk. Habitat selection in Newfoundland is broadly similar to elsewhere, but purportedly less driven by predation risk owing to the fact that wolves are not present in Newfoundland. Despite this, females tend to select more bog habitats in summer, possibly to reduce predation risk to calves (Schaefer and Mahoney 2007). Habitat use of caribou in Newfoundland changed at the start of the decline phase (1990s), with less use of cutovers and forests, and more use of barrens, shrubs and wetlands (Mahoney and Schaefer 2011). This may either be due to increased response to predators or due to lower lichen abundance (COSEWIC 2014).

Many caribou populations undertake migrations from winter range to summer range prior to calving. These can range from relatively short migrations to very large-scale migrations over thousands of kilometers. Females give birth to a single calf, typically from mid-May to mid-June, depending on the population (Bonar et al. 2017, Davidson et al. 2020). Most caribou in Newfoundland migrate, although some populations are more sedentary than others, and within populations that migrate some individuals do not, or may migrate facultatively depending on environmental conditions (Mahoney and Schaefer 2002). Timing of migration of caribou in Newfoundland is also more variable then in most Canadian populations, with migration occurring between mid-March and early July. Migratory females in Newfoundland mostly aggregate in calving grounds in April and May. While some individuals aggregate, others choose to dissociate from the calving aggregation, potentially reflecting a trade-off in predation risk between detection (larger groups are easier to detect) and dilution of risk (larger groups reduce individual risk of being targeted by predators after detection). Both strategies were shown to have equal annual reproductive success, although individuals near the periphery of calving aggregations had lower fitness than those at the centre (Bonar et al. 2020).

The Newfoundland caribou population has undergone numerous dramatic fluctuations in population size. The population in the early 20th century has been estimated at 100,000 individuals, before declining precipitously to 10,000–15,000 individuals by the 1930s (Peek et al. 2012). The population once again increased to an estimated 94,000 individuals by 1996 before beginning another decline, with an estimated population of 33,000 by 2012 (Weir et al. 2014). Current data suggest that the decline has begun to level off with population size beginning to stabilize. A lack of available forage following the population peak is thought to be an important factor in population declines (COSEWIC 2014). Caribou data used in my thesis was collected near the end of the decline phase, as population size was beginning to stabilize.

One of the most important proximate drivers of population growth in caribou is predation on calves, as depressed calf survival is often responsible for population declines (Bergerud 1974, DeMars et al. 2011). Calf survival in Newfoundland supports this hypothesis, as calf survival averaged 62% during the growth phase in the 1980s and 1990s when predation was estimated to be responsible for ~59% of calf mortality (Mahoney and Weir 2009). Calf survival declined to around 35% from 2003–2012, however calf survival has increased since 2007 to near 50% (Lewis and Mahoney 2014). These estimates of calf survival are relatively similar to estimates from Bonar et al. (2018) used in this thesis, who found a survival rate of 60%. Outside of Newfoundland, wolves represent the most significant predation risk for caribou, however wolves in Newfoundland are extirpated. Wolves re-establishing in Newfoundland however remains a possibility. The most significant predators of caribou in Newfoundland are black bears (*Ursus americanus*) and coyotes (*Canis latrans*) since their introduction to the island in 1985, however predation on adults is rare. Bald eagles (*Haliaeetus leucocephalus*) and lynx (*Lynx canadensis*) have also been known to depredate calves (Lewis and Mahoney 2014).

1.8.2 Migratory ungulates in Wyoming

Wyoming is home to numerous migratory ungulate populations, most of which migrate from low elevation winter ranges up to higher elevation summer range. My thesis used data from four species: mule deer, elk, moose, and bison. In addition, Wyoming is home to other ungulate species including bighorn sheep, pronghorn, and mountain goat (*Oreamnos americanus*). Wyoming also has several large predator species including wolves, cougars (*Puma concolor*), and black bears.

Elevation varies from ~1300 m in low winter ranges up to ~4100 m at higher summer ranges. Low areas are primarily dominated by sagebrush (*Artemisia* spp.) steppes, transitioning to herbaceous meadows and mixedwood forests including lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*). Higher elevations are dominated primarily by conifer forests. Annual precipitation varies considerably between low and high elevations, with low elevations receiving a mean of 10–20 cm of annual precipitation and higher elevations receiving 150–250 cm (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). Populations used in this thesis have been shown to surf the green wave in their migrations from winter to summer range (Merkle et al. 2016). Migration distance varies by species, with moose undertaking the shortest migrations (< 30 km) and mule deer undertaking the longest (up to >300 km; see Chapter 5).

1.9 Thesis goals and chapter overview

My thesis focuses on the ecology of the timing of important life-history events in migratory ungulates from an individual perspective and their consequences for adaptation and acclimation in a changing world. Chapters 2–4 follow a narrative arc for caribou life history in spring. Chapter 2 examines the drivers and timing of migration and parturition relative to spring events, Chapter 3 focuses on the link between migration and parturition timing and effects on reproductive success, and Chapter 4 examines how behaviour influences annual reproductive success when calves are young and vulnerable. Chapter 5 switches systems and examines repeatability and plasticity in green wave surfing behaviour in ungulates in Wyoming, USA.

Migration serves as a mechanism to allow individuals to exploit resources that vary over space and time. Chapter 2 examines the timing of migration of five caribou populations in Newfoundland as a function of the timing of spring. I test the green wave surfing hypothesis in caribou in Newfoundland against an alternative; that caribou jump the green wave to arrive on summer calving range prior to the onset of peak plant green-up such that the peak of forage quality corresponds to when energetic needs are highest due to lactation. Caribou did in fact jump the green wave, and did so by following a gradient of melting snow during migration.

Properly timing important life history events is likely to have important implications on annual reproductive success. After demonstrating in Chapter 2 that caribou adopt a strategy of timing reproduction to when resources are most abundant (as opposed to surfing the green wave), I wanted to test how the environment interacted to affect the timing of parturition and migration. In Chapter 3, I assess whether the timing of migration and timing of parturition are either 1) plastic to changes in the timing of spring, indicative of an ability of individuals to acclimate to change; or 2) repeatable, which would suggest the possibility that these behaviours are individual traits that could suggest the potential for transmissible variation upon which selection can act. I also assessed the correlation between timing of migration and timing of parturition, and how the timing of spring and plasticity in parturition timing affected annual reproductive success. Caribou demonstrated plasticity in timing of migration and some plasticity in timing of parturition, while repeatability was moderate for timing of migration and low for timing of parturition. This chapter incorporated ideas of consistent differences in behaviour as a driver of evolutionary processes and acclimation to climate change as an important overall narrative of my thesis. This chapter also served as a bridge between focussing on migration timing in the preceding chapter, and processes affecting annual reproductive success and calf survival during the calving season in Chapter 4.

For many species, the first weeks of life are critical, as these represent times when risk of mortality is highest. Annual reproductive success is therefore likely to often depend on how well individuals adopt behavioural strategies that improve the probability that young will survive the juvenile phase. For Chapter 4, my goal was to examine how forage, predation risk, and dilution of risk from conspecifics affects the probability of calf mortality in their first four weeks of life. To examine these questions, I performed a survival analysis using a Cox proportional hazards model. Calf mortality increased with increased exposure to areas with a higher probability of coyote selection in one of the populations examined but was not affected by selection for high quality forage or distance from conspecifics.

How individuals acclimate migratory behaviour to fluctuations in the environment from an individual perspective remains an important question. The fifth chapter of my thesis was an international collaboration with Dr. Jerod Merkle at the University of Wyoming funded in part through a grant from Fulbright Canada and MITACS. This collaboration allowed me to further test questions regarding migration, e.g., whether green wave surfing is an individual trait, and how plasticity in migration timing to spring conditions can influence whether individuals surf the green wave effectively.

1.10 Co-authorship statement and data sources

Several datasets were used in the development of this thesis. Several of these were provided by a long-term monitoring program by the Newfoundland Wildlife Division and the Sustainable Development and Strategic Science branch of the Department of Environment and Conservation. This includes caribou data from five different populations used in Chapters 2–4, coyote data used in Chapter 4, and a Landsat-derived landcover layer used in Chapter 4. Data on caribou parturition status and dates (Chapters 2–4) and annual reproductive success (Chapters 3/4) were provided by Maegwin Bonar from her MSc thesis work (Bonar et al. 2018). NDVI data used to construct IRG profiles for Chapters 2–4 were the "MODIS Vegetation Index Products" provided by NASA via the MODIS Terra (MOD13Q1) and MODIS Aqua (MYD13Q1) satellites (https://modis.gsfc.nasa.gov/data/dataprod/mod13.php). Data from Wyoming ungulates used in Chapter 5 came from numerous sources: Matthew Kauffman and Kevin Monteith (mule deer, elk, and moose), Anna Ortega and Hall Sawyer (mule deer), Tony Mong (elk), Brendan Oates (moose), Chris Geremia, Rick Whalen, and PJ White (bison). Use of these datasets was arranged by Jerod Merkle. IRG data for Wyoming were provided by Jerod Merkle.

I performed all analyses and am the first author and main intellectual contributor to all chapters in this thesis. I am thankful to all co-authors on my chapters without whom this work would not have been possible. Notably my advisor Eric Vander Wal for invaluable feedback and contributions to all elements of analysis and writing for all thesis chapters. Maegwin Bonar, my co-author for Chapters 2 and 4, provided caribou parturition and calf survival data and comments on drafts. Quinn Webber (co-author for Chapters 3 and 5) provided assistance with behavioural reaction norm analysis as well as feedback on manuscript drafts. As a co-author for Chapter 5, Jerod Merkle helped conceive of the ideas for this chapter, organized the datasets, and helped with editing. Specific acknowledgments are made at the end of each chapter.

Chapter 2: Tracking snowmelt to jump the green wave: Phenological drivers of migration in a northern ungulate, has been published in *Ecology*:

> Laforge, MP, M Bonar and E Vander Wal. 2021. Tracking snowmelt to jump the green wave: Phenological drivers of migration in a northern ungulate. *Ecology* 102:e3268.

Chapter 3: Laforge, MP, QMR Webber, and E Vander Wal. Plasticity and repeatability in spring migration and parturition dates with implications for annual reproductive success, is under review at *Ecology Letters*, manuscript #ELE-01036-2021.

Chapter 4: Laforge, MP, M Bonar, and E Vander Wal. Balancing resources, risks, and neighbours: implications for caribou annual reproductive success, will be submitted to *Oecologia*.

Chapter 5: Laforge, MP, E Vander Wal, QMR Webber, C Geremia, MJ Kauffman, A Middleton, T Mong, K Monteith, B Oates, A Ortega, H Sawyer, R Wallen, PJ White, and JA Merkle. Consistent individual differences and plasticity in migration behaviour of North American ungulates to environmental variability, will be submitted to *Ecology Letters*.

In addition to my thesis chapters, I have contributed to several collaborative publications during my PhD. This includes publishing a natural history note from the field:

Bonar M*, **MP Laforge***, and E Vander Wal. 2017. Observation of a $p < 10^{-9}$ life history event: implications of record-late caribou parturition on ungulate reproductive ecology and field studies. Canadian Journal of Zoology 95:133–137. *Authors contributed equally.

Contributing to undergraduate and MSc thesis projects:

Huang, R, QMR Webber, **MP Laforge**, AL Robitaille, M Bonar, J Balluffi-Fry, S Zabihi-Seissan, and E Vander Wal. 2021. Coyote diet and spatial co-occurrence with caribou. Canadian Journal of Zoology 99: 391-399.

Bonar, M, KP Lewis, M Dobbin, QMR Webber, **MP Laforge**, and E Vander Wal. 2020. Geometry of the ideal free distribution: personality and fitness implications in birthing aggregations of a social ungulate. Ecology Letters 23:1360-1369.

Peignier, M, QMR Webber, EL Koen, **MP Laforge**, AL Robitaille, and E Vander Wal. 2019. Space-use and social organization in a gregarious ungulate: testing the conspecific attraction and resource dispersion hypotheses. Ecology and Evolution 9:5133-5145.

Contributing to collaborative research projects within the WEEL lab:

Newediuk, L, JP Ethier, SP Boyle, JA Aubin, J Balluffi-Fry, E Dedeban, **MP Laforge**, CM Prokopenko, JW Turner, QMR Webber, E Vander Wal. 2021. Sociopolitical factors drive conservation planning timelines: A Canadian case study with global implications. Biological Conservation 257: 109091.

Webber, QMR*, **MP Laforge***, M Bonar, C Hart, AL Robitaille, S Zabihi-Seissan, and Eric Vander Wal. The ecology of individual differences empirically applied to space-use and movement tactics. 2020. The American Naturalist 196:E1-E15. *Authors contributed equally.

Contributing to collaborative research projects with other research groups:

Northrup J, E Vander Wal, M Bonar, **MP Laforge**, M Leclerc, CM Prokopenko, and BD Gerber. Conceptual and methodological advances in habitat selection modeling: guidelines for ecology and evolution. In press at Ecological Applications, Manuscript ID EAP20-0246R1 (104 pages).

And through paid contracts:

Perry, TA, **MP Laforge**, E Vander Wal, TW Knight, and PD McLoughlin. 2020. Individual responses to novel predation risk and the emergence of a landscape of fear. Ecosphere 11:e03216.

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CHAPTER 2: TRACKING SNOWMELT TO JUMP THE GREEN WAVE: PHENOLOGICAL DRIVERS OF MIGRATION IN A NORTHERN UNGULATE

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2.1 Abstract

In northern climates, spring is a time of rapid environmental change: for migrating terrestrial animals, melting snow facilitates foraging and travel, and newly-emergent vegetation provides a valuable nutritional resource. These changes result in selection on the timing of important life-history events such as migration and parturition occurring when high-quality resources are most abundant. We examined the timing of female caribou (*Rangifer tarandus, n* = 94) migration and parturition in five herds across seven years in Newfoundland, Canada as a function of two measures of environmental change—snowmelt and vegetation green-up. We generated resource selection functions to test whether caribou selected for areas associated with snowmelt and green-up during migration and following calving. We found that caribou migrated approximately one week prior to snowmelt, with the flush of emergent vegetation occurring during the weeks following parturition. The results indicate that caribou "jump" the green wave of emergent forage and do so by tracking the receding edge of melting snow, likely reducing movement and foraging costs related to snow cover. Our research further broadens the ecological scope of resource tracking in animals. We demonstrate that resource tracking extends beyond resources directly related to foraging to those related to movement. We also show that snowmelt provides an environmental cue that may provide a buffer against changing environmental conditions.

Keywords: Calving, caribou, energetic demands, forage maturation, green wave hypothesis, migration, movement, Newfoundland, normalized difference vegetation index, phenology, resource tracking, snowmelt.

2.2 Introduction

Spring is an energetically costly time for female migratory ungulates, as they must meet heightened energy demands of long-distance displacement, gestating, and rearing young (Oftedal 1985). Spring in northern climates is also a time of rapid environmental change: reduction in snow cover provides easier access to forage (Goodson et al. 1991) and facilitates travel (Sweeney and Sweeney 1984), and newly emergent vegetation represents a valuable new nutritional resource (Hebblewhite et al. 2008). The dynamics of energetic needs and resource abundance presents a challenge for migrants that must balance energy expenditure with resource gains while dealing with the ephemerality of resources. Animals track resources as their abundance shifts through time (Armstrong et al. 2016). This becomes a challenge, however, when life-history events such as reproduction reduce mobility and ability to track these resources (DeMars et al. 2013, Bonar et al. 2018). Thus, resource tracking may not provide optimal benefit during crucial times associated with reproduction, as individuals will be unable to track resources when burdened by young with reduced mobility. The alternative is to migrate and arrive prior to when resources are most abundant such that peak resource abundance matches the peak in need, which may require alternative cues to properly time migration.

Adaptive evolution in heterogeneous environments has favoured a strategy in many vertebrate animals to reproduce at times when resources are most highly abundant (Sadleir 1969, Thomas et al. 2001). For many species, the optimal phenology of costly life-history events is determined by seasonal availability of food sources that permit individuals to raise young (Visser and Both 2005, Reed et al. 2015). For example, great tits (*Parus major*), have evolved such that their breeding phenology coincides with the peak of caterpillar biomass (Visser et al. 2006). For northern herbivores, the key spring resource is newly emergent vegetation. The digestibility of plants consistently decreases with increased age/biomass, and as such there is a trade-off between forage biomass and digestibility—vertebrate herbivores gain the highest nutritional benefit from foraging on plants at intermediate biomass (the forage maturation hypothesis; FMH—Fryxell 1991; Hebblewhite et al. 2008). For ruminants, even a marginal increase in diet quality can greatly increase body mass and fitness via the multiplier effect, which suggests that a high-quality diet also increases foraging efficiency by reducing the amount of time individuals must spend ruminating (White 1983). For reproductive female ungulates, energetic requirements increase by ~50% during late pregnancy and can increase by more than 215% at the peak of lactation (Oftedal 1985, Robbins 1993, Pekins et al. 1998, Parker et al. 1999).

One of the ways that herbivores may maximize access to newly emergent vegetation is by tracking the flush of vegetation as it greens-up along latitudinal or altitudinal migratory gradients. That is, individuals “surf” waves of intermediate vegetation biomass during migration, e.g., "the green wave" (Bischof et al. 2012; Merkle et al. 2016). Green wave surfing has been demonstrated in numerous taxa, but is well studied in migratory ungulates (Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017) and geese (van der Graaf et al. 2006, Shariatinajafabadi et al. 2014). Green wave surfing has also been demonstrated to have a positive effect on weight gain in elk (*Cervus canadensis*; Middleton et al. 2018). Many individuals, however, “jump” the green wave instead of surf it, a behaviour whereby individuals migrate to summer range prior to green up and wait for the green wave there. For example, red deer (*Cervus elaphus*) primarily jumped the green wave instead of surfing it, potentially to avoid giving birth prior to migration when calves would restrict movement (Bischof et al. 2012). Barnacle geese (*Branta leucopsis*) arrive on breeding grounds prior to the onset of spring such that the hatching of young corresponds to the peak in food quality (Kölzsch et al. 2015). Green wave surfing and jumping exist at two ends of a spectrum of tactics for how animals can exploit changing resource phenology. At one end, animals may be adapted to maximize their exposure to high quality vegetation by surfing the green wave during migration to build capital prior to parturition and the increased energetic demands of lactation. At the other end of this spectrum, individuals can jump the wave and time their migration and parturition on the calving ground to coincide with the emergence of high-quality vegetation when needs are highest. Migrants can also employ an intermediate strategy. For example, barnacle geese match their early migratory stopovers to the timing of spring before overtaking the green wave and arriving on the breeding grounds prior to the onset of spring (Si et al. 2015). The optimal strategy in terms of migration timing is also likely related to feeding physiology. In ungulates, concentrate selectors such as deer (*Odocoileus* spp.) and moose (*Alces alces*) adapted to feed on vegetation at younger phenological stages should migrate earlier than those adapted to feed on grass and roughage (Merkle et al. 2016).

While a preponderance of research on wave surfing involves animals tracking resources specific to foraging (Armstrong et al. 2016), snowmelt may represent a cue of phenological change that is tracked by northern migratory populations. For example, snow pack is known to trigger migration in elk in Yellowstone National Park, with later spring migrations associated with later spring snowmelt (White et al. 2010, Rickbeil et al. 2019). Travelling through snow increases the relative net cost of locomotion exponentially as a function of how far animals sink (Parker et al. 1984, Fancy and White 1987) and alters habitat selection in ungulates (Sweeney and Sweeney 1984). Snow also decreases forage availability (Adamczewski et al. 1988) and foraging efficiency (Goodson et al. 1991), and accessing sub-nivean forage also represents an additional energetic burden (Fancy and White 1985). Snow cover may therefore restrict how early individuals migrate when jumping the green wave and suggests that individuals could follow the receding edge of snowmelt to maximize movement efficiency while still arriving in time to take advantage of the green wave during calving. Such timing may be especially important if green-up occurs shortly after snowmelt. By following snowmelt across migratory routes, animals may be able to optimize timing of calving to optimal conditions. For example, movement costs may be lowered by avoiding the cost of moving through deep snow but also by moving more efficiently over ground and waterbodies that remain frozen (Leblond et al. 2016). A reduction in snow cover would also result in easier foraging where individuals would be released from the burden of cratering for resources as in the winter (Fancy and White 1985).

We test two competing hypotheses for phenological drivers of migration in several populations of caribou (*Rangifer tarandus*) on the island of Newfoundland, Canada. We examine migration timing and resource selection as they relate to the date of snowmelt and the peak of vegetation growth. The green wave hypothesis predicts high selection for areas at the peak of green-up rate during migration at the expense of lower forage quality during lactation and growth of calves. By contrast, if individuals track the receding edge of snowmelt in the spring, then there should be high selection of areas near snowmelt during migration, and high selection of areas near peak vegetation growth during the weeks following parturition when energetic demands are highest. Understanding the spatio-temporal availability of resources for migratory animals during vital life history stages will provide insight into the overall match between resource availability and energetic needs throughout the spring.

2.3 Methods

2.3.1 Study area

Our study took place on the island of Newfoundland, Canada (~47° 44’ N, 52° 38’ W to 51° 44’ N, 59° 28’ W; Figure S2.1.1). Caribou habitat in Newfoundland is primarily composed of coniferous forest with some mixed wood forests dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch *(Betula papyrifera*). Forests are interspersed with wetland habitat (bogs and fens), lakes, as well as rocky and lichen-covered barrens. Newfoundland receives ample year-round precipitation, with mild winters and relatively cool springs (Environment and Climate Change Canada 2019).

2.3.2 Data collection

Adult female caribou (*n* = 112) from five different herds were captured by the Newfoundland and Labrador Wildlife Division between 2007–2013 and fit with GPS collars (Lotek Wireless Inc., Newmarket, ON Canada, GPS4400M collars, 1,250 g). Caribou were captured by darting from a helicopter using a mixture of carfentanil (12 mg/kg) and xylazine (0.2 mg/kg) or using a mixture of ketamine (2 mg/kg) and xylazine (6 mg/kg) which was administered intramuscularly using a CO_2-powered pistol (Palmer Cap-Chur Inc., Power Springs, Georgia). GPS fixes were taken at intervals of 1–5 hours depending on the season and collar. All animal capture and handling followed guidelines from the Canadian Council on Animal Care.

2.3.3 Defining green-up and snowmelt

We defined green-up as the instantaneous rate of green-up, IRG (Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017). IRG is calculated by taking the first derivative of a time-series of normalized difference vegetation index (NDVI) values through time at a given location. To start, raw NDVI data with a spatial resolution of 250 m × 250 m were taken from moderate resolution imaging spectroradiometer (MODIS) satellite data downloaded from NASA (https://search.earthdata.nasa.gov) from February 10th to September 29th of each year. We combined data from MODIS Terra (MOD13Q1) and MODIS Aqua (MYD13Q1) satellites. Sensors on the two satellites are identical, and each satellite uses daily images to generate a composite image every 16 days, with the two satellites generating images eight days apart. Combining the datasets from both satellites therefore provided a temporal resolution of 8 days. We replaced any pixel values in the raw images for which data were unavailable or contaminated by cloud (~10.0% of pixels) by the mean NDVI value of pixels in a 5 × 5-pixel grid surrounding the focal pixel (if no reliable data were available for any of the surrounding pixels it remained NA). To ensure that this procedure was appropriate, we confirmed that the pixels were highly correlated to pixels in this 5 × 5-pixel grid (see Supplementary Materials S2.1). Following the procedure outlined by Bischof et al (2012), we extracted the time-series of NDVI values at each location and applied the following steps. We applied a 3-observation moving median filter to reduce noise in the data. IRG is meant to reflect changes in growing vegetation. To ensure that this green-up signal is not confounded with changes in the NDVI value associated with melting snow, studies using IRG typically set all pixels that are covered by snow to the lowest snow-free value (Bischof et al. 2012, Merkle et al. 2016). To do this, we replaced all pixel values that were coded as snow/ice in the quality band of the MODIS data with the 3rd percentile value of all observations taken for that pixel that were not coded as snow/ice for the duration of the study period. That is, pixels with values indicating snow were set to their lowest snow-free value, excluding outliers. A logistic curve was then fit to the data during spring/summer. Finally, we took the first derivative of this curve as the IRG and predicted the day that IRG reached its highest value for each pixel in each year to quantify the date of peak green-up in each location.

We used the normalized difference snow index (NDSI) to determine the first snow-free date on the landscape each spring. The NDSI was also a MODIS product, with a spatial resolution of 500 m and a daily temporal resolution. NDSI values < 0 are considered to be snow-free, therefore we calculated the first Julian day in the year in which NDSI was < 0 and defined this as the day of snowmelt for that pixel. Validation of the relationship between NDSI and fractional snow cover revealed that the intercept (the actual fraction of the landscape covered in snow when NDSI = 0) was 0.06 (Salomonson and Appel 2004). An intercept of 0.06 suggests the estimated date corresponded to the point when the landscape was 94% snow-free. We extracted NDSI data using Google Earth Engine (Gorelick et al. 2017).

2.3.4 Defining calving and migration dates

To define calving date, we used the method developed by DeMars et al. (2013) and validated by Bonar et al. (2018). This method quantifies birthing events by detecting movement constraints on females who must stop to give birth and whose movements are afterwards constrained by calves that have a slower movement rate. To detect birthing events, we used a population-based method that examined three-day average movement rates of collared females to ascertain 1) whether females gave birth that year, and 2) the date of parturition. We validated these data using the Middle Ridge herd, in which the method correctly classified 100% of parturition events (Bonar et al. 2018).

To determine the temporal extent of the migratory season for each individual, we used Migration Mapper V 2.0 (Wyoming Migration Initiative 2017) implemented in R (all analyses were performed in R version 3.6.1; R Core Team 2019). Migration Mapper plots spatial locations of animals along with plots of net squared displacement (NSD) and allows users to visually identify the start and end dates of migration. We used February 1st as the start date for each sequence, and date of parturition as the maximum possible date. The start of the calving season was defined separately for each individual as starting on the day of parturition and ending three weeks post-parturition, as the energetic burden of calves on mothers has by this point started to decline (Oftedal 1985), and the energetic burden on calves begins to increase as they are weaned. We further screened the data to only include individual ID × year × season combinations (hereafter, “ID year”) that had at least one fix in at least 90% of the days and an overall mean of four fixes per day between the start and end dates of migration defined above, and in the calving season. A minority of individuals in the sample either never migrated (*n* = 9 individuals, 8.7%) or only migrated in some years (*n* = 29, 28.1%), suggesting some populations are partially migratory. We excluded residents and focused on the dominant evolved strategy, migration. These resident individuals would have little spatial variation over which to track resources, and we assumed these individuals were therefore not tracking resources across the landscape and were using different strategies than those we were testing. We therefore removed any individuals that did not migrate >30 km in a given year. Migration routes are plotted for each population in each year in Supplementary Material S2.1. Given low levels of disturbance in this area, we assumed that migration routes represent historical migration routes.

2.3.5 Surfing indices

We evaluated caribou selection behaviour for green-up and snowmelt during migration and calving. We performed three global sets of analyses: selection for areas near/at peak IRG during migration, e.g., green-wave surfing; selection for snowmelt during migration, e.g., tracking snowmelt; and selection for IRG during the calving season. For each ID year, we quantified the average difference, in Julian days, between the date that an individual occupied a given pixel and the date at which that pixel reached peak IRG or became snow free. These seasonal averages then served as individual-level measures of wave surfing/selection. This method represents a slight modification from the method used by Aikens et al. (2017) and Middleton et al. (2018), who used the absolute value of this difference in their calculation. We opted not to take the absolute value, as we were explicitly interested in the timing of migration/calving as a function of these phenological events as opposed to only relative temporal distance to peak IRG/snowmelt day. We then generated density distributions of these wave-surfing indices for each population separately and for all individuals combined. To determine how migration timing related to amount of snow on the landscape, we used NDSI values extracted from Google Earth Engine at randomly sampled locations within each herd and applied the formula from Salomonson and Appel (2004) to calculate mean fractional snow cover at the peak of the density distribution of migration timing.

2.3.6 Resource selection functions

To define caribou use of areas associated with snowmelt and green-up, we used a resource selection function (RSF) framework. RSFs define selection of habitats/resources using a logistic regression of used versus available points. We generated three sets of resource selection functions, two for the migratory period (IRG and snowmelt) and one for the calving season (IRG only as snowmelt occurs before calving).

2.3.6.1 Defining used and available points—During migration, we generated 99.99% Brownian bridges using Migration Mapper (Wyoming Migration Initiative 2017), which produces Brownian bridges using R package “BBMM” (version 3.0; Nielsen et al. 2013) and used this to define the area within which to draw random locations. During the calving season, we defined available resource units within the home range of each individual by generating a 99% minimum convex polygon home range for each individual, using a fixed smoothing parameter *h* of 400 using R package *adehabitatHR* (version 0.4.18; Calenge 2006). Within each Brownian bridge/home range, we paired a total of 10 available (e.g., randomly drawn) points to each observed location (this was done to accommodate a conditional logistic regression framework owing to temporal changes in days to snowmelt/peak IRG through time). For each used and available location, we extracted the date at which each pixel became snow-free as well as the date at which the IRG peaked in the pixel using R package *raster* (version 3.0-7; Hijmans 2016) and calculated the time difference between when a pixel was occupied and when it became snow free or reached peak IRG.

2.3.6.2 Statistical analyses—For each of the three analyses, we generated models using the absolute value of days from snowmelt or green-up. This allowed the model to be non-linear at day 0. However, we assumed that the inflection point of this relationship may not have actually been at 0, but rather that individuals may have selected for *x* days before or after the day of snowmelt/peak in IRG. We therefore tested the predictive ability of models across different temporal lags, by adding or subtracting days to peak IRG/snowmelt and re-extracting the x-axis appropriately. This procedure effectively adjusted the "inflection point" of the absolute value to change and occur earlier or later by changing the x-intercept of the models. For example, if caribou selected for pixels three days after the peak in IRG, the model with a lag of +3 (by subtracting three from days to peak IRG) would have the highest likelihood, because this model formulation results in a vector centered with 0 occurring on day three. All models were fit as conditional logistic regression models to account for variation in the explanatory variables through time, with each used location paired to 10 random points drawn within the home range with snowmelt/green-up values that corresponded to the time of the location. To fit the models, we used the method prescribed by Muff et al. (2020). This method uses a Poisson family with large fixed variance on a random term for stratum (paired sets of options at a given point in time) to fit a mixed effects conditional logistic regression. Models were fit using ID-year as a random effect. Models were fit using package *glmmTMB* version 0.2.4 (Brooks et al. 2017). We modelled lags for days-from-peak IRG/snowmelt that fell between the 10th and 90th percentile of locations used by caribou. We fit the model to each lagged "day" dataset. We performed analyses separately for each of the five replicate herds, and for all the data combined. We repeated this procedure for all three sets of analyses: snowmelt during migration, peak IRG during migration, and peak IRG during calving.

We selected the model with the highest log-likelihood (we used log-likelihood as opposed to AIC as all models had the same number of terms) across all lags for each of the sets of analyses and plotted the probability of selection as a function of days from peak green-up/snowmelt. We interpolated the number of days before or after the optimal lag that were within one log-likelihood value of the optimal lag. We had two competing hypotheses for what phenological change was the main driver of migration, snowmelt or green-up. To test between these hypotheses we compared the log-likelihood and calculated an evidence ratio between the top model for IRG and snowmelt during migration to determine which phenological change was more highly selected by caribou during migration. We used k-fold cross-validation (Boyce et al. 2002, Roberts et al. 2017) to evaluate the predictive performance of the top models, binning the data by ID-year.

2.4 Results

We started with data from 112 individuals across 326 ID-years. After cleaning the data and removing ID year combinations with insufficient data and non-parturient individuals, we were left with a total of 103 individuals over 294 ID-years. A total of 78 ID-years (26.5%) were dropped as individuals did not migrate at least 30 km, lowering the sample size by nine individuals. This resulted in data for 94 caribou with a total of 216 ID-years across the five replicate herds (Buchans: 14 individuals, 44 ID-years; Grey River: 13 individuals, 40 ID-years; Lapoile: 18 individuals, 50 ID-years; Middle Ridge: 34 individuals, 59 ID-years; Topsails: 15

individuals, 23 ID-years). The median date in which individuals started migrating was Mar 25 (range: Feb 9–May 19). The median date of snowmelt on the migratory route was Apr 25 and individuals migrated a median of 61.8 km (range: 30.5–174.9). Migration lasted for a median of 43 days (range: 3–128) and the median date of arrival on the calving grounds was May 10 (range: Mar 20–Jul 13). The median date of calving was May 24 and the median date of peak green-up on the calving ground was 13 days after parturition on Jun 06 (Table S2.2.1).

