Ecological dynamics of wolves and their ungulate prey in Yellowstone National Park



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Declaration of Authorship

The work presented in this thesis is my own. In each of the chapters presented, I have developed the aims, concepts, and methodology, performed the analyses, interpreted results, and written the manuscripts. I have been fortunate to examine data collected by other excellent scientists. For each chapter, a list of co-authors and statements of their contributions are given below.

Chapter 1 – General introduction

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Chapter 2 – Life history stage and annual variation of movement in a wide-ranging carnivore.

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Chapter 3 – Social and environmental determinants of demography in Yellowstone wolves.

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OL and TC conceived and developed the methods, OL performed the analyses and wrote the manuscript. TC Supervised the study and interpreted the results with OL. DWS oversaw the data collection.

Chapter 4 – Population dynamic effects of demography, sociality and dispersal in a territorial carnivore.

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OL and TC conceived and developed the methods, OL performed the analyses and wrote the manuscript. TC Supervised the study and interpreted the results with OL.

Chapter 5 – A demographic model of antagonistic trophic interactions in the Yellowstone ecosystem reveals the primacy of indirect effects on community dynamics.

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OL and TC conceived and developed the methods, OL performed the analyses and wrote the manuscript. TC Supervised the study and interpreted the results with OL.

Chapter 6 – Discussion

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Abstract

A core challenge for ecologists is to understand how biotic and abiotic processes influence demography and the dynamics of populations through time. I explore how ageing, social processes, and population conditions drive demography, movement, and community dynamics in a restored population of wolves *Canis lupus* in Yellowstone National Park, USA. I combine the analysis of empirical data for multiple species with models designed to simulate the dynamics of the system in which they live and interact, focussing on social and demographic processes in wolves.

I assess the utility of movement data for identifying functional senescence—declines in biological functions with age—in wild populations. I use long-term GPS data to describe movement across lifespans, identifying elevated rates of movement in older individuals and a pronounced annual cycle in movement rates.

I show that the fundamental demographic rates of survival and recruitment depend on attributes of individual wolves and their social groups, as well as effects of competition and population. Despite evidence that demographic performance is positively related to group size, packs are consistently small in Yellowstone. This apparent contradiction may derive from an inequality in fitness between breeding and non-breeding individuals in socially reproductive groups. To test this, I construct a group and age structured model simulating Yellowstone's high-density wolf population, and find that by constraining group size, dispersal imparts a substantial regulatory effect on the population. This work forms a foundation for future work to understand the environmental and social basis for dispersal in a large carnivore.

Finally, to examine whether the reintroduction of wolves led to the changes in Yellowstone's community structure observed in the past three decades, I use a novel approach to model community dynamics by parameterising for direct species interactions. I find that widespread and complex indirect effects emerge across the community and show that wolf predation has cascading effects that lead to the gradual recovery of vegetation.

This thesis provides new insights into the social and environmental basis of demography in an ecologically important carnivore and details the role of predator restoration in shaping community dynamics.

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Chapter I

General introduction

Chapter I: General introduction

Animal populations are complex, changeable entities. As they age, spread and contract, boom and bust, and even collapse entirely, populations shift between periods of relative stability and flux in their size, structure, and range (Coulson, 2021b). In a time when natural systems are increasingly imperilled by human activity, habitat destruction and climate change (Travis, 2003; Urban *et al.*, 2016), it is imperative to understand what causes populations to change through time.

Change in populations can be reduced to four vital rates—survival, recruitment, immigration, and emigration—which comprise demography. From the sum of these processes, the dynamics of a population emerge. Quantifying demographic rates is therefore a core theme of population ecology. By determining how traits and genes propagate via survival, reproduction and movement, demography is also fundamental to our understanding of evolution (Metcalf and Pavard, 2007). But what processes determine these rates? This question represents the key challenge for demographic ecologists and motivates much of the research presented here. In short, functional traits, species interactions and environmental effects combine to influence demographic rates of individuals, whose effects emerge across the range of ecological scales, including the size and viability of populations and the structure of communities (Griffith *et al.*, 2016). However, demography and population dynamics may be very complex (Loehle, 2004) and so identifying important underlying mechanisms is an informative approach to their analysis (Benton, Plaistow and Coulson, 2006).

Broadly, factors that influence demography may be classified as abiotic or biotic in origin. Abiotic processes include the interactions of organisms with the physical environment, the effects of climate and weather (Forchhammer and Post, 2004; Boggs and Inouye, 2012) and anthropogenic factors including hunting, habitat loss and pollution (Maxwell *et al.*, 2016). Biotic drivers of demography include the interactions between individuals and their community: both within species (e.g., via sociality, mating success,

competition, facilitation) and between species (e.g., via predation, herbivory, parasitism, mutualism and intraguild competition). In addition to these direct effects, demography and community-structure are also shaped by indirect interactions, which emerge from multiple connected direct interactions. These indirect effects include resource competition, competitive release, apparent competition and behavioural effects (Strauss, 1991). Individual demography is also influenced by characteristics of the individual (e.g., body condition, experience, and senescence). The interplay between these effects is central to understanding how a community changes through time. The research presented here focuses primarily on these biotic drivers of demography across a range of levels of organisation, from attributes of individuals and groups, to features of the population and wider community.

In this thesis, I aim to evaluate how biotic drivers influence demography, population dynamics and community structure, by asking two central questions. First, how do environmental and social processes relate to the demography, and in turn, the population dynamics of an ecologically important predator? And second, how do the interactions between a predator and its major prey species shape the structure and trajectory of their community? To address these questions, I examine more than 20 years of cumulative data concerning the key species of Yellowstone National Park, USA. I use data concerning individual movement, individual and group-level demography, and species populations trends. Before returning to outline how I use these data to examine demography and community dynamics, it will be instructive to first describe the utility of the Yellowstone system for ecological research, and indeed to understand the turbulent history of wolves and their return to Yellowstone.

1.1 Yellowstone National Park & the northern range

Established in 1872 under Ulysses S. Grant, Yellowstone was the first national park in the United States. The unique combination of its volcanic landscape, geothermal geysers, and charismatic megafauna generates more than half a billion dollars (NPS, 2020) from approximately 4 million tourists annually (NPS, 2022). The park is home to numerous species of scientific interest, including populations of beaver *Castor canadensis*, elk *Cervus canadensis*, pronghorn antelope *Antilocapra americana*, cougar *Puma concolor*, Coyote *Canis latrans*, black bear *Ursus americanus*, grizzly bear *Ursus arctos horribilis,* mustelids *Mustela spp.*, amphibians, 300 species of bird, one of the largest remaining wild bison *Bison bison* populations in North America, and importantly, a restored population of grey wolves *Canis lupus* (NPS, 2019). Approximately 80% of the park's 8,983 km^2 area is forest, with much of the remainder comprised of grassland. The landscape is characterised by broad river valleys of sagebrush-steppe and short-grass prairie (Singer and Renkin, 1995), and forested areas of lodgepole pine *Pinus contorta*, Douglas fir *Pseudotsuga menziesii*, Engelmann spruce *Picea engelmannii*, whitebark pine *Pinus albicaulis*, subalpine fir *Abies lasiocarpa*, aspen groves *Populus temuloides* and willow *Salix spp.* (NPS, 2021).

The National Park Service (NPS) is responsible for the management of the land use and monitoring of the biodiversity and key species of the park. The long-term monitoring of the major animal populations is focused on the northern range (figure 1), a 1,531 km^2 area (~10% of YNP) in the north of the park, partially defined by the wintering range of northern Yellowstone elk (Houston, 1982). The wolf and ungulate populations in this area are the focus of the research presented in this thesis.

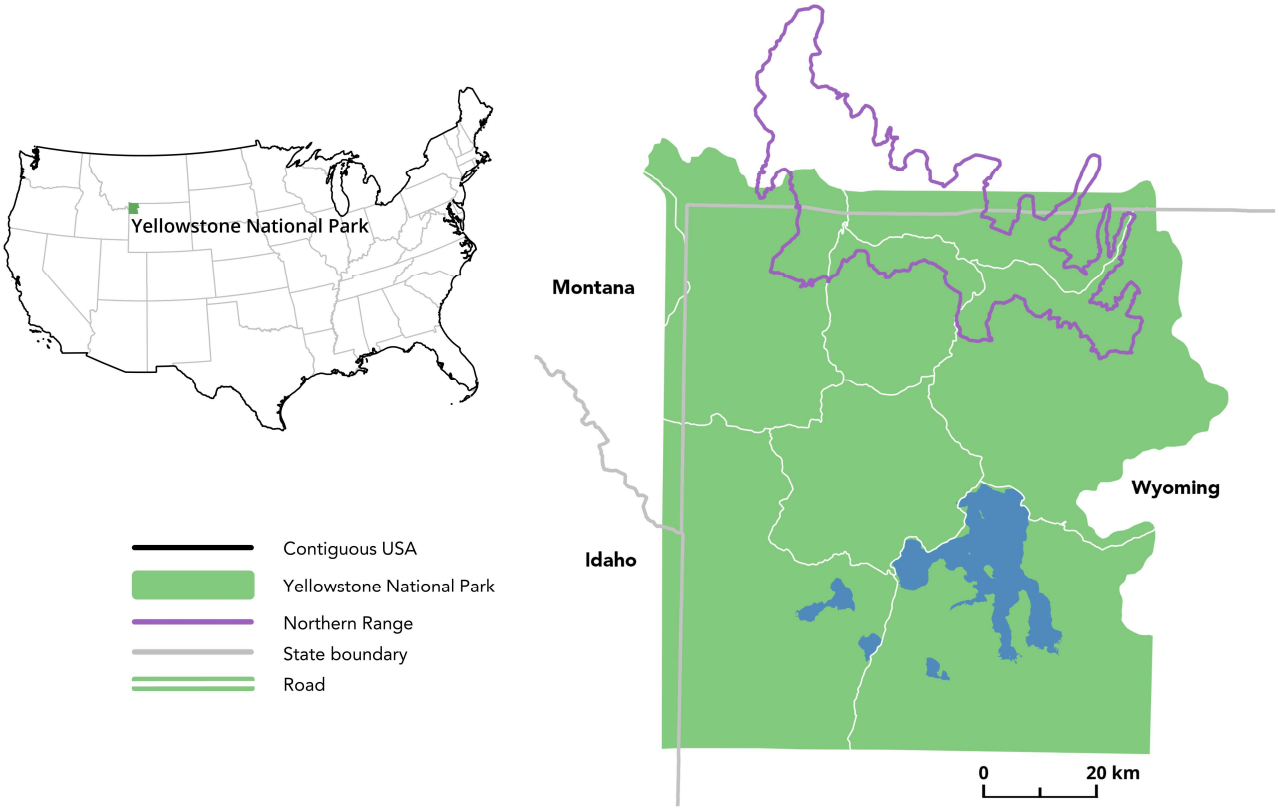


Figure 1: Location and map of Yellowstone National Park, USA, and site of the northern range study system.

1.2 An abridged history of wolves in Yellowstone

Gray wolves *Canis lupus* are a species of large canid predator with a native distribution covering much of Eurasia and North America (Mech, 1974). When Europeans colonised North America from the 15th century, they brought with them an animosity towards wolves, owing to centuries of legend and folklore (Coleman, 2008). In the 19th century, the colonists moved further westward to establish new ranching land. Viewed as a threat to life and livestock, wolves were hunted zealously, mainly by trapping, shooting, and the lacing of animal carcasses with strychnine poison (Steinhart, 2011). Consequently, wolves were eradicated from almost the entirety of the continental United States. In the first quarter of the 20th century, wolves in Yellowstone were killed under a predator control program operated by the national park service, primarily owing to competition with elk hunters (Weaver, 1978). In 1926, the last wolf was shot in Yellowstone (Weaver, 1978).

In 1944, the ecologist Aldo Leopold—renowned for his early advocacy of wilderness restoration—proposed that wolves should be restored in "the larger national parks and wilderness areas; for instance, the Yellowstone and its adjacent national forests" (Leopold, 1944). Two decades later, Leopold penned an influential report that urged a shift toward managing national parks by "natural regulation" (Leopold, 1963). As a result, the Yellowstone elk population was free to fluctuate according to the conditions of the environment (MacNulty *et al.*, 2016). In the absence of top-down regulation from wolves, elk numbers grew substantially (figure 2A), to more than 19 thousand individuals (Lemke and Mack, 1998). The hyperabundance of elk was linked to degradation in woody vegetation species, notably aspen, cottonwood and willow (Barmore, 2003; Beschta and Ripple, 2016; Peterson *et al.*, 2020). At this time, both bison (Plumb *et al.*, 2009) and beaver (Ripple and Beschta, 2004), once historically abundant in Yellowstone, were also nearing extinction. Collectively, these signs pointed to a state of ecological imbalance in Yellowstone.

A contemporary review proposed that the restoration of wolves would reinstate effective natural control of the elk (Houston, 1982). Following reports of wolf sightings in Yellowstone, an investigation in the late 1970s found no evidence of wolves and advocated for their reintroduction (Weaver, 1978). These events came at a time where the concept of ecological conservation was entering the collective consciousness in North America (termed 'the green movement'; Doherty, 2005). Accordingly, the general perception of wolves had become more favourable, while wolf restoration was gaining traction in the scientific and park management communities. Efforts to reintroduce wolves would require years of environmental impact research, campaigning and political process (reviewed in Fritts *et al.*, 2020). Researchers published an environmental impact statement to describe the ecological implications and historical basis for reintroducing wolves (EIS; USFWS, 1994). In May 1994, the Secretary of the Interior under Clinton, Bruce Babbitt, signed a Record of Decision to adopt the suggestions of the EIS, paving the way for the return of wolves to Yellowstone.

In 1995, 14 wolves were captured in Alberta, Canada and released into Yellowstone, followed by a further 17 wolves in 1996 (Fritts *et al.*, 2020). In the following decade, the wolves established a new population (figure 2B) that has since settled at approximately 100 wolves across the park for the last decade (Cassidy *et al.*, 2022). Wolves promptly occupied the northern range, which became saturated with pack territories by the year 2000 (Kauffman *et al.*, 2007) creating a highly competitive landscape. The northern range supports a greater density of wolves than the interior areas of the park, and now represents one of the densest populations in North America (Smith, 2016).

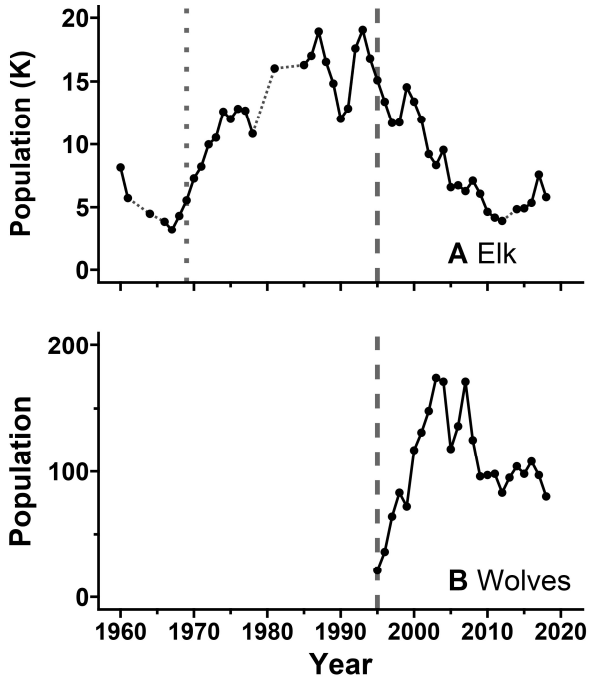


Figure 2: Population time-series of (A) Yellowstone elk and (B) wolves following wolf reintroduction. Dotted line indicates the onset of the natural regulation era of elk management (1969), dashed lines indicate year of first wolf reintroduction (1995).

In the years that followed the reintroduction of wolves, diverse and profound changes have occurred across the Yellowstone ecosystem. As the wolf population re-established, the elk population declined (figure 2A) from nearly 20 thousand to 5 thousand (MacNulty *et al.*, 2016), while the bison population expanded from 1 to 3 thousand individuals (Beschta *et al.*, 2020). The relative abundance of these species—and particularly the abundance of elk—is important to the dynamics and recovery of woody vegetation in

Yellowstone (W. H. Romme *et al.*, 1995; Beyer *et al.*, 2007; Beschta and Ripple, 2016). Additionally, revivals in populations of beavers (Smith and Tyers, 2012) and songbirds (Baril *et al.*, 2011) are linked to regrowth of woody vegetation in Yellowstone. These pronounced population scale changes correspond to a community response to ecological perturbation after the reintroduction of wolves, possibly indicating that the Yellowstone community has been—and possibly remains—in transition from one stable state to another (Coulson, 2021a).

1.3 The ecological consequences of wolf reintroduction: Yellowstone as a natural experiment

The reintroduction of wolves represents a valuable opportunity to examine the link between the presence of a top predator and the community organisation and health of an ecosystem. The past two decades of Yellowstone research represents a superb example of a natural experiment, where ecologists observe the outcomes of large-scale perturbations to natural systems (Sagarin and Pauchard, 2010). Natural experiments can generate large volumes of data concerning multiple species across wide temporal and spatial scales, and allow us to examine conditions which may be impossible to achieve under experimental conditions (Diamond, 1986). These observational studies have granted a wealth of insight into a vast array of ecological and evolutionary questions (Clutton-Brock and Sheldon, 2010). However, natural experiments inherently lack a control group – we do not have another, wolf-less Yellowstone with which to compare the dynamics and structure of the community. It is therefore difficult to establish with certainty the causal links between the return of the wolves and the recovery of woody vegetation and biodiversity as driven by changes occurring in the elk population (Peterson *et al.*, 2020). Indeed, this issue has been the subject of protracted debate.

Whilst there is evidence of localised recovery in willows (Beschta & Ripple, 2016) and aspen (Painter *et al.*, 2015), it is argued that the recovery is partial and may take decades

to stabilise (Marshall, Thompson Hobbs and Cooper, 2013). The link between wolf-induced changes in elk and the recovery of vegetation is also complicated by the effects of wildfires (W. H. Romme *et al.*, 1995) and drought (Frank and Samuel, 1992). Whilst there is some evidence of elk behavioural responses to the presence of wolves (Kohl *et al.*, 2018), it has been argued that vegetation-level effects have been mainly driven by numerical changes in the elk population (Kauffman, Brodie and Jules, 2010; Painter *et al.*, 2015; Boyce, 2018). The decline in the elk population since the wolf reintroduction—and that elk represent nearly 90% of the diet of Yellowstone wolves (Metz *et al.*, 2012a)—suggest that the wolf-elk interaction is important to the community dynamics of this system.

In the absence of controls for natural experiments and observational studies, ecological modelling and simulation are powerful tools to predict the response of a community to changes in the presence and abundance of species, inter-species interactions, and management strategies (Coulson, 2012). This thesis joins nearly three decades of effort to model the dynamics of the Yellowstone ecosystem.

1.4 Yellowstone wolves as a study system

The Yellowstone wolves have been monitored closely since their reintroduction. The wolf project scientists record the body size, disease status, age, inter-annual survival and pack association of individuals, and the pup recruitment, location and spatial extent of the territories of each pack (Smith, Stahler and MacNulty, 2020). Since 2004, 30-40% of the population have been monitored with GPS collars (MacNulty, Stahler, Coulson, *et al.*, 2020), producing a rich history of the spatiotemporal behaviour of wolves (Smith, Metz, *et al.*, 2020). Collectively, these data now form one of the richest and most varied datasets of large carnivores in the world, and have provided insight into a diverse array of ecological and evolutionary processes, including reproductive demography (Stahler *et al.*, 2013), genetics (Vonholdt *et al.*, 2008), parasites (Almberg *et al.*, 2012; Meyer *et al.*,

2022), disease (Almberg *et al.*, 2009), spatiotemporal patterns of predation risk (Kohl *et al.*, 2018) and intraspecific aggression (Cubaynes *et al.*, 2014).

In summary, the Yellowstone wolf reintroduction provides an excellent opportunity to explore the relationships between environmental and social conditions and demographic processes, and to examine how species interactions shape community dynamics. I use data from Yellowstone to address four questions concerning the demographic dynamics of wolves and their impact on the structure of their community:

1) Can movement data be used to detect signals of senescence in free-living animals?
2) How do demographic rates in social species vary according to individual, group, and population-level attributes; and do these patterns indicate an optimal group size?
3) Does inequality in fitness between dominants and subordinates regulate group sizes via dispersal in a socially reproductive species?
4) How does the restoration of a top predator influence the structure and dynamics of a community via indirect effects?

Thesis chapter summary

In this thesis, I examine the relationships between social and environmental processes and demography in a restored population of a social carnivore and use simulation models to predict how these patterns shape the dynamics of their population and drive change across the wider community. A summary of the motivation, methodology and results of each research chapter follows below.

Chapter II: Life history stage and annual variation of movement in a wide-ranging carnivore

The behaviour and physiology of organisms change as they progress through life. Individuals change in size, social status, and experience, and undergo ageing, all of which

may influence an animal's behavioural decisions and its physical capacities. Individuals of almost all animal species undergo senescence — the age-related decline of biological functions including reproduction, immunity, biomechanical capacities, and body condition. Due to the difficulty of recording functional traits across the lifespans of wild animals, there are few cases where functional senescence has been documented in the wild (Soulsbury and Halsey, 2018). In this chapter, I use GPS collar data from more than 14 years of Yellowstone wolf monitoring to explore the possibility of detecting functional senescence—or a decline in physical capacity with age—in animal movements.

During the annual winter periods of intensive study in Yellowstone, where park scientists intensively record the status of the wolf population, an effort is made to fit as many wolves as possible with GPS collars. To date, the resulting movement data have been used primarily to monitor the distribution of wolves and their packs on the landscape and their spatiotemporal relationship with prey. The historical nature of this dataset—combined with rich data concerning the demography of individuals—provides a rare opportunity to examine patterns of movement across the life course. I predict that whilst numerous aspects of movement and space use are likely to vary with age, the distance that individuals move over time would be a component of movement that is likely to show signals of senescence, since movement rates are necessarily constrained by biomechanical and physiological capacity. I therefore predict that if signals of functional senescence emerge before death in free-living animals, then movement rates would exhibit declines at old age.

Contrarily, I identify elevated movement rates in the oldest wolves of the sample. To examine the validity of this finding, I decompose global changes in movement rates into change occurring within individuals and change owing to individuals leaving the dataset. I find that despite the cross-sectional nature of the sample, my results were not significantly biased by processes occurring within individuals. I discuss these results in the context of the social ecology of wolves, where older wolves are more likely to be those

in dominant positions within the pack. I also report a pronounced annual cycle in movement rates and show that wolves move markedly less in Yellowstone's snowbound winters. I discuss this in terms of seasonal variation in the relative energetic costs of locomotion for wolves and their prey.

Chapter III: Social and environmental determinants of demography in Yellowstone wolves

Social living in animals is thought to evolve when the benefits to the fitness of individuals, on average, exceed the costs. Among others, individual benefits to social living include cooperative foraging, defence against predators, the sharing of collective information, and access to mating opportunities. The size of social groups is typically thought to emerge from the optimality of group size at the level of individuals. Accordingly, typical group sizes are thought to derive from *n*-shaped functions of individual fitness against group size.

The ability of a wolf pack to compete and recruit young, and the survival of individuals within it, likely depend to some degree on the size of the pack. However, we do not have a clear picture of how social conditions including pack size combine with other environmental effects to influence each of the major components of demography—survival, recruitment, and movement—which underlie the dynamics of populations.

Based on current understanding of Yellowstone wolf ecology, I predicted that wolf demography is also substantially influenced by prey availability, disease, population density, and presence on the densely populated northern range. Additionally, competitive interactions between rival packs are a leading cause of mortality and population regulation in Yellowstone wolves (Cubaynes et al., 2014). I produced a series of general linear mixed models (GLMMs) to predict how these individual, group, and population-level processes influence demographic performance in wolf packs. This study is the first to examine demography as continuous function of pack size. A key aim of this study was

to evaluate the relationship between pack size and demography, and so to examine if these patterns point to an optimum pack size.

Interestingly, the best performing models predicted positive linear relationships between pack size and key demographic rates. Given that my results do not indicate consistent negative effects of competition between rival packs—and that these analyses focused on survival and recruitment—I suggest that animal movement may be key to understanding demographic dynamics in Yellowstone wolves. This analysis forms the basis for the following research chapter.

Chapter IV: Population dynamic effects of demography, sociality and dispersal in a territorial carnivore.

In the case of socially reproductive species—where only a minority of individuals in a social group produce offspring—there may be differences in the fitness trade-offs of group living for reproductive and non-reproductive individuals. While breeding individuals benefit from direct fitness via the cooperative raising of their offspring, non-breeders do not gain direct fitness under normal circumstances.

In chapter III, I did not identify *n*-shaped or down-turning functions of demography against pack size, indicating that larger packs generally perform better demographically. These results are surprising since larger wolf packs form rarely and dissolve relatively quickly in Yellowstone. I suggest that this apparent contradiction derives from the difference in fitness value of bigger packs for dominant and subordinate wolves. If bigger packs are better at hunting cooperatively, defending the territory and raising offspring to adulthood, then bigger pack sizes are favourable from the perspective of reproductive wolves. However, for subordinate wolves, belonging to a larger pack may be detrimental to lifetime reproductive success by reducing the probability of attaining a breeding position. The subsequent discrepancy in the fitness value of bigger pack sizes for dominants and subordinates may be the cause of smaller than expected pack sizes if

subordinates become more likely to disperse to seek breeding positions elsewhere. In this case, pack sizes are constrained by subordinate dispersal.

In the fourth chapter of this thesis, I tested this hypothesis by combining the results from the demographic modelling performed in Chapter III with findings of past research to construct an age and group-structured model to simulate the demography of wolf packs in northern Yellowstone. I parameterised dispersal such that more individuals dispersed from bigger packs. I parameterised the fates of dispersers—i.e., the proportion of dispersers that survive and remain in the population—according to the current understanding of dispersal in rocky mountain wolves. I compared the population outcomes of model variants with and without the dispersal process and found that dispersal substantially regulated the simulated wolf population. The emerging population was similar in size and structure to the real population, indicating that pack-size-biased dispersal may be an important driver of group and population size in Yellowstone wolves. Our results form a basis for future research to describe the social and environmental conditions that underpin dispersal and quantify its effect on population dynamics.

Chapter V: A demographic model of antagonistic trophic interactions in the Yellowstone ecosystem reveals the primacy of indirect effects on community dynamics

In Yellowstone national park, the reintroduction of wolves has been hailed as a textbook example of a trophic cascade, leading to sensational headlines and viral videos that describe the dramatic changes seen across the landscape. As described above, the wolf reintroduction has been linked to widespread changes to species abundances and recoveries in vegetation and biodiversity in Yellowstone. This dramatic story connected millions to the idea of trophic cascades and restoration ecology more broadly. Whilst the ecosystem has certainly undergone substantial change since the return of the wolves, the trophic cascade debate is far from settled in scientific circles. Some argue for the

remarkable role of wolves in the recovering condition of the ecosystem, while others caution that the recovery of woody vegetation is ongoing and spatially heterogeneous.

The Yellowstone wolf reintroduction is perhaps one of the finest and largest scale examples of a natural experiment. Inherent in natural experiments is the lack of a control, and so attributing causation of the observed changes to the return of wolves is not clear-cut. Since the onset of the wolf restoration program, there have been relatively few attempts to *predict* how the presence of wolves influences the dynamics of the Yellowstone community.

In the final research chapter of this thesis, I construct a community simulation model to explore the relationships between wolves, their elk and bison prey, and vegetation. I use a novel approach to modelling community dynamics by parameterising for direct antagonistic interactions using empirical rates of predation and herbivory. I use this model to explore the dynamic effects of pairwise species interactions. I examine the dynamics of the simulated community by adjusting the intensity of each direct pairwise species interaction and observing the subsequent change to the model communities. I report the emergence of complex and widespread indirect effects across the simulated community, including competition for resources and apparent competition between prey species. I find that greater fitness allows the persistence of a species at lower resource densities. Importantly, I report that the intensification of elk predation induces cascading indirect effects that release woody vegetation from elk herbivory, leading to its gradual recovery. This prediction corresponds to the partial recovery of woody vegetation following the reintroduction of wolves to the community.

Chapter II

Life history stage and annual variation of movement in a wide-ranging carnivore

Chapter II: Life history stage and annual variation of movement in a wide-ranging carnivore

Abstract

Animals undergo senescence, or age-related deterioration, across physiological and reproductive functions. Senescence plays an important role in the dynamics of animal populations by influencing the rates at which individuals reproduce and die. Recording senescence in wild populations may require intensive long-term efforts to detect change in senescent traits within individuals. Detecting senescence in wild animals may be complicated or obscured by predation, disease, human interference, or other processes. We use a data set from more than 14 years of GPS collar monitoring of wolves in Yellowstone National Park, USA to examine the possibility of using movement data to detect senescence. We describe movement rates across wolf lifespans, identifying elevated movement rates in the oldest wolves of our sample and contextualise movement rates in terms of the social ecology of wolves. We also describe an annual cycle of wolf movement rates in a highly seasonal environment.

2.1 Introduction

Animal movement is fundamental to the ecology of individuals, populations, and ecosystems. Generally, an animal's movement patterns are thought to emerge from a complex interaction between an animal's motivations for movement derived from its internal state (e.g., energetic and reproductive requirements); the environmental conditions and landscape features that influence the costs of movement; and the animal's capacity to navigate and physically perform the desired movement (see Nathan *et al.*, 2008). How dynamic changes in these processes lead to variation in movement patterns across the life course remains understudied. As an animal's size, body condition, experience, and reproductive and social status change throughout life, so too may an animal's motivations and capacity for movement. To test this, it is necessary to quantify movement behaviours across lifespans.

Ageing is a key process that influences movement through animal lifespans. Animal ageing can be considered in terms of two concurrent processes: changes in fertility rates and mortality risk (demographic senescence) and changes in the body's functional capacity (functional senescence). Functional senescence is currently less understood in comparison to demographic senescence, with few examples available for wild animals (Soulsbury and Halsey, 2018). Past work has reported lifetime changes in the physiology of wild animals, including changes occurring in the immune system (Cichoń, Sendecka and Gustafsson, 2003), metabolism, hormones and hematocrit blood oxygen storage (Massot *et al.*, 2011; Elliott *et al.*, 2015); as well as physical performance (MacNulty, Smith, Vucetich, *et al.*, 2009; Labocha *et al.*, 2015). To our knowledge, movement has not previously been used as a measure of functional senescence in wild animals.

The study of movement patterns with age requires rich, long-term monitoring. A laboratory study of lifetime movement rates in fruit flies *Anastrepha ludens* revealed increasing daily movement rates during maturation, followed by consistent movement rates during midlife, culminating in a persistent decline in movement rates approaching

death (Mohan, 2017). This pattern may reflect an increase in movement capacity during growth and maturation, relative constancy of body condition during midlife, and a decline in body condition and movement capacity via functional senescence. Whilst laboratory studies can produce rare cross-sections of movement across animal lifespans, laboratory animals are insulated from the ecological conditions that influence movement behaviours in the wild. As such, laboratory-observed patterns may demonstrate changes in movement capacity across the lifespan but cannot capture variation that arises in response to dynamic external conditions (i.e., factors that motivate movement or influence its costs). Importantly however, senescence-related changes in movement capacity of wild animals may be altogether masked by pre-senescence fatality or clouded by the complexity of movement drivers in the wild. For example, older black-tailed gulls *Larus crassirostris* optimise foraging behaviours to reduce costs associated with foraging-related movement (Suzuki *et al.*, 2019). In this regard, individual experience may compensate for physical decline during senescence in older animals.

As well as the capacity for movement, the behavioural decision making with respect to movement may also vary with age. Movement path characteristics in fruit flies *Drosophila melanogaster* (Le Bourg, 1983); the probability of inter-colony movement decisions in African Penguins *Spheniscus demersus* (Sherley *et al.*, 2014); and movement depths and the probability of range shifts in Sablefish *Anoplopoma fimbri* (Maloney and Sigler, 2008) have been found to vary across ages. Similarly, variation in home range sizes across ages have been described in moose *Alces alces* (Cederlund and Sand, 1994), bison *Bison bison athabasca* (Larter and Gates, 1994), roe deer *Capreolus capreolus* (Saïd *et al.*, 2009), Soay sheep *Ovis aries* and red deer *Cervus elaphus* (Froy *et al.*, 2018). Given that home range is intrinsically linked to an animal's movement behaviour, it seems reasonable to expect that movement distances may also vary across life histories and contexts. Movement distance could provide more direct insight into an animal's functional capacity, as maximal distances are inherently limited by an animal's physical capacity.

Reproductive and social status may also influence ecological requirements for movement across lifespans. There is evidence that the effect of reproductive status on movement distances varies between species and across ecological contexts. For example, reproductively mature tailed frogs *Ascaphus truei* frogs move less than pre-reproductive individuals as they are able to meet their ecological needs without longer-range movements (Daugherty and Sheldon, 1982). In contrast, reproductive female black rat snakes *Elaphe obsoleta* move greater distances than non-reproductive females during the breeding season to facilitate outbreeding (Blouin-Demers and Weatherhead, 2002). Alternatively, movement rates may not significantly differ between breeding and non-breeding individuals where other ecological drivers of movement are more important (e.g. polar bears; Parks, Derocher and Lunn, 2006). Subordinate animals may exhibit greater movement distances in search of unguarded females (e.g. estuarine crocodiles *Crocodylus porosus*; Campbell *et al.*, 2013) or new conspecific groups (e.g. wolves; Mech, 1987). These papers reveal that the relationship between social and reproductive status and movement may be temporally dynamic and vary across contexts.

An additional consideration for understanding variation in observed movement concerns how individuals within species may exhibit consistent behavioural differences across time and ecological contexts (Bell, Hankison and Laskowski, 2009). Whilst it seems reasonable to anticipate the possibility of consistent individual differences in movement behaviours, there are few recorded examples of such patterns. Laboratory-measured boldness predicted greater movement rates following re-release in Trinidad killifish *Rivulus hartii* (Fraser *et al.*, 2001). Other features of the individual, such as experience, may also influence movement behaviours. For example, translocated elk were more likely to move farther away from release sites if the local sources of mortality risk were dissimilar to their previous habitat (Frair *et al.*, 2007). The combination of animal personality and differences in experience suggest a need for statistical analyses to account for the behavioural variation that derives from the unique nature of individuals.

Indeed, between-individual variation in movement behaviours is often overlooked in movement ecology (Holyoak *et al.*, 2008).

Given that factors that influence activity and movement patterns, such as weather, can vary across a range of time scales (i.e., daily, seasonal, and annual scales), any analyses that seek to describe movement patterns throughout the lives of wild animals should also make efforts to account for temporal variation of these factors. Whilst tackling the central aim of quantifying changes in movement rates across life history, this approach should also yield ancillary insight into the influence of environmental factors on movement patterns at finer temporal scales. This may improve our understanding of how changing environmental regimes under climate change may impact the movement behaviours of animal species.

In this study, we compile high temporal resolution GPS data of gray wolves *Canis lupus* from Yellowstone National Park USA, collected over more than 14 years—from which we extract a dataset that represents more than 8,000 wolf-days of movement from 48 unique wolves. This rich dataset offers the rare opportunity to assess long term patterns of broad scale movement rates over multiple years for individual animals. These data were used to explore variation in wolf movement across lifespans, and in doing so, identify factors that influence wolf movement rates on finer temporal scales. Movement trajectories (which mainly consisted of hourly GPS recording for long-term monitoring of the wolf population) were aligned with local weather data. General linear mixed effects modelling was used to examine wolf movement rates while accounting for variation between individuals. We tested for differences in movement rates between the sexes, across ages and in relation to weather conditions. This approach was used to profile changes to movement distances throughout annual cycles and across the life history.

From first principles of functional senescence, we predicted a decline in movement rates toward the end of wolf lifespans due to physical deterioration during functional

senescence. We also predicted that high rates of missing GPS fixes (resulting from failures to retrieve location data from GPS collars at a scheduled interval) per day would be associated with lower movement rates.

2.2 Methods

Data collection

Wolves in Yellowstone National Park, USA are fitted with GPS collars as part of a continuous monitoring program overseen by the Yellowstone National Park Service. Whilst their models varied, all collars were manufactured by Lotek (Newmarket, ON, Canada), Telonics (Mesa, AZ, USA) or Followit (formerly Televilt; Lindesberg, Sweden). In the years of 2005 to 2019, intensive monitoring occurred during an early winter recording periods and variously in summer months. Wolf GPS collar relocation frequency varied according to a programmed schedule, alternating between periods of low frequency relocations (6-hour average fix rate), and periods of high frequency relocations (half-hourly and hourly fix rates).

Study Site

Data were recorded from the wolf population of Yellowstone National Park (YNP), USA, an expansive area of open grassland and forested habitat. The vegetation community features short-grass prairie, sagebrush, and forests of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), whitebark pine (Pinus albicaulis), subalpine fir (*Abies lasiocarpa*), aspen groves (*Populus temuloides)* and riparian willow (*Salix* spp.) communities.

Data processing

Analyses were performed on data from intensive movement monitoring periods (hourly or half-hourly recording frequencies) as these represent the richest movement data available with which to analyse the relationship between demography and movement

rates. GPS relocation failures are correlated with local vegetation structure, topography, and changes in satellite constellation positioning, and are therefore common in animal movement data (Frair et al., 2004). GPS recordings were taken variously according to hourly and half hourly recording schedules, for periods of continuous recording. These recording bursts varied in length but were often 1 to 3 months long. The GPS data were cleaned using a script written to detect and replace missing GPS fixes with simulated data (written in the programming language R; R Core Team, 2013). Missing data were identified by detecting inter-fix time differences that exceeded 150% of the expected time difference between fixes for a given recording schedule (i.e., greater than 45 minutes for half-hourly GPS data, and 90 minutes for hourly GPS data). This method was employed because the GPS collars generally did not record a GPS fix beyond 10 minutes after the scheduled recording time.

Missing fixes were replaced by linear spatial interpolation, which placed the detected number of sequential missing fixes evenly along a linear trajectory between the known fixes. Calculations of the distances between missing data therefore computed the minimum possible distance covered during unrecorded movement intervals (Calenge, 2006; Edelhoff, Signer and Balkenhol, 2016). Following the data cleaning, GPS data recorded at half hour intervals were downsampled to standardise the temporal resolution of the GPS data to hourly intervals. Movement trajectories were then trimmed to include only full recording days (midnight to midnight) to facilitate movement rate comparisons. GPS recording periods were converted to movement trajectories (sequences of continuous movement recording) and movement metrics (e.g., distance travelled) were computed in R using the package *AdehabitatLT* (Calenge, 2015). The Euclidean distances between GPS fixes were calculated to give travel distance for each movement interval.

Weather data

Whilst we acknowledge the potential effect of weather—particularly snow cover—on the biomechanics of locomotion in wolves (see discussion), and its probable impact on annual

movement cycles, we do not explicitly include weather data in our analyses due to insufficient spatiotemporal resolution of snow data. Specifically, daily measures of snowfall cannot describe snowpack features along movement trajectories to test for its effects. We use *Month* to test for within-year variation in movement rates and to account for the Yellowstone's pronounced seasonal cycle. For illustrative purposes (see results, figure 2), we used data sourced from a weather station in the Northern Range of YNP (station located at 44°53'48"N, 110°14'02"W), the focal region of wolf population monitoring.

Demographic data

Wolves' ages were estimated from a combination of genetic data and measurements of tooth wear. Genetic data were derived from observations of breeding pairings coupled with genotyping (see Vonholdt et al., 2008). This method identifies the parents of a given focal animal, and cross references this information to known breeding pairings of the two identified parent wolves. Though these estimates were preferred and available for most GPS collared wolves, we used estimates of birth year based on tooth wear measurements for wolves lacking these estimates (see Gipson et al., 2000). Known age was also determined by marking pups (MacNulty, Smith, Vucetich, et al., 2009). Data from two wolves with uncertain age estimates (i.e., wolves with two conflicting potential ages) were excluded. Wolves were assigned nominal birthdays on the 15th of April—the average whelp date of Yellowstone wolves (MacNulty et al., 2020). Wolf Age at a given recording day was then calculated from the birth estimate data.

Statistical modelling

General linear mixed-effects modelling (GLMM) was used to examine predictors of wolf movement distances. We use *Wolf ID* as a random effect to control for individual heterogeneity to improve assessment of age-related processes within individuals (Nussey et al., 2008). We also set Year as a random intercept to account for interannual variation in conditions that may influence movement rates. Wolf *Age* and *Sex* were included as fixed

effects to assess differences in movement distances across ages and between the sexes. We did not test for an interaction of *Age* by *Sex* due to sample limitations (see results). *Month* was included as a factor to assess within-year variation in movement rates. We included the term *Interpolation* —describing the proportion of simulated data in each day—to test for an effect of data replacement in the data cleaning process.

Models were built using the *lmer* function of the package *lme4* (Bates et al., 2007). We produced model variants that retained terms of central interest to the analysis (*Month*, *Interpolation* and *Age*) included non-linear fits of numerical terms. We selected the best performing model variant using the Akaike information criterion (AIC; see supplementary table S1 for model selection). Model variants with fewer parameters were selected in the case where the two best supported models differed by less than 2 in AIC value (Arnold, 2010). A visual inspection of the diagnostic plots for the selected model was used to evaluate the normality of the residuals and assure that the data met the assumptions of modelling form (Zuur *et al.*, 2009).

Selective removal analysis

An analysis was undertaken to assess whether the observed age-related patterns of movement rates were due to real changes in average movement distances, or whether these patterns were influenced by wolves dropping out of the dataset. This exploratory analysis was based on the approach of Rebke et al., 2010. We clustered movement data into those that did and did not survive to the following age to assess whether survivors moved more, less, or similarly to non-survivors across each age boundary. Since we detected seasonal variation in movement rates (see results), this analysis was performed on data collected during winter months only (November to March inclusive) to mitigate any confounding effect of season and because winter data were available from more individuals (45 winter versus 40 summer). Data from three wolves were excluded from this analysis due to being recollared after missing data for one or more winters. The average daily movement rate at each age was calculated for each wolf. Selection refers to

the difference in average movement of survivors and all wolves at a given age (i.e., if selection was positive, movement was greater among survivors). Change refers to the average difference in movement distances between adjacent age classes among survivors. In this way, we decomposed the observed changes into change within individuals longitudinally, and change driven by loss of individuals from the sample.