2.4.1 Surfing indices

Over all herds, the peak of the density distribution for the snowmelt indices was –7.0, suggesting that during migration caribou used locations about one week prior to the pixel being categorized as snow-free (defined as 6% fractional snow cover). The estimated fractional snow cover at this time was 71% (SD = 25%; see Supplementary Materials S2.3). The range of the peak of the density distributions for snowmelt across herds was –17.2 to 1.4 (Figure 2.1, blue curves). While the relatively large pixel size of the NDSI data suggests a certain heterogeneity of phenology within a pixel, we do not think it is likely that smaller patches of green-up exist within these pixels given that the two phenological events (snowmelt and green-up) occur over a month apart in this system. Individuals migrated before the peak of IRG, with the peak of the density distribution for all herds occurring at 51.0 days before the peak in IRG (range across herds: –51.4 to –40.2; Figure 2.1, dashed green curves). Selection indices for IRG during calving, however, were 1.4 for aggregate data using all herds, with a range across herds of –6.4 to 4.5 (Figure 2.1, solid green curves), suggesting that caribou had young calves-at-heel when vegetation quality peaked. These results provide support for our second prediction, that caribou jump the green wave by tracking snowmelt and exploit maximum emergent vegetation resources on the calving ground.

We found a significant positive correlation between individual snowmelt index and IRG surfing index during migration (ß ± [95% CI] = 0.599 [0.521, 0.677], R^2 = 0.51, Figure S2.2.1A). We found a significant, yet weaker relationship between snowmelt surfing index during migration and IRG surfing index during the calving season (ß ± [95% CI] = 0.171 [0.073, 0.269], R^2 = 0.05, Figure S2.2.1B). We found a similar relationship between IRG index across the two time periods (ß ± [95% CI] = 0.246 [0.130, 0.362], R^2 = 0.07, Figure S2.2.1C).

2.4.2 Resource selection functions

The RSFs supported the results of the surfing indices. The log-likelihood values of the snowmelt models indicated that the best model across all herds was one in which the data were centered 7 days before snowmelt, matching the peak of our surfing indices (Figure 2.2A, blue lines). Interpolation from log-likelihood values across lags suggest the most likely lag (within 1 log-likelihood value) ranged between –7.1 to –7.0 (see Table S2.2.2). The optimal lag varied among herds, with a range of 13 days before to 3 days after snowmelt (Figure 2.2, panels B–F, blue lines). The results of the IRG RSFs supported the results of the surfing index analysis above, but with individuals selecting for areas a few days later than the mean date of use indicated by the surfing index. The most predictive lag for all herds combined was 4 days after green-up (interpolated range within 1 log-likelihood unit: 3.0 to 4.3, see Table S2.2.2), with a range among herds from 11 days before green-up to 8 days after green-up (Figure 2.2, green lines). See Figure S2.2.2 for results from RSFs for peak IRG during migration.

Across all herds, selection for both days to snowmelt and peak IRG increased up to the day associated with the lag and decreased afterwards, suggesting that the date associated with the lag represented the phenological state most selected by caribou (Figure 2.3). This response was stronger for the snowmelt models than for the IRG models, suggesting that individuals had a stronger response to snowmelt during migration than to green-up during the calving season. Overall, caribou therefore selected for areas that were 7 days prior to snowmelt during migration and selected for areas a few days after peak IRG during the calving season. For models fit during migration, the best snowmelt model for all herds had much more support than the best IRG model (Δlog-likelihood = 7549, resulting in an infinitely large evidence ratio; see Figure S2.2.3 for results of models run for peak IRG during migration). This further supports the hypothesis that snowmelt date is a much stronger driver of caribou migratory behaviour than plant growth in this system. The snowmelt model had a relatively strong k-fold (k = 5) cross-validation score (mean ρ = 0.898, SD = 0.083). The top model for selection of peak IRG in the calving season had a moderate k-fold cross-validation score (mean ρ = 0.566, SD = 0.214).

2.5 Discussion

The optimal strategies that migratory herbivores can employ to exploit ephemeral resources such as green-up fall along a continuum. At one end, animals use a strategy in which they migrate concurrently with the green wave to maximize the time in which they can exploit this resource (Bischof et al. 2012, Merkle et al. 2016). At the other end of the continuum, they can time their migrations such that reproduction coincides with the peak in vegetation growth on the calving ground (Post et al. 2003), which requires migrating prior to the green wave and likely presents novel phenological challenges. Individuals may also employ a mixed strategy of initially surfing the green wave before overtaking it before arriving on summer grounds (Si et al. 2015). Timing migrations such that the timing of reproduction matches the peak in resources appears to likely be the impetus for species and individuals who jump the green wave. For example, migratory red deer (Bischof et al. 2012) and geese (Kölzsch et al. 2015) were both found to employ a strategy of jumping the green wave. We found evidence of green wave jumping behaviour in migrating caribou in Newfoundland: individuals migrated roughly seven days prior to snowmelt and consequently arrived on the calving grounds to optimize the timing of calving such that the energetically demanding time in the weeks following parturition coincided with the peak of vegetation growth. In caribou, this jumping behaviour was mediated by melting snow on the landscape, and that individuals tracked snowmelt in a manner analogous to populations that surf the green wave (Merkle et al. 2016). Tracking melting snow highlights resource tracking as a robust, and broadly applicable ecological process.

Migrating just prior to melting snow likely serves both as a cue for caribou to time their migrations to arrive on the calving grounds at the correct time, while also providing direct benefits of migrating in conditions that are more favourable. Animals use various cues about their environment to trigger migration. For example, birds may use temperature (Sparks and Braslavská 2001) or day length (Wolfson 1952) to time migration, and migration timing may be linked to broad-scale climate indices such as the North Atlantic Oscillation (Hüppop and Hüppop 2003, Gunnarsson et al. 2006). In leatherback sea turtles (*Dermochelys coriacea*), migration timing was associated with lagged sea temperature and chlorophyll-a concentrations (Sherrill-Mix et al. 2008). The results suggest that melting snow could provide a signal to caribou that triggers migration to ensure that they arrive on summer range at the appropriate time to exploit resources there. Indeed, across all herds in the analyses, the calving season (parturition to three weeks post-parturition) was synchronized with the peak of plant growth. This synchrony is especially notable given that many years in the study represented years when snowmelt (and presumably green-up) occurred early (see Supplementary Material S2.1). This suggests that there may be some level of plasticity in parturition date to changing phenology to allow individuals to match the timing of birth to coincide with green-up even in early springs (Bonnet et al. 2019, Froy et al. 2019).

Evidence from other studies on the role of snow in modulating migration timing has been less clear. Snow cover had no influence on arrival or departure time for migrating caribou for populations in Québec and Labrador (Le Corre et al. 2017). In populations in Alaska and Northern Canada, timing of departure from winter range was only weakly associated with timing of snowmelt, however, timing of arrival on calving grounds was significantly correlated with timing of snowmelt (Gurarie et al. 2019). The discrepancy in how much populations acclimate the timing of migration as a function of snowmelt may be related to migration distance. These major migratory herds in Alaska, Québec, and Labrador all migrated >300 km, compared to the five herds in Newfoundland where migration distance was only 30–175 km. The strategies and drivers of migration for long- versus short-distance migrants are likely to vary. Tracking changes in phenology is likely easier for migrants with large latitudinal or altitudinal gradients along migratory routes compared to shorter-distance migrants. Shorter-distance migrants with less variation across migratory routes also likely have patchier migration routes, and therefore may need to use environmental patchiness as a cue for migration. For elk migrating medium distances (12–202 km) in Yellowstone National Park, snowmelt date on winter range predicted departure date, and snowmelt date on the migration route and on summer range predicted the timing of arrival on summer range, with the latter predictor having the greatest magnitude (Rickbeil et al. 2019). The fact that snowmelt date had a stronger influence on timing of arrival than timing of departure suggests that snow may play a bigger role in modulating the pace of migration than migration initiation. We also note that many individuals in this study adopted a resident strategy and did not migrate (>30 km) at all. This suggests that strategies beyond green-wave surfing and jumping are viable for caribou in Newfoundland, and may be related to density dependence and the level of variability in seasonal habitat suitability (Lundberg 1988, Taylor and Norris 2007). Seasonal environmental conditions in Newfoundland are highly variable across years (see Figure S2.1.3), which may have promoted the persistence of partial migration in caribou on the island.

Female caribou in Newfoundland arrived on summer range about two weeks before giving birth, resulting in them migrating while some snow remained on the ground. Given the delay between reaching the calving grounds and parturition, individuals could have instead waited until snow cover was further reduced and migrated just prior to giving birth. There are several reasons why caribou might have migrated earlier. The energetic burden of migrating in the final week of pregnancy may favour migrating slightly earlier (Parker et al. 1984, Parker 2003). In addition, arriving on the calving grounds earlier may allow individuals to assess the area before giving birth. Individuals may also not have the knowledge in advance to predict when parturition will occur, and therefore arrive two weeks in advance to not risk an early birth while still on the wintering ground. It is therefore possible that migration timing may be related to length of gestation, with snowmelt being correlated with migration timing instead of being the causal factor. Finally, migrating earlier while some snow remains may have energetic benefits by facilitating movement while the ground is still partially frozen, or even allowing caribou to cross lakes that may still be covered in ice (Leblond et al. 2016). Migrating concurrently with melting snow may therefore represent the best trade-off time to migrate where melting snow is revealing emergent forage resources while allowing ease of movement.

Several potential explanations exist for drivers of variance in migratory timing among herbivore species or populations with respect to phenology, and why some surf the green wave and others jump it. Caribou tend to be income breeders (Kerby and Post 2013), and as such would be more likely to synchronize energetically expensive times (rearing and nursing calves) with those that provide the highest abundance of high-quality foraging resources (Post et al. 2003). Indeed, different ungulate species employ different strategies with respect to birth timing. For example, bighorn sheep (*Ovis canadensis*) use stored capital to finance gestation and lactation versus pronghorn (*Antilocapra americana*) that time birth with environmental optima, therefore using an income-breeder strategy (Hogg et al. 2017). Our results are consistent with the income breeding strategy for caribou, where migration is used to time parturition to the peak in resource abundance as opposed to green wave surfing. For most northern ungulates, birth occurs near the end of May or early June (Bonar et al. 2017), suggesting that surfing the green wave may not be a viable strategy in environments with delayed snowmelt and green-up, and that following gradients in melting snow could provide a possible mechanism for the adaptive evolution of parturition dates across populations (Bonnet et al. 2019).

Migration is a behaviour that is globally threatened (Wilcove and Wikelski 2008). Climate change threatens to decouple consumers and the resources upon which they depend (Visser et al. 2004, Lane et al. 2012). While evidence from ungulates suggests that birth dates are not advancing sufficiently to keep pace with advancing plant phenology (Post et al. 2003, Plard et al. 2014), the case for trophic mismatch in ungulates is still far from settled (Gustine et al. 2017). In caribou herds in Newfoundland, the peak of energetic demands following birth occurred concurrently with the peak of vegetation green-up, suggesting no evidence for mismatch in Newfoundland caribou herds. Furthermore, the results outline a mechanism by which individuals may be able to time migrations, by using melting snow to time life-history events appropriately and avoid mismatch. However, this may be more relevant for populations with shorter-distance migrations whose cues on winter range may be more connected spatially and temporally to conditions on summer range.

The results demonstrated empirical support for a strategy of green-wave jumping in caribou, and link this behaviour to tracking snowmelt in spring. Income breeders, like caribou, that jump the green wave also depend on tracking environmentally variable resources. Indeed, resource tracking becomes a correlated two-part process: first track snowmelt to minimize costs of migration, and then track (or select) green up to maximize resource uptake during the peak in reproductive demand. Herbivores such as ungulates and geese surf waves of vegetation (Shariatinajafabadi et al. 2014, Merkle et al. 2016, Aikens et al. 2017). Grizzly bears (*Ursus arctos*) and Glaucous-winged gulls (*Larus glaucescens*) track sockeye salmon (*Oncorhynchus nerka*) abundance in Alaska (Schindler et al. 2013). African elephants (*Loxodonta africana*) track agricultural crops after the peak of green up has passed (Branco et al. 2019). Migration by Newfoundland caribou broadens the concept of resource tracking to include tracking a non-consumable environmental change in a manner analogous to the more traditional idea of consumptive resource tracking.

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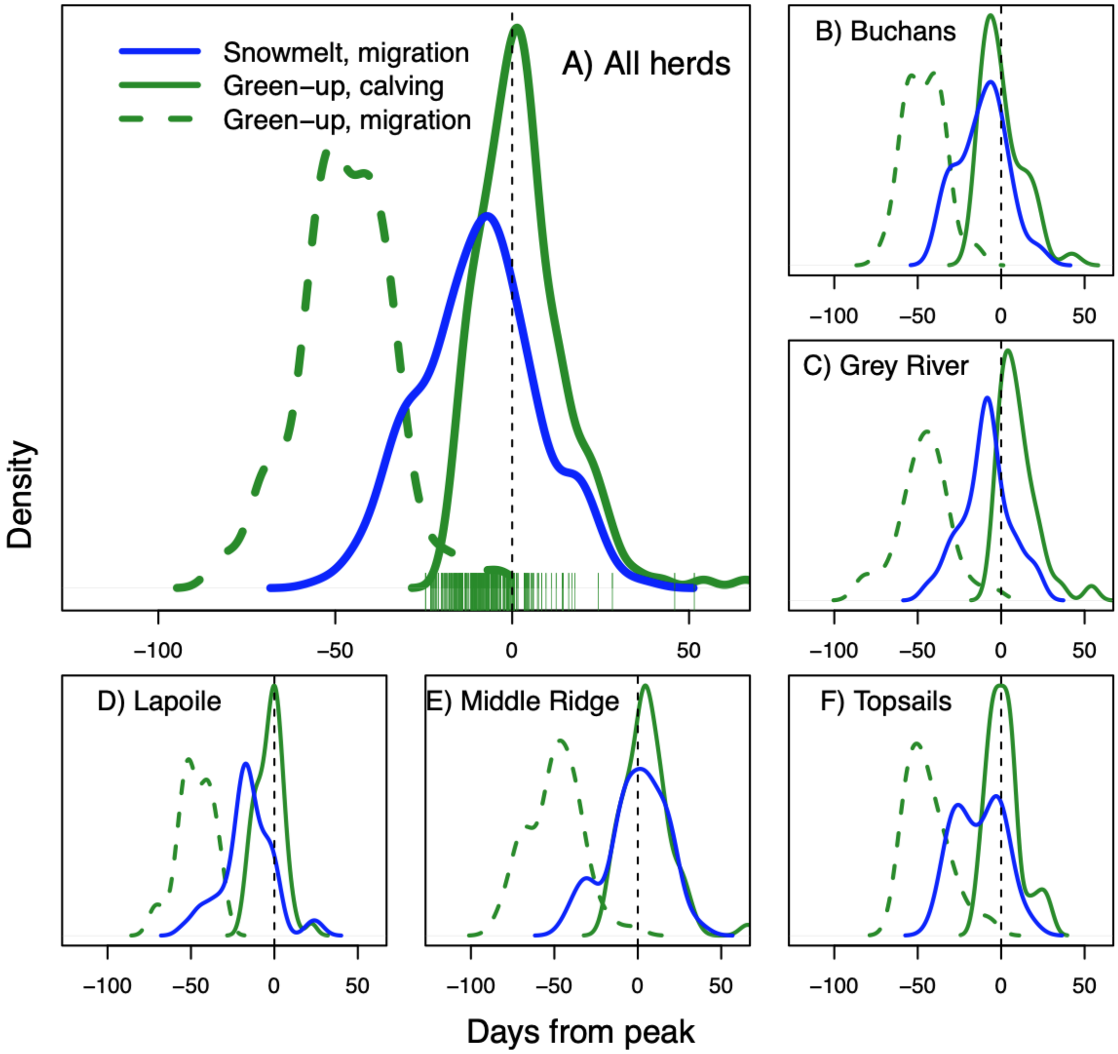

Figure 2.1: Density plots of mean number of days from peak IRG (green lines) and snowmelt (blue lines) for caribou (*Rangifer tarandus*, *n* = 94) GPS location in Newfoundland, Canada. Solid blue lines represent snowmelt during migration, solid green lines green-up during calving, and dashed green lines green-up during migration. Density plots represent the densities of "surfing indices" (the mean number of days away from the peak of IRG/snowmelt) for each individual. Values near zero (vertical dashed lines) indicate individuals with mean locations close to green-up/snowmelt. Green hash marks on the bottom of panel A represent the mean number of days to peak IRG within the home range of individuals at the time they gave birth,

with 80% of births occurring before the peak in green-up. Panel A) is data for individuals from all herds, B–F represent data from individual herds: B) Buchans; C) Grey River; D) Lapoile; E) Middle Ridge; and F) Topsails.

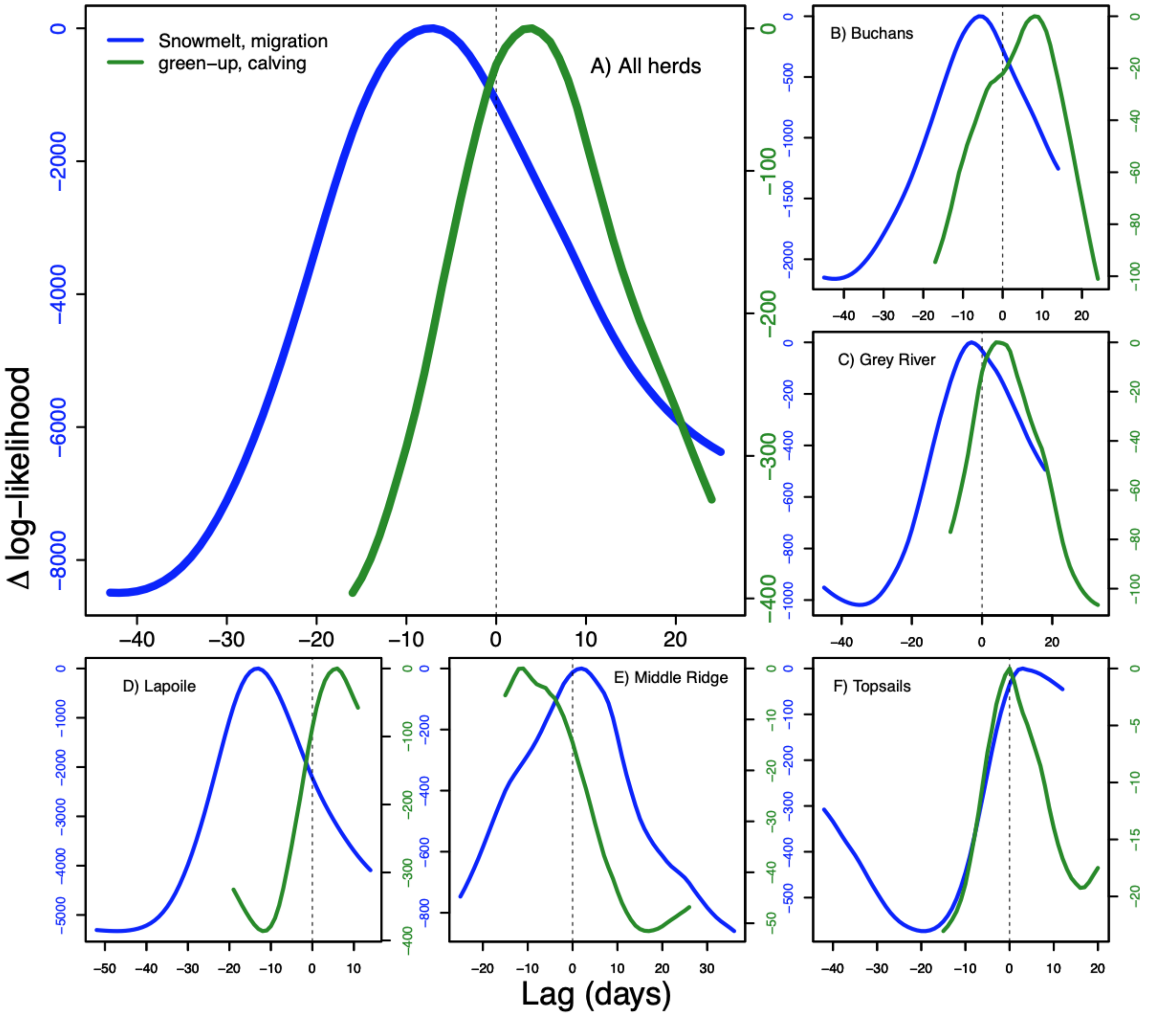

Figure 2.2: Delta log-likelihood of models predicting caribou (*Rangifer tarandus*, *n* = 94) selection behaviour for areas associated with melting snow (blue lines and axis labels) during spring migration and green-up during the calving season (green lines and axis labels, *n* = 216). We generated models using the absolute value of days to snowmelt/peak IRG across several lags. Lagged datasets were constructed by adding or subtracting the value of the lag to the number of days until snowmelt/peak IRG. Using lags allowed us to test for model fit at the focal day of the lag (see Methods). Panel A) is data for individuals from all herds, B–F represent data from individual herds: B) Buchans; C) Grey River; D) Lapoile; E) Middle Ridge; and F) Topsails.

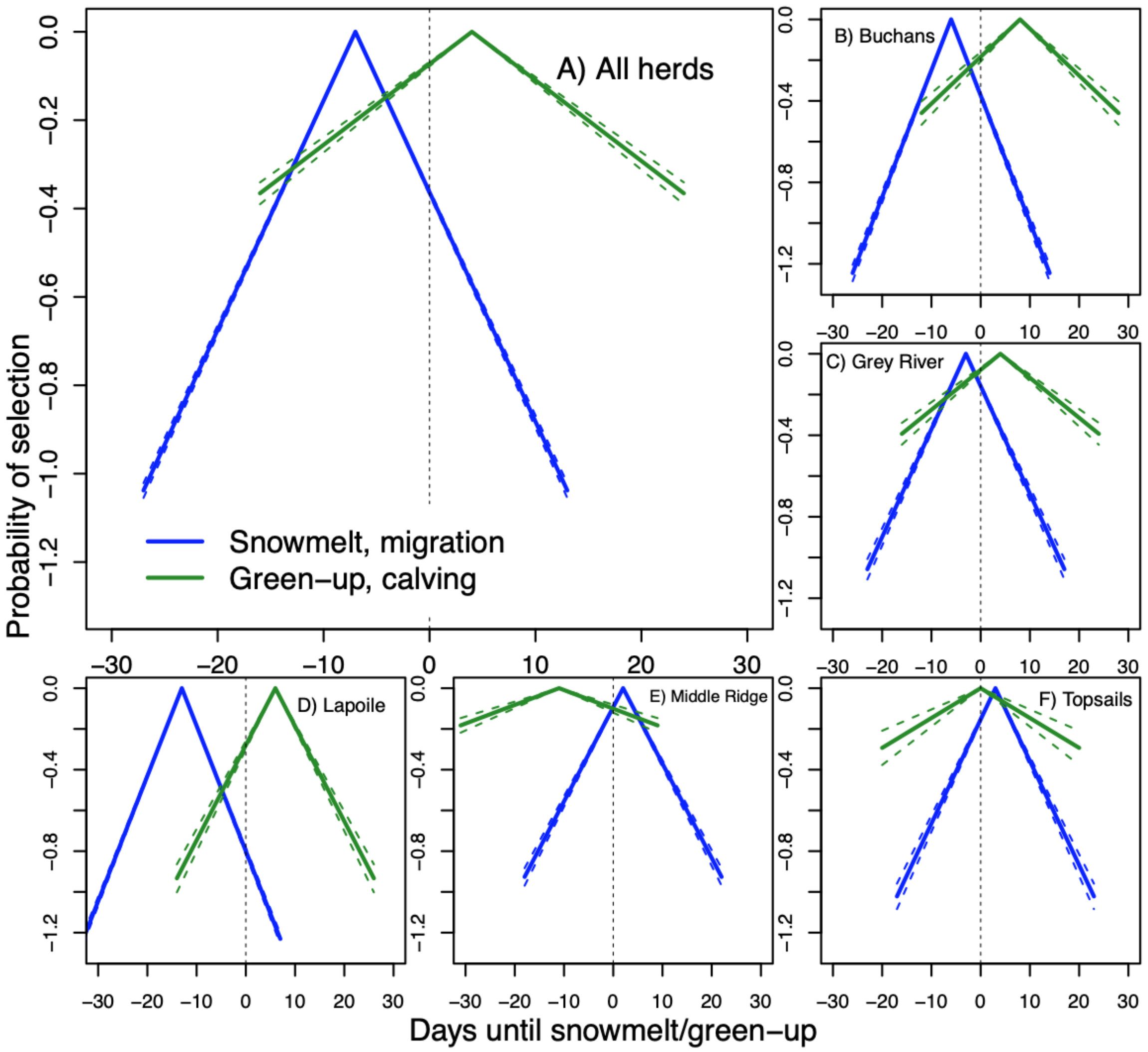

Figure 2.3: Model-predicted selection of caribou (*Rangifer tarandus*, *n* = 94) in Newfoundland, Canada as a function of the number of days from snowmelt during migration (blue lines) and peak IRG during the calving season (green lines) from conditional logistic regression models. Dashed lines represent 95% confidence intervals. Vertical dashed line represents selection at snowmelt or peak IRG. Panel A) is data for individuals from all herds, B–F represent data from individual herds: B) Buchans; C) Grey River; D) Lapoile; E) Middle Ridge; and F) Topsails. Models suggest that caribou selected for areas ~7 days prior to snowmelt overall during migration (panel A), with selection declining for locations that are closer or further in time from this date. Caribou also selected for areas that were about 4 days after green-up during the calving

period (0–3 weeks after parturition), with selection declining for later or earlier phenological stages.

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CHAPTER 3: PLASTICITY AND REPEATABILITY IN SPRING MIGRATION AND PARTURITION DATES WITH IMPLICATIONS FOR ANNUAL REPRODUCTIVE SUCCESS

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3.1 Abstract

Animals are faced with unprecedented challenges as environmental conditions change. Animals must display behavioural plasticity to acclimate to changing conditions, or phenotypic variation must exist within the population to allow for natural selection to change the distribution of trait values. The timing of migration and parturition relative to important annual environmental changes such as snowmelt and vegetation green-up and how they co-vary may influence reproductive success. We tested for plasticity and individual differences in migration and parturition timing as a function of the timing of snowmelt and green-up in a migratory herbivore (caribou; *Rangifer tarandus*, $n = 92$) using behavioural reaction norms. We tested whether timing of parturition, plasticity in parturition timing, or timing of green-up were correlated with calf survival. Migration and parturition timing were plastic to the timing of spring conditions, and we found moderate repeatability for migration timing, but no repeatability in timing of parturition. We detected a novel behavioural syndrome where timing of arrival on summer range and timing of parturition were correlated. Our results suggest that observed shifts in caribou parturition timing in other populations in North America are due to plasticity as opposed to an evolutionary response to changing conditions. We did not detect a correlation between annual reproductive success and either the timing of spring or plasticity to the timing of spring events. While this provides evidence that many populations may be buffered from the consequences of climate change via plasticity, we caution that a lack of repeatability in parturition timing could impede adaptation as climate warming increases.

Keywords: annual reproductive success, behavioural plasticity, calving, caribou, consistent individual differences, green-up, migration, snowmelt.

3.2 Introduction

Evolving life-history strategies to deal with fluctuations in habitat quality through time is fundamental for species living in seasonal environments (Chevin et al. 2010). In many species, migration is viewed as a strategy to optimize use of seasonally available resources (Fryxell et al. 1988, Albon and Langvatn 1992, Shaw 2016). In this context, migration will be most effective when individuals adjust their movement to match the phenology of their environment, which may serve as a cue to forecast spring conditions on summer range (Chapter 2, Kölzsch et al. 2015, Laforge et al. 2021). Optimizing opportunities to reproduce in seasonal environments also depends on individuals rearing young when resource availability is highest to properly finance reproduction (Sadleir 1969, Thomas et al. 2001). Climate change, however, decouples migrants from optimally timing migration, and therefore reproduction. For example, warmer springs disproportionately affects the phenology, or timing of annual events, in lower trophic levels compared to higher trophic levels. The result is phenological asynchrony where consumers do not advance their phenologies to match that of their resource (Visser et al. 1998, Durant et al. 2007). This asynchrony can lead to reduced survival and fitness, a phenological mismatch which can have significant population-level effects (Durant et al. 2007, Miller-Rushing et al. 2010). Plasticity in migratory and reproductive behaviour in response to phenological shifts at lower trophic levels is relevant to species persistence as this plasticity likely buffers populations against adverse environmental change (Boutin and Lane 2014). Likewise, consistent among individual differences can provide capacity for evolution within populations to adapt to changing conditions (Wolf and Weissing 2012). Assessing potential outcomes of climate change on populations will necessitate elucidating how individuals are able to acclimate or adapt behaviours linked to annual reproductive success to inter-annual variation in resource phenology.

For terrestrial herbivores, spring migration is often driven by seasonal changes in the availability of high-quality forage resources (Merkle et al. 2016) or snow cover that may presage future conditions on summer range (Chapter 2, Laforge et al. 2021). The forage maturation hypothesis suggests that herbivores should get the highest nutritional benefit by foraging on plants at an intermediate stage of growth when biomass is sufficient and digestibility is high (Fryxell 1991, Hebblewhite et al. 2008). Animals that forage on high-quality vegetation gain a nutritional benefit (Hamel et al. 2009) and experience increased fat gain (Middleton et al. 2018). While many populations or individuals track the emergence of high-quality forage as it matures along elevational and latitudinal gradients (Bischof et al. 2012, Merkle et al. 2016), others use a strategy of "jumping" the green wave, arriving on summer range prior to when it peaks in forage quality ("green-up"; Bischof *et al.* 2012). Jumping the green wave may be related to snowmelt, with individuals tracking the progression of melting snow along migratory routes (Chapter 2, Laforge et al. 2021). The progression of snowmelt appears to be an important factor in migration timing for many northern ungulates. For example, in caribou (*Rangifer tarandus*) in Alaska and northern Canada, timing of arrival on summer range was correlated with the timing of snowmelt (Gurarie et al. 2019). Similarly for elk (*Cervus canadensis*) in Yellowstone National Park, departure from winter range was correlated with snowmelt date on winter range, and timing of arrival on summer range was associated with the timing of snowmelt on summer range and on migration routes (Rickbeil et al. 2019). Using melting snow to time migrations may allow individuals to arrive on calving grounds to optimally take advantage of green-up during the calving season.

Animals that live in seasonal environments should be adapted to time their reproductive phenology such that the most energetically expensive times correspond with when resources are most highly abundant (Sadleir 1969, Thomas et al. 2001). For ungulates, energetic requirements can more than double during the peak of lactation (Oftedal 1985, Robbins 1993, Parker et al. 1999). In *Rangifer*, parturition date varies among populations as a function of the mean annual timing of green-up (Skogland 1989). Climate change disproportionately alters the phenology of lower trophic levels, resulting in phenological asynchrony where consumer breeding phenologies occur after the peak in resources at lower trophic levels, resulting in depressed reproductive success—a phenological mismatch (Visser et al. 1998, Both and Visser 2001, Samplonius et al. 2021). For example, changing sea ice phenology has altered vegetation phenology in Greenland, resulting in a phenological mismatch and reduced calf survival in reindeer (also *R tarandus*; Post and Forchhammer 2008, Kerby and Post 2013). Long-term data suggests advancing migration and parturition dates in caribou over the last three decades, likely in response to changing resource phenologies (Mallory et al. 2020) or spring temperatures (Paoli et al. 2018). In the case of parturition, this is especially true for northern populations where climate warming has been more acute (Davidson et al. 2020).

Populations can adjust their phenologies to cope with changes in the phenology of their resources in two ways. Individuals may acclimate their phenologies via behavioural plasticity. Alternatively, sufficient variation in phenotypes in the population might result in some individuals being better adapted to novel conditions (Boutin and Lane 2014, Charmantier and Gienapp 2014). If that variation is consistent among individuals, it may provide the pre-requisites for evolution. Plasticity is estimated over shorter, i.e., within generation, timescales by making repeated observations of individual phenologies and correlating them with environmental changes. Meanwhile, directly quantifying evolutionary responses requires data spanning multiple generations (Wilson et al. 2010). The potential for evolution, however, can be inferred from shorter-term behavioural data. For example, natural selection requires traits that vary among individuals, and repeatability provides a measure of the proportion of variance in a trait that is attributable to differences among individuals (Dochtermann et al. 2015). Highly repeatable behaviours are consistent within individuals but vary among individuals (Bell et al. 2009). Estimates of repeatability can therefore be used as tentative estimates for the potential for evolutionary responses when genetic data are unavailable (Wilson 2018)—see for example Perrins and Jones (1976), Erikstad et al. (1993), and Conradsen et al. (2016). Behavioural reaction norms (Dingemanse et al. 2010) provide a framework to test whether contemporary changes in phenology are due to plasticity or a potential evolutionary response by modelling individual-level plasticity to changing environmental conditions while also estimating repeatability. Behavioural reaction norms can also quantify behavioural syndromes, the degree to which behaviours and behavioural plasticity are correlated (Sih et al. 2012). Exploring potential for syndromes in phenological traits, including migration and parturition timing, could demonstrate the importance of individuals properly timing migration to optimize the timing of parturition, with consequences to adaptation under changing environmental conditions.

We used behavioural reaction norm analyses of individual caribou (*n* = 92) in Newfoundland, Canada to test the non-mutually exclusive hypotheses that caribou exhibit plasticity in the timing of migration and parturition as a function of the timing of spring, and that these behaviours are repeatable traits providing variation that could result in an evolutionary response. We also tested for behavioural syndromes linking both timing of migration and parturition and their plasticity, and the phenological mismatch hypothesis by testing whether early springs reduced annual reproductive success. We tested several predictions, including:

1) Both timing of migration (P_1a) and timing of parturition (P_1b) would display plasticity as a function of changes in the annual timing of spring snowmelt. Individuals would both migrate early and give birth early in years where snowmelt occurred earlier. We also predicted that timing of parturition would display plasticity as a function of the timing of green-up (P_1c), with individuals giving birth earlier when green-up was earlier.
2) Both timing of migration (P_2a) and timing of parturition (P_2b) would be repeatable behaviours. Individuals that migrate or give birth early do so consistently.
3) There is a correlation between timing of migration and timing of parturition (P_3). Individuals that migrate early give birth early.
4) There is a correlation in degree of plasticity in migration timing and parturition timing (P_4). Individuals that are more plastic in the timing of their migration are also more plastic in the timing of parturition.
5) Finally, if timing of parturition was not sufficiently plastic, we predicted that timing of green-up would influence calf survival, with lower survival in early springs, which may represent a phenological mismatch (P_5).

3.3 Methods

3.3.1 Study site

We conducted our study on the island of Newfoundland, Canada (~47° 44’ N, 52° 38’ W to 51° 44’ N, 59° 28’ W). Caribou habitat in Newfoundland primarily consists of coniferous forest and mixed wood forests dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*), interspersed with bog and heath habitats. Barren rock and lakes are also common features in Newfoundland (see study area map, Figure S3.1).

3.3.2 Data collection and cleaning

GPS collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g) were deployed on 112 adult female caribou from five populations on Newfoundland between 2007–2013. Caribou were captured by darting from a helicopter. GPS fixes were obtained every 1–5 hours depending on season and collar. All animal capture and handling followed guidelines from the Canadian Council on Animal Care. We initially had data from 112 individuals and 326 individual × year combinations (ID-years). Cleaning the data and removing ID-years with insufficient data, and non-parturient individuals left us with data for 103 individuals across 294 ID-years. A further nine individuals and 78 ID-years were dropped after removing individuals that did not migrate at least 30 km. Our final dataset consisted of data for 92 caribou across 212 ID-years.

3.3.3 Defining timing of snowmelt and green-up

We used two measures of phenological change to quantify the timing of spring events for caribou populations in Newfoundland, the timing of snowmelt and the timing of green-up. We used the timing of snowmelt as the presumed driver of spring migration timing as snowmelt has been shown to correspond to the timing of migration of caribou in Newfoundland (Chapter 2, Laforge et al. 2021). We used the normalized difference snow index (NDSI) derived from daily moderate resolution imaging spectroradiometer (MODIS) data at a spatial resolution of 500 × 500 m to determine the date of snowmelt. We determined the day that each pixel first had a recorded negative value of NDSI as the date upon which each pixel was considered snow-free. We used the timing of snowmelt within each population’s range (99% minimum convex polygon (MCP) of all locations from the start of spring migration to three weeks after parturition) to define the timing of snowmelt for each individual in each year as the median date of when pixels in the population-range became snow-free (Chapter 2, Laforge et al. 2021).

To quantify the timing of plant green-up, we used the instantaneous rate of green-up (IRG). IRG represents the first derivative of a series of normalized difference vegetation index values at a given location. We used data from both MODIS satellites (Terra and Aqua), each of which produced 16-day composite NDVI images at a resolution of 250 × 250 m. The sensors on each of the two satellites produce composite images at opposite times (i.e., phased), so combining the two data records provides an 8-day temporal resolution. We first set to NA any NDVI values where the snow cover band of the MODIS data indicated snow cover and replaced it with the 3rd percentile of all snow-free observations at that pixel. This procedure ensures that the resulting curves are only plotting the change in plant growth and not confounded by melting snow (Bischof et al. 2012, Merkle et al. 2016). We also set any pixels contaminated by cloud (~10.0%) to NA. For each location in our study area and for each year of our study, we used a 3-observation moving median filter to smooth the time series then fit a logistic curve to the time series of NDVI values at that location. We then calculated as IRG the first derivative of this curve and determined the date that IRG had the highest value. This date represented the day in which plant growth was occurring fastest and was therefore assumed to represent the highest nutritional quality for caribou (Hamel et al. 2009, Middleton et al. 2018). To calculate the date of green-up in each herd's range each year, we generated a population-level MCP range (as defined above for snowmelt) and calculated the median date each year that pixels in the home range reached peak IRG. The median date of snowmelt across ranges and years was Apr 27, and the median date of green-up was May 29 (see Figure 3.1).

3.3.4 Defining caribou migration timing

To define timing of migration, we used Migration Mapper V. 2.0 (Wyoming Migration Initiative 2017). Migration Mapper plots GPS locations on a map along with a profile of net squared displacement to allow the user to visually inspect these profiles to specify when individuals begin and complete migratory movements. As we were only interested in spring migration, we only quantified the timing of departure from winter range and arrival on summer range. We used the date of arrival on summer range as our measure of timing of migration. We removed any individuals that did not migrate at least 30 km. The median date for departure from winter range was Mar 25 (range: Feb 9–May 19). The median duration of migration was 43 days (range: 4–128) covering a median distance of 62.2 km (range: 30.5–174.9). The median date for arrival on summer range was May 10 (range: Mar 20–Jul 13, see Table S3.1).

3.3.5 Quantifying timing of parturition and annual reproductive success

We used the method developed by DeMars et al. (2013) and validated by Bonar et al. (2018) to define calving date and whether calves survived to four weeks of age. This method quantifies birthing events by detecting constraints on movement in females who must stop to give birth and whose movements are constrained by calves-at-heel that have a slower movement rate. Females whose calves die in the first four weeks of life display a sudden return to baseline movement rates, whereas females whose calves survive display a gradual return to baseline rates as calves are able keep pace with their mothers. We used a population-based method to detect calving and calf mortality events that examined three-day average movement rates of collared females to ascertain whether females gave birth that year and quantify the date of parturition. In some instances, the model output suggested that individuals gave birth in the first day of the time series provided to the model. In these instances, we manually validated parturition dates by inspecting a plot of daily movement rates. These data were validated using the Middle Ridge population, in which the method correctly classified 100% of parturition events (Bonar et al. 2018). The median date of calving was May 30 (range: May 18–Jul 13), and 60% of calves survived to four weeks of age (see Table S3.1).

3.3.6 Behavioural reaction norms

Behavioural reaction norms quantify how individual behaviour changes across an environmental gradient. To evaluate how individual phenotypes for timing of migration and parturition are expressed across an environmental gradient (timing of snowmelt or green-up), and their effect on annual reproductive success, we quantified behavioural reaction norms (BRNs; Dingemanse et al. 2010) using two sets of bivariate Bayesian mixed effects models (R package *MCMCglmm,* version 2.29; Hadfield 2010; Houslay & Wilson 2017). We predicted that timing of migration and parturition would both be affected by timing of snowmelt, and that timing of parturition would be affected by the timing of green-up, as would calf survival. Therefore, the response variables for our first set of models were the date of arrival on summer range and parturition date, with timing of snowmelt used as our main explanatory variable. For our second model, response variables were parturition date and whether caribou calves survived to four weeks of age, with timing of green-up used as the explanatory variable. We centered and scaled variables independently for each population. Models were fit with uninformative priors (Wilson et al. 2010) and Gaussian error structures for timing of migration and parturition, and with a categorical (binomial) error structure for calf survival. We ran models for a total of 420,000 iterations with a burn-in of 20,000 and a thinning rate of 100 (Webber et al. 2020). We evaluated eight models using different combinations of random and fixed effects structures (Table S3.2). We tested for the effect of individual ID, and for the effect of an individual × environment interaction (i.e., an interaction between individual caribou and relative date of snowmelt or green up; Nussey *et al.* 2007) in the random terms. In our BRN analyses, fixed effects were used to control for changes in the random effects. In each of our two model sets, we chose the model with the lowest deviance information criterion (DIC, see Table S3.2). We extracted best linear unbiased predictors (e.g., random intercept and slope estimates for each ID-year) and calculated repeatability (*r*) of BRN intercepts for migration date, parturition date, and calf survival as the proportion of total phenotypic variation (individual + residual; $v_{ind} + v_{res}$) attributable to differences between individuals (v_{ind}) within a group (Dingemanse and Dochtermann 2013):

$$r = \frac{V_{ind}}{(V_{ind}+V_{res})} \qquad \text{[Formula 3.1].}$$

We examined the correlation between the slope and intercept of best linear unbiased predictors (random effects) for both variables in each model to examine the relationships between individual differences and plasticity within and between the traits (Houslay & Wilson 2017; Table S3.3).

3.4 Results

Both top behavioural reaction norm models included random slopes by individual ID for our response variables (timing of arrival on summer range, timing of parturition, and calf survival) as a function of our explanatory variables (timing of snowmelt and timing of green-up). This provided evidence for the importance of an individual × environment interaction (**Δ** DIC of both models to the next most supported model > 16). At the population-level, later snowmelt was significantly associated with later timing of arrival on summer range (β + 95% credible interval: 0.332 [0.192, 0.455], $p < 0.001$, supporting P_1a) and nearly-significantly correlated with later parturition (0.138 [-0.006, 0.286], $p = 0.067$, partially supporting P_1b), see Table 3.1 and Figure

3.2. We did not detect an effect of the timing of green-up on the timing of parturition (0.094 [-0.066, 0.270], p = 0.270, no support for P_1c), see Table 3.1 and Figure 3.2.

We found some evidence of among individual differences in the timing of migration across individuals, with repeatability for arrival on summer range being moderate (r [SD] = 0.377 [0.045], moderate support for P_2a, Figure 3.3, red symbols). Overall repeatability for timing of parturition was quite low, suggesting that timing of parturition was not a trait that exhibited consistent individual differences in these populations (snowmelt model: 0.112 [0.004], green-up model: 0.051 [0.002] no support for P_2b, Figure 3.3, blue-green symbols). We found evidence of a correlation between the intercept of migration timing and the intercept of parturition timing (0.679 [0.162, 0.986]), where early arrivers also give birth earlier (P_3; Figure 3.4a). We did not, however, find any evidence of a link between the plasticity in arrival on summer range and plasticity in timing of parturition (P_4), individuals that were more plastic in the timing of their migration were not more plastic in the timing of parturition (-0.039 [-0.841, 0.757], Figure 3.4b). There was no support for our prediction that later green-up was correlated with higher calf survival (0.316 [-0.377, 1.101], p = 0.381, no support for P_5, Table 3.1). We also did not find a significant correlation between timing of parturition and calf survival in an average environment (the mean date of green-up; -0.254 [-0.940, 0.568], Figure 3.4c). There was also no evidence that higher plasticity in parturition date resulted in higher overall calf survival (0.274 [-0.530, 0.951], Figure 3.4d).

3.5 Discussion

An animal's ability to match the phenology of life history events with changing snowmelt and green-up timing is vital for persistence, both across seasonal and inter-annual changes (Thomas et al. 2001). We found evidence of individual differences in migration timing (P_2a), such that some individuals consistently migrated earlier, and other individuals migrated later. Despite this, we found little evidence that timing of parturition was consistent among individuals (P_2b). With limited repeatability in parturition timing (r = 0.05–0.11), likely little of the variance is genetic (Dochtermann et al. 2015), and therefore able to respond to selection. Migratory caribou in Newfoundland acclimated the timing of migration to the timing of snowmelt (P_1a), and to a lesser extent, they also acclimated birth date to timing of snowmelt (P_1b) but not to timing of green-up (P_1c). This plasticity may have been sufficient to mitigate the effects of phenological mismatch on calving success in caribou, as we found no evidence for reduced annual reproductive success in early springs (P_5). We also highlight a behavioural syndrome where individuals that migrate early also give birth early (P_3). However, we did not find evidence that plasticity in timing of migration correlates with timing of parturition, suggesting that plasticity in these traits is independent (P_4). Our results suggest a primary role of plasticity in contributing to shifting life history phenology in caribou over the last few decades in other caribou populations (Davidson et al. 2020, Mallory et al. 2020).

The results of our study indicate that migration timing is both a repeatable trait and plastic to the timing of snowmelt, outlining the importance of snow in many systems to synchronize animal phenology. In our populations, individuals migrated approximately one week prior to snowmelt, supporting the hypothesis that caribou use melting snow as a cue for when to migrate (Chapter 2, Laforge et al. 2021). Being plastic in migration timing to changes in snow phenology likely allows individuals to migrate at an optimal time to increase movement efficiency on ground or lakes that are still frozen (Leblond et al. 2016) but without the impediment of deep snow. Moderate repeatability suggests that there are some individual differences in migration timing that could allow for evolutionary change as selective pressures on optimal migration dates change. Repeatability could have a genetic basis or a social one, for example, if individuals learn to migrate from conspecifics (Jesmer et al. 2018). The repeatability of arrival timing in our population (r = 0.377) was slightly higher than the mean value of arrival repeatability for long distance migratory birds (r = 0.31; Both et al. 2016). Consistent individual variation may be more favoured in environments where conditions on winter range are less reliable indicators of conditions on summer range, reducing the ability of individuals to be plastic to environmental variation (Both et al. 2016). Relatively short-distance migrants like caribou in Newfoundland may be more adapted to migrate at the optimal time, reducing between-individual variation and therefore repeatability.

Caribou in our study displayed some plasticity in the timing of parturition to changes in the timing of snowmelt, suggesting individuals can acclimate their reproductive ecology to interannual environmental change. While timing of parturition is primarily correlated with the timing of the rut, environmental conditions have also been shown to impact the timing of parturition, including female body condition and spring temperature (Paoli et al. 2018). Plasticity in breeding date is thought to buffer populations against the consequences of changes in optimal breeding date (Pigliucci 2001, de Villemereuil et al. 2020). Earlier spring green-up has been shown to result in earlier birth in mule deer (*Odocoileus hemionus*; Aikens et al. 2021). Parturition date does vary across *Rangifer* population ranges to match local plant phenology (Skogland 1989, Davidson et al. 2020), and prior studies have documented long-term shifts in parturition date in caribou (Davidson et al. 2020, Mallory et al. 2020). Repeatability of parturition date was low to moderate in red deer (*Cervus elaphus*, r = 0.19, Bonnet et al. 2019) and even lower in our study on caribou (see Figure 3.3). Newfoundland has an unpredictable climate with large inter-annual variation driven primarily by the North Atlantic Oscillation

(Banfield and Jacobs 1998, Finnis et al. 2015), which could have resulted in selection for plasticity in parturition date as opposed to selection for a specific optimal date (Brommer et al. 2005, Nussey et al. 2005). Large variance in climate also suggests that trends of advancing parturition dates may be driven more by plasticity within generations as opposed to adaptive evolution across generations, especially given that these are still relatively short evolutionary timeframes.

It is unlikely that phenological mismatch is currently affecting caribou reproduction and fitness in Newfoundland. Timing of green-up did not significantly affect calf survival, although we note that this was due to large confidence intervals around a relatively large coefficient estimate. We cautiously suggest that early springs do not result in depressed reproductive success, likely because this scenario is mitigated by plasticity in the timing of parturition allowing individuals to avoid significant mismatch. Despite indications of phenological mismatch in caribou (Post and Forchhammer 2008), other studies have failed to detect a significant effect of spring asynchrony on caribou forage availability (Gustine et al. 2017). Early springs may in fact be beneficial for caribou by extending the growing season and therefore the temporal availability of resources. Some of our results however raise the spectre that caribou may not be able to continue to acclimate or adapt to future conditions. If individuals are plastic to a cue that is increasingly unreliably correlated with fitness-maximizing resources, this can result in phenological mismatch despite plasticity. For example, differences in the amount of warming experienced in the Netherlands in early versus late spring resulted in mismatch between great tits (*Parus major*) and their caterpillar prey, as the birds displayed plasticity to the former and the caterpillars the latter (Visser et al. 2006, Visser 2008). Reproductive success in caribou appears to be linked to timing parturition to coincide with peak green-up (Post and Forchhammer 2008);

however, we found that individuals were more plastic in the timing of birth in response to the timing of snowmelt than to green-up itself. The timing of green-up was only loosely correlated with the timing of snowmelt ($R^2 = 0.21$), with green-up only advancing by 0.30 days for each day that snowmelt advanced (Figure S3.3). Other factors such as temperature in early versus late spring or water availability as a function of total snowpack likely affect the relationship between the timing of snowmelt and green-up. It is likely that climate change will continue to disrupt the predictability of the relationship between these two phenological events, which may result in caribou using an increasingly unreliable cue to time reproduction.

Evidence from our study suggests that earlier parturition date in many *Rangifer* populations (Davidson et al. 2020) is driven primarily by plastic changes as individuals acclimate to changing conditions as opposed to natural selection acting to select for individuals that give birth earlier in the season. Repeatability is often considered to represent an upper bound to heritability (Dochtermann et al. 2015), and as such the low repeatability of parturition date we observed suggests it is unlikely that parturition date is heritable in caribou. Plasticity alone, without any evolutionary change, could simply delay population decline if populations are driven beyond the limits of their ability to acclimate (Lande and Shannon 1996, Simmonds et al. 2020). Climate shifts are predicted to result in Newfoundland transitioning from a boreal biome to temperate deciduous forest over the next 10–40 years (Rehfeldt et al. 2012), which could result in significant challenges for persistence of caribou (e.g., loss of important boreal lichen resources). Experimental evidence from both frogs and passerines suggest that current rates of evolution are insufficient to account for observed shifts in reproductive phenologies (Charmantier et al. 2008, Phillimore et al. 2010).

Our behavioural reaction norm framework allowed us to test for correlations in individual responses in environmental change to timing of snowmelt and green-up. For both of our model sets, the top model included random slopes for individuals, suggesting the existence of among-individual variation in the degree of plasticity to environmental change. However, we only detected significant among-individual correlations among two traits: timing of migration and timing of parturition, providing evidence of a link between these two behavioural traits. Counter to our fourth prediction however, we did not find a link between plasticity in timing of migration and plasticity in timing of parturition, suggesting that the ability to acclimate migration timing is not related to plasticity in parturition date. We also failed to detect a significant relationship between plasticity in parturition date and reproductive success. For a telemetry study, we have a large sample of individuals, repeated across several years, and replicated among herds. Despite our relatively large sample size, bivariate mixed effects models, like those used in this study, are data hungry. While some of our conclusions may be based on what could be considered modest statistical inference, we suggest that finding strong inference in our data will be more challenging than in contexts where behavioural tests can be performed across a range of environments that can be replicated numerous times in a single year to obtain a robust sample size (i.e., Carter et al. 2012; Webber et al. 2020).

Climate change represents an imminent threat to migratory animals such as caribou (Wilcove and Wikelski 2008, Shaw 2016). Despite indications that phenologies of some migratory species are shifting to compensate for changes at lower trophic levels (Davidson et al. 2020, Mallory et al. 2020), understanding the mechanism remains an important question. By empirically demonstrating individual plasticity to changing environmental conditions and low repeatability in parturition time, our results suggest that much of the observed contemporary shifts in phenology in other caribou populations (Davidson et al. 2020, Mallory et al. 2020) are due to plastic responses to environmental change as opposed to an evolutionary response. Plasticity appeared to buffer the populations we studied against depressed fitness, as we found no effect of the timing of spring on annual reproductive success. We demonstrate an important link between migration timing and parturition timing, suggesting that phenological synchrony is a two-part process in caribou—individuals must not only give birth when conditions are optimal, but this synchrony is also dependent on migration timing. Caribou are globally threatened (Vors and Boyce 2009), and as a northern ungulate exposed to high levels of climate change-induced warming, examining individual differences and plasticity to inter-annual variability in climate provides an important litmus test for understanding the impact of climate change on migratory herbivores globally.

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Table 3.1: Estimates for fixed effects from the most parsimonious models from two bivariate Bayesian mixed effects models testing the effects of timing of snowmelt (model 1) and timing of green-up (model 2) on the timing of arrival on summer range (model 1), timing of parturition (models 1 and 2) and probability of calf survival (model 2) for caribou (*Rangifer tarandus, n* = 92) in Newfoundland, Canada, 2007–2013. Estimates are presented with 95% credible intervals. The reference category for population is Buchans.

Model 1: Arrival timing and parturition timing as a function of timing of snowmelt		
	Arrival timing	Parturition timing
Arrival timing	-	0.040 (-0.387, 0.457)
Parturition timing	0.032 (-0.347, 0.367)	-
Snowmelt	0.332 (0.192, 0.455)	0.138 (-0.006, 0.286)
Grey River	-0.065 (-0.702, 0.559)	-0.021 (-0.532, 0.500)
Lapoile	-0.046 (-0.676, 0.471)	-0.002 (-0.469, 0.476)
Middle Ridge	-0.047 (-0.563, 0.472)	-0.024 (-0.473, 0.447)
Topsails	0.09 (-0.568, 0.697)	-0.020 (-0.581, 0.535)
Model 2: Parturition timing and calf survival as a function of timing of green-up		
	Parturition timing	Calf survival
Parturition timing	-	-0.037 (-0.375, 0.267)
Calf survival	1.222 (-0.206, 2.817)	-
Green-up	0.094 (-0.066, 0.270)	0.316 (-0.377, 1.101)
Grey River	0.063 (-0.401, 0.507)	-0.971 (-3.282, 1.091)
Lapoile	0.099 (-0.380, 0.526)	-1.284 (-3.258, 0.665)
Middle Ridge	0.027 (-0.395, 0.444)	0.652 (-1.326, 3.132)

Topsails	0.007 (-0.521, 0.554)	-0.968 (-3.340, 1.130)

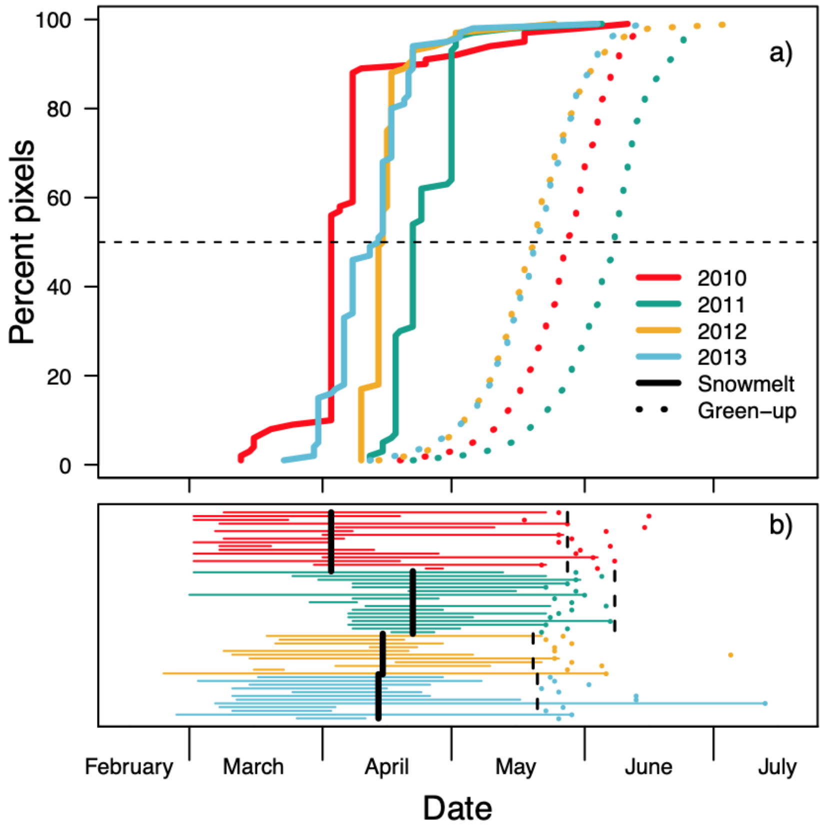

Figure 3.1: Phenology of snowmelt and green-up (a) and migration and parturition (b) for caribou (*Rangifer tarandus*, *n* = 32) in the Middle Ridge population, 2010–2013. a) represents the number of pixels within the population's spring/summer range in which snow has melted (NDSI > 0, solid line) or that have reached the peak of green-up (instantaneous rate of green-up; dotted lines) in each spring. Colours represent different years, and the dashed line represents the median (the measure used for determining date of snowmelt/green-up). b) the timing of migration as horizontal lines for each individual in each year (each line's extent represents the time they were migrating). Points represent the timing of parturition. Black vertical lines represent the median dates of snowmelt (solid) and green-up (dashed) for each year. See Figure S3.2 for plots using the other four populations used in this study.

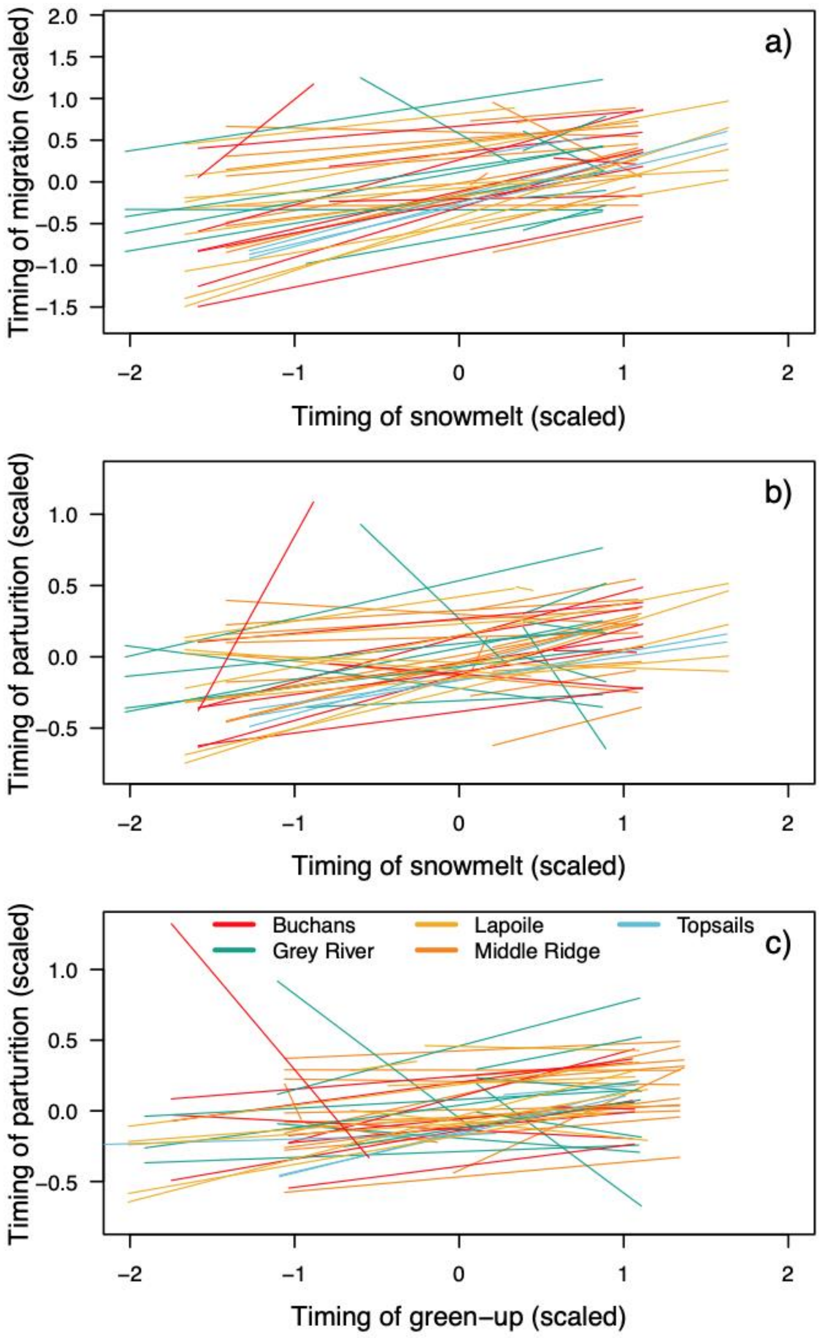

Figure 3.2: Mean-centered behavioural reaction norms for five caribou populations assessing timing of arrival on summer range and timing of parturition as a function of median date of spring snowmelt and green-up (see Methods) for migratory caribou (*Rangifer tarandus*; *n* = 92) in Newfoundland, Canada. Each line represents a different individual. Panel a) represents timing of arrival on summer range as a function of timing of snowmelt, panel b) represents timing of

parturition as a function of timing of snowmelt, and c) represents timing of parturition as a function of timing of green-up. Best linear unbiased predictors represent point estimates of the random effects from the mixed effects model.

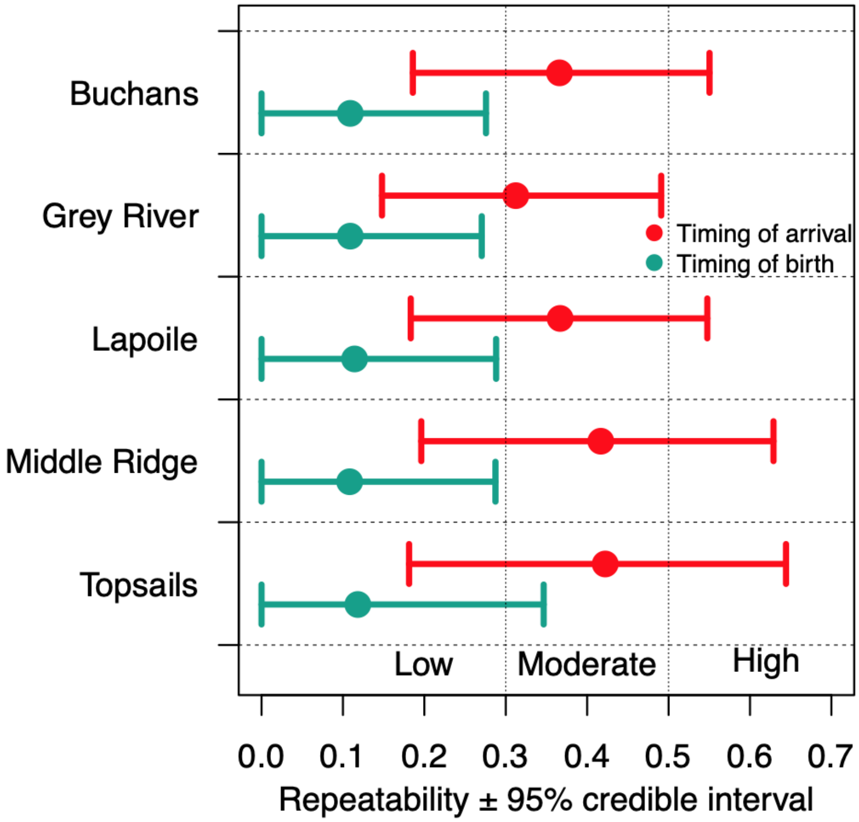

Figure 3.3: Repeatability estimates and 95% credible intervals for timing of arrival on summer range (red) and timing of birth (green) for caribou (*Rangifer tarandus*; *n* = 92) in Newfoundland, Canada. Repeatability estimates were derived from the top Bayesian mixed effects model describing timing of arrival and birth as a function of timing of snowmelt (the first model set).

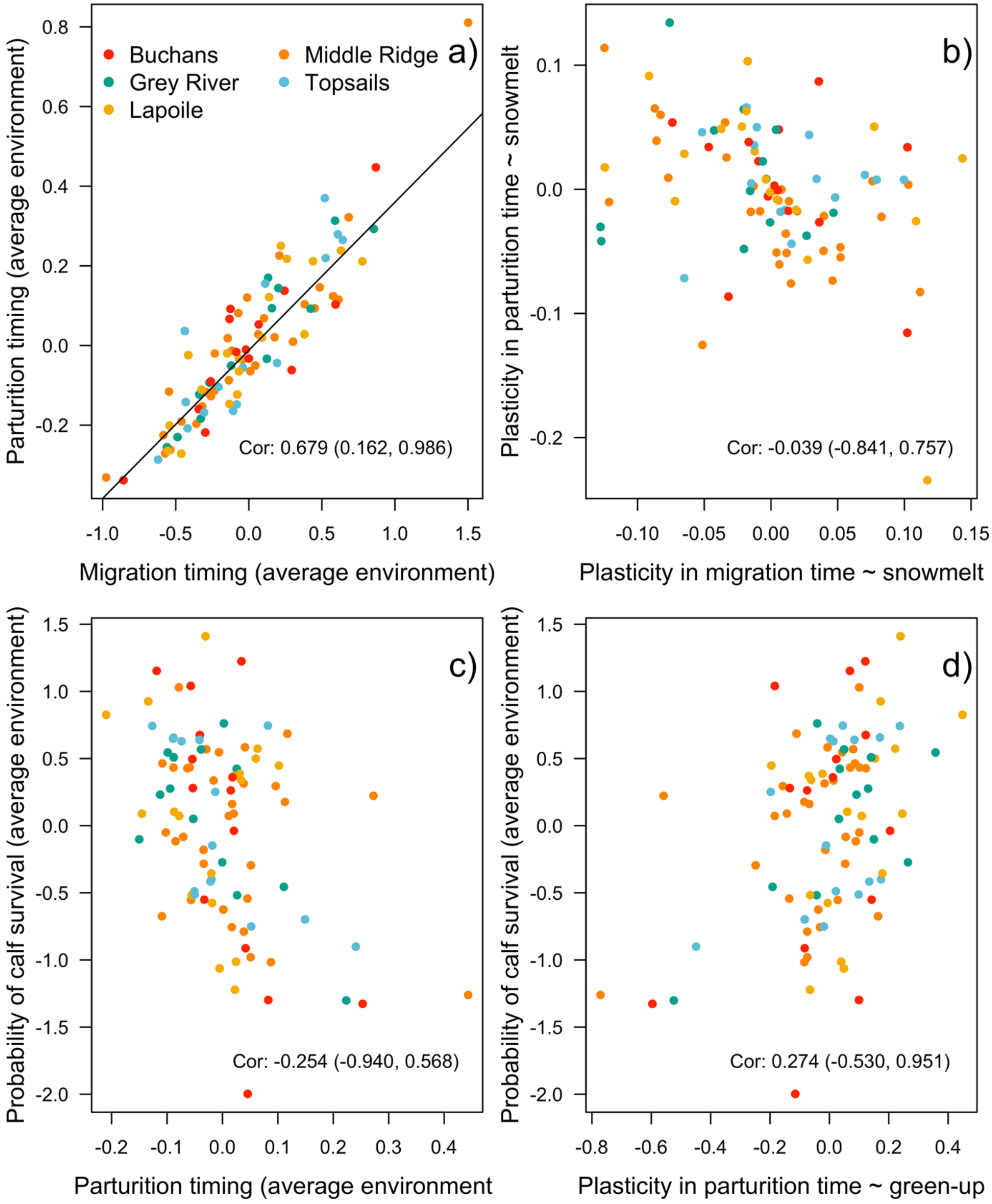

Figure 3.4: Correlations and 95% credible intervals between random slopes and intercepts from bivariate mixed effects behavioural reaction norm models quantifying timing of caribou

(*Rangifer tarandus*; *n* = 92) migration, parturition, and calf survival as a function of the timing of spring snowmelt and green-up. Colours represent different populations. Panel a) represents the correlation between the intercept for timing of migration and the intercept for timing of parturition. Panel b) represents the correlation between the slopes (e.g., plasticity) of migration and parturition timing. Panel c) represents the correlation between the intercept for timing of parturition and the probability of calf survival to four weeks of age in an average environment. Panel d) represents the correlation between the plasticity in parturition time as a function of green-up and the probability of calf survival.