2.3 Results

Sample

After the missing GPS fixes were replaced and data were limited to complete 24-hour segments the sample data set consisted of 8,641 complete days of wolf movement trajectories. 8,230 days of GPS data were available from wolves with age data (48 wolves). All data for wolves of in their first year (encoded as age 0) were from wolves older than 7 months. GPS data were recorded over a period exceeding 14 years (2005 to 2019). Movement data recorded from male and female wolves constituted 55% and 45% of the sample respectively. The total number of complete recording days for an individual wolf ranged from 3 days to 567 days (median 128.5 days). Recordings of individuals occurred over total time spans ranging from 3 days to 2109 days (5 years and 9 months).

Data cleaning

Simulated spatial positions were generated for a total of 4,945 missing GPS fixes, representing 2.4% of the 207,384 attempted fixes (i.e., 24 hourly fixes attempted for each of the 8,641 sample recording days).

Distance

Wolves travelled a median distance of 13.4 km per day. The maximal distance covered by any wolf in a single day was 67.3 km. Distance travelled was strongly positively skewed (skewness = 0.89), and so the response variable data were square-root transformed to approximate a normal distribution to satisfy the assumptions of general linear mixed

modelling. Generally, the distance moved by an individual per day was highly variable (figure 1A).

Model selection

The best performing model (determined by AIC ranking; see supplementary table S1 for model selection table) included random effects of *Wolf ID* and *Year*, and fixed effects for *Month*, *Age* (in years as a category), *Sex*, and a quadratic fit of data *Interpolation*.

Random effects

The random effect of *Wolf ID* showed appreciable variation between individuals ($\sigma_{Wolf\ ID}$ =13.2, $\sigma_{Residual}$ = 35.2; see supplementary table S2 for full model results). Confidence intervals for the *Wolf ID* random intercept were narrow and excluded zero (95% CI [10.1, 16.4]). There was relatively less variation in movement rates between years (σ_{Year} = 4.7, $\sigma_{Residual}$ = 35.2). Whilst the confidence intervals for *Year* were wider—though still exclusive of zero (95% CI [0.06, 9.3]) —the inclusion of *Year* improved model performance versus a comparable model (ΔAIC = 3.9; supplementary table S1).

Sex

While the model indicated a possible tendency for males to move slightly less than females (b = -8.0), this effect was not statistically significant (p = 0.059). We did not test for an interaction between age and sex due to rank deficiency owing to a lack of data for females of age 8.

Age

Wolf movement rates varied by age. Yearling wolves (age 1) moved significantly less than late first year (age 0) wolves (b = -4.96, p = 0.016). All sample data from first year (age 0) wolves were from individuals aged 7 months or older. The oldest wolves in the sample (those aged 6, 7 and 8) moved the greatest distances (fig. 1B), though parameter estimates were marginally non-significant.

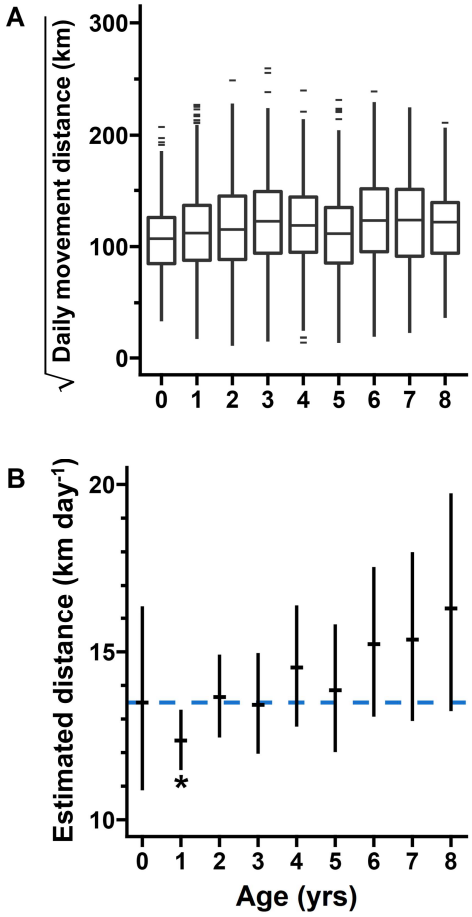


Figure 1: Patterns of daily wolf movement distances by age. (A) Square-rooted observed daily movement distances by age class; (B) Parameter estimates of mixed effects model estimating daily movement distances by age class. Bars represent 95% confidence intervals. Statistical significance is indicated by asterisks ($p < 0.05$). Dashed line indicates intercept value.

Month

Movement rates were generally lower in the late autumn, winter, and early spring months (November to March), and greater in the late spring to early autumn months (April to October; fig. 2). Lower movement rates in the winter months coincided with seasonal snowfall (fig. 2).

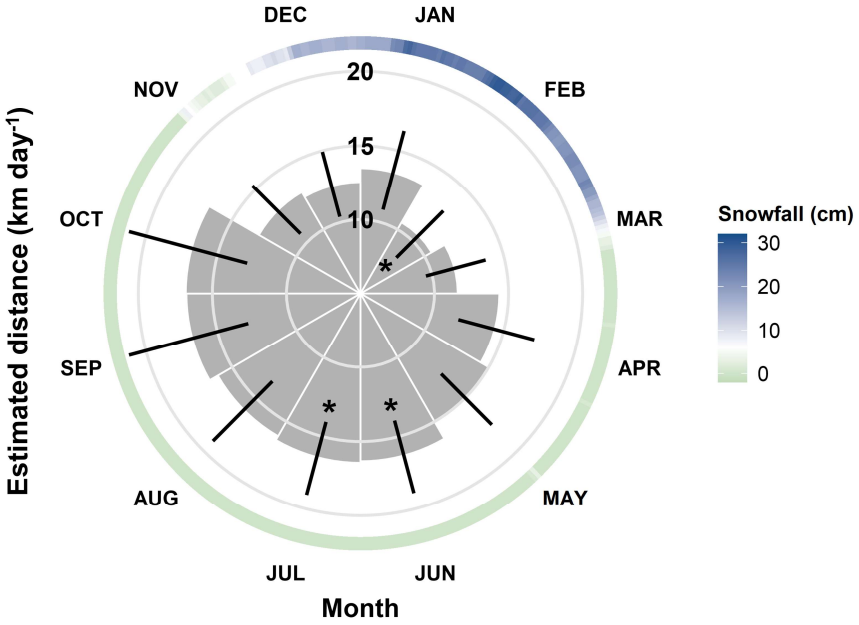


Figure 2: Parameter estimates of mixed effects model predicting patterns of daily distances by month. Grey bars represent parameter estimate, black bars show 95% confidence intervals. Statistical significance is indicated by asterisks ($p < 0.05$). Estimates are relative to model intercept. Outer circle plot indicates annual cycle of daily snowfall (example data from 2017).

Consequences of interpolation of missing data

77.4% of wolf days (24 hour period per wolf) did not have any missing data. 61% of wolf days with missing GPS fixes were missing only one fix (n = 1131; fig. 3A) and 88% were missing a total of 5 fixes or fewer. The analysis revealed a non-linear relationship between the number of data points that were simulated per day, and daily movement distance (*Interpolation*, $b = 27.64$, $p = 0.03$; *Interpolation*^{2}, $b = -97.4$, $p < 0.001$; fig. 3B).

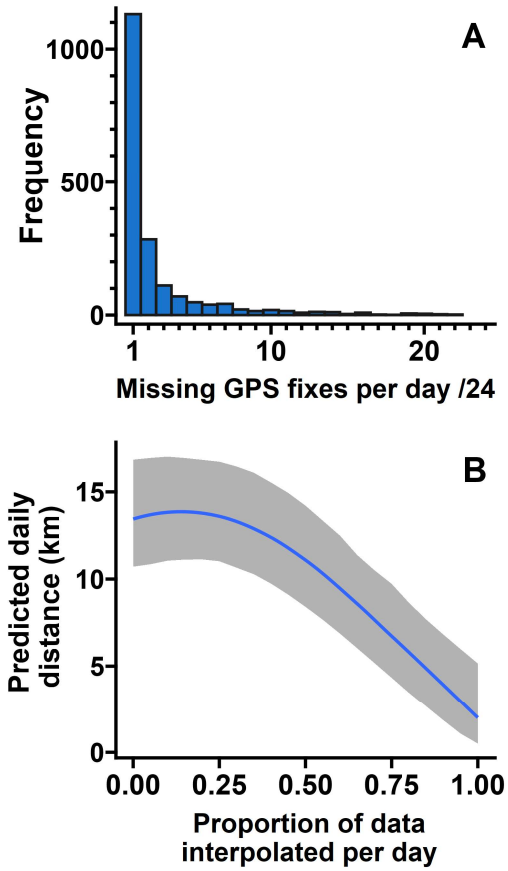


Figure 3: Patterns of data interpolation and its predicted relationship with daily movement. (A) Frequency of missing GPS fix data per wolf day (for days with missing data, n = 1859). (B) Predicted relationship between proportion of interpolated data and movement rate per wolf day. Example prediction made for intercept *Month* (January) and *Sex* (female), for a median aged wolf (3 Years). Gray area represents 95% confidence interval computed from 400 bootstrap resamples.

Selective removal analysis

There was a strong relationship between the observed mean movement differences across ages, and the decomposition of these changes (fig. 4A; $b = 0.98$, $F_{(1,6)} = 8.46$, $p = 0.03$). Whilst there was a tendency for farther moving wolves to be most likely to be lost from the population (fig. 4B), this trend was not statistically significant ($p = 0.304$). Although the data suggest that survivors tend to move progressively more with age at younger age categories, and progressively less at older ages (fig. 4C), this pattern was inconsistent, and the trend was not significant ($p = 0.433$). There was a slight tendency for farther-moving wolves to drop-out from the data set at older ages.

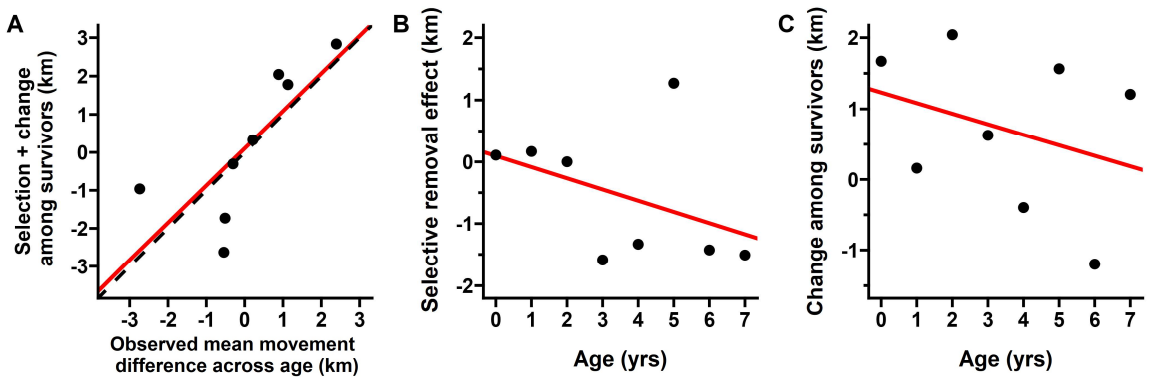


Figure 4: Changes in wolf movement rates across age groups. Linear trendlines represented in red. (A) Comparison between mean movement difference across each age boundary and the sum of the decomposition (*selection* and *change*). Dashed line indicates the identity line ($y = x$). (B) Selective removal effect (the difference between average movement distances of survivors and all wolves) at each age category. (C) Mean change in movement distances of survivors of each age class.

2.4 Discussion

Studies that combine sufficient movement and individual demographic data to capture patterns of movement across wild animal lifespans are lacking. Such data require sustained intensive work to obtain, and their analysis complicated by the effects of GPS collar loss. Nevertheless, this study is to our knowledge the first to collate long-term GPS movement data for the purpose of assessing functional senescence in free-living animals. Broadly, our results profile wolf movement rates as highly variable and cyclical within years. We also found weak evidence that older wolves move more than younger wolves.

Functional senescence

In our study, movement distance was chosen as a measure of functional senescence on the expectation that over broad time scales, movement distances—which cannot exceed an animal's maximum total capacity—would be the component of movement that would be the most likely to reflect any changes in physical capacity with age. However, we recognise that animals are unlikely to consistently move at their maximal capacity and so changes

to movement capacity during age-related physical decline may not clearly manifest as changes in total recorded movement distances.

Our finding of slightly greater movement in the oldest wolves is somewhat surprising, given that wolves are known to senesce across physiological and demographic traits. Firstly, wolf survival is significantly reduced after age 6, which is interpreted as an effect of senescence (Cubaynes *et al.*, 2014). Predatory performance—that is the ability of a wolf to successfully select, attack, and kill elk prey—declines in wolves from around age 4, concurrent with a decline in serum albumin concentration (an indicator of age-related physical decline; MacNulty, Smith, Vucetich, *et al.*, 2009). Age-related changes in gene expression onset early and are detected throughout life in wolves (Charruau *et al.*, 2016), supporting the notion that wolves undergo metabolic ageing in the wild. Additionally, breeding wolves exhibit a decrease in litter size and pup survival from age 5 (Stahler *et al.*, 2013). At first glance, these indicators of ageing contrast with our finding of increased movement rates in the oldest wolves of our sample. Breeding wolves tend to be older and more experienced (Mech, Barber-Meyer and Erb, 2016), with breeding males often leading group movements (Mech, 2000). It is possible that leading animals might move greater distances than their younger counterparts if their movements are necessarily more exploratory, however this remains unclear. If this were the case, given the pack-oriented movements of wolves, it seems unlikely that pack leadership would manifest appreciably greater movement distances at the temporal resolution of this study's GPS data.

The pattern of greater movement rates in the oldest wolves of the sample might be attributed to social processes occurring in older wolves. Older wolves are more likely to be breeders (Stahler, Smith, *et al.*, 2020) and so increased movement behaviour possibly reflects greater investment in movement, owing to the provisioning of dependent offspring (see Mech, 2000). Furthermore, the mammalian reproductive-endocrine and autonomic nervous systems undergo senescence at nearly four times the rate of the central nervous system or musculoskeletal systems (Sehl and Yates, 2001), the latter of which

may be more likely to directly impact locomotion. As such, our findings may indicate that movement rates may be an ineffectual metric for the detection of functional senescence in wild wolves, if social processes or other ecological conditions influence movement rates more than immediately than age-related physical decline. An additional possibility is that the individuals that survived to an older age expressed different movement behaviours to those that died earlier (i.e., fitter wolves with high movement capacities are more likely to survive to an older age). By decomposing the observed changes across ages, we determined that our broader analysis—whilst cross-sectional in nature—was not substantially biased by within-individual processes. This suggests that results of our analysis were reflective of actual processes across lifespans and were not confounded by loss of individuals from the data.

Animal movement is behaviourally complex, emerging from a multitude of internal and external factors (Nathan *et al.*, 2008). Senescence may therefore manifest as changes in movement besides total travel distance, as movement drivers vary across lifespans. Older wolves may select different movement paths to their younger counterparts and compensate for functional senescence from experience in traversing the landscape. An analysis of higher resolution movement trajectories in wide-ranging carnivores may provide insight into how movement varies across lifespans at finer scales and would complement our results.

Within-year movement rates

We observed a distinct temporal coincidence of reduced wolf movement rates during winter months, which suggests that winter conditions play a role in driving seasonal variation in movement rates.

The annual cycle of movement rates approximately corresponds to the timing of elk occupation of the northern range. In spring, a substantial portion of Yellowstone's elk population migrates to summer ranges (White *et al.*, 2010), which tend to be more distant from the centroids of wolf pack territories. Migratory elk then return their winter ranges

on the northern range (and across YNP) from autumn to spring. The variable proximity of the preferred prey populations likely contributes to the annual cycle of movement in Yellowstone wolves, since travel requirements may be greater in summer than winter.

Daily snowfall patterns are likely to have been insufficient to describe snow depth conditions experienced by the wolves in our study, which likely varies through time and space across the landscape. Snow cover may lead to reduced movement rates by impeding movement, and potentially by increasing the need for rest. Additionally, surface snow may alter predator movement if the locomotion of predator and prey species are differentially impacted. Ungulates—including elk, the preferred prey of wolves (Metz *et al.*, 2012b)—have high measures of foot-loading. In elk, the weight of their large body mass is distributed through small hooves, piercing the snowpack (Telfer and Kelsall, 1984; Penczykowski, Connolly and Barton, 2017). Wolves, with their relatively lower body mass and proportionally larger, spread-toed feet, are better able to traverse the snowpack without penetrating deeply into the surface. Decreased wolf movement rates in winter could therefore reflect reduced movement requirements for successful foraging, as their prey experience a greater degree of impediment to their locomotion than during the snow-free months. It has been previously established that snow depth can affect the rate and demography of elk predation by wolves (Huggard, 1993), with deeper snow favouring higher predation rates, and increased proportional predation of adult elk. The general modality of wolf movements also varies annually, as packs alternate between central place movements during denning period, and nomadism after sufficient growth of young (Mech and Boitani, 2003).

Our findings lend support for a close relationship between snow and the ecology of wolves, and by extension, to predictions that climate change and subsequent changes to snow regimes will impact wolf behaviour and trophic interactions (Penczykowski, Connolly and Barton, 2017). Our results may indicate that reduced snowfall or fewer snow days—as has been reported in YNP (Wilmers and Getz, 2005)—could lead to increased

winter movement rates due to a reduction in movement impediment in elk caused by snow. Furthermore, patterns of wolf hunting success and prey demographic preference vary seasonally in Yellowstone, as wolves make more kills but obtain less total prey biomass in summer months due to a shift to calf elk as their preferred prey (Metz *et al.*, 2012b). Shortening winters may increase the seasonal costs of wolf hunting success and via increased movement requirements. Whilst we have some understanding of how body size, age and pack size relate to hunting success in wolves (MacNulty, Smith, Mech, *et al.*, 2009; MacNulty, Smith, Vucetich, *et al.*, 2009; MacNulty *et al.*, 2012), further work is needed to assess the impact of movement on the hunting success of wolves, and further, whether changing snow regimes will impact hunting success and predation dynamics in Yellowstone wolves.

Practical implications of data replacement

Our combined use of high-resolution GPS recording with a low rate of missing fixes and a conservative spatial interpolation method means that the subsequently calculated movement metrics were likely to represent accurate (though inherently conservative) estimates of the study animals' actual movements. Long periods of rest—not uncommon for wolves (Llaneza *et al.*, 2016; Kohl *et al.*, 2018)—in combination with local habitat features which may decrease the probability of a successful GPS fix (e.g. shielding by canopy vegetation). This might explain the association between greater rates of failed GPS fixes per day and lower movement rates. A dedicated study might investigate the relationship between fix failure rates and local topography and vegetation structure. Given that only a very small proportion of our data were interpolated—and that most wolf-days with simulated data only contained one or two missing data points—we do not expect this pattern to impact our results.

The prediction of lower movement rates under higher rates of missing GPS fixes may derive from daily activity cycles. If individuals are more likely to be at rest during the night (Yellowstone wolf activity is generally lower at the start and end of the 24 hour daily cycle;

Kohl *et al.*, 2018), a high rate of data replacement using our method may estimate lower total daily movement due to unrecorded periods of activity. We recommend that others using similar GPS data cleaning regimes consider accounting for missing fix rates when analysing drivers of movement distances, and to also consider the relationship between the movement and the general activity cycle of the study species.

With the possibility of life-long monitoring of animal movements via GPS only becoming viable in recent years, studies that combine historic movement data with rich demographic data, such as this, are rare. We found no evidence of senescence in movement, and some tentative evidence of increased movement rate at old age. We also describe seasonal variation in movement rates, which we attribute to temporally variable locomotion costs associated with snow cover and prey distribution in winter. Our results lead us to advocate the use of modelling that accounts for individual variation in behaviour in movement studies. We also highlight an effect of missing data on distance measurement in animal-borne GPS data, and advocate consideration of such effects when statistically analysing GPS data with simulated fixes.

Supplementary information

Table S1: Model selection. General linear mixed model (GLMM) variants with associated model performance. *Wolf ID* and *Year* effects were fitted as random intercepts. *Age* (in years) was fitted as a factor (Age F), and as continuous numerical independent variable for age in years (Age C) and in months (Age M). Squared indicates fit of a given fixed effect with an additional quadratic term to test for non-linearity of the effect. Most supported model variant underlined.