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CHAPTER 4: BALANCING RESOURCES, RISKS, AND NEIGHBOURS: IMPLICATIONS FOR CARIBOU ANNUAL REPRODUCTIVE SUCCESS

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4.1 Abstract

Balancing the reward of high-quality forage against the risk of predation is a fundamental challenge for most species. This trade-off becomes more critical during reproduction, when animals must not only acquire more resources to provision offspring but also face an increased indirect risk of predation to vulnerable young. To minimize the probability of loss of young and to improve annual reproductive success, individuals may select for areas with higher quality forage, avoid risky areas associated with predators, or in social species, aggregate with conspecifics to dilute the per capita probability of predation. Using two populations of radio-collared caribou (*Rangifer tarandus*) in Newfoundland, Canada, we investigated how maternal habitat use and aggregation affected the probability of calf mortality using a Cox proportional hazards model. We tested three variables quantified before and after parturition: 1) use of high-quality vegetation as indexed by the rate of change in normalized difference vegetation index; 2) avoidance of areas associated with predators based on selection functions for coyotes (*Canis latrans*); and 3) mean distance to other collared conspecifics. We detected a significant positive correlation between predation risk and calf mortality in one of our two populations. Neither selection for high-quality forage nor distance to conspecifics was correlated with calf survival in either population. Predation risk appeared to have predicted calf mortality in one of the populations we examined. We highlight that trade-offs between risks and resources that are modified by social contexts are likely to vary among populations.

Keywords: Annual reproductive success, caribou, foraging, Newfoundland, predation risk, social grouping, survival analysis, trade-offs.

4.2 Introduction

Finding quality forage and avoiding predation risk are two fundamental drivers of animal movement and habitat selection. Selection favours a balance between reducing the risk of predation against the costs of missed opportunities to forage (Lima 1998). How animals prioritize this trade-off depends on energy requirements and perception of risk (Ruckstuhl and Neuhaus 2006), both of which vary through time and by reproductive state (Pinard et al. 2012, Viejou et al. 2018). That is, animals may need to be more sensitive to predation risk when with vulnerable young. This can be accomplished by selecting for less risky habitats where risk of predation is reduced (Viejou et al. 2018), or by diluting per capita risk of predation by grouping with conspecifics (Hamilton 1971, Bonar et al. 2020). At the same time, individuals providing parental care must also increase foraging or find higher quality forage to provision offspring, either directly or indirectly via lactation which increases energetic demands (Parker et al. 1999). For many species, mortality is highest in the first days to months of life (Gaillard et al. 2000). There should thus be fitness benefits—for example, increased annual reproductive success—associated with managing the trade-off between energy gain and risk avoidance as energetic needs and reproductive state change over time (Lima and Dill 1990). Knowing how energy–predation trade-offs affect annual reproductive success is important, as drivers of species declines are often unknown or difficult to investigate; therefore, elucidating how parental strategies affect annual reproductive success can help inform drivers of population vital rates.

To increase survival and annual reproductive success, prey animals should have evolved behavioural strategies that minimize encounters with predators. For example, prey species alter fine-scale habitat selection (Creel et al. 2005, Mao et al. 2005) and home range placement (Perry et al. 2020) in response to predation pressure. Antipredator responses, however, should be sensitive to current risk (Lima and Dill 1990), which in turn is often associated with reproductive status. Females with young face an increased indirect risk as young are susceptible to predation (Adams et al. 1995). As such, females with young are likely to be more risk averse. For example, caribou (*Rangifer tarandus*) in mountainous areas calved at higher elevation where predation risk was lower (Bergerud and Page 1987), and caribou with calves avoided areas associated with higher predation risk more than those without calves (Leblond et al. 2016, Viejou et al. 2018). Aggregating with conspecifics may also serve as an anti-predator strategy. While larger groups may be easier to detect (Hebblewhite and Pletscher 2002), this is mitigated by the advantages of group vigilance (Pulliam 1973), and dilution of the per capita odds of being attacked by a predator in larger groups (Hamilton 1971, Foster and Treherne 1981, Bonar et al. 2020). Despite anti-predator advantages, living in groups can be costly as competition for foraging resources increases (Grand and Dill 1999). Predators also seek to find prey, and may select for habitats that are deemed high quality by prey (Kittle et al. 2017), resulting in a shell game where prey may seek to use space less predictably to avoid predator learning (Mitchell and Lima 2002). Prey species must therefore weigh the risks and rewards of choosing habitats that otherwise provide valuable forage resources.

Selection for habitat with adequate nutrition has consequences for body condition and reproductive success (Parker et al. 2009). For herbivores, forage quality is linked to the phenological state of forage plants. Individuals gain the most benefit by foraging on plants at an intermediate stage of growth, where digestibility is high and biomass is sufficient (the Forage Maturation Hypothesis; Fryxell 1991, Hebblewhite et al. 2008). Plants mature at different rates in heterogeneous landscapes, allowing animals to spatially track and select for areas where forage quality is highest. Such tracking typically occurs across elevational and latitudinal gradients and is termed “surfing the green wave” (Bischof et al. 2012, Shariatinajafabadi et al. 2014, Merkle et al. 2016, Aikens et al. 2017). Other populations may time reproductive phenology to match the peak of green-up to gain a nutritional benefit from these forage resources when energetic needs are highest (Chapter 2, Post and Forchhammer 2008, Mysterud et al. 2017, Laforge et al. 2021). This would then result in a scenario where individuals should select for areas associated with emerging vegetation at the local (i.e. home range) level, as opposed to surfing a wave of vegetation *per se* during migration (Webber et al. 2020). Selection of areas associated with high-quality, newly-emergent vegetation has been associated with higher fecal crude protein levels (Hamel et al. 2009) and increased fat gain (Middleton et al. 2018) in ungulates. Selection for high-quality forage is important because energetic requirements can increase by 50% in late pregnancy for female ungulates, and increase to over 215% of baseline two to three weeks post-parturition when demands from lactation are highest (Oftedal 1985, Robbins 1993, Parker et al. 1999). This increased energy requirement suggests that reproductive individuals must energetically finance the cost of lactation by increasing energy intake prior to parturition to increase fat stores before birth, following parturition, or both.

Here, we assess how strategies related to selection of quality forage, avoidance of predation risk, and group aggregation both before and after parturition affect annual reproductive success of female caribou. Caribou are a species at risk globally (Vors and Boyce 2009), thus investigating links between forage use, avoidance of predation and group size on survival will be important when working to design effective management strategies that improve reproductive success and increase population growth (e.g., Serrouya et al. 2019). Caribou are often considered income breeders (Kerby and Post 2013), and in our study area the calving season corresponds with the time in which vegetation quality is highest (Chapter 2, Laforge et al. 2021), providing an excellent system in which to test predictions around forage use, predator avoidance, and aggregation and how these change based on reproductive state. While caribou in Newfoundland have been shown to avoid areas associated with predators and select for areas with more forage (Bastille-Rousseau et al. 2015), the consequences of this selection on annual reproductive success have yet to be tested. We implemented a survival analysis to test the influence of predation risk (based on coyote (*Canis latrans*) habitat selection), forage quality, and distance to conspecifics on calf survival during the first four weeks following parturition to determine the relative contribution of each in determining calf survival and therefore female reproductive success. We tested the influence of these variables both before and after parturition to examine whether shifting strategies (or adopting new ones) following parturition improved calf survival and subsequently fitness. We tested three, non-mutually exclusive hypotheses and their associated predictions:

1) Calves die due to direct encounters with predators, which are likely higher in areas more frequently selected by those predators. We therefore predicted that calf mortality would increase as females with calves selected for areas with increased predation risk from coyotes after parturition. Predation risk should not be a factor prior to parturition, as predation on adult caribou in Newfoundland is rare.
2) Increased use of high-quality vegetation, either before or after parturition, will increase maternal condition and in turn result in faster offspring growth due to higher-quality milk which should result in improved calf survival. We predicted that calf mortality would be lower when use of high-quality forage is higher both before and after parturition. Caribou may display a strategy of selecting for high-quality forage primarily prior to parturition when less constrained by predation risk (capital breeding

strategy), or primarily after parturition when needs are highest despite higher predation risk (income breeding strategy).

3) Associating with conspecifics will dilute the risk of calf mortality. We therefore predicted that calf mortality will decrease when caribou associate more with conspecifics after parturition to mitigate the effect of predation risk. Calf survival should be agnostic to grouping behaviour prior to parturition, or calf survival may increase in individuals further from conspecifics if competition results in reduced access to forage in pregnant females.

4.3 Methods

We investigated three variables at two different time scales to examine daily probability of survival using a Cox proportional hazards survival model. We first quantified high-quality forage by quantifying the rate of change in the normalized difference vegetation index (Section 4.3.4). We next quantified risk of predation from coyotes using a habitat selection analysis, which we varied at the daily scale to capture daily variation in selection behaviour (Section 4.3.5). We also determined the mean distance that each individual was from collared conspecifics within the population as a measure of social aggregation (Section 4.3.6). These variables were then used to predict calf survival in our model (Section 4.3.7; see Figure 4.1). Each row in the data frame included the mean value of our three response variables two weeks prior to parturition, the daily values of each variable, and the status of the calf (alive or dead), for the first four weeks following parturition.

4.3.1 Study site

Our study occurred on the island of Newfoundland, Canada. Newfoundland has a maritime climate with ample year-round precipitation. It is dominated by boreal forest, primarily balsam fir (*Abies balsamea*) and spruce (*Picea* spp.), along with stands of aspen (*Populus* spp.) and white birch (*Betula papyrifera*). Forests are interspersed with lakes, wetlands, and open rocky and lichen barrens. Wolves (*Canis lupus*) have been extirpated from Newfoundland since ~ 1930s, as such the main predators of caribou in Newfoundland are coyotes and black bears (*Ursus americanus*), which prey primarily on calves (Bastille-Rousseau et al. 2015, 2016, Mahoney et al. 2016). While black bears are also significant predators of caribou calves in Newfoundland, we unfortunately did not have access to collar data on black bears for this study, and therefore focused on risk from coyotes.

4.3.2 Study animals

Our study used data on GPS-collared adult female caribou (*n* = 49) in two populations in Newfoundland for which telemetry data on co-occurring coyotes were also available, Middle Ridge (*n* = 31) and Lapoile (*n* = 18, Figure 4.2). Predation risk was estimated using habitat selection functions from coyotes (*n* = 81) captured in the same areas as our two study populations of caribou (Middle Ridge, *n* = 30 F and 28 M; Lapoile, *n* = 6 F and 17 M). Coyotes and caribou were captured via helicopter from 2006–2010 and fitted with radio-collars that took locations every 1–4h. Survival monitoring of caribou calves from the mid-80s until the mid-2010s revealed that coyote predation was responsible for the mortality of ~12% and ~16% of calves in the Lapoile and Middle Ridge populations, respectively (Bastille-Rousseau et al. 2016). Coyote predation however, became an increasing source of mortality into the early 2000s, accounting for ~40-60% of mortality events (Mahoney et al. 2016).

4.3.3 Caribou birthing and calf survival

To determine calving status, we used the method developed by DeMars et al. (2013) and validated by Bonar et al. (2018) to determine whether and when individuals gave birth, whether calves survived up to 4 weeks of age, and the date that calves died. These methods capitalized on the fact that a mother's movement rate is constrained when giving birth. Mothers must stop to give birth and reduce movement rates with a calf at heel as young cannot travel as quickly as adults. If calves die before four weeks of age, however, mothers return to baseline movement rates faster than if they still had a calf-at-heel. To determine whether and when individuals gave birth in a given year of our study, we applied a population-based method that evaluated three-day average movement rates of females (Bonar et al. 2018). This method was validated using the individuals from the Middle Ridge herd and was found to have correctly classified 100% of parturition events. To determine calf mortality, we used an individual-based method that used GPS step length and maximum likelihood estimation to predict calf mortality up to four weeks of age. This method correctly classified 100% of mortality events in the Middle Ridge herd. For more details, see Bonar et al. (2018).

4.3.4 Quantifying high-quality forage

To quantify high-quality forage in our caribou survival analysis, we calculated the instantaneous rate of green-up (IRG) which represents the time when plant growth is highest. IRG is quantified as the first derivative of a series of normalized difference vegetation index (NDVI) values through time at a given location/pixel. NDVI data from two MODIS satellites (Terra and Aqua) were downloaded from NASA (https://search.earthdata.nasa.gov). Each MODIS satellite produces composite images every 16 days with a spatial resolution of 250 × 250 m. These composite images are phased across the two satellites, and given that the sensors on the two satellites are identical, the two data streams can be combined to generate a time series with an 8-day temporal resolution. We fit the data using the following procedure: 1) we set all pixel values that were coded as cloud, snow/ice, or unreliable as NA; 2) we "floored" the data by calculating the 3rd percentile of all snow-free values at a given pixel and substituted it for any lower values (Bischof et al. 2012). This is done to remove the signal of melting snow in the calculation of the green-up profile; 3) we replaced missing pixel values with the mean pixel values in a surrounding 5 × 5 pixel window, leaving as NA any pixels where all pixels in the 5 × 5 window were also NA (for details, see Chapter 2, Laforge et al. 2021); 4) we next applied a three-observation moving median filter to the time series for each pixel to reduce noise in the time series; 5) we fit a logistic curve to spring green-up and took the first derivative of this curve, estimated daily, as our measure of IRG. All analyses were performed in R version 3.6.1 (R Core Team 2019).

4.3.5 Coyote habitat selection functions

We used Landsat-derived landcover data with a 30 m spatial resolution for our coyote habitat selection functions (Newfoundland Department of Environment and Conservation 2014). Landcover types in this dataset included wetland, broadleaf forest, mixedwood forest, conifer forest, conifer scrub, rocky barrens, lichen barrens, and anthropogenic features. We also used a digital elevation map (Natural Resources Canada 2006) from which we also calculated terrain ruggedness using the *raster* package (version 3.1-5; Hijmans 2019) in R. We also used distance to the nearest anthropogenic feature (roads and trails; Newfoundland Department of Environment and Conservation, unpublished data).

We generated habitat selection functions for coyotes to estimate predation risk for caribou. Habitat selection functions are logistic regressions comparing attributes of used locations to those that could have been used by an animal (Manly et al. 2002, Northrup et al. 2021). We also wanted to quantify how coyote selection changed through time as a function of seasonality through the spring. To do this, we generated habitat selection functions using a moving window analysis. Using a moving window analysis allowed us to model changing predator habitat selection into our models. These moving window habitat selection functions were then used to model predation risk for caribou in our calf survival model. The "width" of our moving window was 21 days (the focal day and a buffer of 10 days to either side). Since our coyote data spanned multiple years, we assumed that it would be more appropriate to group data across years based on plant phenology (as opposed to calendar date). That is, we assumed coyote behaviour would be more similar across years, for example, 15 days prior to green-up as opposed to on May 15th. Sampling windows for our coyote habitat selection functions were therefore grouped based on days before or after green-up (the median date when IRG reached its maximum value within the coyotes' range) and the data were subsetted and calculated using the following procedure:

1) Our primary period of inference for our final caribou analysis was from two weeks before parturition to four weeks after parturition. We first subsetted the coyote data to start two weeks prior to the earliest parturition event in the caribou data until four weeks after the latest parturition event, buffered by 10 days on both ends to include all relevant data.
2) We calculated the mean day of green-up in both coyote ranges (99.9% minimum convex polygon (MCP) around all coyote locations after subsetting in step 1) as the median date in which pixels reached peak IRG within that range each year using that subset of locations. We then subtracted this date of peak IRG for each year from the

Julian day of the location of the animal to get a “days from peak IRG” for each coyote location.

3) To further refine the temporal extent of the required coyote data, we repeated steps 1) and 2) above but instead used the date of peak green-up in coyote range relative to peak green-up of caribou in caribou ranges to subset the data. That is, if the earliest parturition event occurred 10 days before green-up in caribou range, we subsetted the coyote data to include locations starting 34 days (two weeks plus 10-day buffer) before green-up in the coyote range as first determined using our preliminary subset based on calendar dates. This represented a minor change as the spatial extent of caribou and coyotes overlapped but was not identical, allowing for more precision in calculating green-up based on the coyote data itself.

For each population, we generated habitat selection functions at the landscape (2nd order *sensu* Johnson 1980) scale, as we assumed this would be the most relevant scale that would affect caribou habitat selection. We generated 10 random points per used point within a 99.9% MCP surrounding all coyote used locations. We first generated a fully parameterized habitat selection function using all data for each of the populations. Models included elevation, terrain ruggedness, distance to linear features, conifer forest, mixed wood forest, conifer scrub, lichen barrens, and rocky barrens. We did not include anthropogenic features or broadleaf in our models as these cover types were both very rare on the landscape. We quantified landcover types as proportions of habitat within a 100 m buffer to incorporate habitat selection around each point when fitting the models. Distance to nearest linear feature was log transformed, and we divided both elevation and terrain ruggedness by their highest value to scale them to between 0 and 1 to put them on the same scale as our habitat proportion variables. Since our goal for this analysis was focused on prediction and to simplify generating models using our moving window approach, we opted to simply fit the full model for each population. We calculated variance inflation factors (VIF) to ensure that no variables resulted in issues with multi-collinearity (VIF < 2).

We next generated our daily habitat selection functions for each herd using our moving window analysis. For each day (relative to green-up timing), we subsetted the data to include the focal day along with ten days before and ten days after, and fit the same habitat selection function model as defined above. We opted to not fit a mixed effects model for this moving window analysis to avoid overfitting given the short temporal extent of each habitat selection function. We then extracted the coefficient values and their standard errors. These daily habitat selection functions were then used to predict predation risk for caribou in our survival analyses. We also calculated, for each model, a k-fold (k = 5) cross validation score (see Figure S4.1).

4.3.6 Mean neighbour distance

To calculate mean neighbour distance, we grouped observations of multiple individuals taken at the same time (with a tolerance of five minutes), and calculated the mean distance to other collared conspecifics within the same population using the Spatsoc package (version 0.1.14, Robitaille et al. 2019). Since we only had a subset of individuals in each population collared (~0.7%), our estimates of mean distance to conspecifics assume that collared individuals represent a random sampling of individuals within each population. We are confident that this is the case, as individuals were captured at random and on winter range, suggesting that their relative positions on calving grounds should be representative of each population as a whole. We therefore assumed that our sample of individuals was indeed a representative sample of individual spacing on the calving ground (Bonar et al. 2020).

4.3.7 Caribou survival analyses

Our models included predation risk (as defined by our coyote habitat selection functions), high-quality forage as predicted by IRG, and mean neighbour distance. To test how these affected the probability of calf mortality, we implemented survival analyses using Cox proportional hazards models using R package *survival* version 3.2-11 (Therneau 2021). We quantified covariates for each day between parturition and either when the calf died or reached four weeks of age at which point it was removed from the analysis. We used four weeks of age as a cutoff as this represents the most vulnerable time for calves, and because our model becomes less reliable at detecting mortality events after this point. We took the average of each covariate across locations within the same day to aggregate data to the daily scale. We also included the mean values of our covariates for the two weeks prior to parturition to determine whether habitat selection prior to having a calf also influenced the probability of calf survival, which was invariant across observations for the same female-calf pair throughout the calving season. Because we assumed that forage quality would have a lag effect, we applied a 10-day moving average to our measure of habitat quality. We used the *frailty* function to incorporate a random effect for animal ID in our models to account for the fact that females had multiple calves across years. We fit four different models plus an intercept-only model. The first three models corresponded to each of our three main hypotheses (predation risk, forage, and distance to conspecifics) plus a full model that included all three. We compared models using AIC and performed likelihood ratio tests to determine whether models were statistically more explanatory than the null model. We centered and scaled all explanatory variables. We fit models separately for our two populations. We calculated Pearson correlation coefficients to test for collinearity between our variables to ensure that no variables had $p > |0.7|$. We selected the model with the lowest AIC and confirmed that the model met the assumption of proportional hazards by using the cox.zph function in the *survival* package. We dropped any variables that violated the assumption of proportional hazards.

4.4 Results

4.4.1 Coyote habitat selection functions

We found differences in habitat selection both through time and between the two populations. Coyotes in Middle Ridge selected lichen barrens and conifer scrub, and increased the use of rocky barrens and areas at higher elevation throughout the spring, and decreased their use of areas with rugged terrain throughout the spring. Coyotes in Lapoile selected rocky barrens and mixed wood forests and avoided conifer forests, lichen barrens, and areas of high terrain ruggedness. Both populations were more likely to select for areas closer to linear features later in the season (Figure 4.3). For a summary of model coefficients for the model fit using all data during the calving season, see Table S4.1. All model terms had a VIF < 2. Results of k-fold cross-validation analysis can be found in Figure S4.1.

4.4.2 Caribou survival models

We had data on the survival of a total of 104 calves (Middle Ridge = 55, Lapoile = 49) from 49 unique females (Middle Ridge = 31, Lapoile = 18) spanning 2041 total daily observations. We recorded a total of 40 mortality events, 16 in Middle Ridge (29.1%) and 24 in Lapoile (49.0%).

We dropped mean distance to neighbours before parturition as it was highly correlated with distance to neighbours at the daily scale in both populations (r = 0.85 for Lapoile, 0.73 for Middle Ridge). For Lapoile, the predation model, which included selection for coyote habitat selection risk layer both at the daily scale and before parturition was the most supported model based on AIC, however, predation risk before birth violated the assumption of proportional hazards. We therefore dropped this variable from all models and reran and re-ranked the models based on AIC (see Table 4.1). The predation model remained as the top model and now only included predation risk at the daily scale. For each standard deviation increase in the coyote habitat selection function value, risk of calf mortality increased by a factor of 1.68 (95% CI: 1.06, 2.66, $p = 0.026$; model $R^2 = 0.61$; Figure 4.4). The full model for the Lapoile population also had a lower AIC than the Null model, however predation risk was still the only significant term in the model (Table S4.2). No variables explained calf mortality in the Middle Ridge herd, as the top model was the intercept-only model, and no variables in the next-top model were significant (Table 4.1).

4.5 Discussion

Natural selection should favour individuals that are best able to balance forage acquisition while mitigating risks from predators (Lima and Dill 1990). For species where adult survival is high but offspring survival is variable, such as caribou in Newfoundland, fitness will primarily be determined by the ability to successfully raise offspring (Gaillard et al. 2000). As such, elucidating how forage selection/predation avoidance strategies of females with calves influence calf survival is key to monitoring population-level changes. Previous studies have shown that caribou do select for areas with more available forage and lower predation risk from coyotes and black bears (Bastille-Rousseau et al. 2015). Despite this, few studies have directly examined how selection of areas of high-quality forage and avoidance of areas associated with a high risk of predation in a spatially explicit way affect probability of calf survival. We failed to detect a correlation between selection of high-quality forage and calf survival at the scale we examined, and we only found evidence that avoiding areas associated with predators improved survival probability in the Lapoile population. Despite a predicted benefit of associating with conspecifics to dilute risk of predation (Hamilton 1971), we failed to detect an effect of mean neighbour distance on probability of calf mortality.

Our dynamic coyote habitat selection functions were predictive of calf mortality in the Lapoile population, but we did not find evidence for such a relationship in the Middle Ridge population. Several factors may have contributed to why we detected an effect in one population but not the other. The abundance of coyotes relative to other predators likely influenced whether avoiding areas selected by coyotes was an effective strategy to mitigate calf loss. Black bears are another important source of mortality for caribou neonates in Newfoundland (Rayl et al. 2015). If relative predation risk from bears was a more significant risk factor for caribou in Middle Ridge compared to Lapoile, then avoiding areas with coyotes may not have had as significant effect on survival rates if individuals instead selected for areas with less risk from bears.

Predation risk can also interact with previous environmental conditions and weather to influence calf mortality. The maternal condition hypothesis suggests that previous environmental conditions affect maternal body condition and subsequently calf body condition, making calves more vulnerable to predation or inducing females to forage in riskier locations to sustain the costs of lactation (Pettorelli et al. 2005, Griffin et al. 2011, Bastille-Rousseau et al. 2016). If access to resources was more limited in Lapoile, it could lead to females who are in poorer condition with calves that are more vulnerable to predation. If calves were in better condition in Middle Ridge, they may have been better able to escape from predators if attacked, reducing the consequences of selecting for areas associated with coyotes. More proximately, weather conditions during the calving season may alter selection behaviour of cow–calf pairs, altering their potential interactions with predators (Griffin et al. 2011, Bastille-Rousseau et al. 2016). The Lapoile population may have been exposed to more adverse spring weather events, resulting in riskier behaviour and a stronger signal of predation risk influencing calf mortality. Future studies should continue to investigate how weather at multiple temporal scales interacts with forage availability in predicting annual reproductive success outcomes.

While aggregating with conspecifics may reduce the likelihood of predation by diluting per capita risk (Hamilton 1971), separating from conspecifics can also have advantages which may have resulted in us failing to detect an effect of neighbour distance on calf survival. Larger groups are easier to detect (Hebblewhite and Pletscher 2002), therefore some individuals may choose a strategy of reducing detection probability instead of seeking the safety afforded by aggregating in groups. Calf survival in the Middle Ridge population was found to be equal among individuals who chose to aggregate versus those who did not, suggesting that both strategies resulted in equal annual reproductive success (Bonar et al. 2020). Despite this, individuals that were closer to the periphery of calving aggregations faced an increased risk of having their calves depredated, suggesting that the relationship between distance to conspecifics and calf mortality may be non-linear.

Counter to our prediction that use of areas with high-quality forage would decrease calf mortality, we failed to detect an effect of use of IRG on the probability of calf mortality in either population. Bastille-Rousseau et al (2016) also did not find a significant effect of rate of green-up on survival rates at broader spatial scales. It is possible that IRG within each herd’s range during calving is relatively homogeneous, and therefore present little difference in forage benefits throughout the range. Plants also green-up at different rates, and therefore plants selected by caribou may not represent the dominant plant species within a 250 × 250 m pixel, which may obscure actual selection that may occur at finer scales then indexed by our NDVI data (Merkle et al. 2016). Variation in IRG in the study area may be more important temporally than spatially, such that selection for IRG during the calving season is less important than giving birth at the correct time to match conditions at broader spatial scales (Chapter 2, Laforge et al. 2021). There may also be a trade-off between selection for forage and predator avoidance. If areas of high-quality forage are selected by predators such as coyotes or bears, this may result in a situation where a strategy of selecting higher-quality forage in areas of higher risk is balanced against a safer strategy of sacrificing forage quality for safety from predators (Lima and Dill 1990).

The factors we examined in this study likely also interacted with caribou density in driving calf mortality. Caribou population numbers in Newfoundland have fluctuated dramatically in recent decades, from a contemporary peak in the mid 1990s of ~96,000 individuals before declining to an estimated 33,000 individuals near the end of our study period in 2012 (Weir et al. 2014). During the peak of the decline phase, predation risk to neonates was influenced more strongly by weather events during calving as females and calves were under greater nutritional stress (Bastille-Rousseau et al. 2016). While declining calf survival due to increased predation on calves is thought to be the main causal factor contributing to declines, it is thought that this is mediated by lower forage availability following periods of high density (Mahoney and Schaefer 2002, COSEWIC 2014). Increased forage availability at the end of the decline phase as range quality began to improve may have resulted in less need for caribou to select areas with higher IRG, which may therefore be a more significant factor on calf survival at the population peak or early in the decline phase when forage was more limiting.

Elucidating proximal causes of variation in annual reproductive success and fitness is key to properly managing populations, especially in a time of rapid environmental change. Our results suggest a limited role of forage use as indexed by NDVI at fine spatial scales or of proximity to conspecifics in driving calf survival at these population densities during a decline phase. We found an effect of predation in one of our populations but not the other, suggesting that predation risk may depend on context. Nutrition and predation are both important drivers of calf survival and population demographics in Newfoundland (Mahoney and Schaefer 2002, Bastille-Rousseau et al. 2016), but we failed to detect much evidence that fine-scale selection behaviour contributed meaningfully to variation in calf survival rates.

4.6 Acknowledgments

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Table 4.1: ΔAIC, Akaike weights and likelihood ratio test results for Cox proportional hazards models describing probability of caribou (*Rangifer tarandus*) calf death up to four weeks of age on the island of Newfoundland, Canada. Results presented for two populations, Lapoile and Middle Ridge. Likelihood ratio tests (LRT) were performed compared to the null model. Models were fit separately for each population. IRG = instantaneous rate of green-up (first derivative of normalized difference vegetation index, see Methods).

Population	Model	Terms	Delta AIC	Akaike weight	LL	LRT test
Lapoile	Predation	Current predation risk	0	0.606	-75.4	χ^2 (3.84) = 11.93, p = 0.016
	Full	Predation + Green-up + Social	1.7	0.256	-72.8	χ^2 (7.2) = 16.94, p = 0.020
	Null	None	4.3	0.072	-81.3	-
	Social	Mean distance to conspecifics	5.6	0.037	-81.3	χ^2 (0.64) = 0.06, p = 0.641
	Green-up	Mean IRG last 10 days, IRG before parturition	6.1	0.029	-78.6	χ^2 (3.61) = 5.38, p = 0.207
Middle Ridge	Null	None	0	0.434	-61.7	-
	Predation	Current predation risk, predation risk before parturition	0.7	0.303	-60.1	χ^2 (2) = 3.28, p = 0.194

Social	Mean distance to conspecifics	2.0	0.160	-61.7	χ^2 (1) = 0, p = 0.973
Green-up	Mean IRG last 10 days, IRG before parturition	3.5	0.076	-61.4	χ^2 (2) = 0.51, p = 0.776
Full	Predation + Green-up + Social	5.6	0.027	-59.5	χ^2 (5) = 4.44, p = 0.488

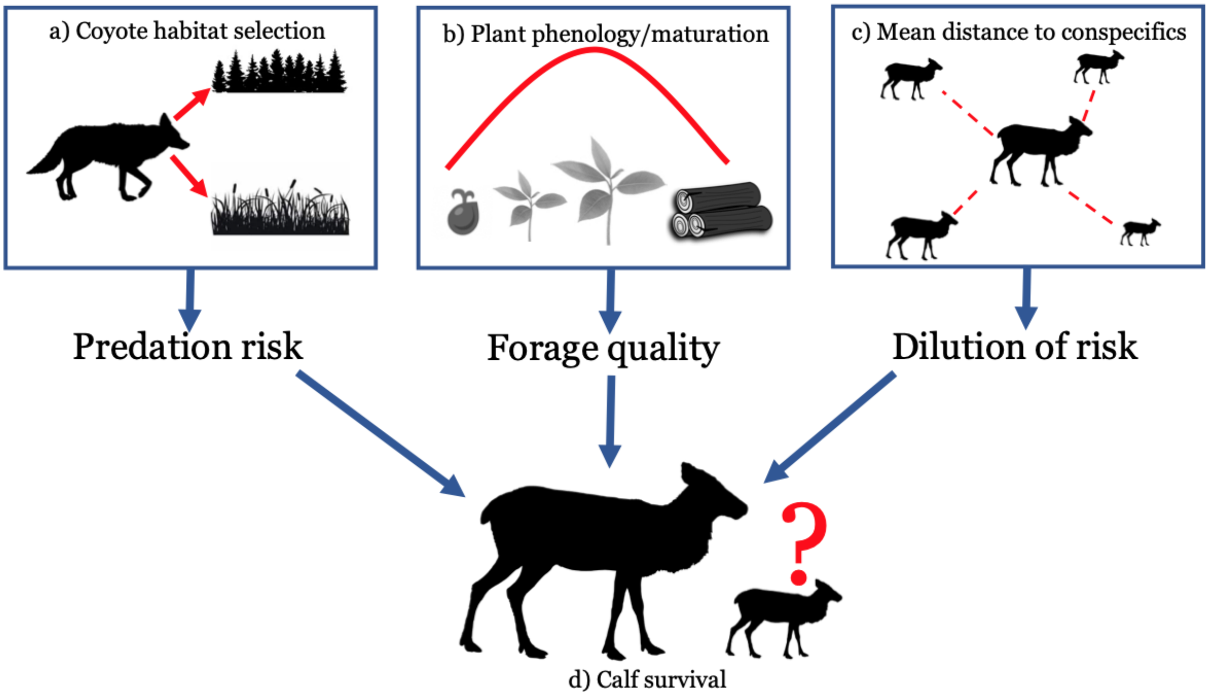

Figure 4.1: Methods overview of survival analysis for caribou (*Rangifer tarandus*) calves (*n* = 104) in Newfoundland. We quantified a) predation risk from coyotes using habitat selection analyses; b) forage quality as indexed by the rate of change of the normalized difference vegetation index; and c) mean distance from collared conspecifics as a measure of dilution of per capita risk of predation. These spatially explicit variables were then used to predict the fate of caribou calves in a Cox proportional hazards model. All three variables were fit at two timescales: the mean two weeks prior to parturition, and at the daily scale after parturition until four weeks post-parturition (10-day rolling average in the case of forage quality).

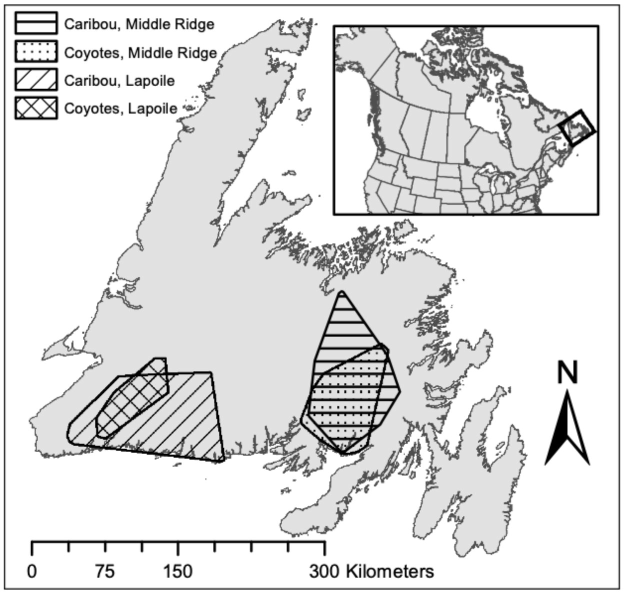

Figure 4.2: The island of Newfoundland with 100% minimum convex polygon ranges for the two populations of caribou (*Rangifer tarandus*) and coyotes (*Canis latrans*) used in this study (Middle Ridge and Lapoile).

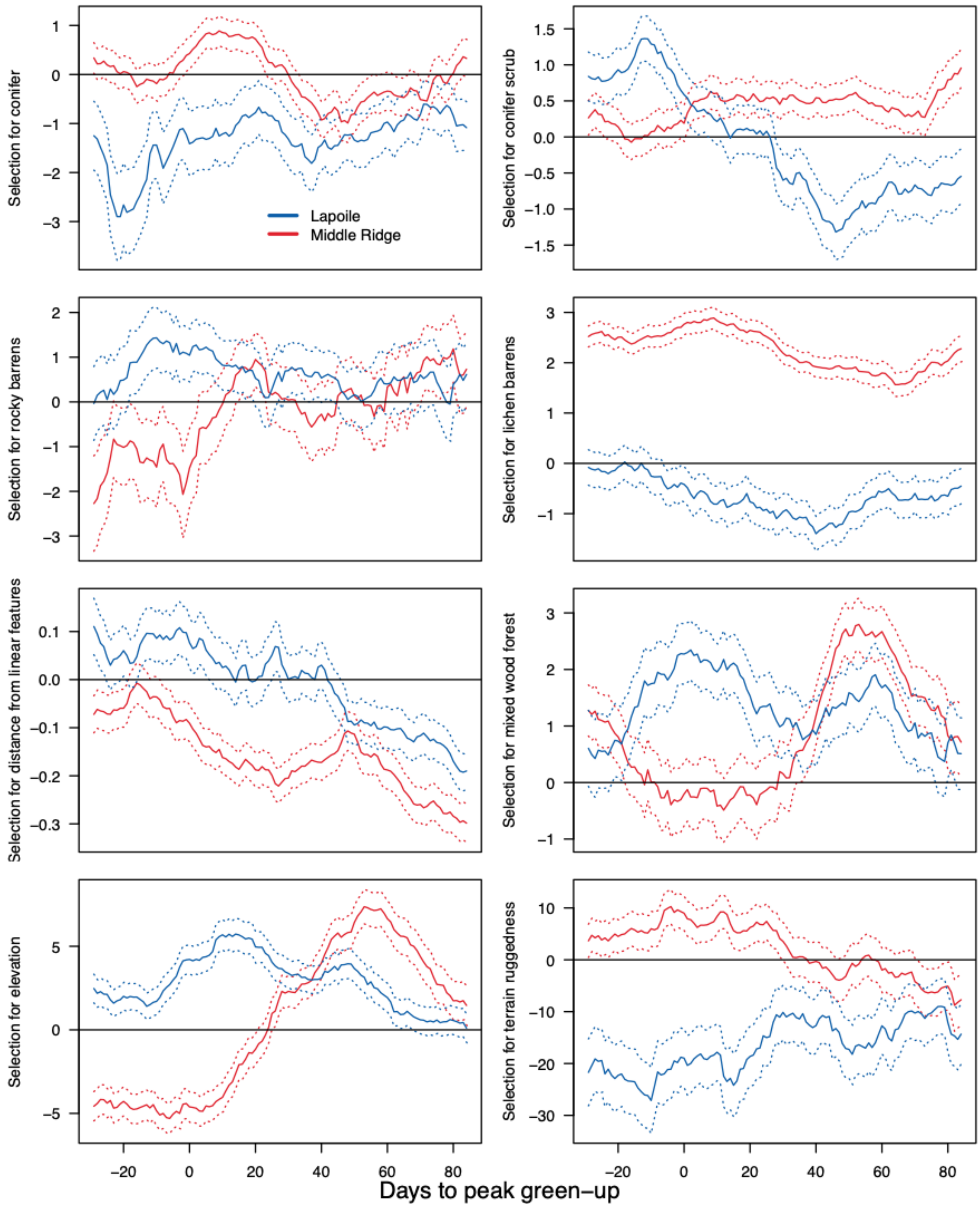

Figure 4.3: Results of rolling window habitat selection functions for coyotes (*Canis latrans*) in Lapoile (*n* = 23, blue) and Middle Ridge (*n* = 58, red) from 2008–2013 in Newfoundland. Habitat selection functions were fit for each day relative to the peak of vegetation green-up

within their range with a ten-day buffer to either side (see Methods). Solid lines represent beta coefficient parameter estimates and dashed lines represent 95% confidence intervals. Solid black horizontal lines represent no selection or avoidance.

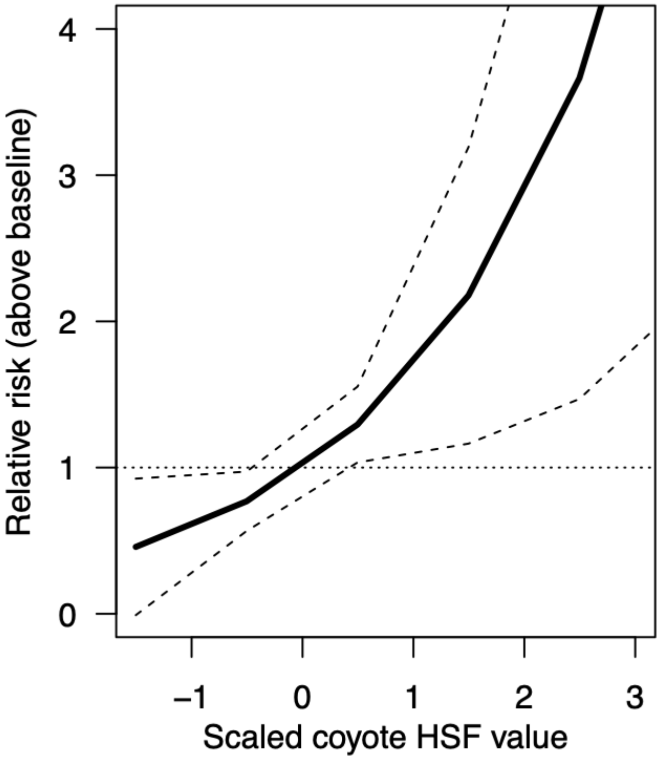

Figure 4.4: Relative risk of mortality of caribou (*Rangifer tarandus*) calves (*n* = 49) from the Lapoile population in Newfoundland, Canada as a function of the coyote (*Canis latrans*) habitat selection function (HSF) value used by the female fit using a Cox proportional hazards model.

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CHAPTER 5: CONSISTENT INDIVIDUAL DIFFERENCES AND PLASTICITY IN MIGRATION BEHAVIOUR OF NORTH AMERICAN UNGULATES TO ENVIRONMENTAL VARIABILITY

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5.1 Abstract

Migration is a behaviour that is at risk. Climate change alters the timing of resource availability, decoupling consumers from their resources during migration. To persist, migratory individuals must acclimate or populations must adapt to this change; either by being plastic to changes in the environment to avoid phenological asynchrony, or via differences among individuals in the population that drive an evolutionary response. We examined plasticity in migration timing to the timing of spring green-up and quantified individual differences in migration timing in eight populations of four species of ungulate in Wyoming, USA. Timing of migration was plastic to timing of green-up and repeatable. However, plasticity did not result in higher selection for high-quality forage during migration. Early springs did not result in a decline in selection for forage that may have indicated a phenological asynchrony. Our results are overall good news for migratory ungulates faced with changing environments.

Keywords: Acclimation, behavioural reaction norms, climate change, consistent individual differences, herbivores, migration, plasticity, repeatability, surfing the green wave, Wyoming.

5.2 Introduction

Animals migrate to enhance their acquisition of resources that vary through space and time (Shaw 2012). Migration is most beneficial when animals migrate at the correct time to match the temporal abundance of forage resources. For example, many migratory herbivores track the green-up of plants as they mature along latitudinal and altitudinal gradients (Shariatinajafabadi et al. 2014, Merkle et al. 2016, Aikens et al. 2017). Yet, the Anthropocene is marked by unprecedented environmental change (Parmesan and Yohe 2003, Urban et al. 2016), resulting in a phenological asynchrony where consumers fail to match the timing of life-history events to resource availability. For example, egg-laying dates of great tits (*Parus major*) did not advance concurrently with an advance in the date of peak caterpillar abundance in The Netherlands, reducing fitness (Visser et al. 1998). Changing green-up phenology in North America has altered arrival timing of migratory birds, but not always enough to avoid a potential asynchrony or mismatch (Mayor et al. 2017). Persistence in the face of environmental change can occur in two ways: individuals can acclimate their behaviour to match the change in resource distributions, or differences among individuals can drive an evolutionary response within populations as natural selection favours better adapted phenotypes (Boutin and Lane 2014). In a changing world, the fate of migratory species could well depend on their ability to either acclimate to new conditions or adapt via variation in migratory phenotypes.

Many herbivores track the flush of high-quality vegetation resources as they progress from low to high elevations and latitudes in a behaviour known as “surfing the green wave” (Bischof et al. 2012, Merkle et al. 2016). Tracking resources allows animals to exploit them for a greater period of time (Drent et al. 1978). Green wave surfing has been documented in numerous taxa. In birds, Barnacle geese (*Branta leucopsis*) have been shown to initially follow the green wave during migration before overtaking it to arrive on breeding range with the onset of spring to ensure peak nutritional availability for goslings (Si et al. 2015). In terrestrial mammals, many species including mule deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), elk (*Cervus canadensis*), caribou (*Rangifer tarandus*), red deer (*Cervus elaphus*), moose (*Alces alces*) and bison (*Bison bison*) match the timing of their migrations to correspond with the timing of the green wave (Bischof et al. 2012, Merkle et al. 2016, Rivrud et al. 2016, 2018, Aikens et al. 2017). Green-up that occurs over a longer period increases overall availability of high-quality forage throughout the season, increasing growth and survival of juvenile ungulates (Pettorelli et al. 2007, Monteith et al. 2015). Altitudinal gradients in migration routes in red deer were positively correlated with weight gain (Mysterud et al. 2001), and selecting locations closer to the peak of green-up has been shown to improve fat gain in elk (Middleton et al. 2018). Migrating at the correct time to exploit forage resources is therefore vital for individual fitness and population persistence. But tracking is not easy as the inter-annual timing of green-up at a single location can vary from 20 days to 50 days across northern North America and Eurasia (Delbart 2021). To efficiently surf the green wave across years where environmental conditions alter the timing of green-up, individuals should have the capacity to acclimate the timing of their migrations to match the timing of the peak in resource quality during migration.

Behavioural plasticity, the ability to alter behaviour as environmental conditions change, illustrates how individuals acclimate to changing circumstances over their lifetimes (Piersma & Drent 2003; Dingemanse et al. 2010; Mathot et al. 2012; Box 5.1). For example, killer whales (*Orcinus orca*) in the north-east Atlantic alter the depth at which they forage as a function of the life stage and distribution of herring (*Clupea harengus*) prey (Samarra and Miller 2015). Similarly, African oribi (*Ourebia ourebia*) alter habitat selection, group size and dispersion behaviour as a function of the distribution of resources across the wet and dry seasons (Brashares and Arcese 2002). In migratory herbivores, elk alter the timing of migration to changes in environmental conditions such as timing of snowmelt and green-up (Rickbeil et al. 2019). Plasticity may therefore serve as a mechanism for species to acclimate to changes in resource phenology (Boutin and Lane 2014, Charmantier and Gienapp 2014).

In addition to plasticity, populations can adapt to change via consistent differences among individuals, which, if transmissible, could drive an evolutionary response to allow populations to adapt. Individuals within a population often display variation in behavioural phenotypes, that is, there are differences among individuals that remain consistent across time and contexts (Réale et al. 2007; Box 5.1). For example, individual grizzly bears (*Ursus arctos*) were found to have different habitat selection patterns for bogs and cut blocks that remained consistent across years (Leclerc et al. 2016). Consistent individual differences have also been described in the context of dispersal (Cote et al. 2010, Quinn et al. 2011), recursive movement (Berger-Tal and Bar-David 2015), and foraging behaviour (Webber et al. 2020). Quantifying individual differences in behaviour provides a baseline for the level of heritability of that behaviour (Dochtermann et al. 2015), a fundamental requirement for natural selection and adaptation in the face of changing environmental conditions. In addition to genetic heritability, behaviours can also be transmitted via maternal environment or through cultural transmission (Whiten 2005, Tennie et al. 2009). For example, ungulate populations have been shown to culturally transmit information on migratory routes to conspecifics (Jesmer et al. 2018). Transmissible differences in migration timing or selection for green-up could provide a mechanism for populations to adapt in the face of environmental change in green-up phenology.

Migration behaviour is currently at risk (Wilcove and Wikelski 2008). Anthropogenic disturbance is resulting in a global decline in animal movement (Tucker et al. 2018), and climate change poses a distinct challenge to migrants (Robinson et al. 2009). Earlier and warmer springs result in an advance of phenological events at lower trophic levels that can be detrimental to migrants that depend on the predictability of resources to finance reproduction (Post et al. 2001). For example, insectivorous birds face population declines as a lack of plasticity to advancing insect emergence has resulted in mistimed arrival on summer range and egg laying (Visser et al. 1998, Both and Visser 2001, Both et al. 2006, Zhemchuzhnikov et al. 2021). Similarly, drought alters plant phenology and decreases access to high-quality resources by terrestrial herbivores by reducing green-up duration (Aikens et al. 2020), which in many locations will be exacerbated by climate change. While some studies suggest that phenological mismatch may threaten ungulate species (Post and Forchhammer 2008, Plard et al. 2014), the evidence is far from clear (Gustine et al. 2017, Rickbeil et al. 2019). If seasonal changes in plant growth occur along a gradient from winter to summer range and cues on the winter range are reliable indicators of future conditions on summer ranges, ungulates may buffer against changes in plant phenology by altering their migration timing. Likewise, consistent, transmissible variation among individuals (e.g., some individuals consistently migrate earlier) could provide variation to allow populations to adapt to new conditions and persist. The relative contribution of plasticity and evolution in determining species responses to environmental change remain an important question in both mammals (Boutin and Lane 2014) and birds (Charmantier and Gienapp 2014).

We examined plasticity and consistent individual differences in two important green wave surfing behaviours, 1) the timing of migration, e.g., date of departure from winter range and date of arrival on summer range; and 2) selection for emergent vegetation. We examined eight populations of four North American ungulate species (mule deer, elk, moose, and bison). We first tested two non-mutually exclusive hypotheses for how migratory ungulates are acclimating or have the potential to adapt to changing environmental conditions:

> H_1: We hypothesized that individuals use plant phenology as an environmental cue to time migration. We therefore predicted that timing of migration would be correlated with the timing of spring green-up.
>
> H_2: If different migration strategies exist among individuals in a population, we hypothesize that timing of migration (H_2a) and selection for high-quality forage (H_2b) during migration will be individual traits. We therefore predict a high repeatability value for when individuals leave winter range, arrive on summer range, and select for green-up.

We next tested two hypotheses regarding selection of green-up:

> H_3: Migrating at the correct time to match the timing of the green wave should increase selection for green-up. Individuals that are better able to acclimate to inter-annual variation in the timing of green-up by acclimating the timing of their migration should be better able to select for green-up across a range of spring conditions. We therefore predict a positive correlation between individual plasticity in migration timing and selection for green-up.
>
> H_4: If climate change is advancing spring green-up, resulting in phenological asynchrony in earlier springs, we hypothesize that selection for green-up will be stronger in later springs when conditions are closer to historical norms compared to early springs. In this case, we predict a positive relationship between timing of spring and selection of green-up.

Behavioural reaction norms (BRNs) are a conceptual and analytical tool used to identify individual behavioural responses across a gradient of environmental conditions, providing a framework for testing both plasticity and consistent individual differences (Dingemanse et al. 2010, see Box 5.1). In the context of behaviours that are threatened by climate change, BRNs provide a powerful tool to simultaneously test for how individuals acclimate or how consistent differences among individuals could drive an evolutionary response to change. By testing for plasticity and consistent differences in migratory behaviour across multiple species and systems, we gain not only a fundamental knowledge of the behavioural ecology of migration, but also work to understand how migrants may alter their behaviour as a function of environmental change to overcome phenological asynchrony (Shaw 2016).

5.3 Methods

5.3.1 Study area

Our study occurred in eight study sites (e.g., ranges) across the western half of the state of Wyoming, USA, with a few study sites extending slightly into the neighbouring states of Montana, Idaho, and Colorado (Figure 5.1). Low-elevation summer ranges are dominated by sagebrush steppe (*Artemisia* spp.), with higher-elevation summer range predominantly a mix of aspen (*Populus tremuloides*) and conifer (*Pinus* spp.) forests and sagebrush. Elevation ranges from approximately 1300 m to 4100 m.

5.3.2 Study populations

We studied four species of ungulates that undertake altitudinal migrations: mule deer (n = 2 populations, 86 individuals between 2009–2019, for a total of 284 spring migration events), elk (n = 3 populations, 74 individuals, 2007–2016, 193 spring migrations), moose (n = 2 populations, 23 individuals, 2005–2014, 45 spring migrations), and bison (n = 1 population, 47 individuals, 2005–2015, 144 spring migrations). Individuals were captured either via ground darting (bison) or via a netgun fired from a helicopter (all other populations) and equipped with GPS radio-collars.

5.3.3 Defining migration

Only individuals with a clearly spatially distinct summer and winter range were used in the analysis. To define the start and end dates of migration for each ID in each year (ID-year), we plotted net-squared displacement of a time-series of GPS collar locations next to detailed maps of the movement data itself with the aid of a custom GUI (Wyoming Migration Initiative 2017). We visually determined the last point an individual was in winter range to define the start of spring migration and the first point located in summer range to define the end of spring migration based on inspection of mapped locations and net-squared displacement. The mean migration distance across populations was 9.6–144.1 km. We excluded from analysis any individuals who had a nomadic movement profile with no defined winter or summer range. All analyses were conducted in R version 3.6.1 (R Core Team 2019).

5.3.4 Defining green-up

We used the instantaneous rate of green-up (IRG; Bischof et al. 2012, Merkle et al. 2016) to index forage quality (when green-up is happening at the fastest rate) and to define the relative timing of spring (Julian date at which IRG peaked) at different locations/years. The IRG is calculated by taking the first derivative of an annual time series of normalized difference vegetation index (NDVI) values at a given location. Plants are most nutritious at early stages of growth (Fryxell 1991, Hebblewhite et al. 2008). By quantifying the rate of change in plant growth as indexed by NDVI, the IRG provides a measure of forage quality by quantifying new plant growth in a given location (Bischof et al. 2012, Merkle et al. 2016). NDVI data were taken from surface reflectance bands 1 and 2 of the MODIS Terra satellite (MOD09Q1) which has a 250 × 250 m spatial resolution and an 8-day temporal resolution. We used the procedure used by Bischof et al (2012) and Merkle et al. (2016) to process IRG values. In brief, we first set all pixels contaminated by cloud or that had negative values to NA. We then set all NDVI values below the 0.025 quartile value of pixels that were categorized as being snow-free (based on the MOD09A1 MODIS snow cover band, 500 m^2) at each location to the value of the 0.025 quartile to remove the influence of melting snow from the analyses. Then, we applied a 3-observation moving window median analysis to the time-series of each location to smooth the data and scaled the NDVI data in each time series to between 0 and 1. Lastly, we fit a double logistic regression to each time-series and took the first derivative of this curve to calculate IRG. We calculated the date of peak IRG for each cell in each year as the Julian day that the IRG values were the largest.

To define the timing of spring for each herd, we first generated a 99% kernel range (using a fixed h-value of 400) for all locations for all individuals in each herd across all years and seasons. We used the same range across years to ensure that changes in the timing of spring were associated with changes in phenology, not due to changes in the overall location of herds or sampled individuals across years. We then extracted the Julian date of peak IRG for all pixels within the herd’s range for each year and used the median date to quantify the timing of spring for each herd in each year.

5.3.5 Habitat selection analyses

To define individual-level selection of IRG, we fit habitat selection functions using conditional logistic regression for each individual (Northrup et al. 2021). Selection functions are defined by comparing a set of used points to a distribution of locations available to the animal. To define available habitat during migration for our analyses, we first generated Brownian Bridge movement models using package *adehabitatHR* (version 0.4.16, Calenge 2015) for each ID-year at a resolution of 100 m. We then isolated/defined 99.99% contours to the Brownian Bridge occurrence distribution and generated 10 random points paired to each used point within this migration corridor. We then fit individual-level selection functions using separate conditional logistic regression models for each ID-year, with used versus available points as the response variable and IRG as the covariate. To account for changing availability of IRG through time, we fit our model as a conditional logistic regression, with our ten random locations associated with each point having IRG values associated with that point in time. Models were fit using package *mclogit* (version 0.6.1, Elff, 2017). We used beta coefficients from these models as individual-based measures of selection for IRG.

5.3.6 Behavioural reaction norms

To quantify individual differences in migration timing and selection for IRG as a function of the timing of spring, we used a behavioural reaction norm (BRN) framework (Dingemanse et al. 2010). A BRN framework quantifies both plasticity (random slopes) and consistent differences among individuals (random intercepts) in a single modelling framework (see Box 5.1). We fit bivariate behavioural reaction norms using Markov Chain Monte Carlo generalized linear mixed models using package *MCMCglmm* (Hadfield 2010). We developed two sets of models. Both used the beta coefficient value for selection of IRG from our individual conditional selection functions to quantify selection of high-quality forage as a co-response variable. In the first model set, the second co-response variable was date of departure from winter range, and in the second model we used date of arrival on summer range. Both were fit using a Gaussian distribution. Our model sets included models describing differences among populations or individuals (random slopes) in timing of migration and selection for IRG. Models also tested for plasticity to timing of green-up, with models that included random slopes for timing of green-up to model the effect of an individual × environment interaction, e.g., an interaction between individual and relative date of spring green-up (Nussey et al. 2007; Table 5.1). All continuous variables were centered (i.e., mean subtracted from each observation) independently for each population. For each analysis we chose the model with the lowest Deviance Information Criterion (DIC). We extracted best linear unbiased predictors (BLUPs) and calculated repeatability (r) of BRN intercepts for migration date and selection for IRG as the proportion of total phenotypic variation (individual + residual; $v_{ind} + v_{res}$) attributable to differences between individuals (v_{ind}) within a group (Dingemanse and Dochtermann 2013):

$$r = \frac{V_{ind}}{(V_{ind}+V_{res})} \qquad \text{[Formula 5.1].}$$

Repeatability therefore represents the proportion of unexplained variance that is explained due to differences among individuals. Repeatability values <0.3 are considered low, whereas values >0.5 are considered high (Falconer and Mackay 1996). We plotted the relationship between slope BLUPs for timing of migration and intercept BLUPs for selection of IRG to test for a correlation between these two traits. Typically, such phenotypic covariance plots are used to evaluate whether personality (i.e., behavioural phenotype) and plasticity for a given trait are correlated (slope-by-intercept correlation for a given trait), or to test for the existence of a behavioural syndrome (correlation of average phenotype or plasticity across behaviours) by regressing the intercepts or slopes of two different traits against each other (Sih et al. 2004). Here, we hypothesized that plasticity (slope) in our metric for timing of migration would be correlated with "personality" (e.g., intercept) of selection for IRG; that is, that plasticity in when individuals migrate should result in a better ability to surf the green wave.

5.4 Results

Our final dataset included a total of 230 individuals over a total of 666 spring migration events (ID-years). The median date of departure from winter range was Apr 26 (range Feb 2–Jul 28), while the median date of arrival on summer range was May 31 (Feb 10–Aug 22). Overall, most individuals selected for high-quality emergent vegetation (IRG), with a median selection coefficient from conditional logistic regression models of 0.51 (sd = 14.58; Table S5.1).

The top behavioural reaction norm model (lowest DIC) was the individual × environment interaction model, which included random slopes for each individual for timing of migration start or end and selection for IRG as a function of the timing of spring green up in the population's range (see Table 5.1). This was the case for both sets of models—those using date of departure from winter range and those using arrival on summer range. Random slopes in the top model suggest an individual × environment interaction, where individuals had different responses to changing spring conditions. In support of H_1, the timing of spring had a significant effect on the timing of migration, with individuals migrating later in years with later springs: departure from winter range (β (95% credible interval, MCMC p-value)) = 0.375 (0.174, 0.575, $p < 0.01$), arrival on summer range = 0.603 (0.435, 0.763, $p < 0.01$). See Figure 5.2a and 5.2b.

Across all herds, repeatability in the timing of migration was moderate for timing of departure from winter range ($r = 0.379$, $SD = 0.135$) and high for timing of arrival on summer range ($r = 0.608$ $SD = 0.142$). High repeatability provides strong evidence for H_2a that timing of migration is an individual trait. The repeatability of selection for IRG was low (departure model:

r = 0.217, SD = 0.115, arrival model: r = 0.205, SD = 0.110). This provided no support for H_2b, that selection for IRG is also an individual trait (Figure 5.3).

We found no correlation between the slope of timing of departure from winter range and overall selection for IRG (–0.143, 95% CI: –0.632, 0.363; Figure 5.4a), and a negative correlation between plasticity in timing of arrival on summer range and selection for IRG (–0.409, 95% CI: –0.828, –0.010; Figure 5.4b). This negative/lack of correlation provided no support for our third hypothesis (H_3), that increased plasticity in migration timing would result in higher selection for IRG. The timing of spring had no effect on selection for IRG: departure –0.009 (–0.032, 0.012, p = 0.410), arrival –0.010 (–0.031, 0.012, p = 0.383, Figure 5.2c), providing no evidence to support our fourth hypothesis (H_4) of higher selection of IRG in late springs due to phenological asynchrony in earlier springs.

5.5 Discussion

Migratory herbivores are faced with increased challenges as environmental conditions change, as plant phenology is closely linked to weather patterns (Shaw 2016). One way to elucidate how populations may deal with changing conditions in the future is to examine how individuals acclimate to current inter-annual variation in the environment and to quantify individual differences that could lead to an evolutionary response (Boutin and Lane 2014, Charmantier and Gienapp 2014). We found that migratory ungulates in Wyoming were plastic in timing their spring migrations to the timing of spring green-up, and that migration timing was a behaviour that varied among individuals—certain individuals consistently migrated early relative to green-up and others consistently migrated late. Selection for IRG, however, was not a behaviour that varied among individuals, providing little indication of individuals that were more or less specialized in surfing the green wave. Counter to our prediction, increased plasticity in the timing of migration did not result in higher selection for IRG, suggesting that individuals that migrate at the correct time may not need to be highly selective during migration. We also found no evidence of phenological asynchrony, as early springs did not result in lower selection for IRG. Overall, our results suggest a positive outlook for migratory ungulates as they appear to have the capacity to acclimate migratory behaviour and have consistent among-individual differences that could allow for an evolutionary response.

High plasticity in migration timing suggests individuals can detect and acclimate to changing environmental conditions during migration (Figure 5.2, panels a and b). There is a gradient of spatial fidelity in ungulates from elk (Eggeman et al. 2016, Rickbeil et al. 2019) to species such as mule deer that have very high fidelity to migratory routes and therefore very little plasticity in whether or where to migrate (Sawyer et al. 2019). Our results provide an upshot, as they suggest that all migratory ungulates in Wyoming including mule deer are highly plastic in when they migrate relative to spring green-up. While limited in the ability to shift migration routes altogether (akin to changing species ranges, which is one option), these individuals/species seem to be able to exploit the variation in springs observed in our dataset. Animals can learn about their environment either via direct experience about the environment or via socially by observing conspecifics (Lewis et al. 2019), allowing them acclimate their behaviour to different conditions. Species can use learned knowledge and spatial memory to guide navigation during migration (Merkle et al. 2019) and may therefore also use memory and observation of local conditions to determine when and how fast to migrate.

Moderate to high repeatability in migration timing, especially for arrival on summer range, suggests migration timing is a consistent trait within individuals and that they use different cues to time migration (Figure 5.3). Timing of migration could have a heritable, genetic basis, or it could be transmitted via social learning either by maternal transmission or from social groups, in a manner akin to how individuals have been shown to culturally transmit knowledge of migration routes (Jesmer et al. 2018). The presence of multiple strategies in timing of migration within a population may be indicative of variation in feeding preference or intra-specific niche partitioning (Páez-Rosas and Aurioles-Gamboa 2010). For example, stable isotope analysis of springbok (*Antidorcas marsupialis*) and gemsbok (*Oryx gazella gazella*) hair samples in Namibia revealed evidence of dietary niche specialization in both species (Lehmann et al. 2015). IRG provides a coarse measure of plant growth at broad spatial scales, therefore different forage resources will be available at different times. Individuals may migrate at different times to exploit different forage resources based on dietary specialization, leading to individual differences in migration timing and high repeatability. Intra-annual variation in migration timing may also allow for more temporal variation in resource use across migratory ranges, resulting in decreased competition. Migrating earlier or later than the population mean may reflect a strategy of selecting for times when resources are fewer but competition is lower, resulting in similar fitness benefits across strategies in a process analogous to fitness balancing across migratory strategies (Hebblewhite and Merrill 2011).

Both plasticity and repeatability for timing of migration were higher for timing of arrival on summer range than for timing of departure from winter range. Migratory ungulates spend a significant amount of time during migration in stopovers in order to maximize replenishment of energy reserves (Sawyer and Kauffman 2011), which may serve to adjust the pace of migration to local conditions. Conditions on winter range may not reflect relative conditions across the migratory route. For instance, when there is a high-snow winter but warm spring, green-up on winter range may occur early, but higher elevation green-up is still delayed due to persistent snow. In this case, environmental cues on winter range may be unreliable, with individuals instead having to gauge the progression of the onset of spring throughout their migration by calibrating the pace at which they migrate. Mule deer populations from this study have been shown to surf the green wave poorly at the start of their migrations but arrive on summer range concurrently with the green wave (Ortega et al, In Prep). This suggests that individuals do in fact use environmental cues during migration to modulate the pace of migration to synchronize movements to the progression of plant phenology.