	Model structure		AIC	ΔAIC
Model variant	**Random**	**Fixed**		
Null	Wolf ID	-	82657.3	568.3
Full	Wolf ID	Month + Interpolation + Age F + Sex	82119.9	30.9
Age continuous	Wolf ID	Month + Interpolation + Age C + Sex	82159.2	70.2
Age continuous/quadratic	Wolf ID	Month + Interpolation + Age C^2 + Sex	82160.3	71.3
Age (months)	Wolf ID	Month + Interpolation + Age M + Sex	82127.8	38.8
Sex-reduced	Wolf ID	Month + Interpolation + Age F	82125.7	36.7
Interpolation quadratic	Wolf ID	Month + Interpolation + Age F + Sex	82092.9	3.9
Wolf ID reduced		Month + Interpolation^2 + Age F + Sex	82510.5	421.5
Year random effect	Wolf ID + Year	Month + Interpolation^2 + Age F + Sex	82089.0	**0.0**

Table S2: Parameter estimates from GLMM predicting daily movement distances in Yellowstone wolves (n = 8230 wolf days). *Sex* is a binary factor with female as the reference group. *Month* and *Age* are factors with January and 0 Years as reference groups respectively. Statistically significant p values ($p < 0.05$) highlighted in bold.

	Parameter	β	95% CI		SE	t	P
Fixed effects							
	Intercept	116.15	10.14	16.39	6.05	19.20	0.00
Month	February	-13.45	0.06	9.28	5.57	-2.41	**0.02**
	March	-8.59	34.67	35.76	4.95	-1.73	0.08
	April	3.75	104.41	127.85	5.65	0.66	0.51
	May	6.42	-24.40	-2.55	5.04	1.27	0.20
	June	11.59	-18.29	1.10	5.04	2.30	**0.02**
	July	12.01	-7.33	14.80	5.05	2.38	**0.02**
	August	10.84	-3.45	16.25	5.70	1.90	0.06
	September	13.28	1.71	21.42	8.22	1.62	0.11
	October	13.45	2.11	21.86	8.14	1.65	0.10
	November	-2.48	-0.38	21.96	5.17	-0.48	0.63
	December	-4.12	-3.08	29.24	5.18	-0.80	0.43
Age	Age 1	-4.96	-2.74	29.25	2.06	-2.41	**0.02**
	Age 2	0.71	-12.62	7.60	2.69	0.26	0.79
	Age 3	-0.29	-14.27	5.98	3.30	-0.09	0.93
	Age 4	4.42	-8.97	-0.94	3.85	1.15	0.25
	Age 5	1.55	-4.45	6.06	4.12	0.38	0.71
	Age 6	7.25	-6.60	6.25	4.63	1.57	0.12
	Age 7	7.80	-2.95	11.90	5.20	1.50	0.14
	Age 8	11.62	-6.34	9.48	6.49	1.79	0.08
	Interpolation	27.64	-1.64	16.18	12.76	2.17	**0.03**
	Interpolation^2	-97.42	-2.17	17.79	20.80	-4.68	**0.00**
	Sex	-8.00	-0.83	24.11	4.11	-1.95	0.06
Random intercepts		σ	σ^2				
	Wolf ID	22.09	4.7				
	Year	174.43	13.21				

Chapter III

Social and environmental determinants of demography in Yellowstone wolves

Chapter III: Social and environmental determinants of demography in Yellowstone wolves

Abstract

The size and dynamics of animal populations emerge from the vital demographic rates of survival, recruitment, and movement. These vital rates are influenced by the complex interaction of individual, group, population, and environmental level processes that are unique to each species and system. For animals that live in social groups, numerous social and environmental factors influence the functional efficiency, cohesion, internal competition, and demographic success of a group, and so the optimality of group sizes. For social species that establish and defend territories like some social carnivores, the capacity of the group to maintain its territory and defend itself against rival groups is also important to the value of group size. Wolves are large social carnivores that live in groups, cooperatively rear offspring, and defend a hunting territory. In Yellowstone National Park, the population of reintroduced wolves has been monitored closely for more than 2 decades. As a result, there are rich data concerning the age, sex, and survival of individuals, and the location, size, and recruitment rate of packs, offering a rare opportunity to quantify individual and group level determinants of demographic rates.

We use 20 years of individual survival and pack-level recruitment data to examine how social and environmental factors relate to the demography of wolf packs. On the basis that an important source of mortality in Yellowstone wolves derives from fatality in interpack conflicts, we tested for links between demography and the size of neighbouring rival packs. We identify density-dependent and senescent effects on individual survival, and inclining survival with both focal and neighbour pack sizes. We find elevated pup recruitment rates in larger packs, offset by poorer pup survival for larger litters. Interestingly, we report poorer recruitment in small packs with larger rival packs, but a positive correlation between recruitment and neighbour pack size for larger packs. This indicates that larger packs may be better able to insulate pups from the effects of competition, and that competing larger packs may experience better recruitment and individual survival conditions simultaneously. We also outline the basis for modelling the effects of dispersal on group and population dynamics in social carnivores.

3.1 Introduction

Animal population dynamics are driven by ecological factors that influence the rates at which individuals reproduce, die, and move. These rates may be influenced by prey or vegetation availability, density dependence, disease, and competition as well as weather and natural disaster. It has long been held that wolf populations are generally limited by the availability of prey (Fuller, Mech and Cochrane, 2003). However, if a population of predators is food-limited, then prey availability may determine the ceiling of wolf density but is not instructive as to population dynamics occurring below the density threshold set by prey availability. As the predominant social unit in wolves, the dynamics of individual packs underpin change at the population level. We may gain insight into the dynamics of wolf populations if we can examine major determinants of demographic rates in wolf packs.

Wolves live in social groups, generally composed of a mating pair of adults and their offspring (though packs may also include non-family 'adoptees'; see Mech and Boitani, 2003). Wolf packs maintain and defend territories, in which they live, hunt, and reproduce. Competing wolf packs engage in aggressive encounters wherein physical contests can lead to fatal injury (Smith, Metz, *et al.*, 2015). Wolf packs are also known to invade the territories of neighbouring packs, and attack other denning packs, commonly leading to fatalities in both adults and pups of targeted packs (Smith, Metz, *et al.*, 2015). In Yellowstone National Park, most wolves die by natural causes (Cubaynes *et al.*, 2014). Importantly, approximately 50% of total mortality is caused by wolf-wolf killing during intraspecific conflict (Smith, Cassidy, *et al.*, 2020), representing a substantial source of regulation (Cubaynes *et al.*, 2014). There is evidence that the outcomes of these aggressive encounters are influenced by the relative size of packs and the composition of packs (Cassidy *et al.*, 2015). However, it is not feasible to record every aggressive pack interaction, nor quantify their impact on pack success. It is possible that interpack competition has costs for the success of a pack that accumulate over time. It is therefore

of interest to ask whether the long-term reproductive success of packs, or the survival of individuals within them, relate to features of neighbouring packs versus the features of their own.

Additionally, outbreaks of disease, primarily canine distemper virus (CDV), impact the health of Yellowstone wolves and the survival of pups (Stahler *et al.*, 2013). Given that there is a growing understanding that the demography of Yellowstone wolves is substantively influenced by processes besides prey limitation, it is of interest to investigate the major determinants of wolf demographic rates to understand what drives the dynamics of the population. Yellowstone's wolves have been monitored closely since their reintroductions in 1995-1997. Individual wolf demography, survival, pack size and pack reproduction data having been collected intensively. We collate 20 years of individual wolf survival data and 25 years of pack-level recruitment data to determine how pack size, individual demography, and the size of neighbouring packs influence individual survival and recruitment within packs.

Although wolves are considered habitual dispersers at the level of the individual, dispersal is difficult to record, and remains relatively poorly understood. In Yellowstone, where wolves are generally densely populated, dispersal can be primarily considered as movement between packs within the population internally (Smith, Cassidy, *et al.*, 2020). We therefore focus on determinants of individual survival and pack-level recruitment for the purpose of this analysis.

3.2 Methods

Data collection

Yellowstone wolves are monitored year-round as part of a long-term study by the Yellowstone Wolf Project (see Smith, Stahler and MacNulty, 2020). Survivorship data (1998-2020) from wolves living within Yellowstone National Park were used to model demographic and pack-level predictors of individual interannual individual survival. In each year since the reintroduction, wolf pups have been captured and radio-collared between November and February, and so have known age and sex (see MacNulty *et al.*, 2009). A mortality signal is relayed when radio-collars detect sustained immobility, whereupon the causes of deaths are investigated on site (see Murray *et al.*, 2010). For this analysis we included all data where wolves were recorded as surviving to the following biological year (15th April to 14th April) or were known to have died by natural causes (see results for sample size and data censoring). Wolves that went missing, or that were killed by humans, and those that permanently dispersed outside of the park were excluded from analyses. We also excluded lone wolves from survival analyses as we were interested in the effect of pack size on survival.

Count data of annual pack recruitment were collected between 1995 and 2019. If successful, wolf packs produce litters of pups early in each year. Litter size was recorded when pups emerge from the den in April (Smith, Cassidy, *et al.*, 2020). Since most infant wolf mortality occurs in the first 6 months of life (Fuller, Mech and Cochrane, 2003; Smith, Cassidy, *et al.*, 2020), pups are considered to have been recruited to the population if they survive to the subsequent winter count when pups are approximately 8 months old (MacNulty, Stahler, Coulson, *et al.*, 2020). We therefore decomposed recruitment at the level of the pack into pup production and pup survival.

For each year, we determined interpack distances using annually published minimum convex polygons (MCPs) of 95% of wolf locations for each pack (e.g. Smith, Stahler, *et al.*, 2020). MCP centroids—the geographical centre of a pack territory in each year—were

computed using the *gCentroid* function of the *rgeos* package (Bivand *et al.*, 2017). We then calculated pairwise inter-pack distances for all pack dyads per year, and so identified the nearest neighbour of each pack.

Modelling approach

We used general linear mixed effects modelling (GLMMs) to test fixed effects of various candidate independent variables that we predicted to be important in each major demographic process. The structure of our models was determined by the form in which data were collected. For each GLMM, we fit a random intercept for *Year* to account for inter-annual variation in demographic rates. Models were fitted (see below) using the *glmer* and *glmer.nb* functions of the R package *lme4* (Bates *et al.*, 2007).

Individual survival

Individual interannual survival was coded as a binary outcome for Year t+1 and so survival was modelled using a binomial error structure. We evaluated the relationship between individual survival and their *Age* and *Sex*, and the size of their pack. We used winter *Pack size* count as a predictor of individual survival as more attrition of adults occurs over winter (Smith, Cassidy, *et al.*, 2020). We also assessed whether annual wolf *population size*, *Elk* count, the binary occurrence of Canine Distemper Virus outbreaks per year (*CDV Year*), and residence on the *Northern range* (where the population is more densely populated; Smith *et al.*, 2020) were linked to wolf survival. Finally, we tested for an effect of *neighbour pack size* on individual survival.

We report odds ratios (ORs) for survival predictions (calculated by exponentiating parameter estimates). Odds ratios describe the relative probability of events (i.e. survival or death), under given conditions (Rita and Komonen, 2008). Specifically, model predictions describe changes in the probability of individual survival by each unit change in a continuous variable (e.g., *Pack size*), or between levels of a categorical independent variable (e.g., CDV vs. non-CDV years). We did not use mark-recapture analysis for

individual survival since the recapture rate of radio-collared wolves is very high, and so there is high confidence in the timing of mortality.

Pack recruitment

We applied a negative binomial structure to model predictors of number of pups born (using the *glmer.nb* function of the *lme4* package; Bates *et al.*, 2007). The negative binomial form allows for the prediction of the rate of events in a GLMM framework. We modelled pup production against *pack size*, wolf *population size*, *CDV Year*, *Elk* count, and residence on the *Northern range*. We use the April count for pups born as this is the pack size observed during the recruitment season. Parameter estimates from the negative binomial regression results were exponentiated to give incidence rate ratios (IRRs) of pup production. Like odds ratios, IRRs describe the change in the rate of events (i.e., pups born) as predicted by levels of categorical predictors or by single unit changes in continuous independent variables.

Pack level recruitment was determined by the number of pups that were recorded as having survived to the December census, as compared to the number counted in April. We modelled pup survival using the proportion of surviving pups that as the response variable (as proportions bounded between 0 and 1). We used a binomial error structure in modelling pup survival, weighted by the number of pups born (to account for variation in litter size). We tested for effects of *pack*, *pup count*, residence on the *Northern range*, *CDV Year*, *wolf population* size, *elk* count, and *neighbour pack size* on the survival of pups. We use *pack size* data from the December counts to test for effects on pup survival since this corresponds to when pup survival was counted. Odds ratios were reported for predicted pup survival effects. Confidence intervals on plotted predictions were computed with 400 bootstrap resamples.

Model selection

We constructed full models included the independent variables described above for each of the three demographic processes described. We then produced model variants with parameter reductions and used quadratic terms to test for non-linear effects of numerical covariates (see model selection in supplementary table S1) . We selected the best supported model variant for each demographic process using the Akaike information criterion (AIC). In cases where the AIC difference (ΔAIC) between two best performing model variants was less than 2, we selected the simpler model (Arnold, 2010) for the purposes of parsimony. We performed a visual inspection of the diagnostic plots for the best supported models to ensure that the assumptions of the model forms were met (Zuur *et al.*, 2009). Residual plots are not informative for binary data (i.e. the individual survival model) and so we used tools in the DHARMa package in R that enable interpretable visualisation of model residuals and so avoid misspecification of binomial GLMMs (Hartig, 2020). We used the results of the best supported models to identify and describe major ecological drivers of demography within wolf packs.

3.3 Results

Interannual individual survival

Of an initial 949 wolf-year entries, we excluded those with missing age data (n = 4), unknown pack association (n = 23) and lone wolves (n = 5). We further censored entries whose $Year_{t+1}$ status was missing or unknown (n = 132) or permanently dispersed outside of Yellowstone (n = 80), and wolves who subsequently died via human (n = 21) or unknown (n = 2) causes. Of the resulting 682 wolf-years, data for both pack size and neighbour pack size were available for 529 entries. We therefore retained all wolf-year entries for which there were age and pack association data, known sizes of packs and neighbour packs, and for which wolf status in $Year_{t+1}$ was either alive, or dead by natural causes. The resulting subset contained data from 1998 to 2018.

For each additional year of age, the *odds ratio* of individual wolf survival to the subsequent year declined by approximately 15% (OR = 0.85 [95% CI: 0.76-0.94]; Fig. 1B). Survival odds increased by 13% for each additional wolf in a pack (OR = 1.13 [95% CI: 1.05-1.21]; Fig. 1C). Wolf survival was therefore predicted to be greater for younger wolves in larger packs (fig. 1D).

Individual survival odds ratio decreased by 1.5% for each additional wolf in the population (OR = 0.99 [95% CI: 0.98-0.99]; Fig. 1a). Wolf survival was positively associated with the size of closest neighbour pack (OR = 1.07 [95% CI: 1.00-1.14]; Fig. 1e). Model performance was greater when terms for *Sex*, *CDV Year*, *Elk* and presence on the *Northern range* were excluded from candidate models (supplementary table S1).

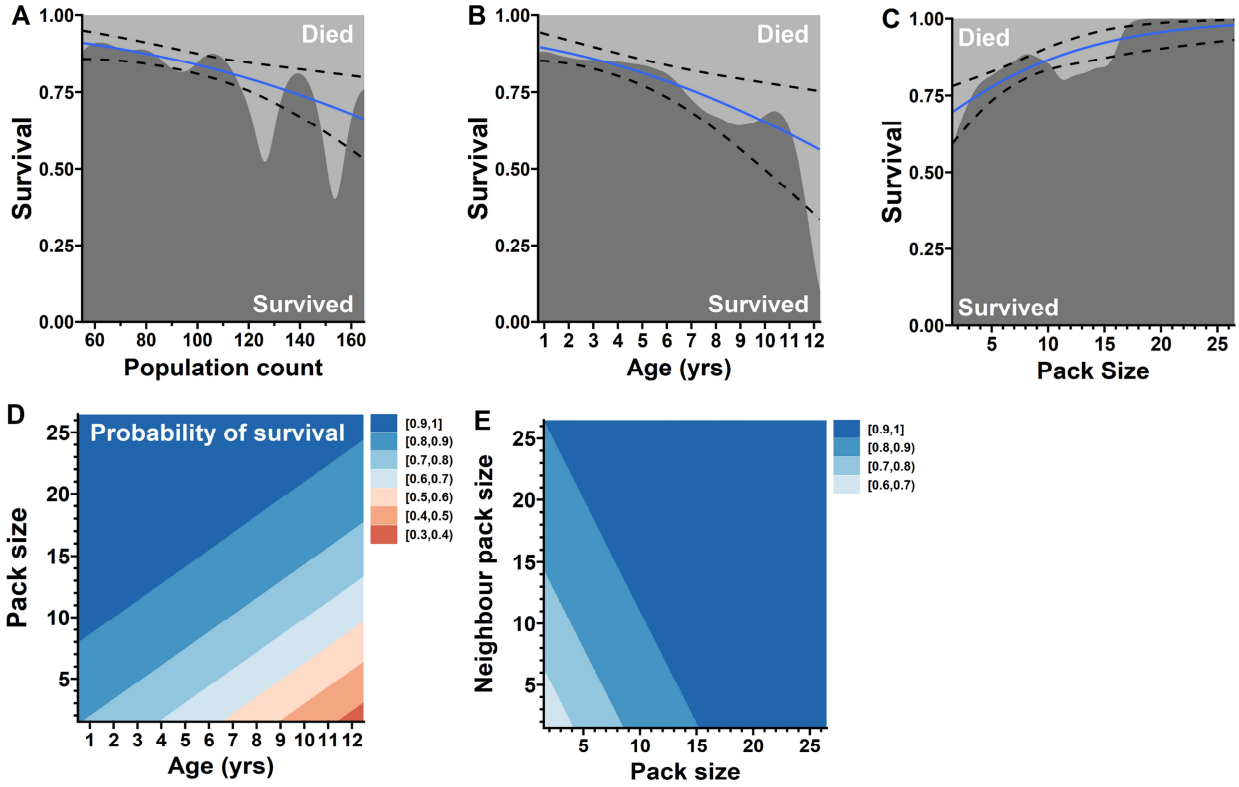


Figure 1. Interannual individual survivorship of Yellowstone wolves by population count, age, and pack size. (A) Survival by population count. (B) Survival by age. (C) Survival by pack size. Conditional density of survival (A-C) is given by grey shaded areas. Blue lines represent GLMM predicted survival where non-focal parameters were set at median values (model results supplementary table S2). Dashed lines represent 95% bootstrap confidence intervals from 400 resamples. (D) Predicted probability of survival by age and adult pack size. (E) Predicted probability of survival by pack size and neighbour pack size. Survival probability (D-E), as indicated by coloured areas, was predicted by a GLMM where non-focal variables were set at median values.

Recruitment: pup production

Of the 277 entries for wolf pack-years with a known pack size, pack territory locations were unavailable for 57. For our analysis of pup production, there were 171 wolf pack-years with data for *pack size* at the April count. Data from 2013 were excluded from the subset due to no elk count. Data in the recruitment model subsets were recorded from 1998 to 2018.

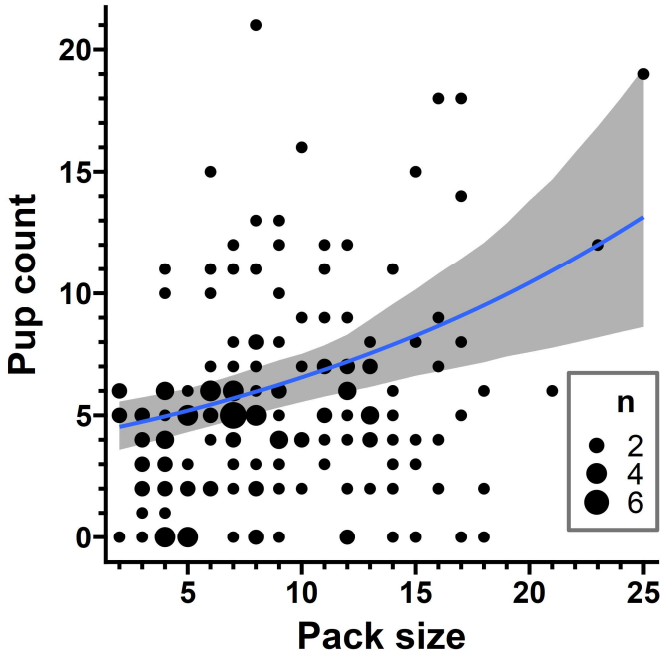


Figure 2. Yellowstone wolf pup production by pack size. Pups counted at den emergence in a biological year by adult pack size. Point size indicates the number of observations. Blue line represents GLMM predicted pup production for northern range packs (model results supplementary table S3). Grey shaded area represents 95% bootstrap confidence interval from 400 resamples.

Of wolf packs that bore pups, the median pack size was 6 adults, bearing a median of 5 pups. Larger packs produced more pups (IRR = 1.05 [95% CI: 1.03-1.07]; fig 2), as did packs on the northern range (IRR = 1.61 [95% CI: 1.31-1.97]). While model variants suggested that pup production was lower in years where the wolf population was larger

(IRR = 0.996 [95% CI = 0.99-1.00]), the population term did not improve model performance (ΔAIC = 1.1) and so was excluded.

Recruitment: pup survival

For our analysis of pup survival, we used the same base dataset as that for our analysis of pups born, but subset for entries with available pack size and pup survival at the December count (n = 162 pack years). Of packs that whelped pups in our subset, the median survival of pups was 0.91. Larger pack size was associated with greater rates of pup survival (OR = 1.12 [95% CI: 1.05-1.19]; Fig. 3A). For each additional pup whelped, the odds ratio of pup survival decreased by 6% (OR = 0.94 [95% CI: 0.90-0.98]; Fig. 3B). Pup survival was therefore predicted to be greater in larger packs, with fewer pups (fig. 3B).