Greater plasticity in migration timing did not result in greater selection for IRG (Figure 5.4), suggesting the potential for alternative strategies in how individuals acquire high-quality forage. For timing of arrival, our results were counter to our prediction, with individuals that were more plastic in timing of arrival having lower overall selection for IRG. Individuals that are more plastic may in fact be more synchronized in their movements to the green wave, and because of this may not need to be as selective during migration. Green-wave surfing behaviour may therefore lie on a continuum between two distinct strategies—those that choose the best time to migrate relative to plant phenology and do not need to worry about selecting IRG; versus those that are less plastic in response to the timing of spring but that are better able to select for patches of higher local IRG. Plasticity itself incurs a cost of increased investment in neural tissue (Snell-Rood 2013), and while habitat selection is often considered to be cost-free (Fretwell and Lucas 1970), this is likely to often not be the case (Morris 1987, Lin and Batzli 2002). Individuals may therefore be best served to invest in one strategy or the other. We think valuable insight could be gained by further investigating trade-offs between plasticity and habitat selection.

We found no evidence of phenological asynchrony in these populations, as early springs did not result in lower selection for IRG (Figure 5.2c). It therefore appears that even the earliest springs during the study period were within the capacity for individuals to acclimate to. We do not know, however, whether these years were significantly earlier than the historical average sufficient to result in a phenological asynchrony. We only monitored populations for 3–11 years, and due to satellite coverage our plant phenology data only go back to 2001. Alternatively, asynchrony may simply have been masked by environments where selection for IRG is easier in early springs. In Wyoming, early springs are often associated with a slower rate of green-up (Aikens et al. 2020), which could make selection easier than in faster, later springs that make surfing the green wave more difficult. Given the contemporary nature of our data, it is also possible that some level of selection had already occurred in these populations, and that individuals maladapted to earlier springs or that had insufficient plasticity had already failed to persist prior to our study. Overall however, a lack of decline in selection for IRG by migratory ungulates in early springs is a good sign as environments continue to change.

Our results provide an overall positive outlook for migratory ungulates in the face of anthropogenic climate change. Plasticity in timing of migration suggests that individuals can acclimate to changing conditions to avoid phenological asynchrony and potential mismatch. In addition, consistent differences among individuals in migration timing could potentially provide behavioural variation that, if transmissible, could result in an evolutionary response to changing conditions (Dochtermann et al. 2015). Despite these encouraging results, we advocate for continued caution and monitoring. It is difficult to know to what extent current plasticity can be extrapolated to future conditions. Continued environmental change may result in conditions beyond which individuals have evolved the capacity to acclimate to, and plasticity alone without an evolutionary response could simply delay an eventual phenological mismatch with significant effects on fitness (Lande and Shannon 1996, Simmonds et al. 2020). While high repeatability for migration timing could help drive such an evolutionary response, this is far from certain for long-lived ungulate species in the face of rapid change. We also caution that our results may not extend to longer-distance migrants such as birds who may have less cues to rely upon during migration to time their arrival on summer range. Low repeatability in selection for IRG also suggests that actively selecting for IRG may not be an individual, transmissible trait. A key component of population monitoring during the Anthropocene will be to evaluate how populations are acclimating or adapting to changing conditions.

Of our five main findings, three are positive signs for populations of migratory herbivores in the face of change: 1) plasticity in migration timing to spring conditions suggesting individuals acclimate to environmental conditions; 2) consistent differences among individuals in migration timing that could allow for evolutionary change provided they are transmissible; and 3) no evidence of phenological asynchrony in early springs. Our other main two findings are potentially problematic for populations of migratory ungulates: 1) relatively low differences among individuals in ability to select for IRG suggests selection behaviour is not likely to be transmissible across generations; and 2) increased plasticity in migration time to spring green-up did not translate to higher selection for IRG. Our findings were consistent across all four species examined, suggesting a convergence of evolutionary strategies to deal with inter-annual variation in plant phenology. Plasticity and consistent individual differences together provide populations two potential avenues to acclimate or adapt in the Anthropocene. Individuals may acclimate if conditions do not exceed their capacity to do so; or populations may adapt if transmissibility of phenotypes well adapted to new conditions is sufficient to drive a potential ecological rescue

(Vander Wal et al. 2013). Working in concert, these processes will hopefully allow migratory herbivores to continue to persist in a changing world.

5.6 Acknowledgements

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Table 5.1: Candidate models describing migration timing and selection for instantaneous rate of green-up (IRG) in North American ungulates. Models were generalized linear bivariate Markov chain Monte Carlo regressions, with timing of migration and selection of IRG fit as co-response variables. Two sets of models were fit, one with timing of departure from winter range and one with arrival on summer range used to define timing of migration. Model 1 was the null (intercept only) model, models 2 and 3 were fit with random intercepts but no fixed effects to model population/individual differences only. Model 4 incorporated plasticity as a function of timing of spring, with no differences among populations/individuals. Models 5 and 6 incorporated plasticity in addition to population/individual differences, but level of plasticity remain unchanged (random intercepts only). Models 7 and 8 incorporate a population/individual × environment interaction, fitting population- and individual-level plasticity (random slopes), respectively.

Number	Model description	Fixed effect	Random intercept	Random slope	Δ DIC - depart	Δ DIC - arrive
1	Null	None	None	None	292.8	520.8
2	Population differences only	None	Population	None	296.8	524.7
3	Individual differences only	None	Animal ID	None	91.2	129.2
4	Overall plasticity, no differences	Spring day	None	None	291.1	507.7
5	Population differences, overall plasticity	Spring day	Population	None	295.1	511.7

6	Individual differences, overall plasticity	Spring day	Animal ID	None	77.8	65.7
7	Population × environment interaction	Spring day	Population	Population	276.3	491.7
8	Individual × environment interaction	Spring day	Animal ID	Animal ID	0	0

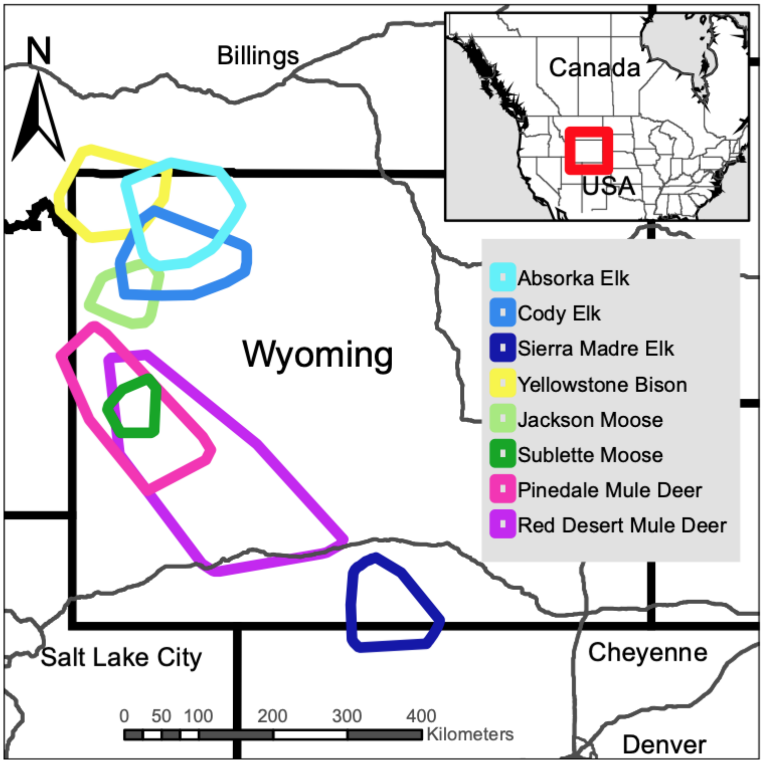

Figure 5.1: Map of the study area (Southern and Western Wyoming, USA) with locations of the eight ungulate populations used in this study.

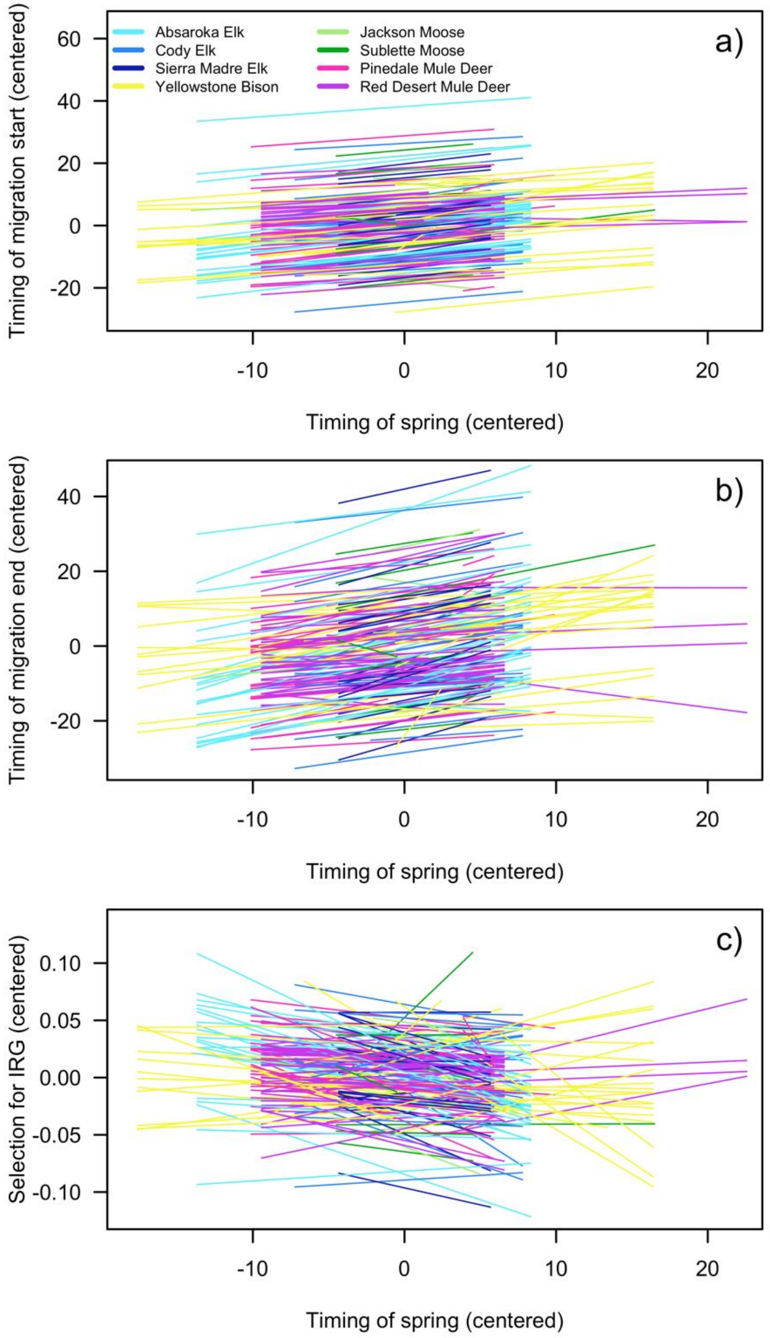

Figure 5.2: Behavioural reaction norms for a) timing of departure from winter range, b) timing of arrival on summer range and c) selection of instantaneous rate of green-up (IRG) as a function of the timing of spring green-up. Each line represents an individual. Higher intercepts in panels a and b represent individuals who migrate later in an average environment, and a positive slope

suggests that individuals migrate later when spring green-up occurs later. Higher intercepts in panel c represent individuals that have higher overall selection of IRG, and positive slopes represent individuals who have higher selection of IRG in later springs. Populations are represented by different colours.

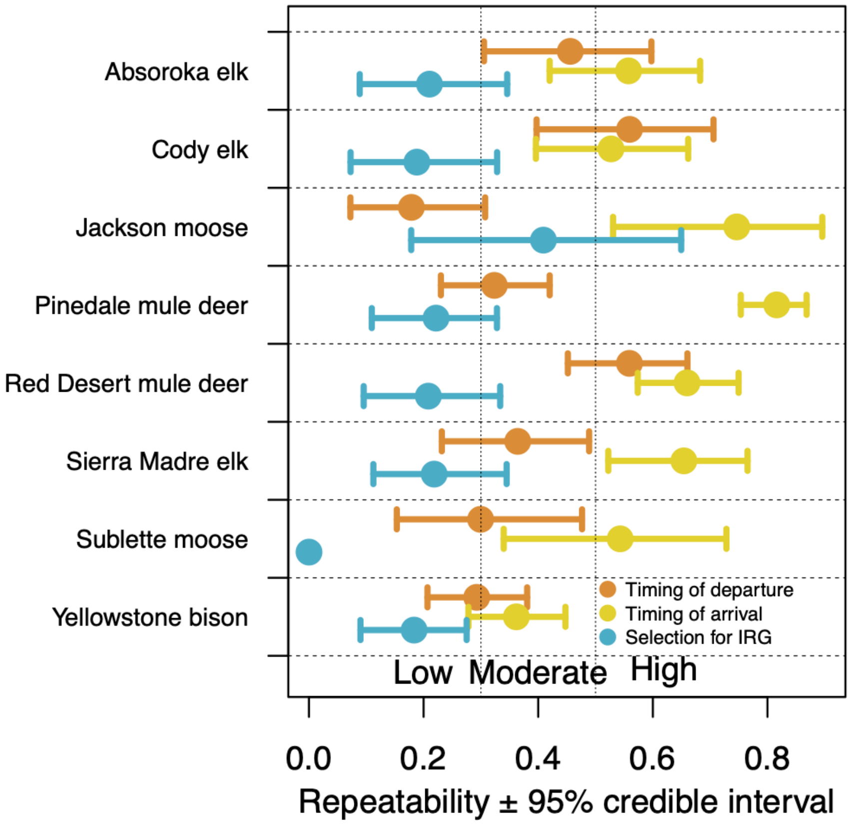

Figure 5.3: Repeatability estimates plus 95% credible interval for timing of departure from winter range (orange), timing of arrival on summer range (yellow), and selection for instantaneous rate of green-up (IRG, blue) for eight ungulate populations (*n* = 230 individuals) in Wyoming, USA, 2005–2019. Vertical dotted lines delineate low, moderate, and high repeatability values, and horizontal dotted lines delineate populations.

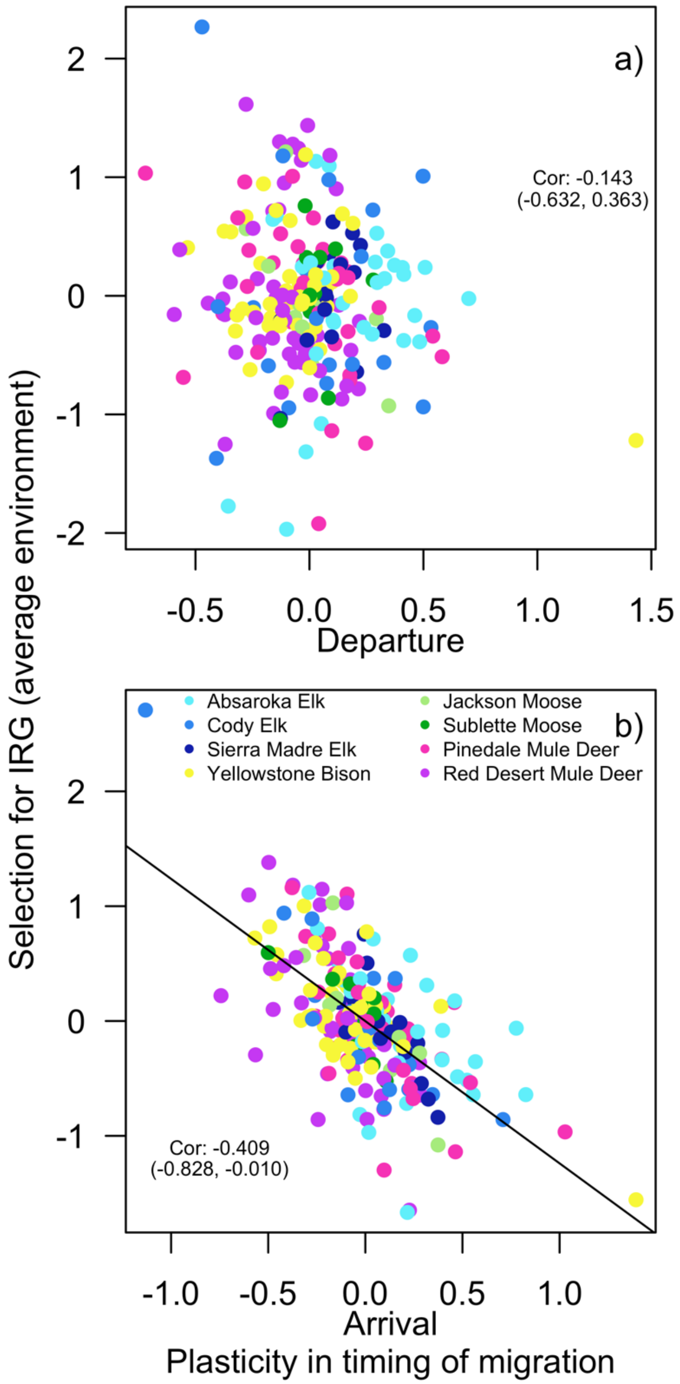

Figure 5.4: Correlation between plasticity in timing of departure from winter range (a) and timing of arrival on summer range (b) as a function of the timing of spring green-up (random slopes) versus the intercept of selection for instantaneous rate of green-up (IRG) for ungulate species in Wyoming, USA, 2005–2019. Correlations (+ 95% credible interval) are displayed on

each panel. A negative correlation (as in panel b) suggests that individuals that are more plastic in the timing of their migration as a function of the timing of spring have lower selection for IRG. Populations are represented by different colours.

Box 5.1: Primer for behavioural acclimation and adaptation. The field of behavioural ecology emphasizes the importance of incorporating consistent differences among individuals and plasticity into the study of animal behaviour (Dingemanse et al. 2010). Plasticity describes the within-generation change in an individual's behaviour as a function of an environmental gradient and provides a measure of acclimation, or responsiveness to environmental change. Repeatability quantifies the proportion of variance observed in a population that is due to differences among individuals (Bell et al. 2009). High values of repeatability (>0.7) suggest that individuals are consistent in their behaviour relative to conspecifics across contexts, whereas low values (<0.3) suggest little differences among individuals. Repeatability provides an upper limit for heritability and therefore provides a potential measure of adaptability by natural selection across generations (Dochtermann et al. 2015). Behavioural reaction norms are models that quantify plasticity and repeatability in a single analytical framework (Dingemanse et al. 2010).

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CHAPTER 6: CONCLUSIONS AND FUTURE DIRECTIONS

6.1 Summary

Dealing with changing environmental conditions is an important challenge for migratory animals. Resource availability varies through time heterogeneously both within and across years (Delbart 2021), therefore individuals should have evolved ways to track these changes by being plastic to cues in the environment. Climate change is exacerbating this interannual variability, resulting in phenological asynchrony and potential mismatch (Visser et al. 1998, Samplonius et al. 2021). In the absence of sufficient behavioural plasticity, species may be able to adapt to changes in the phenology of resources upon which they depend if consistent differences among individuals drive an evolutionary response to this change. Elucidating external drivers of plasticity and differences among individuals provides evidence of which processes will potentially allow populations to persist in the face of continued environmental change.

My thesis work demonstrated the importance of environmental variation at intra- and inter-annual scales on the life-history and annual reproductive success of ungulate species. By incorporating individual differences and plasticity into the study of migration, I was able to demonstrate that migration is both plastic to changing spring conditions and an individual trait. The main findings of my thesis were:

1) Contrary to many other migratory ungulate populations, caribou in Newfoundland do not surf a wave of green-up but instead follow a gradient of melting snow during migration. By migrating concurrently with snowmelt, caribou likely reduced movement costs associated with travelling through deep snow while also timing parturition to occur at the peak of green-up. By timing parturition to green-up, caribou had access to vegetation at peak green-up during the calving season when energetic needs from lactation were high.

2) Timing of migration was a repeatable trait. Across the 13 populations studied in this thesis, repeatability in the timing of arrival on summer range ranged from ~0.3–0.8, with most herds having a higher repeatability value than average repeatability scores across behavioural ecology studies (0.37, Bell et al. 2009).

3) Timing of parturition was not repeatable in caribou, although I did find a correlation between timing of arrival on summer range and timing of parturition.

4) Selection for green-up had relatively low values of repeatability in ungulates in Wyoming, suggesting that there are not clear phenotypes that are better at surfing the green wave.

5) Ungulates were plastic in the timing of their migrations to the timing of spring. Caribou in Newfoundland displayed plasticity in migration timing to the timing of snowmelt, whereas ungulates in Wyoming responded to the timing of green-up.

6) I found some evidence that caribou were plastic in the timing of parturition as a function of the timing of snowmelt, but not as a function of timing of green-up.

7) Selection for areas associated with coyote selection reduced annual reproductive success for one of two populations tested, but not for the other.

8) I found no evidence that early springs in Newfoundland resulted in lower annual reproductive success in caribou, suggesting that phenological mismatch is not currently affecting annual reproductive success for caribou in Newfoundland. Likewise, early springs did not result in lower selection for green-up in ungulates in Wyoming.

6.2 Implications for migratory species

My research suggests an overall optimistic picture for many terrestrial migratory herbivores in light of global climate change; however, with several important caveats and reasons for caution. All populations studied displayed plasticity in the timing of migration to the timing of spring events, in caribou (*Rangifer tarandus*) in Newfoundland this was timing of snowmelt and in ungulates in Wyoming, green-up. This outlines the two ends of a continuum of migratory strategies in migrants and suggests that acclimating migration timing to changing environmental conditions is a convergent strategy across multiple species and systems. Species (or individuals) can either surf the green wave to gain a nutritional benefit during migration (Bischof et al. 2012; Merkle et al. 2016; Aikens et al. 2017; Chapter 5) or jump the green wave to time reproduction to when green-up is at its peak on summer range (Mysterud et al. 2017; Chapter 2). Caribou in Newfoundland followed melting snow to jump the green wave, potentially to facilitate travel over frozen lakes (Leblond et al. 2016). High repeatability in migration timing across all populations examined reveal a diversity of finer-scale, intra-population strategies in timing migration. This is good news, as climate change will likely alter selective pressures on optimal migration times, and having existing variation in migration time will allow for an evolutionary response provided migration time is transmissible across generations. This can occur either through heritable, genetic variation or via cultural/maternal transmission of behaviours (Tennie et al. 2009, Jesmer et al. 2018). Despite a potential evolutionary response in migration timing, a lack of repeatability in parturition timing could hinder a similar response to changing selective pressures on timing of parturition. Caribou also displayed more plasticity in parturition timing to the timing of snowmelt as opposed to timing of green-up, which may become an increasingly unreliable cue for the timing of green-up.

My results suggest important differences in migratory behaviour and acclimation or adaptation to change as a function of resource phenology across taxa and systems. Green wave jumping, as seen in Newfoundland caribou, may be more common strategy than green wave surfing in climates with shorter growing seasons that would limit the ability of individuals to give birth after the green wave and allow sufficient time to raise young. Changes in green-up have also been inconsistent across North America. Green-up has generally advanced in the East but has become later in the West (Mayor et al. 2017), and in bird taxa, slower migrants that arrived on breeding grounds earlier and that overwintered further north had higher responsiveness in changing spring phenology (Youngflesh et al. 2021). This underscores that challenges for migratory species associated with changing phenology are dependent on variation at very broad spatial scales and are dependent on unique migratory ecologies.

Studies examining selection behaviour for green-up for species that surf the green wave have become common over the last decade (Bischof et al. 2012, Shariatinajafabadi et al. 2014, Si et al. 2015, Merkle et al. 2016, Aikens et al. 2017). Less attention however has been given to the importance of selecting green-up on summer range in species that jump the green wave. Migratory red deer (*Cervus elaphus*) that jumped the green wave were shown to have summer ranges with more green-up then residents (Mysterud et al. 2017); however, studies of finer scale selection for green-up at its peak for green wave jumpers remains relatively understudied (but see Webber et al. 2020). While my research failed to detect an explicit link between use of green-up and calf survival (Chapter 4), further research into patterns of selection for green-up on summer range by jumpers is warranted, as few studies have explicitly examined fine-scale selection for green-up outside of migratory movements.

6.3 Implications for caribou in Newfoundland and across Canada

Many of the results from my thesis are positive news for caribou in Newfoundland. All populations I examined were plastic in the timing of their migrations to the timing of spring snowmelt (Chapter 3). Newfoundland experiences a high degree of interannual variation in environmental conditions driven by the North Atlantic Oscillation (Banfield and Jacobs 1998, Finnis et al. 2015), creating conditions where plasticity has likely evolved. Migration timing was also moderately repeatable, suggesting that consistent differences among individuals could potentially drive an evolutionary response to changing evolutionary pressures on migration timing. Caribou in our study had calving seasons that were well matched to the timing of spring green-up (Chapter 2), which likely provided them with high-quality forage when energetic requirements of lactation were highest.

Some of my results, however, warrant caution regarding how caribou will fare in the face of climate change. Timing of parturition was plastic to environmental conditions, but responded more strongly to the timing of snowmelt than to the timing of green-up (Chapter 3). Snowmelt therefore appears to correlate with gestation time in caribou, with early snowmelt possibly resulting in better forage conditions earlier in the season that result in reduced gestation time. I found that timing of snowmelt and green-up were only loosely correlated. Given that timing parturition to when forage resources are most abundant appears to increase fitness in caribou (Post and Forchhammer 2008), climate change may reduce fitness of caribou in Newfoundland if timing of snowmelt is no longer a reliable signal for timing of green-up (Visser et al. 2006, Visser 2008), resulting in a phenological mismatch. Earlier green-up has, however, been shown to positively correlate with early season forage availability and body condition in reindeer (also *R. tarandus*, Pettorelli et al. 2005, Cebrian et al. 2008), so phenological asynchrony may be offset by improved habitat quality. I did not observe a significant effect of timing of spring on caribou calf survival in Newfoundland, and the trend potentially suggested that calf survival may have been lower in springs with early green-up.

Caribou numbers in Newfoundland have fluctuated dramatically, and it is likely that population density affected the results of my research. Caribou numbers most recently peaked in the 1990s before beginning to decline (Weir et al. 2014). My research occurred near the end of the decline phase as population numbers began to stabilize. An important ultimate cause of caribou declines has been attributed to a reduction in foraging resources resulting in higher calf mortality, mediated by increased predation (Bergerud 1974, COSEWIC 2014, Lewis and Mahoney 2014, Mahoney et al. 2016). My research shows that caribou jump the green wave (Chapter 2), and therefore re-enforces the importance of habitat quality on calving grounds as critical for reproductive success. While I did not observe a fitness effect of use of green-up among female caribou on calving success, it may be that the influence of green-up may be stronger during the height of the decline phase when habitat quality would be predicted to be at its lowest and forage may therefore be more limiting. This suggests that I may have been more likely to detect an effect of selection for green-up when population decline was steepest, suggesting the importance of continued monitoring across population phases. The fact that I did not detect a fitness effect of use of green-up does not, however, mean that it is unimportant. If all individuals selected for areas with high-quality forage, there may have been insufficient variation across individuals to detect an effect.

Caribou in Newfoundland are exposed to a high degree of variation in environmental conditions, both within and across years. This stochasticity in conditions may have led to caribou in Newfoundland being highly plastic in their strategies. Most populations have facultative migration, where not all individuals migrate, or where individuals may switch strategies. The wide range of migration dates in this thesis also suggest a diversity of strategies. This suggests that Newfoundland may have been an ideal system within which to test hypotheses around individual differences and plasticity in migratory behaviour, habitat selection, and parturition. This also raises the question of whether other *Rangifer* populations display the same levels of plasticity and individual differences.

Caribou face declines across Canada and the world (Vors and Boyce 2009). While habitat alteration due to industrial activities is often cited as a primary cause of population decline (Festa-Bianchet et al. 2011), the possibility of trophic mismatch remains a concern, especially as climate change continues to alter key trophic interactions. I advise managers to closely monitor changes in the timing of environmental events such as snowmelt and green-up and quantify their effect on population vital rates. While results of this thesis suggest caribou are able to acclimate, this ability may reach a tipping point where acclimation is no longer feasible, especially as regions undergo significant changes in community composition (Rehfeldt et al. 2012). I also recommend that managers monitor the fates of caribou calves and perform survival analyses similar to those described in my thesis. Such analyses could incorporate other important variables that are deemed important for the population (e.g., level of industrial development, which was not predicted to be significant for our populations). While predation is often the proximate cause of calf mortality, other factors are likely to play a role in interacting with predation risk to determine overall risk, therefore monitoring calf survival as a function of multiple factors will provide important insight for managers.

6.4 Plasticity and individual differences in migration behaviour across species and populations

While many ungulate species have been shown to surf the green wave (Merkle et al. 2016), there is likely to be variation in the plasticity and personality among species and populations as a function of landscape attributes and species-specific ecologies. Understanding the ecological factors that determine the favourability for both plasticity and personality to emerge in a population remains an important question (Dingemanse and Wolf 2010). Traits inherent to species such as digestive constraints and gregariousness modify predictions surrounding green-wave surfing behaviour as they alter profitability of wave surfing and ability to learn from conspecifics. Likewise, landscape attributes such as the interannual variability in the timing of green-up and the order of green-up along migratory corridors will also affect plasticity and consistent among individual differences in green-wave surfing.

6.4.1 Differences among species

Two important axes can be predicted to result in differences in migratory personality and plasticity among species – gregariousness and feeding/digestion. Green-wave surfing is a profitable behaviour for ruminants as newer plant growth is higher in cell soluble content and lower in fiber (Van Soest 1982). Ruminant digestion, however, varies across species, which should have consequences on the importance of green wave surfing. Species that are *concentrate selectors* are adapted to consume forage rich in cell soluble content and have digestive systems less optimized to digest fiber. By contrast, *grass and roughage eaters* are much more adapted to consume fibrous food (Hofmann 1989). The result is that we would expect a much stronger selective pressure on concentrate selectors to match green-up and surf the green wave (and hence use environmental cues to be plastic to environmental conditions) than on grass and roughage eaters.

Gregariousness and group size should also mediate personality and plasticity in migration. Migratory performance improved in whooping cranes (*Grus americana*) in groups with older, more experienced individuals (Mueller et al. 2013), and data from translocated ungulates suggests that migratory performance is linked to cultural transmission of knowledge about the environment gained across multiple generations (Jesmer et al. 2018). We would therefore expect that more gregarious species would be more likely to be plastic to environmental variability as groups are more likely to contain individuals with appropriate cultural knowledge to respond optimally. Likewise, we would also predict less gregarious populations to have more consistent differences since smaller groups/individuals are more likely to vary in their movement phenotypes than would animals with collective movement.

In some species such as bison (*Bison bison*) and wildebeest (*Connochaetes taurinus*), grazing in large numbers can stimulate plant growth and the production of high-quality forage, reducing the need for these populations to track the green wave. Grazing removes older shoots and promotes new growth, resulting in significant increases in productivity (Frank et al. 1998). Bison in Yellowstone National Park were found to not track the green wave later in the spring, but rather maintained forage quality by grazing in aggregate (Geremia et al. 2019). In such cases, the importance of plasticity would be reduced, as there would be less need to acclimate migratory behaviour to inter-annual variation in green-up. Given the importance of aggregating with conspecifics for such a strategy to be viable, we would also predict very low among individual variation. Repeatability in this case would likely be low, as there is little residual variance left to explain that would be attributable to differences among individuals (Table 6.1).

6.4.2 Differences based on environmental variation

Environmental variability itself is likely to be a key determinant of plasticity. That is, individuals exposed to greater variation in green-up should be more likely to display plasticity in migration timing in response to that variation. Plasticity itself can be variable across individuals and populations—being responsive to environmental variation may be costly as individuals must seek cues, and individuals may instead opt to conserve energy, be unresponsive and do better in average environments (Wolf et al. 2008). We could therefore hypothesize that in areas where the timing of green-up is more consistent across years, the costs of being plastic may outweigh the benefits. We would therefore predict greater plasticity in environments that are more variable, where the consequences of being unresponsive to the environment are higher.

Migration length could also affect plasticity and individual differences. Longer distance migrants will have less knowledge about conditions on summer range, as such it would be more difficult for such species to display plasticity to environmental conditions, at least for arrival on summer range. This could be mitigated however if individuals are able to use cues on stopovers to regulate the pace of migration.

Finally, spatial heterogeneity in green-up (Aikens et al. 2017) could also be expected to affect migratory plasticity and personality. The order of green-up along the migratory route was shown to affect green-wave surfing performance in mule deer (*Odocoileus hemionus*), with a more ordered progression of green-up from winter to summer range improving surfing performance (Aikens et al. 2017). A more ordered green-up could also be predicted to result in greater plasticity in migratory timing, as cues would be easier to detect and follow. This should also reduce individual differences, as a narrower range of migratory phenotypes would be adaptive compared to a landscape with un-ordered green-up (Table 6.1).

6.5 Other future directions in integrating personality and migration ecology

Integrating individual differences and plasticity into finer-scale movement behaviours during migration could elucidate what factors not only affect initiation of migratory behaviour, but also factors that modulate the pace of migration *en route*. My research on timing of migration focussed on the timing of departure from winter range and arrival on summer range. Migration by herbivores includes the use of stopovers, which serve as important locations for replenishing energy reserves. Mule deer spend up to 95% of their time during migration in stopovers with higher quality forage than in movement corridors (Sawyer and Kauffman 2011). Examining movement rate at finer temporal scales, e.g., daily movement rate, as a function of environmental conditions will help elucidate what mechanisms drive migration and plasticity in migration at finer scales. The advantage of such an approach is an increase in available data. Behavioural reaction norm models are very data hungry, and quantifying migration timing and environmental variation on an annual scale provides relatively coarse (e.g., one observation per individual per year) temporal resolution. Examining these processes at finer scales will allow for increased power to detect environmental effects, plasticity, and among individual variation on the pace of migration.

While many studies have examined how climate change has altered the mean timing of life-history events such as migration and parturition (Davidson et al. 2020, Mallory et al. 2020), less attention has been paid to how these trait distributions have changed. Caribou calving dates tend to be right-skewed (Bonar et al. 2017), suggesting a cost to giving birth too early in the season. If conditions early in the spring improve, the cost of giving birth early may be reduced, resulting in a distribution of birth dates that more closely approximate a normal distribution. Less predictable conditions are also likely to result in greater variance in birth dates, which could have consequences on fitness. More synchronous calving is thought to serve as a means to swamp predators and dilute per capita risk to calves (Estes and Estes 1979), especially in species whose young follow mothers such as caribou (Rutberg 1987). If calving becomes less synchronized due to more variable climatic conditions, the advantages of predator swamping may decrease.

6.6 Concluding remarks

The primary goals of my thesis were to apply a lens of consistent differences in behaviour among individuals to the study of resource tracking, and link individual behaviour and selection for green-up to fitness outcomes. The first three core chapters of my thesis follow an arc of 1) examining the overall timing and drivers of migration; 2) examining plasticity and repeatability in timing of migration and parturition to changing environmental phenology; and 3) examining the fitness consequences of tracking forage resources against the risk of predation and group size in predicting annual reproductive success. I then examined plasticity and consistent individual differences in ungulate populations in Wyoming, USA known to surf the green wave and found high repeatability in migration timing and significant plasticity to the timing of spring green-up in timing of migration (Chapter 5).

Movement is a behaviour that allows animals to maximize use of fitness-enhancing locations while reducing time spent in locations that reduce fitness (Nathan 2008, Avgar et al. 2014). Such patterns at broad spatial scales drive the evolution of migratory behaviour, as the fitness benefits of locations on the landscape change through time (Avgar et al. 2014, Shaw 2016). This underscores the fact that habitat selection is a complex process whose relative benefits vary spatiotemporally on both intra- and interannual scales. The research I conducted during my PhD sought to examine how fitness-enhancing selection behaviour varied at both these scales. The Anthropocene represents a significant threat to species who rely on the predictability of environmental cues to time important life-history events. My research cautiously suggests optimism for migrating ungulates that demonstrated the ability to acclimate to changing conditions. My research suggests that resource tracking is a ubiquitous behaviour across populations of migratory ungulates, which serve a vital role in the persistence of these iconic species.

Table 6.1: Modifications of predictions around consistent individual differences in migration timing and plasticity as a function timing of green-up as a function of species and landscape attributes.

Variable	Effect on individual differences/repeatability	Effect on plasticity
Gregariousness	Decrease – individuals more likely to move cohesively and therefore display minimal individual differences.	Increase - social learning will allow larger groups to better acclimate to environmental variation.
Feeding type – more selective	Decrease – greater impetus to match movement to the environment in selective feeders should decrease variance in migration timing among individuals.	Increase – more impetus to match movement to the environment in more selective feeders.
Green wave engineers (e.g., bison and wildebeest, Geremia et al. 2019)	Decrease – individuals more likely to move cohesively and therefore display minimal individual differences.	Decrease – less need to follow the green wave as grazing increases forage quality *in situ*.
Increased interannual variation in green-up	Increase – more interannual variation will result in a wider range of phenotypes that are	Increase – more interannual variation will increase the selective pressure to be plastic.

	adaptive over a broader range of environmental variation.	
Distance migrated	No prediction.	Decrease – cues less reliable across larger geographic distances.
Greenscape – order of green-up along route	No prediction.	Increase – greater reliability of cues with green-up occurring sequentially will increase probability of individuals being plastic.
Greenscape – Geographic extent/”width” of wave	Increase – Increased wave width allows for more variation in optimal (or near optimal) migration times.	Decrease – Less impetus to follow broader range of high-quality habitat

6.7 Literature cited

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SUPPLEMENTARY MATERIALS

The following are supplementary materials for Chapters 1–5.

S1 Supplementary material for Chapter 1

Table S1.1: Glossary of terms.

Adaptation	The process by which selective pressures acting upon phenotypes results in an inter-generational change in genotypes within a population such that the population as a whole has better fitness under the new conditions.
Animal personality	See *Consistent differences among individuals.*
Behavioural plasticity	The ability of an animal to change its behaviour as a function of environmental context.
Behavioural reaction norm (BRN)	The range of behavioural phenotypes expressed by a single individual across a set of environments. BRN intercepts reflect *animal personality* or *consistent differences among individuals*, and slopes represent *behavioural plasticity* (Dingemanse et al. 2010).
Behavioural syndrome	A suite of correlated traits, typically calculated by regressing the slopes or intercepts from behavioural reaction norms (Sih et al. 2004).
Consistent differences among individuals	Differences among individuals that are consistent across time and contexts (Réale et al. 2007).
Forage Maturation Hypothesis	The hypothesis that plant quality as a resource for herbivores changes with the *phenology* of plants as they mature, with intermediate growth stages providing the most benefit. Early growth stages are limited by biomass

	(cropping and bite rates are limiting), whereas later stages of growth result in a decrease in digestibility (Fryxell et al. 1991, Hebblewhite et al. 2008).
Green wave	The progression of plant growth across altitudinal or elevational gradients. Herbivores can follow this flush of vegetation to take advantage of high-quality forage resources as they become available across the landscape (see *Forage Maturation Hypothesis*; Bischof et al. 2012).
Instantaneous rate of green-up (IRG)	The rate of change (first derivative) in a time series of Normalized Difference Vegetation Index values through time. IRG is used to quantify the *green wave* as a spatial formulation of the *Forage Maturation Hypothesis* (Bischof et al. 2012, Merkle et al. 2016).
Normalized Difference Vegetation Index	A satellite-derived measure of green-ness used to quantify the progression of plant growth on the landscape. The first derivative is taken to calculate when plant growth is highest and forage is of highest quality for herbivores (the instantaneous rate of green-up).
Phenology	The relative timing of seasonal/cyclic events.
Phenological asynchrony and mismatch	Phenological asynchrony occurs when the phenology of a consumer species and that of their resource become decoupled, typically due to climate change affecting the phenologies of each species unequally. If this asynchrony

	results in a decline in fitness, the result in a phenological (or trophic) mismatch (Visser et al. 1998, Samplonius et al. 2019).
Repeatability	The proportion of phenotypic variance that is attributable to differences among individuals (Bell et al. 2009). High repeatability is indicative of distinct behavioural phenotypes within a population (e.g., high consistent differences among individuals).

S2 Supplementary material for Chapter 2

S2.1 – Study area, representative phenology, and migration routes

When preparing our raw NDVI models for curve-fitting, we replaced any pixels that were missing (either due to cloud cover or unreliable data) with the mean NDVI value of pixels in a 5 × 5-pixel grid surrounding the focal pixel. To ensure that this procedure was not biased and result in pixels that were inaccurate due to differences in phenology with neighboring pixels, we calculated the correlation between the NDVI value of the pixel and the pixels in this 5 × 5-pixel grid. We extracted these values for a sample of 5000 locations within our study area for each NDVI image throughout our study period from February 10th to September 29th (30 total images, for a total of 150,000 records). We found that the NDVI at focal pixels was highly correlated with surrounding pixels (Spearman correlation coefficient: 0.9903, $R^2 = 0.9808$). After these data were filled in, NDVI curves through time were also subjected to a 3-observation moving median filter to further reduce any bias associated with this filling procedure.

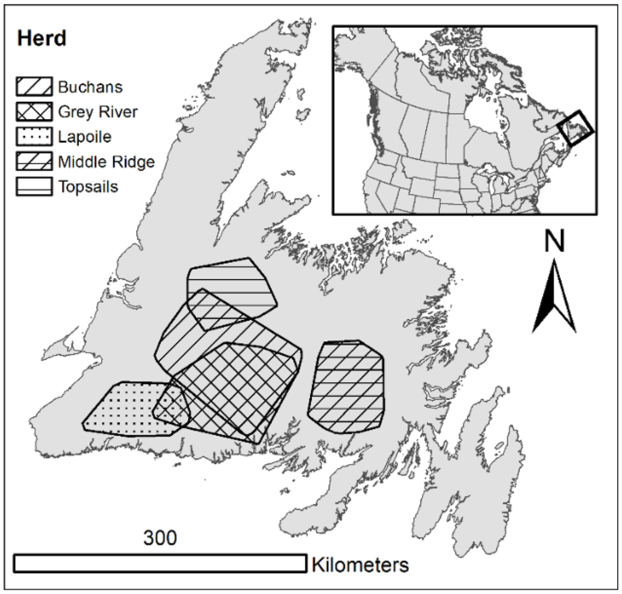

Figure S2.1.1: Map of our study area, the island of Newfoundland, Canada, showing the location of our five replicate caribou (*Rangifer tarandus*; *n* = 94) herds.

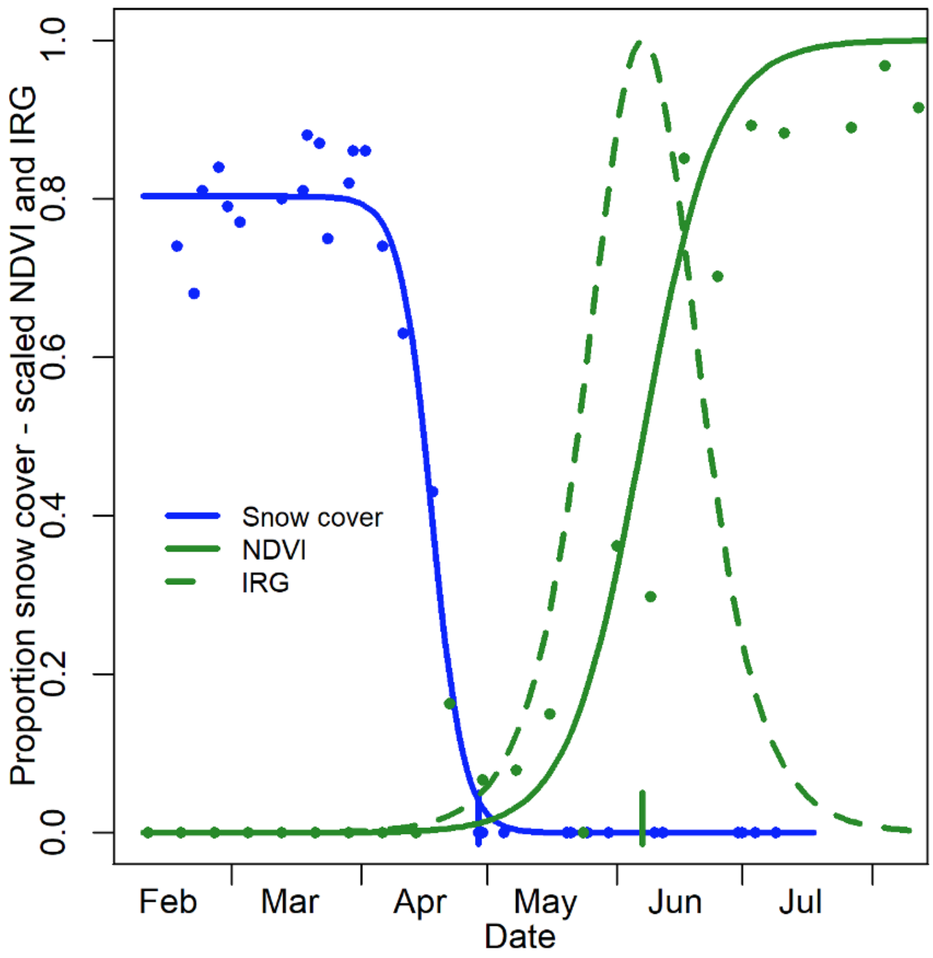

Figure S2.1.2: Phenology of snowmelt and green-up at a representative pixel in our study area. Blue points represent proportional total snow cover based on MODIS normalized difference snow index data and estimated using the formula presented by (Salomonson and Appel 2004) fitted with a logistic curve (blue line). Green points represent raw normalized difference vegetation index (NDVI) values, also from MODIS satellite data. Points that were prior to snowmelt (based on the quality band of NDVI) were set to the 3rd percentile value of all snow-free locations at that pixel for the duration of our study. The solid green line is the fitted NDVI curve scaled from 0–1, and the dashed green line represents the instantaneous rate of green-up (IRG; the first derivative of NDVI). Small blue and green lines on the bottom of the plot represent the dates of snowmelt and peak IRG, respectively.

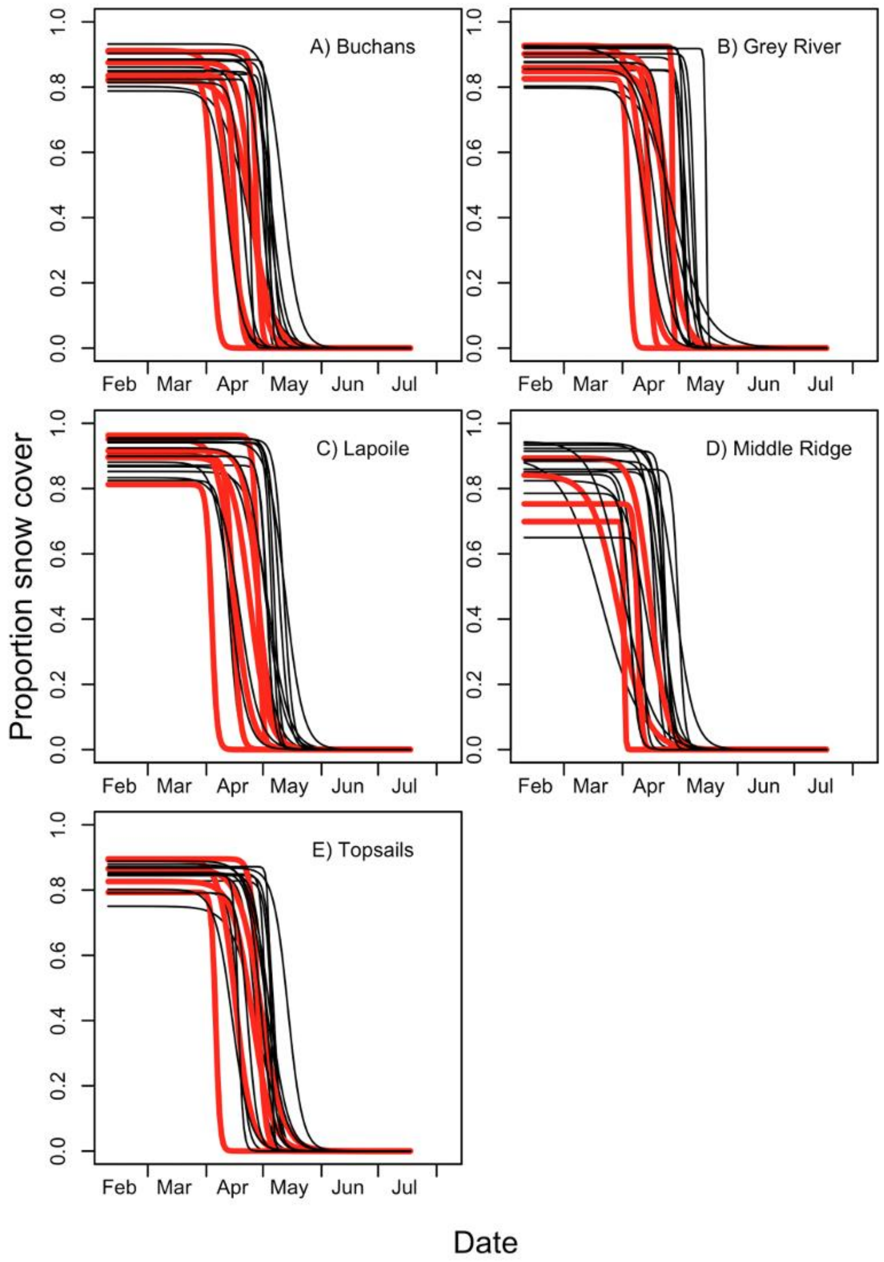

Figure S2.1.3: Curves showing proportion of the landscape covered in snow through time for each of our five replicate caribou (*Rangifer tarandus*) herds in Newfoundland, Canada. We plotted the progression of snowmelt for each year with reliable MODIS data (2001–2020). Thick red lines are years included in our study; thinner black lines represent other years. Proportion snow cover was estimated from normalized difference snow index values and estimated using the formula presented in (Salomonson and Appel 2004).

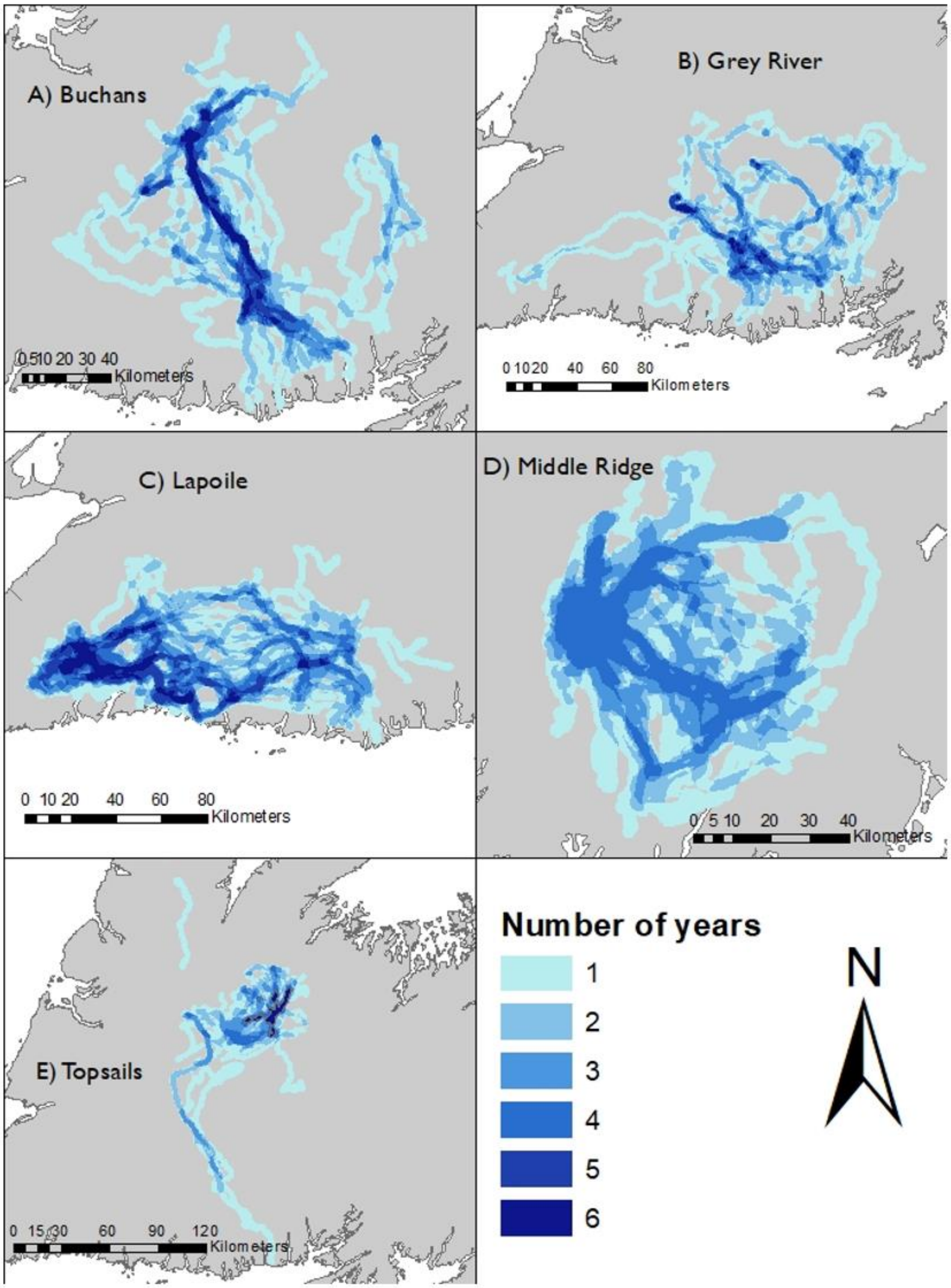

Figure S2.1.4: Fidelity of migration routes across all collared individuals in each population for each of our five caribou (*Rangifer tarandus*) populations in Newfoundland, Canada. We generated 99.99% Brownian bridges around all individuals in each year. Colours represent the degree of overlap between migration routes across years, with darker colours indicating areas used multiple years, and lighter colours representing areas used in fewer years. Panel A represents data from the Buchans herd (14 individuals over 6 years of data, 44 ID-years total), panel B – Grey River herd (13 individuals over 6 years of data, 40 ID-years total), panel C – Lapoile herd (18 individuals over 6 years of data, 50 ID-years total), panel D – Middle Ridge herd (34 individuals over 4 years of data, 59 ID-years total), and panel E – Topsails herd (15 individuals over 5 years of data, 23 ID-years total). Calving areas correspond to areas with the highest inter-annual overlap in ranges.

S2.2 – Additional Results

Table S2.2.1: Summary of sample size and timing of migration, calving, snowmelt and green-up for caribou (*n* = 94) in Newfoundland, Canada from 2007–2013.

	All Herds	Buchans	Grey River	Lapoile	Middle Ridge	Topsails
Number of individuals	94	14	13	18	34	15
Number of ID years	216	44	40	50	59	23
Median + [range], start date of migration	Mar 25 [Feb 09, May 19]	Mar 31 [Feb 09, Apr 22]	Mar 29 [Feb 14, May 19]	Mar 22 [Mar 01, Apr 19]	Mar 17 [Feb 23, Apr 25]	Apr 07 [Mar 11, May 10]
Median + [range], end date of migration	May 10 [Mar 20, Jul 13]	May 08 [Apr 14, Jun 22]	May 07 [Mar 29, Jun 22]	May 17 [Apr 13, Jun 17]	May 03 [Mar 20, Jul 13]	May 10 [Apr 08, Jun 07]
Median + [range], duration of migration (days)	43 [3, 128]	40.5 [13, 84]	39.5 [7, 123]	50.5 [18, 94]	43 [3, 128]	19 [4, 74]
Median + [range], distance of migration (km)	61.8 [30.5, 174.9]	105.3 [42, 143]	58.0 [36.4, 174.9]	99.8 [32.1, 173.5]	48.3 [30.5, 82.3]	48 [32.1, 139.1]
Median + [sd], date of snowmelt over migratory route	Apr 25 [17.6 days]	May 02 [13.3 days]	Apr 26 [13.1 days]	May 08 [19.3 days]	Apr 14 [9.7 days]	May 03 [10.9 days]

Median + [range], date of calving	May 24 [May 22, Jul 13]	May 22 [May 22, Jun 23]	May 24 [May 22, Jul 04]	May 28 [May 22, Jun 17]	May 24 [May 22, Jul 13]	May 24 [May 22, Jun 15]
Median + [sd], date of peak IRG during calving	Jun 06 [13.5 days]	Jun 08 [13.4 days]	May 30 [12.9 days]	Jun 12 [9.5 days]	Jun 02 [14.2 days]	Jun 07 [10.5 days]

Table S2.2.2: Estimated date of the optimal lag (number of days before/after peak instantaneous rate of green-up (IRG) or snowmelt) for caribou (*Rangifer tarandus*, *n* = 94) selection of areas with high IRG or near the date where snow melts, along with log-likelihood values of the top model. We generated models using the absolute value of days to snowmelt/peak IRG across several lags. Lagged datasets were constructed by adding or subtracting the value of the lag to the number of days until snowmelt/peak IRG. This was done to allow us to test for model fit at the focal day of the lag (see Chapter 2, Methods). Estimates represent the lag/day (number of days added or subtracted) that resulted in the best fitting model using days from peak as a squared term based on log-likelihood of models. The estimated range represents the day at which interpolated log-likelihood values have a difference of 1 (ΔAIC = 2). The difference is the number of days between the minimum and maximum estimate. LL is the log-likelihood of the top model.

	Snowmelt—Migration			IRG—Calving			IRG—Migration		
Herd	Estimate (range)	Difference	LL	Estimate (range)	Difference	LL	Estimate (range)	Difference	LL
All	-7 (-7.1, -7)	0.1	-1203170.6	4 (3, 4.3)	1.3	-636481.44	-60 (-60.2, -59)	1.2	-1210719.7
Buchans	-6 (-6.1, -5.6)	0.5	-224873.13	8 (6.9, 9.3)	2.4	-118198.26	-64 (-65.5, -63.4)	2.1	-226292.2
Grey River	-3 (-3.2, -2.8)	0.4	-202849.83	4 (3.3, 6.8)	3.5	-107657.91	-15 (-30.5, NA)	NA*	-203687.85
Lapoile	-13 (-13.1, -13)	0.1	-312009.16	6 (5.5, 6.2)	0.7	-133579.25	-45 (-45.1, -44.5)	0.6	-315670.7

Middle Ridge	2 (1.6, 2.2)	0.6	-372759.19	-11 (-12.6, -10)	2.6	-214962.7	-31 (-31.3, -29.5)	1.8	-373436.7
Topsails	3 (2.6, 3.4)	0.8	-89117.399	0 (-1.4, 0.9)	2.3	-61826.128	-69 (NA, -67)	NA*	-89659.702

*Not computed due to insufficient data on adjacent lags. This occurred when 1 log-likelihood away from the best model was outside the range with which the data could be interpolated. See Figure S2.2.2 panels C and F.

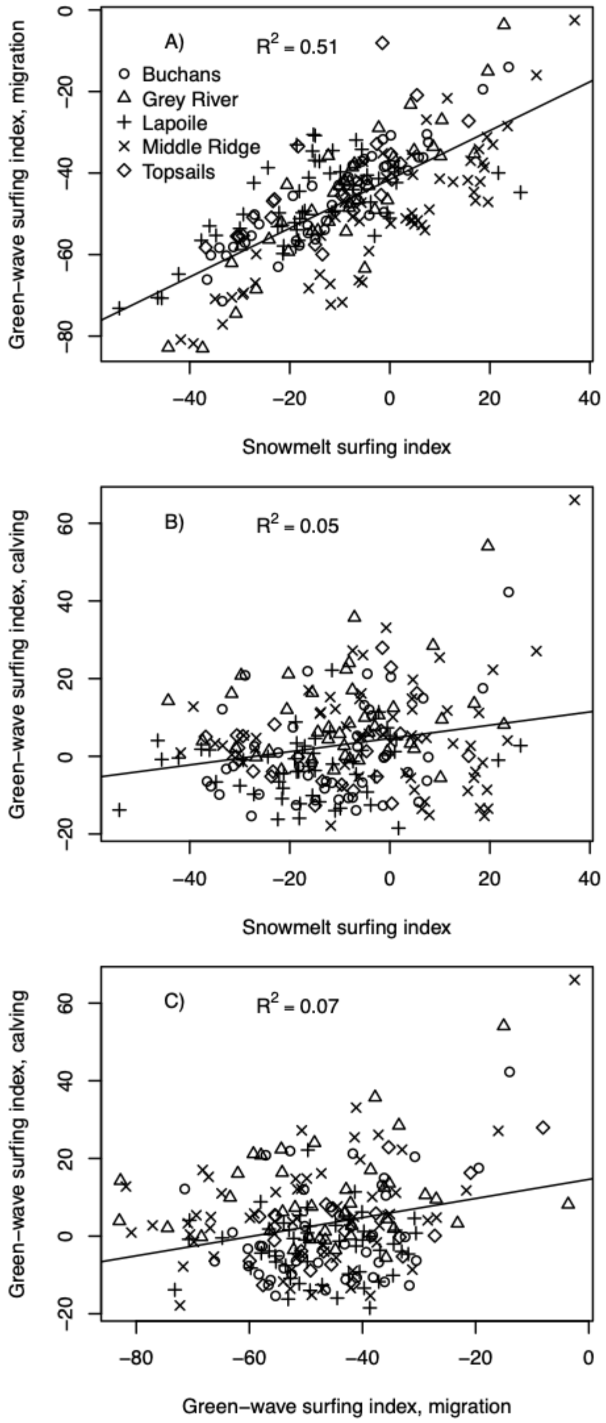

Figure S2.2.1: Correlations between surfing indices (mean days from snowmelt or peak IRG) for caribou (*Rangifer tarandus*, *n* = 94) in Newfoundland, Canada. Panel A is the correlation between snowmelt surfing index and peak IRG (“green wave”) surfing index (both during migration), B) is the correlation between snowmelt index during migration and peak IRG during calving, and C) is the correlation between peak IRG indices across the two seasons. Different herds are represented by different symbol types.

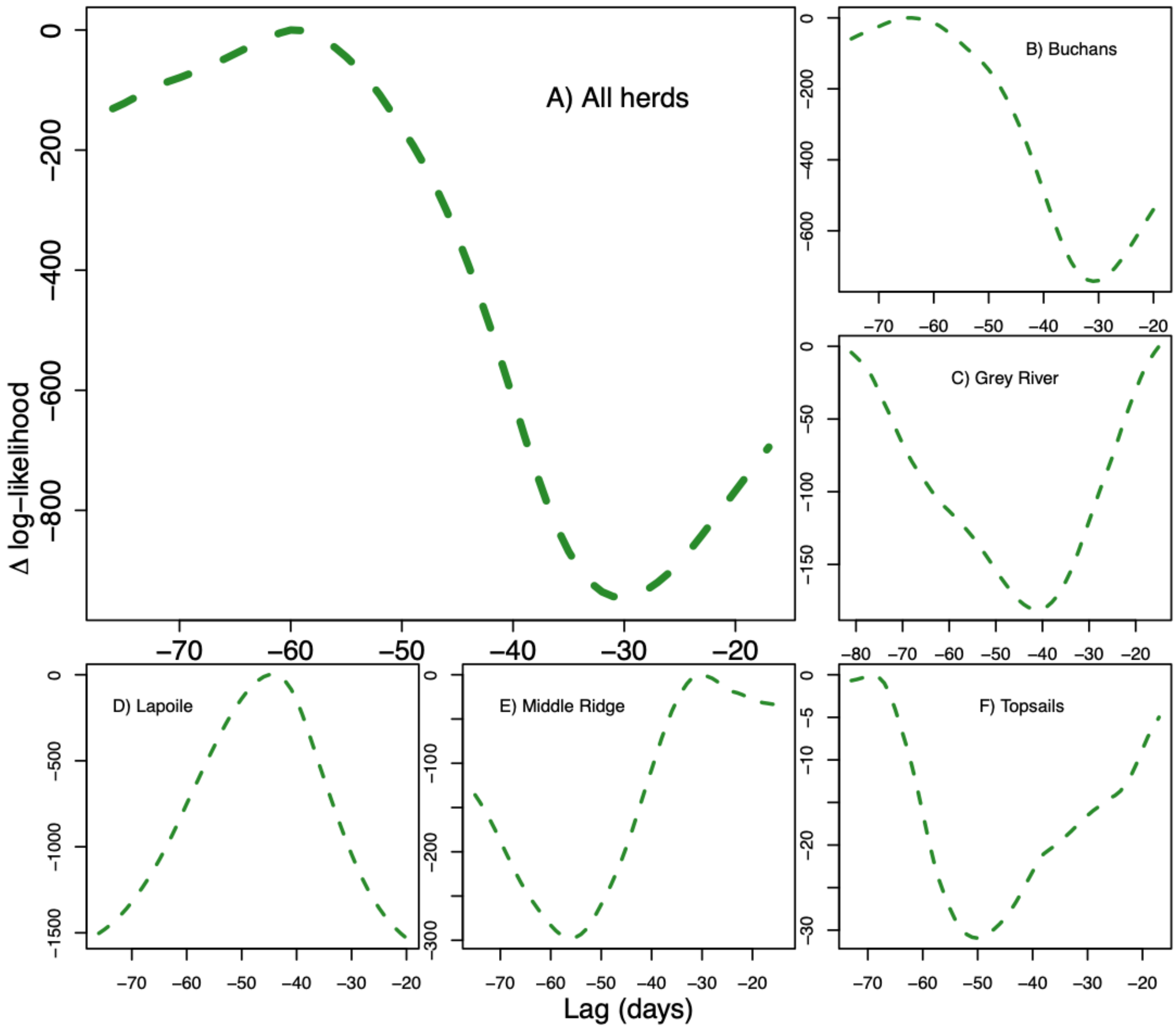

Figure S2.2.2: Delta log-likelihood of models predicting caribou (*Rangifer tarandus*, *n* = 94) selection behaviour for days from peak instantaneous rate of green-up during migration (*n* = 216). We generated models using the absolute value of days to peak IRG across several lags. Lagged datasets were constructed by adding or subtracting the value of the lag to the number of days to peak IRG. This was done to allow us to test for model fit at the focal day of the lag. Panel A) is data for individuals from all herds, B–F represent data from individual herds: B) Buchans; C) Grey River; D) Lapoile; E) Middle Ridge; and F) Topsails. These results are shown to contrast with models for snowmelt, and outline that model fit for tracking green-up during migration in this population results in poor fitting models.