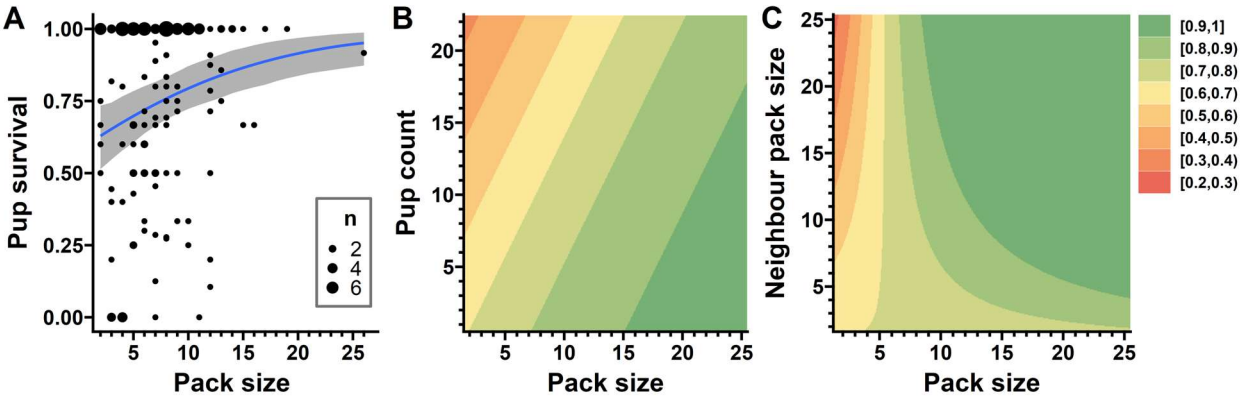


Figure 3. Pup survival by adult pack size, pup count and neighbour pack size. **A.** Observed pup survival by pack size. Point size indicates the number of observations. Grey shaded area represents 95% bootstrap confidence intervals from 400 resamples. **B.** Model predicted pup survival by pack size and count of pups at den emergence. **C.** Model predicted pup survival by pack size and neighbour pack size. Predicted survival, as indicated by blue line (A) and coloured areas (B-C) as predicted by GLMM where non-focal variables were set at median values (model results supplementary table S4).

Model performance was not improved by non-linearity in the effect of pack size on pup survival (supplementary table S1). Pup survival was lower in northern range packs (OR = 0.23 [95% CI: 0.15-0.37]), and during CDV outbreak years (OR = 0.16 [95% CI: 0.06-0.39]). Pup survival was dependent on an interaction between focal and neighbour pack sizes (OR = 1.02 [95% CI: 1.00-1.04]; fig 3C). At smaller pack sizes, pup survival was lower

when neighbour packs were larger, whilst at larger pack sizes, the model predicted an association between pup survival and larger neighbour packs (fig. 3C). The inclusion of annual wolf *Population size* and *Elk* count in model variants did not improve the performance of the pup survival model.

3.4 Discussion

Our results describe determinants of key demographic rates in Yellowstone wolves and highlight the advantages of social living in large carnivores.

Age, disease, and population effects

Increasing mortality risk with age represents a typical signal of senescence—Yellowstone wolves exhibit relatively fast life histories (MacNulty, Smith, Vucetich, *et al.*, 2009; Coulson *et al.*, 2011) with rapid growth to early maturity, short generation time and short life spans (reviewed in MacNulty *et al.*, 2020). Our results reflect the general rule that the probability of interannual survival declines under senescence.

The negative association between population count and both individual survival (Cubaynes *et al.*, 2014) and pack-level pup production (Stahler *et al.*, 2013) reflects current understanding of density dependence in Yellowstone. Our results also illustrate negative effects of CDV outbreaks on recruitment success, as CDV causes substantial juvenile mortality (Almberg *et al.*, 2009). The consequences of CDV outbreaks are more severe for packs in the northern range, (Almberg *et al.*, 2009), presumably owing to increased disease transmission in this densely populated region. Indeed, pup survival was lower in the northern range—a prey-dense and high quality, but more competitive region (Smith, Stahler and MacNulty, 2020). However, pup production rates were higher in northern range packs. Northern range packs are more likely than interior packs to produce multiple litters (Smith, Cassidy, *et al.*, 2020), attributed mainly to greater prey abundance. For the same reason, northern range packs may also be better able to raise pups in the den

to the point of den emergence, reducing cryptic pup mortality in the den. This result highlights the trade-off of living and raising young in a high quality but competitive environment.

Relationships between pack size and demography

Group living is widespread across animal taxa, conferring diverse benefits to individuals within social groups (Krause and Ruxton, 2002). In large carnivores, the benefits of sociality include cooperative hunting (Mech, 1970; Creel and Creel, 1995; Lührs, Dammhahn and Kappeler, 2013; MacNulty *et al.*, 2014), food defence (Wilmers *et al.*, 2003; Vucetich, Peterson and Waite, 2004), communal defence (Bertram, 1975; Packer, Scheel and Pusey, 1990) and cooperative breeding (Stahler *et al.*, 2013). While previous work identified elevated mortality in wolves belonging to smaller packs (i.e. <5 individuals; Smith *et al.*, 2010), to our knowledge, our results are the first to quantify variation in demographic rates against pack size as a continuous measure. Our findings reveal the benefits of sociality in wolves, where belonging to a larger pack is associated with reduced mortality risk to individuals. Larger wolf packs are more successful at hunting bison (MacNulty *et al.*, 2014), food defence (Wilmers *et al.*, 2003), and interpack aggressive conflict (Cassidy *et al.*, 2015). The success rate of hunting elk—the favoured prey of Yellowstone wolves—declines after a threshold of hunting group size (MacNulty *et al.*, 2012), though individual demography is also important (MacNulty, Smith, Mech, *et al.*, 2009). Elk hunting success therefore seems unlikely to promote the formation of ever larger packs (MacNulty *et al.*, 2012). However, our results suggest that individuals in larger groups generally experience a survival advantage, which likely derive from improved group resource acquisition, territory maintenance and territory defence.

The benefits of larger packs are also reflected in measures of recruitment, with larger packs producing more pups and raising a greater proportion of pups to maturity. It is possible that larger packs were more likely to have multiple breeding females. Each year,

approximately 25% of Yellowstone packs produced multiple litters, typically from 2-3 litters (though as many as 6 pregnant females have been observed; Smith, Cassidy, *et al.*, 2020). Females whelp in the den, rendering it difficult to directly attribute litters to single or multiple females. While the genetic determination of parentage is attempted for GPS-collared wolves in Yellowstone (see DeCandia *et al.*, 2021), we were interested in the net production of pups as a function of pack size to maximise the subset for this analysis. While we focussed on group-level predictors of recruitment, it is worth noting that maternal factors also predict greater rates of pup recruitment, including the age, body mass and coat colour of the breeding female (Stahler *et al.*, 2013). Pup survival was lower when litters were larger, likely owing to increase provisioning demands for larger litters.

Larger packs had greater pup survival across the range of pack sizes, though more acutely before a threshold of 3-5 adult wolves (Stahler *et al.*, 2013). Whilst non-linearity in the effect of pack size on pup survival did not improve the performance of our model, our results do not preclude the possibility that additional pack members confer diminishing returns on pup survival.

Effects of competitor packs on demography

Our models are the first to evaluate variation in individual pack level demographic rates in relation to the sizes of competing wolf packs. There is precedence for our approach to predict demography in terms of rival group size in territorial social carnivores, as the size of rival groups is positively associated with mortality rate in female lions (*Panthera leo*), and negatively associated with reproductive success (Mosser and Packer, 2009).

Larger wolf packs are generally more successful in interpack aggressive encounters in Yellowstone wolves (Cassidy *et al.*, 2015), a leading cause of mortality (Smith, Cassidy, *et al.*, 2020). Because of this, the positive association between individual survival and the size of neighbouring packs was unexpected (though the confidence intervals for this

prediction were wide and close to non-significance). The odds of a pack winning an aggressive encounter with another is also substantially improved with the presence of older, experienced individuals, and so pack composition can compensate for a numeric disadvantage (Cassidy *et al.*, 2015). In light of this, our finding that survival relates positively to neighbour pack size may indicate that numeric differences in pack size alone are insufficient to predict interannual individual survival. In addition, the effects of competition between rival packs may also accumulate across interactions with multiple packs around a pack's territorial boundary. Because of this, a greater complexity of information may be needed to detect links between the attributes of rival packs and annual demography.

At small pack sizes, pack size differentials appear important to successful recruitment, suggesting their vulnerability to competitive pressures from larger rival packs (Cassidy *et al.*, 2015). For larger packs, our results indicate that neighbouring packs experience greater recruitment rates synchronously. This pattern may derive from bigger packs being better able to insulate their pups from the detrimental effects of interpack competition. It is also possible that uniformity in other conditions operating at the landscape scale—perhaps at finer temporal scales than year intervals—drive coincidence of demographic performance between packs. For example, weather is known to influence wolf-elk predation dynamics (Vucetich, Smith and Stahler, 2005). Carnivore-ungulate predation dynamics may also be influenced by the lunar cycle (Palmer *et al.*, 2017). In these cases, variation in demography driven by such conditions may not be captured by fitting a random effect for year.

Social group size and dispersal

In our analysis, the best performing demographic models did not indicate down-turning functions of pack size on demographic performance, which would otherwise point to an optimal group size. Consequently, our results suggest that larger packs generally perform

better demographically. This is particularly interesting given the relatively small and consistent size of wolf packs in Yellowstone for the past decade (Stahler, Smith, *et al.*, 2020). This apparent contradiction between demographic predictions and the empirical size of social groups requires further attention and may derive from processes occurring via the third vital demographic rate, movement.

Given that our analysis did not investigate effects of inter-group movement, it is possible that dispersal plays a role in regulating the demographic costs of remaining in a larger pack as individual. Indeed, metapopulation modelling suggests that in the absence of disease, group fission and fusion rates contribute notably to the dynamics of wolf group size, in addition to birth and death rates (Brandell *et al.*, 2021). It would be of interest to apply our results to a framework whereby pack and population dynamics can be compared under the absence or inclusion of intergroup movements. This will enable evaluation of the role of movement in the population dynamics of territorial social carnivores.

Quantifying the relative importance of individual, group, population, and environmental processes to demography is a considerable challenge for ecologists. Collectively, our results illustrate the centrality of group living to the demography of wolves and point to a potential role for movement in the regulation of group sizes.

Supplementary information

Table S1: Model selection for individual survival (binomial regression, n = 529), pups born (negative binomial regression, n = 171), and pup survival (weighted binomial regression, n = 162). In all cases, a random intercept was fitted for *Year*. Null models were fitted with no fixed effects. Listed variables were fitted as fixed effects. Best supported model variants underlined. Numerical variables were mean centred. *Elk* was also scaled by one standard deviation.

Model structure	AIC	ΔAIC
Individual survival		
Null	487.4	25.8
Age + Pack size + Neighbour pack size + Pop. size + NR + CDV Year + Sex + Elk	468.3	6.7
Age + Pack size + Neighbour pack size + Pop. size + NR + CDV Year + Elk	466.3	4.7
Age + Pack size + Neighbour pack size + Pop. size + NR + CDV Year	464.4	2.8
Age + Pack size + Neighbour pack size + Pop. size + CDV Year + Elk	465.3	3.7
Age + Pack size + Neighbour pack size + Pop. size + NR + Elk	464.4	2.8
Age + Pack size + Neighbour pack size + Pop. size + Elk	463.4	1.8
Age + Pack size + Neighbour pack size + Pop. size	**461.6**	**0.0**
Age + Pack size + Pop. size	464.1	2.5
Age^2 + Pack size + Neighbour pack size + Pop. size	464.6	3.0
Age + Pack size^2 + Neighbour pack size + Pop. size	463.5	1.9
Age + Pack size + Neighbour pack size^2 + Pop. size	462.5	0.9
Age + Pack size × Neighbour pack size + Pop. size	463.6	2.0
Pups born		
Null	927.1	28.6
Pack size + Pop. size + NR + CDV Year + Elk	899.8	1.3
Pack size + Pop. size + NR + CDV Year	899.4	0.9
Pack size + Pop. size + NR	897.4	-1.1
Pack size + NR	**898.5**	**0.0**
Pack size^2 + NR	900.4	1.9
Pup survival		
Null	646.1	118.7
Pup count + Pack size + Neighbour pack size + CDV Year + NR + Elk + Pop. size	532.4	5.0
Pup count + Pack size + Neighbour pack size + CDV Year + NR + Elk	530.9	3.5
Pup count + Pack size + Neighbour pack size + CDV Year + NR	530.9	3.5
Pup count + Pack size + Neighbour pack size + CDV Year	578.2	50.8
Pup count + Pack size + Neighbour pack size + NR	540.8	13.4
Pup count + Pack size^2 + Neighbour pack size + CDV Year + NR	529.2	1.9
Pup count + Pack size + Neighbour pack size^2 + CDV Year + NR	532.9	5.5
Pup count^2 + Pack size + Neighbour pack size + CDV Year + NR	530.0	2.6
Pup count + Pack size × Neighbour pack size + CDV Year + NR	**527.4**	**0.0**

Table S2: Results of GLMM model of probability of inter-annual individual wolf survival (binomial regression, n = 529). Random intercept fitted for *Year*. Odds ratios (OR) are exponentiated parameter estimates. *Pack size* refers to pack adults at December count. Numerical variables were mean-centred.

Model parameter	OR	Estimate	Std. Error
Intercept	5.69	1.74	0.14
Age (Years)	0.85	- 0.17	0.05
Pack size	1.13	0.12	0.04
Neighbour pack size	1.07	0.07	0.03
Wolf population	0.99	- 0.01	0.00
Year (random intercept) : $\sigma = 0.023$, $\sigma^2 = 0.153$			

Table S3: Results of GLMM model of pup production (negative binomial regression, n = 171). Random intercept fitted for *Year*. Incidence rate ratios (IRR) are exponentiated parameter estimates. *Pack size* refers to pack adults at April count. *Northern range* is a binary factor with negative reference group. Numerical variables were mean-centred.

Model parameter	IRR	Estimate	Std. Error
Intercept	3.947	1.37	0.09
Pack size	1.047	0.05	0.01
Northern range	1.608	0.47	0.10
Year (random intercept): $\sigma = 0.030$, $\sigma^2 = 0.174$			

Table S4: Results of GLMM model of pup survival (weighted binomial regression, n = 162). Random intercept fitted for *Year*. Odds ratios (OR) are exponentiated parameter estimates. *Pack size* refers to pack adults at December count. *CDV Year* and *Northern range* terms are binary factors with negative reference groups. Numerical variables were mean-centred.

Model parameter	OR	Estimate	Std. Error
Intercept	12.79	2.55	0.26
Pup count	0.94	-0.06	0.02
Pack size	1.15	0.14	0.03
Neighbour pack size	1.05	0.05	0.03
Pack size × Neighbour pack size	1.02	0.02	0.01
CDV Year	0.14	-1.94	0.47
Northern range	0.22	-1.50	0.23
Year (random intercept): $\sigma = 0.418$, $\sigma^2 = 0.646$			

Chapter IV

Population dynamic effects of demography, sociality and dispersal in a territorial carnivore.

Chapter IV: Population dynamic effects of demography, sociality and dispersal in a territorial carnivore.

Abstract

Individuals living in social groups face a trade-off in the costs and benefits of group living. In some species, including wolves, only one or few individuals in a group reproduce. Past work indicates that measures of performance and demography are improved in larger wolf packs, however, wolves do not typically form large packs. We hypothesise that this apparent contradiction derives from an inequality in fitness between dominant breeding individuals and non-breeding subordinates in larger packs, and that pack sizes are constrained by elevated subordinate dispersal from bigger packs. In the absence of comprehensive data concerning dispersal, we test this hypothesis by constructing an age- and group-structured population simulation model of northern Yellowstone wolves. We predict the annual rates of survival of individuals and the recruitment of wolf packs using our existing analyses of wolf demography. We set dispersal to occur at greater rates from bigger packs and parameterise disperser survival according to the current understanding of rocky mountain wolf dispersal. We find that mortality resulting from dispersal induces a substantial constraint on pack sizes, resulting in populations that resemble that of northern Yellowstone wolves. Our results point to the potential importance of dispersal in regulating group size in socially reproductive species and form a basis for future work to evaluate the survival and reproductive fates of dispersing wolves.

4.1 Introduction

Group living is widespread across diverse animal taxa and arises from a complex interaction of benefits and costs to individuals (Krause and Ruxton, 2002). In general, it is predicted that evolution should select for group living when the fitness benefits to the individual exceed the costs. Of the diverse species that live in groups, some exhibit a reproductive division of labour, where only some individuals within a group breed. In eusocial species, including naked mole rats (Clarke and Faulkes, 1997) and species of ants, bees, wasps and termites, breeding is typically exclusive to only one female (Wilson and Hölldobler, 2005). In other species, others may also breed, but at a lower frequency than a focal or dominant breeder. These include meerkats (Clutton-Brock *et al.*, 2001), dwarf mongooses (Creel and Waser, 1991), spotted hyenas (Hofer and East, 2003) and wolves (Stahler, Smith, *et al.*, 2020). Because of inequality in direct fitness that results from this reproductive divide, the total fitness value of group living may differ for breeding and non-breeding individuals. Additionally, the demographic success of a group—i.e., the survival of individuals in the group and how many offspring breeders recruit—may vary according to features of the group, including its size and composition (reviewed below). For socially reproductive species then, the optimum size of a social group may be different for breeding versus non-breeding individuals within the group.

Gray wolves, *Canis lupus*, live in packs typically formed of a cooperatively-breeding parent-offspring group, headed by a monogamous breeding pair (Stahler, Smith, *et al.*, 2020). Wolf packs in Yellowstone National Park, USA (YNP) range in size from 2 to 26 individuals, with an average of 9 adults (as measured in April after the birth of pups; Stahler *et al.*, 2020). At the individual level, wolves benefit from group living via cooperative hunting (MacNulty *et al.*, 2014), maintenance and defence of territory (Mech and Boitani, 2003), food defence (Wilmers *et al.*, 2003), and cooperation in potentially fatal inter-pack conflicts (Cassidy *et al.*, 2015).

For dominant breeding wolves, social living provides substantial direct fitness via the cooperative rearing of their offspring (Mech and Boitani, 2003). However, for most wolves, pack living typically comes at the expense of the opportunity to breed. Whilst it is possible for subordinates to breed in addition to dominant breeders—known as plural breeding—this occurs in only 25% of Yellowstone wolf packs annually (Stahler, Smith, *et al.*, 2020). Plural breeding is thought to occur facultatively, and is often observed under particular social circumstances, including where subordinates breed with individuals from other packs, or when packs become unusually large or are especially diverse in age and sex composition (Stahler, Smith, *et al.*, 2020). Dominant wolves may interfere or suppress the breeding of subordinates via physical aggression (Derix *et al.*, 1993), and may even kill the offspring of successfully breeding subordinates (McLoed, 1990).

While the fitness costs of subordination may be offset by the inclusive fitness gained by helping to raise the offspring of close relatives (Hamilton, 1964), non-breeders are generally deprived of direct reproductive fitness. Subordinates therefore stand to gain substantial fitness benefits should they choose to leave their pack and successfully attain breeder status elsewhere, either in an existing pack or through the formation of a new pack. In this circumstance, the selection for behaviours that maximise direct reproductive fitness conflicts with kin selected group living.

Wolves commonly disperse from the natal pack to seek opportunities to establish a new territory and to breed (Mech and Botani, 2003; Stahler, Smith, *et al.*, 2020). Dispersing wolves traverse areas in which they are unfamiliar with the distribution of prey, risks from vehicles and humans, and the territories of wolf packs that may attack and kill them (Fuller, Mech and Cochrane, 2003). Wolves dispersing outside YNP experience greater hazard to their survival, due in part to human-caused mortality (Smith et al., 2010). Dispersal therefore represents a substantial risk to individual survival. Additionally, the wolf population of northern Yellowstone is one of the densest in north America (Smith, 2016). Opportunities for successful dispersal may be generally limited to

joining other existing packs because the landscape is typically saturated with wolf pack territories. Northern range dispersal therefore mainly consists of movement within the population (Smith, Cassidy, et al., 2020). For these reasons, establishing a breeding position in a northern range pack is probably rare.

At the group level, there is evidence that numerous measures of performance increase with the size of wolf packs. Larger packs exhibit improved probability of success in aggressive inter-pack strife (Cassidy *et al.*, 2015), the cooperative hunting of bison (MacNulty *et al.*, 2014), recovery from disease (Almberg *et al.*, 2015), and food defence (Wilmers *et al.*, 2003) compared to smaller packs. Results from our prior modelling (Chapter 3 in this thesis), also indicate that larger packs show improved demographic performance in the survival of individuals and the recruitment of pups. There is evidence that very large packs exhibit declining elk hunting efficiency (MacNulty et al., 2012) and experience poorer foraging cohesion (Metz et al., 2011). Moreover, packs of intermediate sizes are most competitively efficient against kleptoparasite scavengers (Wilmers et al., 2003). However, there is no evidence these large-pack effects translate into a decrease in demographic performance.

Given that exceptionally large 'superpacks' form rarely and are short lived in Yellowstone, and that pack sizes have been consistent and relatively small for the past decade (Stahler et al., 2020), we expect there to be some process that constrains the formation of ever-larger packs. For subordinates, unlike breeding wolves, an ever-larger social group may not positively relate to individual fitness. If a subordinate perceives a decline in their chances of inheriting or seizing their pack's breeding position as the size of the pack increases, they may be more likely to disperse. In this case, subordinate dispersal may act to constrain pack sizes.

In summary, there are four observations that point to this scenario. Firstly, larger packs generally exhibit greater performance across a range of pack functions. Secondly, wolf packs in northern Yellowstone are generally consistent in size and only rarely and briefly become very large. Thirdly, our prior analyses did not indicate *n*-shaped or down-turning relationships between pack size and demographic rates. And finally, ours and other analyses have not fully described or tested for the effects of the dispersal process on pack and population dynamics due to the difficulty in comprehensively recording the survival and reproductive fates of dispersers. We therefore suggest that the costs and benefits of dispersal represent a potentially important gap in our understanding of the pack dynamics of Yellowstone wolves.

In prior work, we constructed models to predict demographic rates of wolves under key social and environmental conditions. We use the results from these models to parameterise an age- and group- structured population model to simulate the population dynamics of northern Yellowstone wolves. We introduce dispersal as a potential regulatory process and describe its effects on the equilibrium conditions of the model population. We structure and parameterise dispersal based on past research of dispersal in wolves.

4.2 Methods

Model structure

We constructed an age and group-structured population model and iterated demographic functions over a simulated population of wolves. Our model simulated the vital demographic rates of survival of individuals and pack-level pup recruitment. We added the possibility of dispersal—where wolves leave their pack to either die or survive to join a pack. Dispersal therefore provided movement within the population and an additional a source of loss of individuals by mortality.

The demographic models on which the simulation model was based accounted for whether a pack lived on northern range, or the occurrence of canine distemper virus (CDV) outbreak per year. For our simulations, we set our demographic functions for northern range packs in non-CDV years. See table 1 for demographic function parameters.

Each step of the model simulated wolf pack demography over the course of one year, *t*. We ran the model for 200 timesteps for each run since we observed in model testing that this was sufficient to surpass the initial transient dynamics and achieve asymptotic population size. The model was written and analyses performed in the programming language R (R Core Team, 2013).

Population structure

We constructed a population vector, *P*, formed of age frequency distributions for each pack at timestep *t*, that is,

$$P_t = \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \\ \vdots \\ N_{m,t} \end{bmatrix}$$

where *m* is the maximum age. We set maximum age—and so the number of age classes—to 15, the age of the oldest known wild wolf (Theberge and Theberge, 1998).

Given that we were interested in the equilibrium state of the model population, and to establish some initial marginal inequality in pack sizes, we initialised each pack with a random count (between 0.99 and 1.01) of one-year old individuals. Note, age count distributions—and so group and population sizes—were continuous values.

Table 1: Parameters of demographic functions used to determine annual individual survival and pack-level recruitment. Bracketed numbers indicate in-text equation numbers. Centering values were applied in demographic function equations to correspond to the mean-centering of numerical data used in initial models. Numerical variables in the raw data were mean centred for the predictive models. Constants are applied for binary factor terms to model northern range dynamics in a non-CDV outbreak year. See methods for demographic function equations.

Rate	Eqn.	Demographic function Parameter	Symbol	Type	Mean	Value
Individual survival	(2)	**Survival**				
		Intercept	α_1	Constant	-	1.739
		Age	β_1	Coefficient	3.817	-0.167
		Pack size	β_2	Coefficient	8.189	0.122
		Neighbour pack size	β_3	Coefficient	6.607	0.067
		Population size	β_4	Coefficient	102.242	-0.015
Pack-level recruitment	(3)	**Pups born**				
		Intercept	α_2	Constant	-	1.373
		Pack size	β_5	Coefficient	8.865	0.046
		Northern range	C_1	Constant	-	0.475
	(4)	**Pup survival**				
		Intercept	α_2	Constant	-	2.548
		Pups born	β_6	Coefficient	6.068	-0.062
		Pack size	β_7	Coefficient	7.136	0.137
		Neighbour pack size	β_8	Coefficient	6.728	0.047
		Pack size × Neighbour pack size	β_9	Interaction	-	0.019
		Northern range	C_2	Constant	-	-1.498
		CDV Year	-	Constant	-	0.000

Pack structure

Our demographic models of individual and pup survival included terms for the sizes of nearest neighbour packs, and so each pack in the model was designated a neighbour. We assigned adjacent neighbours in a circular arrangement to avoid edge effects. Between the years of 2010 and 2021, the northern range has been consistently occupied by 4 or 5 packs (Smith *et al.*, 2019, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2020; Cassidy *et al.*, 2021, 2022). Setting a baseline condition of 4 packs, we varied the model pack structure to test for the effects of the number of packs on the dynamics of the population. For the purposes of simplicity, and because the number of packs on the northern range has been

relatively consistent in the past decade (Cassidy *et al.*, 2020), we did not model pack extinction in this case.

Individual survival

For each time step, a transition matrix was populated with survival by age class for each pack. For each pack per annual time step of the model, we populated an age-structured matrix with survival values, S, for each age. This transition matrix, T, where m is the maximum age, took the form per pack:

$$T = \begin{bmatrix} 0 & 0 & 0 & 0 & \cdots & 0 \\ S_1 & 0 & 0 & 0 & \cdots & 0 \\ 0 & S_2 & 0 & 0 & \cdots & 0 \\ 0 & 0 & S_3 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \cdots & \vdots \\ 0 & 0 & 0 & 0 & S_{m-1} & 0 \end{bmatrix}$$

The survival of individuals in a pack to year t+1 was therefore performed by the product of the population and transition matrices:

$$P'_{t+1} = T_t P_t \qquad (1)$$

This survival-adjusted population vector preceded the addition of newborns (note, the rates of individual survival and group recruitment each derived from the pack and population conditions at the start of the timestep, and effectively occurred simultaneously). The survival of individuals of each age group, i, in year t, were determined by the function

$$S_{i,t} = \frac{1}{1 + e^{-(\alpha_1 + \beta_1 I_t + \beta_2 G_t + \beta_3 R_t + \beta_4 N_t)}} \qquad (2)$$

where I_t is the focal age category, G_t is the size of the focal pack, R_t is the size of the neighbouring pack, and where N_t is the total population size.

Recruitment

For each year, offspring were recruited to packs according to functions predicting the number of pups whelped and the rate of their first-year survival. Surviving pups were therefore added to the population at age 1 at the end of a model year. While the maximum number of pups recruited to a Yellowstone pack in a year is a reported 25, this is unusually high (Smith, Cassidy, *et al.*, 2020). We set the maximum number pups that a pack could produce annually to 10 to approximate more typical pup production (Stahler *et al.*, 2013). The number of pups born, B, to a given pack in a model year t was governed by the function

$$B_t = e^{(\alpha_2 + \beta_5 G_t + C_1)} \quad (3)$$

where G_t is the size of the focal pack, and C_1 is a constant set for presence on the northern range. Note, the form of the predictive equation for negative binomial GLMMs is the same as for a Poisson model.

The survival of pups in a litter, R, bounded between 0 and 1, was computed via the function

$$R_t = \frac{1}{1 + e^{-(\alpha_3 + \beta_6 PB_t + \beta_7 G_t + \beta_8 E_t + \beta_9 G_t \times E_t + C_2)}} \quad (4)$$

where R_t is the number of pups in the litter, G_t and E_t are pack size and neighbour pack size respectively, and C_2 is a constant adjusting pup survival for northern range packs.

The number of pups, Q, added to a pack in year, t, was therefore determined by the number of pups born and the rate of their survival:

$$Q_t = B_t S_t \quad (5)$$

The surviving pups per pack, Q_t, were added as yearlings to the survival-adjusted population vector P'_{t+1}, to produce the population for the subsequent time step, P_{t+1}.

Dispersal mechanism

We ranged dispersal rates from 0.05 to 0.4, reflecting the approximate minimal and maximal probabilities of dispersal estimates for Yellowstone wolves from 1995 to 2016 (Smith, Cassidy, *et al.*, 2020). We weighted dispersal probability such that dispersal rates would be greater from larger packs. This corresponds to observations of higher dispersal in larger than average wolf packs (Jimenez *et al.*, 2017), and reflects our assumption that the fitness costs of remaining in a pack for a non-breeding wolf are greater in larger packs. The rate of dispersal from each pack, D_t, was set to incline up to a threshold, beyond which dispersal was assumed to occur at the maximal rate (see figure 1B for visualisation).

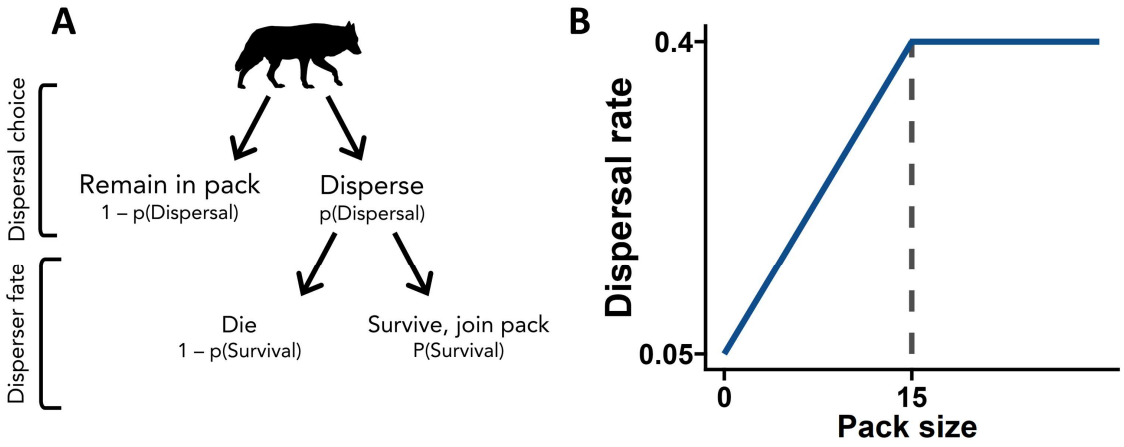


Figure 1: Model dispersal scheme. (A) Possible fates of wolves in the model dispersal process. (B) Annual pack-level dispersal rate as a piecewise linear function of pack size.

The reported mean pack size from which wolves dispersed occurred in one study was 10 (Jimenez *et al.*, 2017), equal to the average pack size in Yellowstone (Stahler, Smith, *et al.*, 2020). Because of this, we set dispersal to occur at the maximal rate from a pack size of 15. The dispersal rate of wolves from a given pack in a simulated year, D_t, was therefore determined by the function

$$D_t = \begin{cases} \frac{0.35}{15}(G_t) + 0.05, & if\ G_t < 15 \\ 0.4, & if\ G_t \geq 15 \end{cases} \quad (6)$$

Where G_t is the size of a focal pack.

Because we model the addition of new pups in terms of their survival through their first year, and because dispersal rates are approximately consistent in adult wolves after their first year (Smith, Cassidy, *et al.*, 2020), we assume dispersal rates as equal across ages. Whilst pack sizes surely change within years, we set dispersal to occur based on pack sizes at the start of each year for simplicity.

In a sample of rocky mountain wolves—including Yellowstone wolves and wolves in lower density populations—56% survived dispersal, of which 42% joined an existing pack, representing 23% of all dispersers (Jimenez *et al.*, 2017). We initially set *Disperser survival* as 20%, and test for the population effect of variation in this value. For the purposes of simplicity, and because the northern range has been saturated with wolf territories since the year 2000 (Boyce, 2018) with a consistent number of packs (Cassidy *et al.*, 2020), we assume that dispersers that are able to form new packs predominantly do so outside the northern range. Our model therefore simulated a closed population, and dispersal here refers to inter-group movements. We set surviving dispersers to distribute evenly amongst all packs.

We performed a sensitivity analysis to test for the effect of each demographic function, and each parameter within them, on the equilibrium population size. We upwardly adjusted each parameter by 5%, meaning that each adjustment increased the relevant demographic rate. Subsequent populations were compared against the baseline parameterisation.

4.3 Results

Baseline conditions

After initial transient dynamics, the model population stabilised to equilibrium (figure 2A). When the model was parameterised using demographic model predictions for northern range packs—and where dispersal was included (see below)—the population reached asymptotic state at 82.9 individuals. The equilibrium population under baseline conditions was composed of equally sized packs (figure 2B).

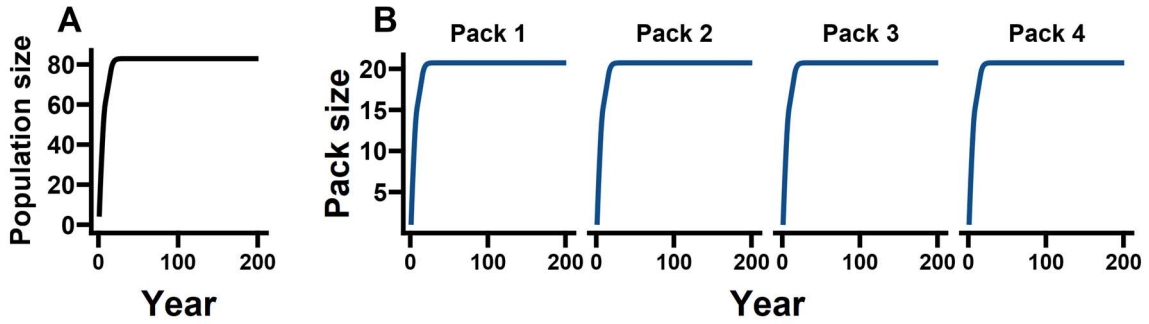


Figure 2: Model population trajectory (A) of the total population and (B) decomposed into packs.

Adjusting demographic constraints and model group structure

Increasing the maximum age of individuals beyond the baseline 15 did not result in changes to equilibrium conditions (figure 3A). There were positive relationships between both maximum litter size (figure 3B) and the number of packs (figure 3C), and the equilibrium population size.

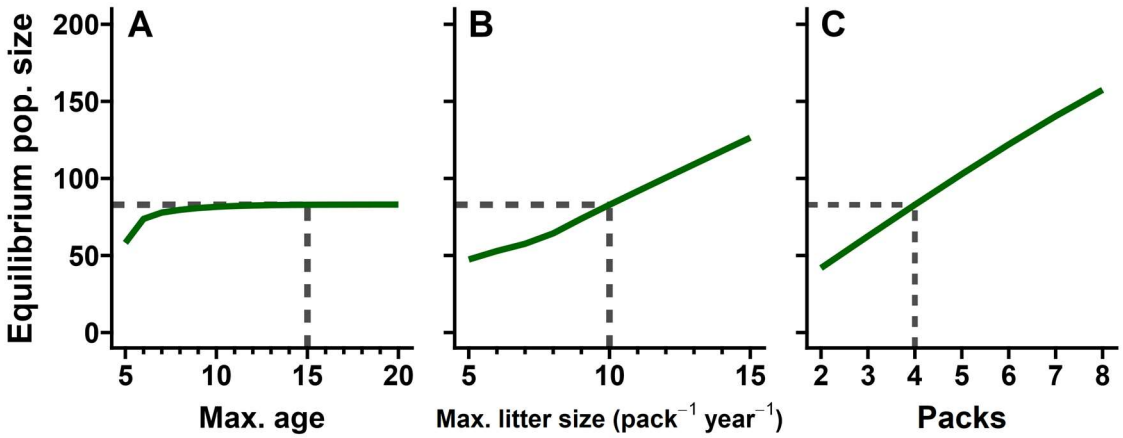


Figure 3: Equilibrium population sizes under different parameterisation conditions for (A) maximum age of individual survival; (B) maximum annual litter size per pack; and (C) the number of packs in the population. Dashed lines indicate values of baseline parameterisation.

Dispersal-related population dynamics

The inclusion of the dispersal process resulted in smaller equilibrium population (figure 4A). At the baseline survival of 20%, dispersal mortality and intergroup movements reduced the equilibrium population size by 86% (figure 4A). The size of equilibrium populations increased as an escalating function of disperser survival (figure 4B).

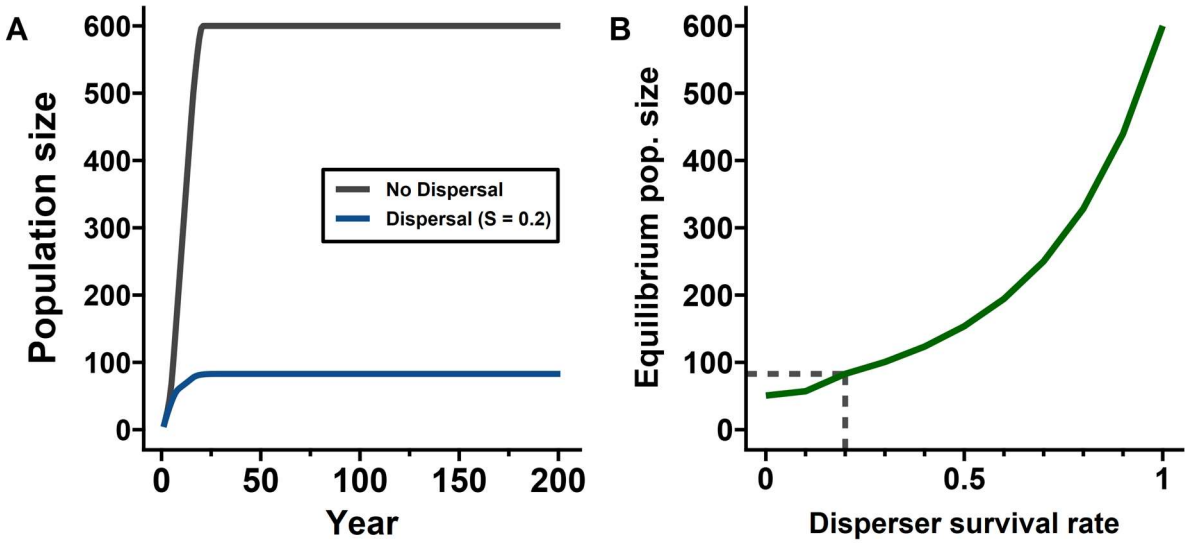


Figure 4: Model dispersal dynamics. (A) Population trajectories for comparable models without and with dispersal (at baseline survival, $S = 0.2$); and (B) Equilibrium population sizes across the range of disperser survival. Dashed lines indicate values of baseline parameterisation.

Table 2: Results of sensitivity analysis. Equilibrium population change versus baseline under 5% upward adjustment of demographic function parameters and whole demographic rates.

			Baseline population	82.90
	Demographic function Parameter adjusted	Symbol	Δ Population	(%)
Individual Survival	**Survival**		**9.83**	**11.86**
	Intercept	α_1	0.15	0.18
	Age	β_1	0.00	0.00
	Pack size	β_2	-0.14	-0.17
	Neighbour pack size	β_3	0.08	0.10
	Population size	β_4	0.03	0.03
Recruitment	**Pups born**		**0.00**	**0.00**
	Intercept	α_2	0.00	0.00
	Pack size	β_5	0.00	0.00
	Pup survival		**4.43**	**5.34**
	Intercept	α_2	0.01	0.01
	Pups born	β_6	0.00	0.00
	Pack size	β_7	-0.01	-0.01
	Neighbour pack size	β_8	0.00	0.00
	Pack size × Neighbour pack size	β_9	-0.02	-0.02

Sensitivity analysis

Our sensitivity analysis revealed that the population was more strongly influenced by positively adjusting individual survival than by recruitment (table 2). Adjusting the rate of birth rate of pups did not affect the population following 5% adjustments. Interestingly, positively adjusting the effect of pack size on individual survival, and the effects of pack size and neighbour pack size on pup survival, led to decreases in the equilibrium population. When demographic rates as functions of pack size were adjusted positively, individual survival and pack recruitment increased. This in turn inherently increased the number of dispersers from the pack, and so the number of individuals lost from the population. Under these conditions, the mortality of dispersers exceeded the positive pack size effects, producing smaller populations.

4.4 Discussion

Our model was motivated by an apparent disconnect between measures of pack performance and demography against pack sizes, and observations of consistently small packs in northern Yellowstone wolves. Our simulated population reasonably approximated the size and structure of the real population and illustrated a strong regulatory effect of dispersal-induced mortality on the dynamics of the population.

Model population dynamics

The stable equilibrium that emerges in our model reflects the relative stability in the Yellowstone population for more than a decade (Smith, Cassidy, *et al.*, 2020). Similarly, the equal division of the population between packs reflects the relative uniformity in pack sizes seen on the northern range (Cassidy *et al.*, 2020). Whilst our model did not include pack extinction, the number of packs on the northern range has been consistent in the past decade (Cassidy *et al.*, 2020), and the loss of a pack from the landscape is quickly capitalised upon. We therefore expect that the population dynamic effects of pack extinction are generally short-lived.