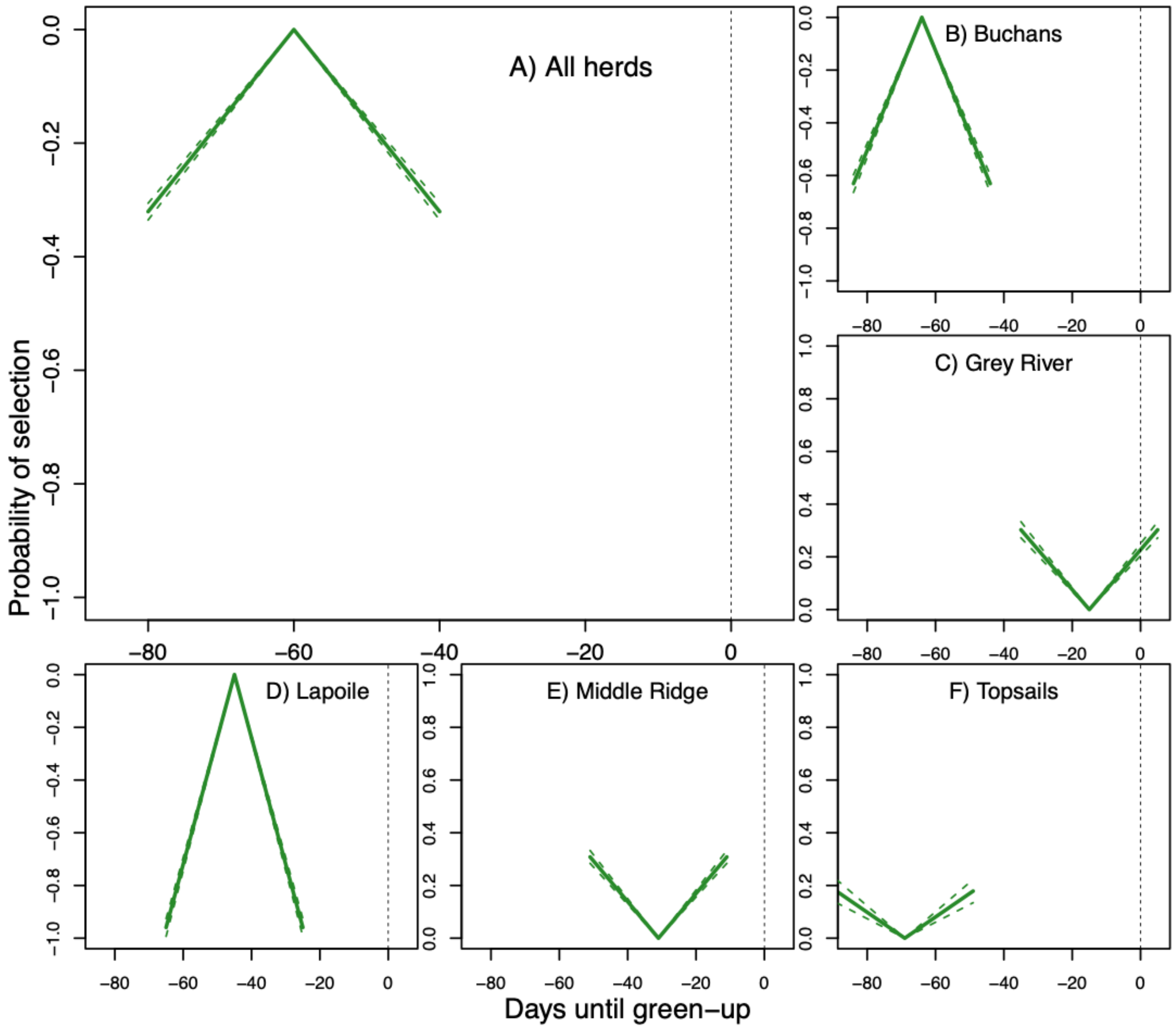

Figure S2.2.3: Model-predicted selection of caribou (*Rangifer tarandus*, *n* = 94) as a function of the number of days from peak IRG during migration from conditional logistic regression models. Dashed lines represent 95% confidence intervals. Panel A) is data for individuals from all herds, B–F represent data from individual herds: B) Buchans; C) Grey River; D) Lapoile; E) Middle Ridge; and F) Topsails. These results contrast with models for snowmelt, and outline that model fit for tracking green-up during migration in this population result in poor fitting models.

S2.3 – Calculating fractional snow during migration

We calculated values of the normalized difference snow index (NDSI) and translated them to the fraction of ground covered by snow (fractional snow cover) to determine fractional snow cover during migration for all herds in our analysis and for individual herds. To do this, we sampled 1000 random points in each of our five replicate herds. We then used Google Earth Engine (Gorelick et al. 2017) to extract the value of the NDSI at each location for early spring to summer (Julian day 45–200) for each year of our study (2007–2013). We then calculated the day the NDSI first had a negative recorded value (our "day of snowmelt", see Chapter 2 Methods). We took the peak values of our density distributions of mean days to NDSI = 0 for each individual/year for each herd (surfing indices, see Chapter 2 Methods) and calculated the NDSI value at that day for each herd and for all herds combined. We used the formula presented by Salomonson and Appel (2004) to calculate fractional snow cover from NDSI:

FRA: $0.06 + 1.21 \times \text{NDSI}$ [Formula S2.3.1]

For our pooled data with all herds, we found that the peak of migration occurred when fractional snow cover was 71% (SD = 25%), see full Results below (Table S2.3.1 and Figure S2.3.1).

Table S2.3.1: Summary of normalized difference snow index (NDSI) and fractional snow cover during migration of caribou (*Rangifer tarandus*, *n* = 94) during spring in Newfoundland Canada from 2007–2013. Surfing index represents the day at which density distributions for mean days to snowmelt (first day of year in which the NDSI recorded a negative value) for each individual-year combination were highest for all herds combined and each individual herd (surfing index). Mean NDSI and fractional snow cover values are estimated for those days (rounded to nearest integer value, + SD).

Population	Surfing index	Mean NDSI (+ SD)	Mean fractional snow cover (+ SD)
All	-7.04	0.53 (0.16)	71% (25%)
Buchans	-6.30	0.49 (0.16)	65% (25%)
Grey River	-8.39	0.54 (0.15)	72% (24%)
Lapoile	-17.23	0.67 (0.15)	88% (24%)
Middle Ridge	1.41	-0.15 (-0.15)	0% (0%)
Topsails	-3.08	0.38 (0.20)	52% (30%)

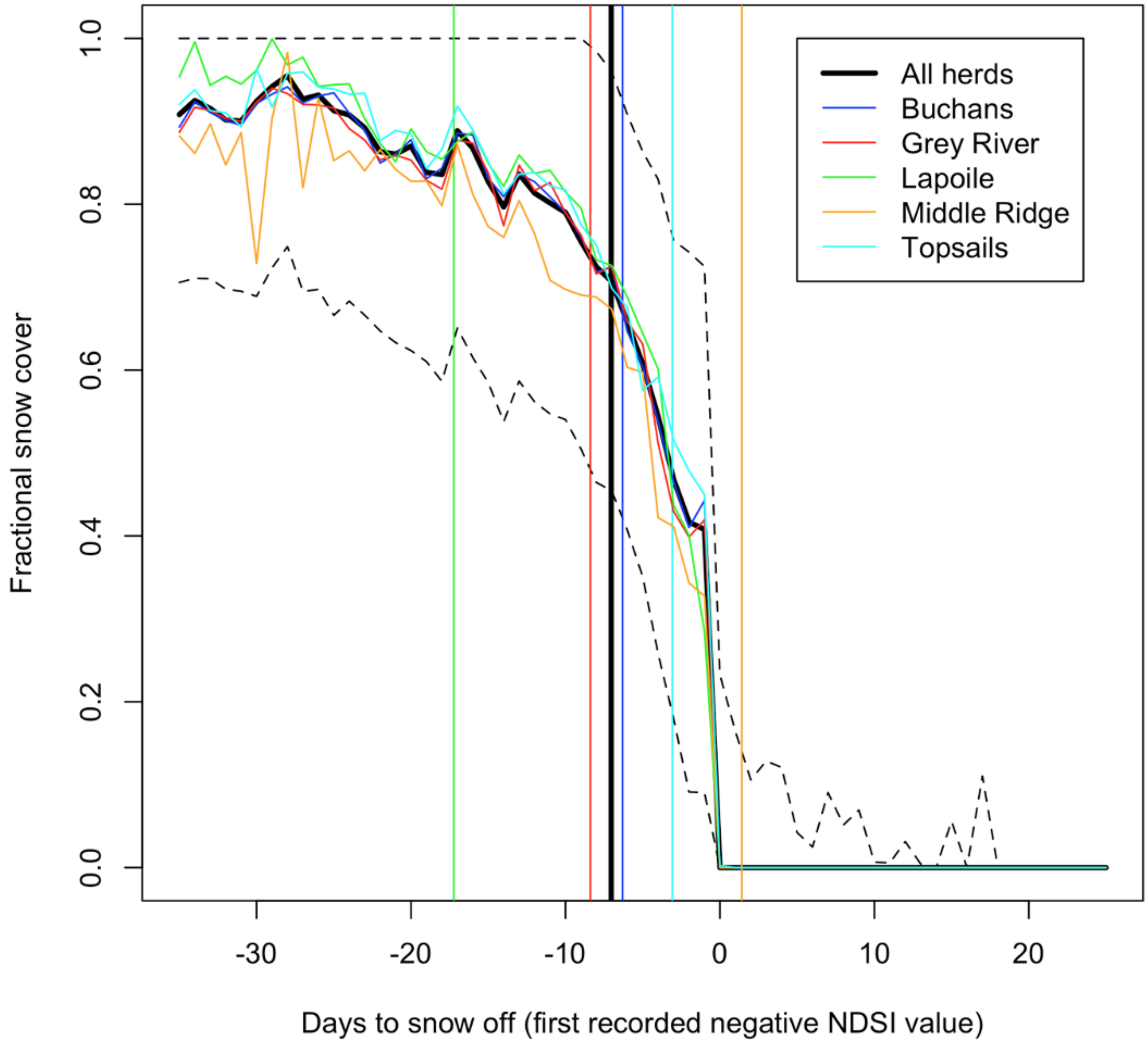

Figure S2.3.1: Total fractional snow cover through time as a function of number of days until the first recorded negative normalized difference vegetation index (NDSI) value at each location in caribou (*Rangifer tarandus*) ranges on the island of Newfoundland, 2007–2013. A total of 1000 locations were sampled in each herd range and the NDSI extracted for each location. Thick black lines represent data for all herds combined, colors represent individual herds. Vertical lines represent peak migration timing for all herds/each herd (surfing indices, see Chapter 2 Methods). Fractional snow cover for each herd during the peak of migration occurs at the intersection of lines of the same color. Dashed black lines represent the standard deviation for all herds combined (standard deviations for each herd separately not shown). Note, all values that would result in a fractional snow cover value outside the range of 0–1 were set to 0 or 1.

S3 Supplementary materials for Chapter 3

Table S3.1: Summary statistics of caribou (*Rangifer tarandus*, *n* = 92) sample size and spring migration timing, duration, and distance across five populations in Newfoundland, Canada from 2007–2013.

	All Populations	Buchans	Grey River	Lapoile	Middle Ridge	Topsails
Number of individuals	92	14	13	18	32	15
Number of ID years	212	44	40	49	56	23
median + [range], start date of migration	Mar 25 [Feb 09, May 19]	Mar 31 [Feb 09, Apr 22]	Mar 29 [Feb 14, May 19]	Mar 22 [Mar 01, Apr 19]	Mar 18 [Feb 23, Apr 25]	Apr 07 [Mar 11, May 10]
median + [range], end date of migration	May 10 [Mar 20, Jul 13]	May 08 [Apr 14, Jun 22]	May 07 [Mar 29, Jun 22]	May 18 [Apr 13, Jun 17]	May 04 [Mar 20, Jul 13]	May 10 [Apr 08, Jun 07]
median + [range], duration of migration (days)	43 [4, 128]	40.5 [13, 84]	39.5 [7, 123]	51 [25, 94]	43 [4, 128]	19 [4, 74]
median + [range], distance of migration (km)	62.2 [30.5, 174.9]	105.3 [42, 143]	58 [36.4, 174.9]	99.8 [35.9, 173.5]	48.9 [30.5, 82.3]	48 [32.1, 139.1]
median + [range], date of calving	May 30 [May 18, Jul 13]	May 31 [May 20, Jun 23]	May 28 [May 22, Jul 07]	Jun 01 [May 22, Jun 23]	May 29 [May 18, Jul 13]	May 31 [May 22, Jun 15]

Proportion calves survive	0.6	0.66	0.55	0.51	0.7	0.52
Median + [5th and 95th percentile] date of snowmelt	Apr 27 [Apr 12, May 19]	Apr 27 [Apr 16, May 21]	Apr 27 [Apr 15, May 24]	May 03 [Apr 09, May 25]	Apr 16 [Apr 08, May 03]	May 01 [Apr 13, May 23]
Median + [5th and 95th percentile] date of green-up	May 29 [May 04, Jun 13]	May 28 [May 01, Jun 13]	May 30 [May 04, Jun 13]	Jun 03 [May 13, Jun 15]	May 28 [May 06, Jun 12]	May 27 [Apr 26, Jun 13]

Table S3.2: Random and fixed effect structures and Δ deviance information criterion (DIC) for candidate behavioural reaction norm models for migratory caribou (*n* = 92) in Newfoundland, Canada. Two model sets are compared: one set with timing of migration (arrival on summer range) and timing of parturition as co-response variables and timing of snowmelt as the explanatory variable, and one set with timing of parturition and calf survival as co-response variables with timing of spring green-up as the explanatory variable. Timing of snowmelt/green-up is the median date in which pixels in the population's range became snow-free (migration and parturition models) or reached peak green-up (parturition and calf survival models) that spring.

Model	Fixed effects	Random effects	**Δ** DIC migration and parturition	**Δ** DIC parturition and calf survival
Null	Population	None	81.2	50.4
Population differences, no plasticity	Population	Population	81.2	60.8
Individual differences, no plasticity	Population	Individual	56.0	35.9
Overall plasticity, no population/individual differences	Population + Timing of snowmelt/green-up	None	58.4	50.0
Overall plasticity, population differences	Population + Timing of snowmelt/green-up	Population	58.5	50.1

Overall plasticity, individual differences	Population + Timing of snowmelt/green-up	Individual	16.0	34.4
Random slopes, population × environment interaction	Population + Timing of snowmelt/green-up	Population × Timing of snowmelt/green-up	59.6	37.6
Random slopes, individual × environment interaction	Population + Timing of snowmelt/green-up	Individual × Timing of snowmelt/green-up	0	0

Table S3.3: Slope and intercept correlations (plus upper and lower 95% credible interval) between timing of arrival on summer range, timing of birth, and annual reproductive success for caribou (*Rangifer tarandus*, n = 92) in Newfoundland Canada. Results from the top Markov chain Monte Carlo bivariate generalized linear regression models, along with an interpretation of what each correlation suggests.

Traits	Interpretation	Estimate	Lower	Upper
Migration time intercept, birth time intercept	Timing of migration (arrival on summer range) and timing of parturition in an average environment are correlated. Individuals that migrate earlier give birth earlier (see Figure 3a, Chapter 3).	0.68	0.16	0.99
Migration time intercept, migration time slope	No strong correlation between timing of migration in an average environment and amount of plasticity in migration timing.	-0.36	-0.97	0.47
Birth time intercept, birth time slope	No correlation between timing of birth in an average environment and plasticity in timing of birth.	0.19	-0.76	0.91
Migration time slope, birth time slope	No correlation between plasticity in migration timing and parturition timing (see Figure 3b, Chapter 3).	-0.04	-0.84	0.76

Migration time slope, birth time intercept	No correlation between plasticity in migration timing and timing of birth in an average environment.	-0.21	-0.92	0.66
Migration time intercept, birth time slope	No strong correlation between timing of migration in an average environment and plasticity in timing of parturition.	0.27	-0.68	0.92
Calf survival intercept, birth time intercept	No strong correlation between probability of calf survival and timing of parturition in an average environment (see Figure 3c, main text).	-0.25	-0.94	0.57
Calf survival intercept, calf survival slope	No strong correlation between average probability of survival and whether probability of survival changes as a function of green-up.	-0.26	-0.90	0.54
Birth time intercept, birth time slope	Potentially negative correlation suggests that individuals that give birth late may be less plastic in the timing of parturition.	-0.52	-0.99	0.42
Calf survival slope, birth time slope	Likely negative correlation suggests that increased plasticity in parturition time results in less heterogeneity in annual reproductive success across a gradient of green-up dates.	-0.57	-0.97	0.10
Calf survival slope, birth time intercept	Potentially positive correlation suggests individuals who give	0.49	-0.41	0.98

	birth later are more likely to have their calf survive when green-up is later.			
Birth time slope, calf survival intercept	Potentially positive correlation suggests that greater plasticity in parturition time may increase reproductive success (see Figure 3d, main text).	0.27	-0.53	0.95

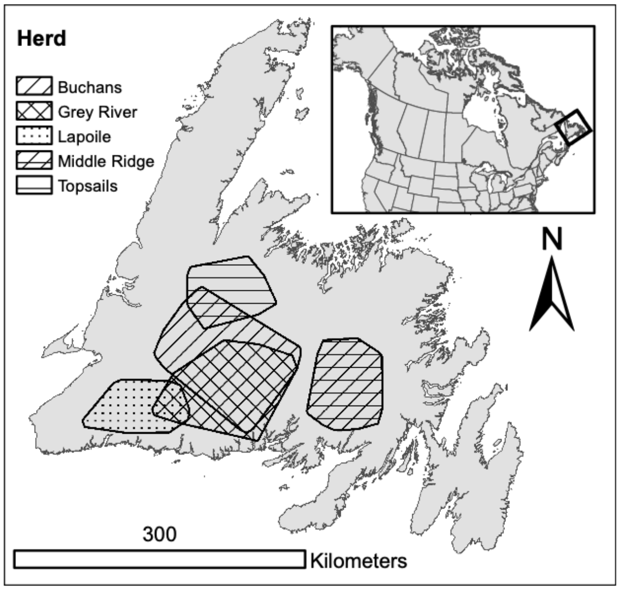

Figure S3.1: The island of Newfoundland with the location of the five caribou (*Rangifer tarandus*) populations used in this study.

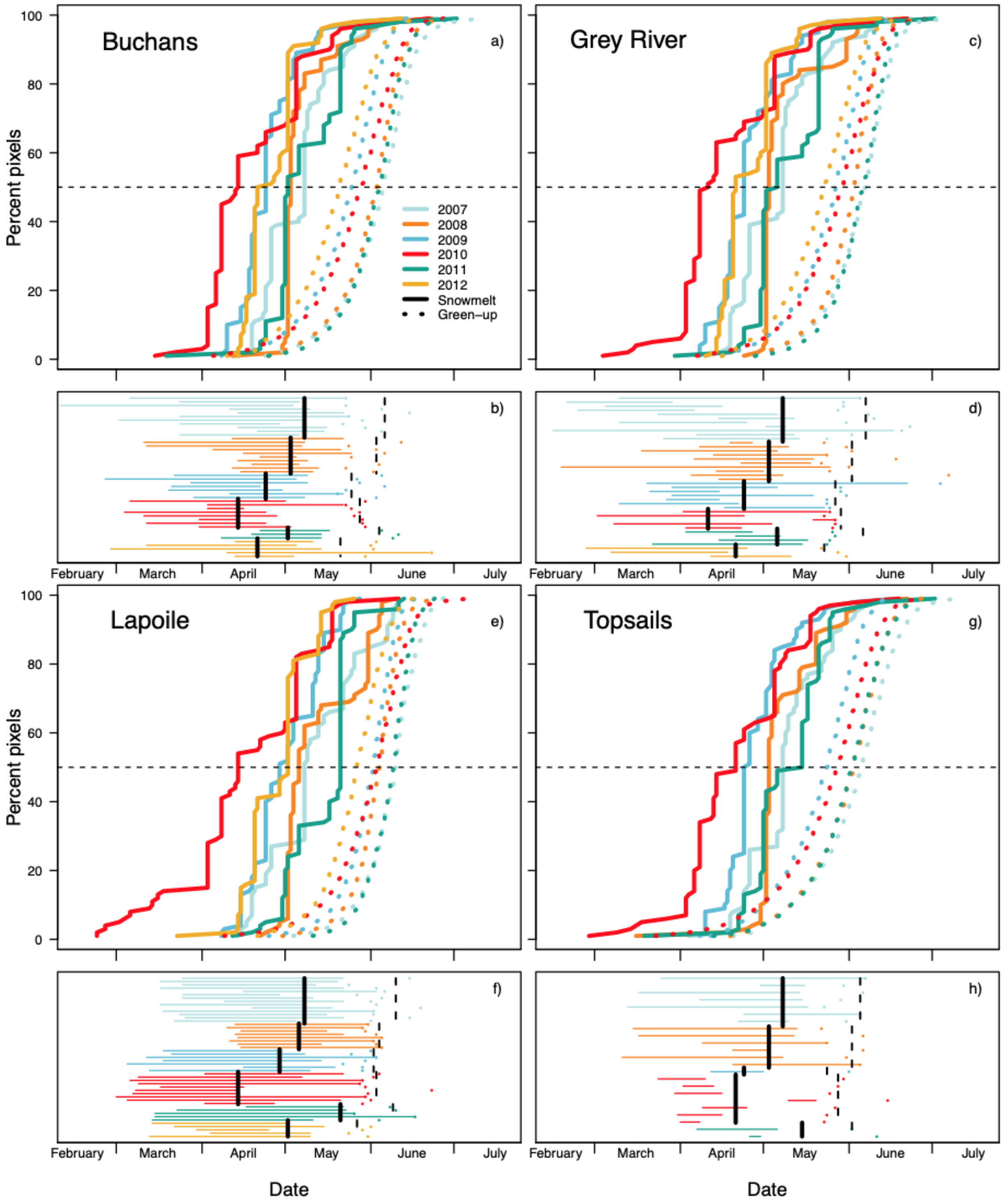

Figure S3.2: Phenology of snowmelt and green-up and migration and parturition for caribou (*Rangifer tarandus*, *n* = 60) in the Buchans (a, b), Grey River (c, d), Lapoile (e, f), and Topsails (g, h) populations, 2007–2012 (no data for Topsails, 2012). a), c), e), and g) represents the number of pixels within the population's spring/summer range in which snow has melted (NDSI > 0, solid lines) or that have reached the peak of green-up (instantaneous rate of green-up; dotted lines) in each spring. Colours represent different years, and the vertical dashed lines represent the median (the measure used for determining date of snowmelt/green-up). b), d), f), and h) represent the timing of migration as horizontal lines for each individual in each year (each line's extent represents the time they were migrating). Points represent the timing of parturition. Black vertical lines represent the median dates of snowmelt (solid) and green-up (dashed) for each year. See Figure 3.1 for plots for the Middle Ridge herd.

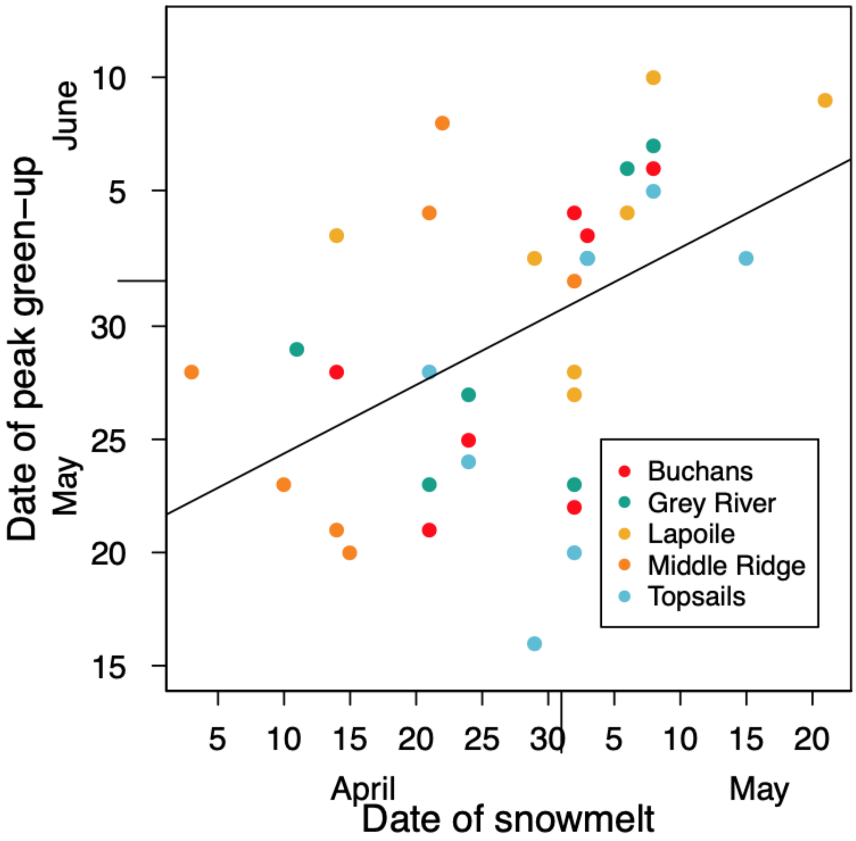

Figure S3.3: Relationship between date of snowmelt and date of green-up in the ranges of five caribou (*Rangifer tarandus*) populations in Newfoundland, 2007–2013. There was a significant relationship between green-up date and snowmelt date, however later snowmelt only resulted in green-up occurring 0.303 (95% CI: 0.114, 0.492) days later (adjusted R^2 = 0.21).

S4 Supplementary material for Chapter 4

Table S4.1: Parameter estimates (+95% CI) for selection functions for coyotes (*Canis latrans*) in the Lapoile and Middle Ridge populations in Newfoundland, Canada. Parameter estimates were estimated for the entire study period. See Figure 4.2 for parameter estimates from the moving window analysis.

	Estimate + 95% CI, Lapoile	Estimate + 95% CI, Middle Ridge
Intercept	-2.930 (-3.146, -2.715)	-1.532 (-1.681, -1.384)
Conifer forest	-1.271 (-1.500, -1.042)	0.000 (-0.136, 0.136)
Conifer scrub	0.009 (-0.125, 0.144)	0.446 (0.352, 0.540)
Rocky barrens	0.684 (0.430, 0.937)	-0.272 (-0.585, 0.041)
Lichen barrens	-0.642 (-0.781, -0.503)	2.284 (2.199, 2.370)
Mixedwood forest	1.351 (1.125, 1.577)	0.946 (0.744, 1.148)
Distance to nearest linear feature	-0.029 (-0.047, -0.010)	-0.157 (-0.172, -0.142)
Elevation	2.557 (2.222, 2.892)	-0.305 (-0.682, 0.072)
Terrain Ruggedness	-17.234 (-19.508, -14.960)	2.710 (1.291, 4.130)

Table S4.2: Parameter estimates and hazard ratios (+95% confidence intervals) of the fully parameterized Cox proportional hazards model describing probability of caribou (*Rangifer tarandus*) calf mortality in the Lapoile population, Newfoundland, Canada. IRG = instantaneous rate of growth; see Chapter 4 Methods.

	Estimate (+ 95% CI)	Hazard ratio (+95% CI)
IRG	-0.121 (-0.882, 0.639)	0.886 (0.414, 1.895)
Predation	0.585 (0.086, 1.084)	1.795 (1.090, 2.956)
Distance to neighbours	0.161 (-0.426, 0.749)	1.175 (0.653, 2.115)
IRG before birth	0.323 (-0.298, 0.943)	1.381 (0.742, 2.568)

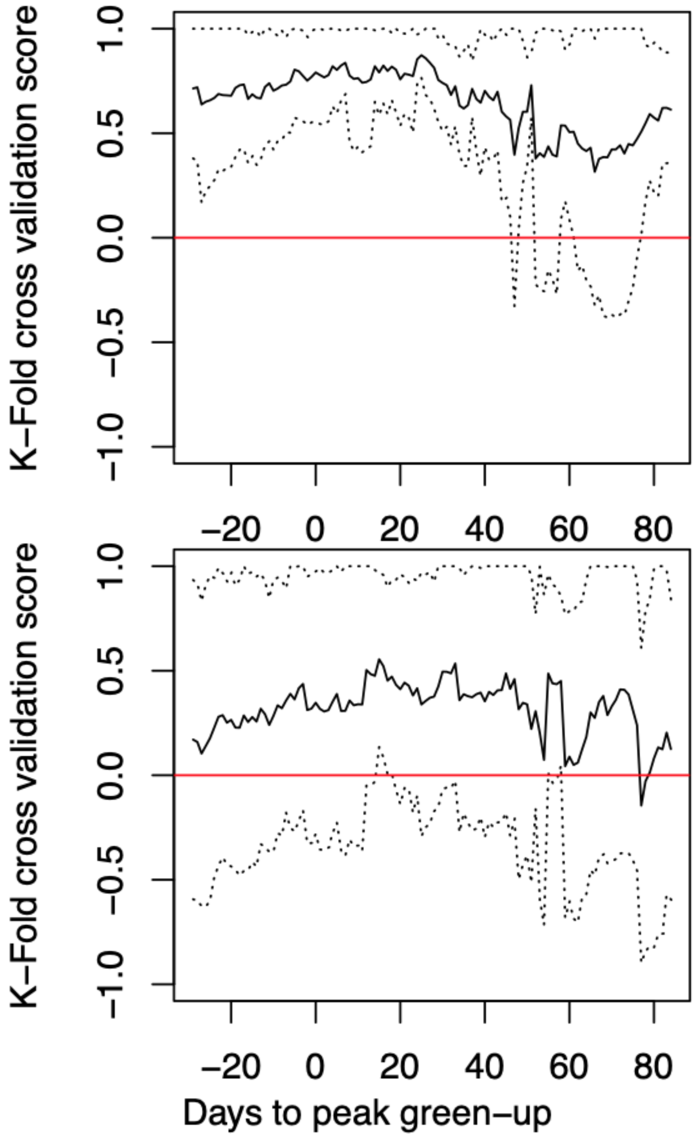

Figure S4.1: K-fold cross-validation scores for moving window selection functions of coyotes (*Canis latrans*) in two populations (Lapoile, n = 23, top panel and Middle Ridge, n = 58, bottom panel) in Newfoundland. We generated resource selection function models for each focal day (with a 10-day buffer on either side) and implemented k-fold cross-validation to verify the predictive strength of the model (see Chapter 4 Methods for details). Dashed lines represent standard errors. Red horizontal line represents 0 (no predictive power).

S5 Supplementary material for Chapter 5

Table S1: Summary statistics of migration timing, selection for IRG (instantaneous rate of green-up) and number of locations for data used from eight ungulate populations for behavioural reaction norm analyses in Wyoming, USA from 2005–2019.

	All Populations	Absaroka Elk	Cody Elk	Jackson Moose	Pinedale Mule Deer	Red Desert Mule Deer	Sierra Madre Elk	Sublette Moose	Yellowstone Bison
Number of individuals	230	32	22	11	37	49	20	12	47
Mean (range) of animal-years	2.9 (1, 8)	2.5 (1, 3)	2.5 (1, 3)	1.9 (1, 3)	3.7 (2, 6)	3 (2, 4)	3 (3, 3)	2 (1, 3)	3.1 (1, 8)
Mean (range) distance of migration (km)	69.3 (2.7, 327.4)	37.7 (11.6, 60.2)	61.6 (14.8, 107.6)	26.2 (10, 41.5)	69.9 (27.5, 138)	144.1 (70.7, 327.4)	37.2 (11.5, 77.3)	9.6 (2.7, 24.3)	41.9 (12.3, 64)
Mean (range) duration of migration (d)	34.9 (1, 122)	31.3 (3, 107)	29.5 (1, 84)	25.2 (2, 90)	55.4 (4, 122)	27.6 (4, 81)	46.1 (7, 99)	14.9 (1, 67)	27 (2, 96)

Mean (range) start date of migration (Julian day)	115.6 (33, 209)	134.8 (83, 209)	143.1 (86, 197)	146.5 (59, 187)	88.4 (37, 149)	117 (69, 152)	86.9 (47, 127)	95.6 (33, 152)	129.8 (63, 188)
Mean (range) end date of migration (Julian day)	150.5 (41, 234)	166.1 (100, 234)	172.6 (123, 226)	171.7 (141, 219)	143.7 (105, 192)	144.7 (94, 206)	132.9 (85, 196)	110.5 (41, 154)	156.8 (78, 215)
Mean (range) number of locations/animal-year	4914.7 (44, 33264)	964.7 (44, 5434)	11044.2 (396, 33264)	3409.5 (253, 9141)	7251.5 (429, 16104)	2684.2 (66, 9856)	8074.4 (1232, 17380)	3927.5 (253, 17666)	3904.4 (264, 13442)
Median (sd) IRG selection coefficient	0.51 (14.58)	1.09 (2.01)	-0.24 (2.31)	-0.07 (1.29)	1.85 (1.74)	0.05 (1.94)	1.66 (1.66)	-0.71 (74.9)	-0.28 (2.03)

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