The positive relationship between the number of packs in our model and the equilibrium population derives from the lack of a spatial component in the model. Whilst there have been years with more packs on the northern range (e.g. 8 in the winter of 2007, Smith, Cassidy, *et al.*, 2020), there have since consistently been 4 to 5 packs saturating the northern range for more than the past decade (Cassidy *et al.*, 2020). The northern range seems unlikely to support many more packs under typical conditions, and so our baseline model structure seems appropriate.

Increasing the maximum age of individuals did not constrain equilibrium populations, suggesting that under the baseline maximum age of 15, individual mortality accumulated such that wolves did not reach the maximum age in substantial numbers. This reflects the rarity of individuals reaching this age in the wild (Theberge and Theberge,

1998). The larger population under positively adjusted individual survival corroborates past models that predicted the importance of adult survival to population growth rate (Smith, Cassidy, *et al.*, 2020).

Increasing the maximum annual pup production per pack led to larger populations, suggesting that packs were producing pups at the maximal rate. Changing the pack size effect by 5% in the elasticity analysis did not therefore have any impact on the population via changes in pup production. The elasticity analysis revealed that the survival of pups was important to the size of the equilibrium population. The importance of pup survival to the population is unsurprising given the relatively young age structure of wolf populations (Mech, 2006).

Individual vs. group advantages: the regulatory effect of dispersal

We included dispersal in our demographic model and parameterised this process according to existing empirical measures of dispersal. Dispersal reduced the asymptotic population size to a value on the same order of magnitude as the real population—the northern Yellowstone population has fluctuated around 40 individuals since 2009 (Smith, Cassidy, *et al.*, 2020). Our results suggest that dispersal—as parameterised according to current understanding of the fates of dispersing rocky mountain wolves—can have a substantial role in the regulation of the wolf population. The addition of dispersal to the predictive functions of survival and recruitment markedly improved the match of model prediction the observed population. Disperser survival strongly influenced the population, suggesting that empirical measures of disperser fates are likely to be important to understanding the population dynamic consequences of dispersal between packs.

Dispersal is a highly risky behaviour (Meyer *et al.*, 2022), involving a substantial risk to survival via starvation and attack from others (Smith *et al.*, 2010) for a potentially small chance at attaining a breeding position. In northern Yellowstone wolves, whose dense population saturates the landscape with territories, newly formed packs cannot readily establish new territories under normal conditions, meaning that dispersal probably riskier

than in lower density populations in the surrounding region (Jimenez *et al.*, 2017). However, we would generally expect the fitness gains from successfully attaining a breeding position to be substantial.

From first principles, we anticipate that the costs of reproductive subordination are greatest for wolves in larger packs. In this case, selection should favour greater dispersal rates from bigger packs. Conflict in group size advantage between dominants and subordinates is also seen in meerkats—another socially reproductive mammal—whereby dominant breeding meerkats intensify their suppression of subordinates in larger groups, increasing the rate of their eviction (Clutton-Brock, Hodge and Flower, 2008). This pattern corresponds to the assumption of greater dispersal from bigger wolf packs. Future work to evaluate the social conditions underlying dispersal is needed to validate our assumption, but our results point to the potential significance of this effect.

Our model did not account for sex differences in dispersal. While males most commonly become breeders by dispersing, females are more likely to attain breeding status as a subordinate or by inheriting the dominant breeding position within the natal pack (Stahler, Smith, *et al.*, 2020). The costs of reproduction are greater for females due to energetic and time investment in gestation and lactation, and so perhaps females are more likely to remain in the natal pack due to greater chance of cooperation from relatives. Sex differences in dispersal are likely an important nuance that we excluded for the purpose of simplicity.

It is possible that our model overestimated dispersal, owing to large equilibrium pack sizes producing high rates of dispersal. We set the maximum dispersal rate to the upper bound of dispersal rate predictions for Yellowstone wolves, though annual dispersal rates under normal conditions are probably lower (Smith, Cassidy, *et al.*, 2020). Understanding the social and environmental conditions that underpin the dispersal process is key target of future research into Yellowstone wolves (Stahler, Smith, *et al.*, 2020). It is difficult to record the fates of all dispersing wolves (i.e., the post-dispersal survival and reproductive

status of dispersers) and thereby quantify the average fitness value of dispersal. For our model, we could not explicitly parameterise for the trade-off between the benefits of group living versus the risk of dispersal that subordinates face under specific conditions. Quantifying these trade-offs will be central to understanding the dynamics of dispersal. Our results indicate a potentially strong regulatory effect of dispersal on group and population dynamics and provide a basis for further work to quantify the fitness trade-offs underlying dispersal.

Chapter V

A demographic model of antagonistic trophic interactions in the Yellowstone ecosystem reveals the primacy of indirect effects on community dynamics

Chapter V: A demographic model of antagonistic trophic interactions in the Yellowstone ecosystem reveals the primacy of indirect effects on community dynamics

Abstract

Species interactions play a central role in the organisation and dynamics of ecological communities. The relative importance of direct and indirect interaction effects is key to our understanding of community-scale processes. We develop a novel community modelling approach to simulate the ecological community of northern Yellowstone, where the reintroduction of wolves has potentially induced a trophic cascade. The occurrence and rate of a trophic cascade in Yellowstone—as determined by the recovery of over-exploited woody deciduous plants—are much debated. We present an alternative approach to simulating the populations of multiple interacting species to explore these processes. We structure survival and recruitment functions of each species according to their specific life histories, and weight population growth parameters by dietary preferences and predation rates, as informed by empirical data. We simulate the populations of two vegetation classes (grass and browse), two herbivores (elk and bison) and an apex predator (wolves) and their various interactions. We demonstrate that prevalent, impactful, and nuanced indirect effects can arise in model communities where only direct interactions are parameterised. Furthermore, our model predicts a predator-driven trophic cascade, where the release of woody plants from herbivory is associated with a gradual increase in its availability. Our methodology allows the simulation of specific ecological communities with potentially greater ecological validity than traditional approaches to parameterising consumer-resource interactions.

5.1 Introduction

The Yellowstone ecosystem after the reintroduction of wolves is often touted as a poster child for trophic cascades. The most ardent versions of the story assert that the reintroduction of wolves reduced elk numbers, which led to the regrowth of forests (Ripple and Beschta, 2012), rivers changing their courses, and a paradise emerging from an overgrazed wasteland. In truth, patterns of recovery and their ultimate cause appear to be more nuanced. The community has indeed changed following the reintroduction of wolves, but forest cover does not uniformly recover in a quarter of a century, and compelling evidence that wolves have changed the morphology of rivers is lacking (Beschta and Ripple, 2018; East *et al.*, 2018). Rather, there is disagreement on the role that wolves have played in altering community dynamics—particularly at the level of the vegetation—with different studies reaching contrasting conclusions. Generally, there has been a paucity of mechanistic modelling to predict the ecological consequences of wolf reintroduction. We address this gap here, not only providing insight into the Yellowstone ecosystem, but also providing general insight into the role of direct and indirect interactions on community dynamics using a novel modelling approach.

Species interactions are fundamental to community ecology. Theoretical work has long indicated that the complexity of food webs and the strengths of interactions occurring within them influence the organisation and stability of ecological communities (May, 1973). Direct trophic interactions are those occurring immediately between two species and may be antagonistic (e.g., trophic interactions, parasitism) or mutualistic (e.g., pollination). Indirect interactions occur between two non-adjacent species (i.e., those connected by a chain of two or more direct interactions). The impacts of indirect effects can, in some contexts, outweigh those of direct effects (Yodzis, 1988; Menge, 1995). However, the prevalence and importance of indirect interactions in ecological communities remains a fundamental question in ecology (Sutherland *et al.*, 2013). It is difficult to assess the dynamics of indirect effects in real-world communities as empirical

measures of interaction coefficients remain controversial (Damgaard and Weiner, 2017). Alternatively, models simulating the interactions of multiple species of real systems are relatively rare. Whilst simulated communities necessarily simplify natural systems, they offer useful insight into indirect interactions and community-level processes when model parameterisation is guided by empirical data.

The significance of indirect interactions in the organisation of communities is exemplified by trophic cascades. Trophic cascades are powerful community-wide changes driven by indirect interactions whose effects perturbate throughout food webs (see Pace *et al.*, 1999), often induced by change in the abundance of apex predators. In the archetypal trophic cascade scenario, a predator suppresses the impact of a prey species on the prey's resources by constraining the population or altering the behaviour of the prey. These effects may then propagate to other species in the community. In this way, indirect effects can substantially influence the dynamics of a whole community.

Whilst competitive interactions between species are likely the most commonly studied form of indirect interactions (Law and Watkinson, 1987; Rees, Grubb and Kelly, 1996; Freckleton and Watkinson, 2000; Adler *et al.*, 2018), there is difficulty in usefully assessing the strength of competitive species interactions in the field. Empirical measures of the strengths of antagonistic interactions, such as the strength of competition that species appear to impose on one another, may be insufficient to predict how those competitors will respond to change in or absence of their counterparts in reality (Tuck *et al.*, 2018). A potentially useful alternative approach is to examine how model competitor species respond to change in the other when their mutual influence is modelled solely through their relationships with the resources and predators that they have in common. Importantly, this approach makes no explicit assumptions as to the strength of indirect interactions. It would be valuable to apply this framework in the context of a well-studied system where indirect interactions may play an important role.

Creating models to simulate the population dynamics of multiple interacting species provides a means to explore how direct and indirect interactions shape communities. Simulated communities enable particular insight into the role of density mediated indirect interactions (DMIIs; Abrams, 1995). DMIIs occur when the density of intermediate species drive variation in successive, indirectly linked species, principally via consumptive effects. Multispecies simulation models are commonly based on Lotka-Volterra predator-prey model structures (Case, 1991; Law and Morton, 1993; Křivan and Schmitz, 2004; Miller, TerHorst and Burns, 2009; Maynard, Serván, *et al.*, 2019). Whilst these models may produce generalisable dynamic systems, measuring the carrying capacity and intrinsic rates of population increase in the field is non-trivial, and the dynamics of Lotka-Volterra systems can produce outcomes that differ notably from empirical equilibrium abundances (Maynard, Wootton, *et al.*, 2019). There may be advantage in applying empirical data concerning the life histories and the relative consumption rates of dietary components to parameterise the population growth rates of each species in simulated communities. In doing so, we might anticipate a more ecologically valid reflection of the dynamics of a real-world system. We develop this approach to simulate community dynamics of the northern Yellowstone National Park.

The Yellowstone ecosystem has been keenly observed by ecologists since wolves were reintroduced from 1995, following 70 years of absence (Fritts *et al.*, 2020). In this period, a hyper-abundant elk population is thought to have degraded the Yellowstone community (Wagner, 2006). Elk herbivory is thought to have generally suppressed the growth of willow *Salix spp.* (Beyer *et al.*, 2007), cottonwood (*Populus* spp.; Beschta and Ripple, 2016) and aspen *Populus tremuloides* (William H Romme *et al.*, 1995), which provide important habitat and resources for beaver *Castor canadensis* (Smith and Tyers, 2012), songbirds (Baril *et al.*, 2011) and other species. The restoration of wolves to an ungulate-rich system presents an opportunity for long term observation of population trends (Figure 1), community-wide responses to predator reintroduction (Smith, Peterson and

Houston, 2003), and possibly, a trophic cascade in action (Peterson *et al.*, 2014; Smith, Stahler and MacNulty, 2020).

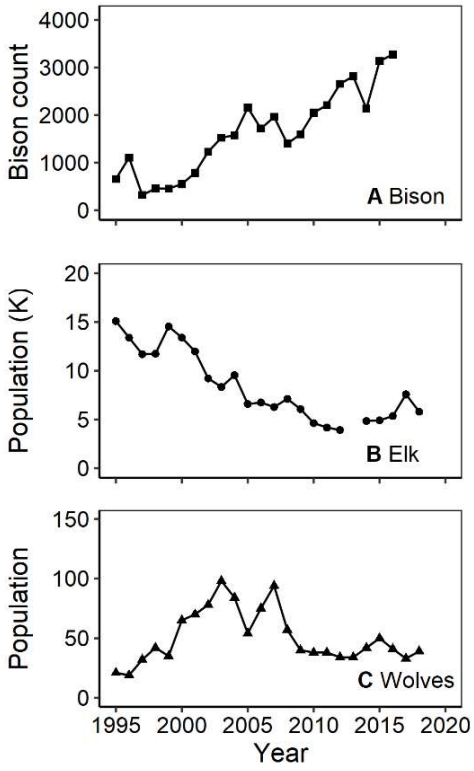


Figure 1: Population time-series of (A) bison, (B) elk and (C) wolves, in northern Yellowstone National Park after the 1995 wolf reintroduction. Data from the National Park Service.

The recovery of deciduous woody plants is often considered to be important measure of the recovering health of the Yellowstone ecosystem (Painter *et al.*, 2015; Beschta and Ripple, 2019). There is evidence of localised recovery of both willows (Beschta & Ripple, 2016) and aspen stands (Painter *et al.*, 2015). However, despite their lower density, it has been suggested that elk continue to exert strong browsing pressure in some sites, and that recovery may therefore take many more decades (Marshall, Thompson Hobbs and Cooper, 2013). There is also evidence that the recovery of browse species is unrelated to a behaviourally mediated response of elk to the presence of wolves (Kauffman, Brodie and Jules, 2010). Indeed, it has been argued that the predominant impact of wolves on willow and aspen has been via numerical decline in the elk population (Kauffman, Brodie and Jules, 2010; Painter *et al.*, 2015; Boyce, 2018). Whether the recovery of browse species is

driven by either a density dependent or behaviourally mediated trophic cascade remains uncertain. However, we would generally anticipate any recovery of woody vegetation to arise gradually, due to slow rates of woody vegetation growth and continued herbivory. In general, discussion of processes in Yellowstone has often concerned whether the observed changes have been driven by bottom-up (e.g. vegetation-herbivore interactions) or top-down processes (e.g., predator limitation of herbivores) (see Peterson *et al.*, 2020), and how these processes will influence the trajectory of the system. The relative importance of these processes may not be adequately captured by static measures, and it seems reasonable to expect that their importance may vary through time. Additionally, the role of competitive interactions—particularly between ungulate species—has been generally overlooked. This issue is likely to come into greater focus for Yellowstone research, to understand the potential impacts of shifts in the relative abundance of ungulate species. Dynamic models may provide a useful approach to explore the importance of direct and indirect species interactions and regulatory processes in Yellowstone's community dynamics.

We developed a multispecies time series model to simulate community population dynamics in northern Yellowstone National Park. The model iterates species-specific growth functions of vegetation, sympatric herbivores, and an apex predator across time series, creating a dynamical system to represent Yellowstone's key species. We model growth and herbivory of vegetation (categorised as either grass or browse) and population dynamics of elk *Cervus canadenis*, bison *Bison bison*, and wolves *Canis lupus*, in terms of survival and recruitment across time steps. Our modelling approach differs substantially from commonly used Lotka-Volterra form community models, with the aim of more closely approximating the dynamics of a well-studied real-world community. We use our model to evaluate the role of indirect effects in the dynamics of northern Yellowstone. In doing so, we aimed to assess whether trophic cascades—as driven by density mediated

indirect interactions—can arise in simulated communities, as parameterised by direct interactions alone.

5.2 Methods

Model system

Our model simulates the life histories of three major animal species that dominate northern Yellowstone National Park (hereafter "northern Yellowstone"). This is an area characterised by broad river valleys dominated by grassland and sagebrush (Singer and Renkin, 1995) and coniferous forest at higher elevations (Kokaly *et al.*, 2003). Our model simulates population dynamics of key species which inhabit this region: wolves and their prey. We model dynamic resource pools for two herbivore species, where elk feed on browse, and both elk and bison feed on grass. We model direct predation and herbivory interactions only (figure 2).

Species life histories

Wolves predominantly kill older elk (89% of wolf-killed female elk are over 10 years old; MacNulty *et al.*, 2020), but also heavily predate on seasonally-available calves (Metz *et al.*, 2012b). Elk survival is generally greater than 0.8 between the ages of 2-15 (MacNulty, Stahler, Wyman, *et al.*, 2020). There is evidence to suggest that elk recruitment rate is linked to wolf abundance, but this typically ranges from 0.1 to 0.3 (MacNulty, Stahler, Wyman, *et al.*, 2020).

Bison fecundity has been reported between 0.23-0.35 depending on female age class in a growing population (Fuller *et al.*, 2007). The probability of adult bison survival has been reported between 0.75-0.96 (Larter *et al.*, 2000; Fuller *et al.*, 2007), though these values do not capture survival across all ages and sexes. Calf survival in Yellowstone was reportedly 0.76 in 1996 (Kirkpatrick *et al.*, 1996) before the reintroduced wolf population had grown substantially (see Boyce, 2018). We assume total bison survival to be lower

than the highest reported values for the purposes of our model due to predation and the lower calf survival.

Wolf survival has been reported as between 0.8-0.84 (Pletscher *et al.*, 1997; Hayes and Harestad, 2000; Marucco *et al.*, 2009) though survival may be lower when dispersing (Pletscher *et al.*, 1997), at high population densities (Hayes and Harestad, 2000), and in younger (Marucco *et al.*, 2009) and older wolves (Cubaynes *et al.*, 2014). There is also a substantial degree of variability in pup survival and recruitment (Fuller, 1989; Almberg *et al.*, 2009; Stahler *et al.*, 2013). Across all age categories, the survival of Yellowstone wolves is 0.77 (1998-2010; Cubaynes *et al.*, 2014). We initially set the target survival to recruitment ratios for bison, elk, and wolves to 0.9:0.1, 0.85:0.15 and 0.75:0.25, respectively. We performed a sensitivity analysis to assess the effect of variation in all survival and recruitment terms.

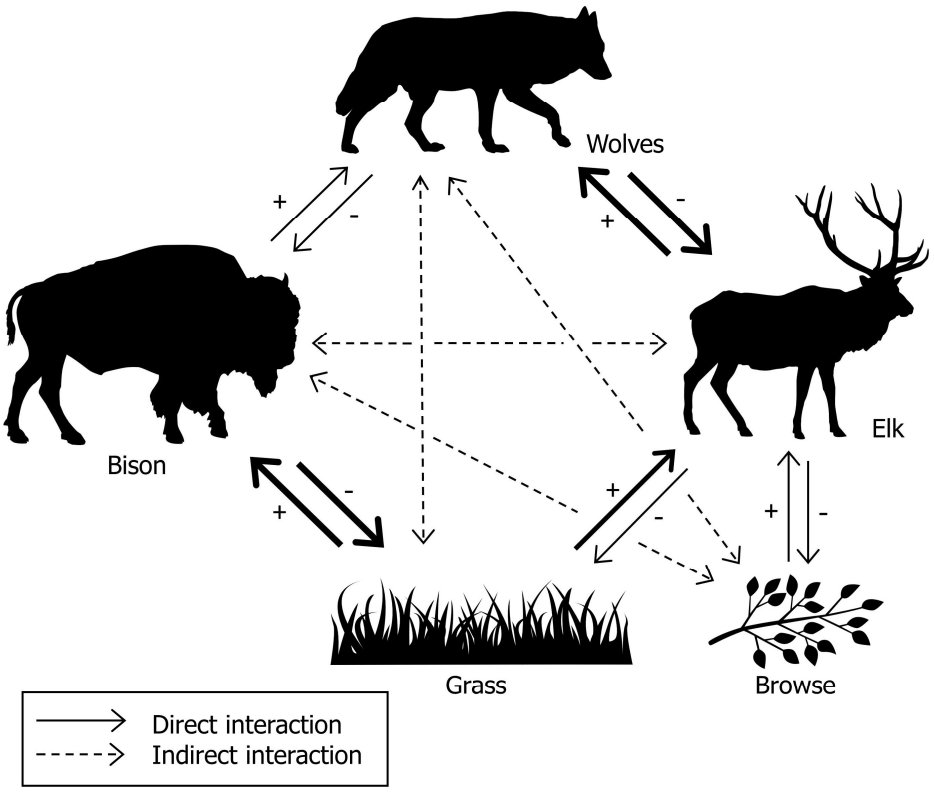


Figure 2: Direct and indirect pairwise species interactions of major species of northern Yellowstone National Park. Signs indicate direction of influence of a given interaction according to the model. Line thickness broadly indicates relative strength of direct interactions as parameterised in the model. Direct interactions are parameterised, indirect interactions are not.

Modelling approach

Our model consisted of three animal species and two categories of vegetation, grass and browse, each of which represents multiple species. The population size of species x and time t is always referred to as $N_{x,t}$ In the case of browse and vegetation population size is treated as a proxy for biomass, while the size of the animal populations represents the number of individuals. The subscripts W, E, B, G and A represent wolves, elk, bison, grass and browse, respectively. The dynamics of the vegetation components of the model were determined by density-dependent functions,

$$N_{G,t+1} = (1 - \beta_{GG})G^* + \beta_{GG}N_{G,t} + \beta_{EG}N_{E,t} + \beta_{BG}N_{B,t} \quad (1)$$

$$N_{A,t+1} = (1 - \beta_{AA})A^* + \beta_{AA}N_{A,t} + \beta_{EA}N_{E,t} \quad (2)$$

β_{GG} and β_{AA} determine how quickly the grass and browse respectively regenerate when rare and in the absence of any herbivores (with smaller values conferring greater growth rates). G^* and A^* provide maximum values for grass and browse respectively in the absence of herbivores. $(1 - \beta_{GG})G^*$ and $(1 - \beta_{AA})A^*$ are consequently intercepts and β_G and β_A are slopes. For any starting value of $N_{G,t+1} < G^*$ or $N_{A,t+1} < A^*$, in the absence of herbivory, the populations will converge on values of G^* and A^* for $0 < \beta_x < 1$. The density-dependent constraint on the vegetation captures the observation that grass and browse will not grow indefinitely, whilst also providing a stabilising mechanism for the system.

The β_{XY} slopes describe the effect of species X on species Y. The dynamics of the animals (elk, bison, and wolves) are captured with equations of the form:

$$N_{X,t+1} = f_X(\dots)N_{X,t}, \quad (3)$$

Where $f_{X,t}(\dots)$ is a function describing the population growth rate of species X at time t. $f_{x,t}$ is further decomposed into survival $S_{X,t}(\dots)$ and recruitment $R_{X,t}(\dots)$ functions before being combined such that $f_{X,t}(\dots) = S_{X,t}(\dots) + R_{X,t}(\dots)$ is the growth rate of species X at time t (Coulson *et al.*, 2008), which is then applied to generate the population of species X at time t+1. The annual survival of each species was bounded between 0 and 1 and was

assumed to be logistic. Bison and elk produce a sole offspring at each breeding event, so their recruitment was also assumed to be of logistic form. In contrast, wolves produce litters of multiple offspring at each successful reproductive attempt (Packard, 2010). The wolf recruitment function was therefore assumed to be Poisson distributed. As an example of a function $f_{X,t}(\dots)$, for wolves it took the form:

$$f_W(N_{E,t}, N_{B,t}) = \frac{1}{1 + e^{\alpha_W + \beta_{EW} N_{E,t} + \beta_{BW} N_{B,t}}} + e^{\tau_W + \gamma_{EW} N_{E,t} + \gamma_{BW} N_{B,t}}. \quad (4)$$

Although the model is more complex than many models of species interactions (see table 1 for a full list of model terms) it is biologically more realistic. The functions $f_{x,t}(\dots)$ capture the shape of the demographic functions that determine survival and recruitment rates for each animal species. This allows different species interactions to influence different aspects of the demography of each species. The α_xs represent survival intercepts, the τ_xs recruitment intercepts, the β_{xy} survival slopes and the γ_{xy} recruitment slopes. On each occasion, the model was run for 20,000 timesteps to ensure we report asymptotic outcomes rather than transient dynamics. Simulations were automatically halted if any species went extinct.

Parameterisation

The model was initially set up with arbitrary values to approximate the relative magnitude of survival and reproduction for each of the five model animal species. We then manually explored a grid of parameter space to generate a stable system capable of reaching equilibrium. The various coefficients within individual equations were then adjusted to approximate the relative influence of survival and recruitment for each species, the empirical relationships between species, or the relative importance of a species' dietary components (see below).

Animal Populations

Coefficients in survival and recruitment equations were set to broadly approximate species-specific survival and recruitment ratios at equilibrium (the target survival: recruitment ratios for bison, elk and wolves were 0.9:0.1, 0.85:0.15 and 0.75:0.25 respectively). At equilibrium, mean survival and recruitment for each species sum to unity. The intercepts of growth equations were adjusted to modify the baseline ratio of the animal population (those observed at equilibrium after the timeseries model was run) to approximate real-world population ratios of northern Yellowstone's species. As averaged across population counts from the winters of 2011-2016, Bison, elk and wolves are present at a ratio of 68:116:1. We adjusted this ratio according to the annual presence of elk in northern Yellowstone (see below) for a target ratio of 68:48.5:1. We did not try to replicate the mean population sizes of each species numerically but instead scale the parameters to keep the predicted values on a scale that aids readability.

Vegetation growth

We assumed grass to be the more plentiful resource and so maximum vegetation value was set to a greater value for grass than browse. We also assumed that grass would recover faster than browse, and so set the growth rate factor β_{GG} to a smaller value than β_{AA} to simulate faster grass regrowth (see table 1 for model parameters).

Relative grazing impact on grass

Broadly, we assume that the offtake of vegetation across timesteps is proportional to the abundance of herbivores. We based the relative grazing impact of the herbivore species on the proportion of time elk and bison spend in northern Yellowstone, and their feeding rates. Bison have a greater grazing impact per individual than elk (Frank, Wallen and White, 2016), despite the expectation of lower energy requirements per unit mass (Peters, 1986). Allometric scaling of foraging requirements indicates that bison require approximately 1.5 times the amount of forage than elk per unit time (Beschta *et al.*, 2020). Yellowstone's northern elk herd migrates annually, and typically occupy northern

Yellowstone from late autumn to early spring—a period of approximately 5 months—whereafter elk are substantially less abundant in the northern area (White *et al.*, 2010). We assume bison are present in northern Yellowstone year-round (Geremia *et al.*, 2014). These values represent an approximation of ungulate presence in northern Yellowstone, which can vary substantially between years (White *et al.*, 2010; Geremia *et al.*, 2014). Greater individual grazing impact (1.5 times that of elk) and greater presence throughout the year (2.4 times greater than elk) were combined for a bison grazing impact of 3.6 times that of elk.

Dietary composition of herbivores

In northern Yellowstone, grasses and sedges combined represented 97% and 92% of bison diet in winter and summer respectively (Singer and Norland, 1994; Olenicki and Irby, 2005). For the purpose of this model, we assume that bison are exclusive grazers because we were interested in the influence of shared and unshared resources on the herbivore populations and wider community dynamics. Elk feed on grass and browse vegetation (Christianson and Creel, 2007), and so we added browse to simulate an additional uncontested resource. The positive effect of grass on the survival and recruitment of elk was set to 9 times that of browse on the basis that elk diet is composed of approximately 90% grass and 10% browse (Christianson and Creel, 2007). We made the simplifying assumption that grass and browse are of approximately equal nutritional value, and that dietary preference does not change when one resource becomes rare, as we were predominantly interested in the impact of an additional, uncontested resource for the elk.

Predation

Yellowstone wolves mainly kill elk, with elk representing 85-96% of wolf kills (Metz *et al.*, 2012b). Bison represent 1.3% of annual wolf-killed prey (Metz *et al.*, 2012b), though wolf scavenging (Metz *et al.*, 2016) and predation of bison (Tallian *et al.*, 2017) have increased in recent years, concurrently with increasing bison abundance. On this basis, we set wolf population growth rate to be 19x more strongly driven by elk compared to bison (i.e., 5%

bison diet). Wolf kills are likely to be driven partially by the relative availability of prey species, whose populations vary appreciably through time (see Varley and Boyce, 2006; Tallian *et al.*, 2017). Due to the potential difficulty in accurately determining prey preference under varying prey species abundance ratios, we elected to make prey preference static. We anticipated that predation interactions would strongly influence community dynamics, and so to explore the impact of the strength of these interactions, we systematically adjusted each parameter in our analyses.

Elasticity analysis

The model was initialised with arbitrary starting population sizes for grass, browse, elk, bison, and wolves, and iterated until the system reached a state of equilibrium. To identify potentially important parameters and interactions on the outputs of the model (e.g., asymptotic population sizes of grass, browse, elk, bison, and wolves), we performed a parameter perturbation sensitivity analysis. We independently perturbed each of the 25 parameter values by 5% (i.e., multiplied positive parameter coefficients by 1.05 and negative coefficients by 0.95 to increase output values positively).

Table 1: Model terms, symbols, and values.

Model Term	Symbol	Value
Grass (G)		
Maximum	G^*	100
Growth Factor	β_{GG}	0.2
Bison Grazing	β_{BG}	-0.36
Elk Grazing	β_{EG}	-0.1
Browse (A)		
Maximum	A^*	60
Growth Factor	β_{AA}	0.3
Elk Grazing	β_{EA}	-0.1
Wolves (W)		
Survival		
Intercept	α_W	-0.7
Bison Prey	β_{BW}	0.0019
Elk Prey	β_{EW}	0.036
Recruitment		
Intercept	τ_W	-1.6
Bison Prey	γ_{BW}	0.0019
Elk Prey	γ_{EW}	0.001
Bison (B)		
Survival		
Intercept	α_B	-0.16
Grass Feeding	β_{GB}	0.035
Wolf Predation	β_{WB}	-0.018
Recruitment		
Intercept	τ_B	-2
Grass Feeding	γ_{GB}	0.00019
Wolf Predation	γ_{WB}	-0.00085
Elk (E)		
Survival		
Intercept	α_E	-0.21
Grass Feeding	β_{GE}	0.03
Browse Feeding	β_{AE}	0.0033
Wolf Predation	β_{WE}	-0.066
Recruitment		
Intercept	τ_E	-1.8
Grass Feeding	γ_{GE}	0.0014
Browse Feeding	γ_{AE}	0.000155
Wolf Predation	γ_{WE}	-0.047

Manipulating the strengths of direct species interactions

The interaction between two species—and the impact of their interaction on community dynamics—is mediated by a combination of the effect of species X on species Y, and vice versa. Because of this, we chose to simultaneously perform adjustments to both components of a given interaction (*i.e.,* β_{XY} and β_{YX}). For example, to adjust the model to intensify wolf predation of elk, we simultaneously adjusted model terms that determined how elk influence wolf population growth, and the negative impact of wolves in the elk growth equations. In more general terms, we systematically weakened or strengthened the interaction by adjusting consumption rate in both the consumer and resource or prey equations. Given that the survival functions of animal growth equations influenced populations more strongly than did the recruitment functions, we focussed on exploring community dynamics by manipulating interaction terms in the species survival functions. This allowed clearer illustration of how species interactions influence the wider system.

To calculate the influence of each model term on the dynamics of each population, we ran the model under independent adjustments of 0.99 and 1.01 for each model term and calculated the gradient of the equilibrium population for each species occurring across those adjustments. By comparing the relative influence of the consumer parameters on prey populations with that of prey parameters on consumer populations, we were able to manipulate the strength of a pairwise interaction by the same relative magnitude for both species in that interaction. To achieve this, we calculated the ratio of these elasticities in each pairwise interaction (Jones and Tuljapurkar, 2015). We then adjusted the consumer parameters across a range of values (using multipliers ranging from 0.95 to 1.05, at intervals of 0.005), and simultaneously adjusted prey parameters at the appropriate magnitude relative to these values, according to the ratio of their elasticities. In this way, we simultaneously manipulated predation efficiency and predator impact on prey populations, or the efficiency of herbivores and their impact on vegetation resources. For each adjustment of the strength of an interaction, we ran the model fully and recorded the equilibrium population conditions of each species. We could then observe how the

organisation of the community at equilibrium differed when the strength of direct species interactions varied, and so gain insight into the dynamics of indirect interactions occurring in the model system. Relationships between asymptotic population values and adjusted interaction strengths were reported as gradients. These gradients represent the partial derivative of a given species' equilibrium population values with respect to the relevant terms in each interaction (see table 1). For example, when we simultaneously manipulate the impact of species X on the survival of species Y, and vice versa, the partial derivative of equilibrium population X with respect to these simultaneous adjustments would be signified by

$$\frac{\partial N_X}{\partial(\beta_{XY}, \beta_{YX})}$$

Or the effect of the same adjustments to species X and Y on a third species Z by

$$\frac{\partial N_Z}{\partial(\beta_{XY}, \beta_{YX})}$$

Indirect interactions can therefore be revealed when the population of a third species responds to change the strength of the interaction between two others.

5.3 Results

Equilibrium Conditions

To the nearest whole number, the animal community was composed of bison elk and wolves at a ratio of 68:48.5:1, matching the real-world target ratio. At equilibrium, grass and browse resource levels were constrained to 62% and 88% of their respective maxima by herbivory. The equilibrium survival to recruitment ratio for the animal species were 0.88:0.12 for bison, 0.85:0.15 for elk, and 0.78: 0.22 for wolves (to 2dp.). All survival to recruitment ratio values were therefore to within 0.02 of their respective original targets.

Generally, the simulated community did not appear to be controlled by bottom-up processes, since the influence of the grass parameters (G^*, β_{GG}, β_{EG}, β_{EG}) on the asymptotic populations were often negligible (table 2). The link between elk and wolves was strong, as the parameters of each species often had substantial impacts on the asymptotic populations of the other (table 2).

Elasticity Analysis

When model parameters were independently perturbed, 19 of the 27 terms adjusted led to a greater than 1% change in one or more species populations at equilibrium compared to baseline (table 2). Other than a clear influence of grass maximum value (G^*) on bison (and elk to a lesser extent), perturbations of grass parameters did not generally have strong impact on model animal populations. Therefore, the model system was not strongly regulated by bottom-up processes. Perturbations to wolf and elk terms commonly influenced the other of the two species. The wolf population also reacted strongly to changes in some bison parameters (0.0% to +91.3%), while conversely, bison were mostly unaffected by perturbation of the wolf terms (0.0% to +1.1%).

The elasticity analysis indicated indirect effects occurring throughout the model community. Positive adjustment of the browse maximum led to growth of the wolf population, while conversely, perturbing wolf terms led to slight changes to browse

resource level. Wolves were frequently influenced by model term adjustments, with 14 of the 27 single term perturbations leading to a greater than 1% change in the equilibrium wolf population. Single term perturbations also indicated that the population growth of elk and bison had the potential to mutually influence one another, despite no direct interaction parameters (table 2). The prominence of indirect interactions and their role in the dynamics of the community became more pronounced when interaction strengths were adjusted symmetrically in each pairwise interaction.

Symmetrical adjustment of interaction parameters

By adjusting both sides of a predator-prey or herbivore-vegetation interaction, we effectively improved the efficiency of predation or herbivory and increase their impact on prey or vegetation. These adjustments could be thought to represent species evolving improved resource acquisition traits, or in the case of predation, mimic the increase in predation pressure that occurred after wolf reintroduction. Most manipulations of interaction strengths had linear or close to linear relationships with asymptotic population values (see figures 3 & 4). We therefore report gradients representing infinitesimal changes.

Table 2: Elasticity analysis output table. Values represent change in equilibrium population values under +5% perturbation of each model term adjusted (bracketed values show percentage change).

		Species				
		Grass	**Browse**	**Bison**	**Elk**	**Wolves**
Baseline population:		61.937	52.817	70.618	50.278	1.038
Term Adjusted (+5%)		**Equilibrium population change**				
		Δ (%)	Δ (%)	Δ (%)	Δ (%)	Δ (%)
Grass						
Maximum	G^*	0.002 (0.0)	0.085 (+0.2)	11.273 (+16)	-0.595 (-1.2)	0.003 (+0.3)
Growth Factor	β_{GG}	0.000 (0.0)	0.008 (0.0)	1.073 (+1.5)	-0.057 (-0.1)	0.000 (0.0)
Bison Grazing	β_{BG}	0.001 (0.0)	0.028 (+0.1)	3.774 (+5.3)	-0.199 (-0.4)	0.001 (+0.1)
Elk Grazing	β_{EG}	0.000 (0.0)	0.005 (0.0)	0.708 (+1.0)	-0.037 (-0.1)	0.000 (0.0)
Browse						
Maximum	A^*	0.058 (+0.1)	2.999 (+5.7)	-0.013 (-0.2)	0.007 (0.0)	0.108 (+10.4)
Growth Factor	β_{AA}	0.003 (0.0)	0.151 (+0.3)	-0.007 (0.0)	0.000 (0.0)	0.005 (+0.5)
Elk Grazing	β_{EA}	0.007 (0.0)	0.359 (+0.7)	-0.016 (0.0)	0.001 (0.0)	0.013 (+1.3)
Wolves						
Survival						
Intercept	α_W	0.003 (0.0)	0.132 (+0.2)	0.251 (+0.4)	-0.924 (-1.8)	0.005 (+0.5)
Elk Prey	β_{BW}	0.006 (0.0)	0.326 (+0.6)	0.619 (+0.9)	-2.280 (-4.5)	0.012 (+1.2)
Bison Prey	β_{EW}	0.000 (0.0)	0.025 (0.0)	0.048 (+0.1)	-0.177 (-0.4)	0.001 (+0.1)
Recruitment						
Intercept	τ_W	0.008 (0.0)	0.393 (+0.7)	0.747 (+1.1)	-2.748 (-5.5)	0.014 (+1.3)
Elk Prey	γ_{BW}	0.000 (0.0)	0.023 (0.0)	0.044 (+0.1)	-0.162 (-0.3)	0.001 (+0.1)
Bison Prey	γ_{EW}	0.000 (0.0)	0.002 (0.0)	0.003 (0.0)	-0.012 (0.0)	0.000 (0.0)
Bison						
Survival						
Intercept	α_B	-0.267 (+0.4)	0.005 (0.0)	0.602 (+0.9)	-0.032 (-0.1)	-0.074 (-7.1)
Grass Feeding	β_{GB}	-3.418 (-5.5)	0.058 (+0.1)	7.708 (+10.9)	-0.407 (-0.8)	-0.948 (-91.3)
Wolf Predation	β_{WB}	-0.031 (-0.1)	0.001 (0.0)	0.007 (+0.1)	-0.004 (0.0)	-0.009 (-0.9)
Recruitment						
Intercept	τ_B	-3.338 (-5.4)	0.057 (+0.1)	7.527 (+10.7)	-0.327 (-0.8)	-0.926 (-89.2)
Grass Feeding	γ_{GB}	-0.020 (0.0)	0.000 (0.0)	0.044 (+0.1)	-0.002 (0.0)	-0.005 (-0.5)
Wolf Predation	γ_{WB}	-0.001 (0.0)	0.000 (0.0)	0.003 (0.0)	0.000 (0.0)	0.000 (0.0)
Elk						
Survival						
Intercept	α_E	0.058 (+0.1)	-0.001 (0.0)	-0.132 (-0.2)	0.007 (0.0)	0.109 (+10.5)
Grass Feeding	β_{GE}	0.522 (+08)	-0.009 (0.0)	-1.176 (-1.7)	0.062 (+0.1)	0.974 (+93.8)
Browse Feeding	β_{AE}	0.049 (+0.1)	-0.001 (0.0)	-0.109 (-0.2)	0.006 (0.0)	0.091 (+8.8)
Wolf Predation	β_{WE}	0.020 (0.0)	0.000 (0.0)	-0.045 (-0.1)	0.002 (0.0)	0.037 (+3.6)
Recruitment						
Intercept	τ_E	0.501 (+0.8)	-0.009 (0.0)	-1.130 (-1.6)	0.006 (+0.1)	0.935 (+90.1)
Grass Feeding	γ_{GE}	0.024 (0.0)	0.000 (0.0)	-0.054 (-0.1)	0.003 (0.0)	0.045 (+4.3)
Browse Feeding	γ_{AE}	0.002 (0.0)	0.000 (0.0)	-0.005 (0.0)	0.000 (0.0)	0.004 (+0.4)
Wolf Predation	γ_{WE}	0.014 (0.0)	0.000 (0.0)	-0.031 (0.0)	0.002 (0.0)	0.026 (+2.5)

Predation interactions

Stronger predation of elk (figure 3) led to markedly lower asymptotic populations size of elk ($\frac{\partial N_E}{\partial(\beta_{WE},\beta_{EW})} = -47.8$), slightly larger wolf populations wolves ($\frac{\partial N_W}{\partial(\beta_{WE},\beta_{EW})} = 0.2$), and release of bison ($\frac{\partial N_B}{\partial(\beta_{WE},\beta_{EW})} = 13.0$). Conversely, when the strength of wolf-bison predation was increased, the bison population slightly increased ($\frac{\partial N_B}{\partial(\beta_{WB},\beta_{BW})} = 0.7$), whilst elk declined ($\frac{\partial N_E}{\partial(\beta_{WB},\beta_{BW})} = -3.5$), suggesting apparent competition between the prey species. Here, the increase in predation on bison was apparently outweighed by the competitive release occurring due to elk decline. Wolves exhibited a negligible population gain when wolf-bison predation was increased ($\frac{\partial N_W}{\partial(\beta_{WB},\beta_{BW})} = 0.05$). Whilst the community population dynamics were more profoundly impacted by changes in wolf-elk predation than wolf-bison predation, it is interesting that the former led to a decline in the focal prey species, whilst the latter impacted the non-focal prey species more strongly. When the exploitation of their non-preferred bison prey increased, the population of the wolves' preferred prey, elk, declined. Whilst this pattern was slight and did not coincide with change in the wolf population, it did indicate that the rate of predation of a preferred prey species can be influenced by the predation of another.

Whilst browse experienced release and its resource level grew under increased elk predation ($\frac{\partial N_A}{\partial(\beta_{WE},\beta_{EW})} = 6.8$), grass exhibited no substantial change compared to the baseline population value under adjustment of neither elk predation ($\frac{\partial N_G}{\partial(\beta_{WE},\beta_{EW})} = 0.1$) nor bison predation ($\frac{\partial N_G}{\partial(\beta_{WB},\beta_{BW})} = 0.1$). Predation interaction adjustments therefore only impacted vegetation when the vegetation category had only a single consumer, as compensatory herbivory by one herbivore species constrained the level of the shared resource when the population of the other herbivore declined.

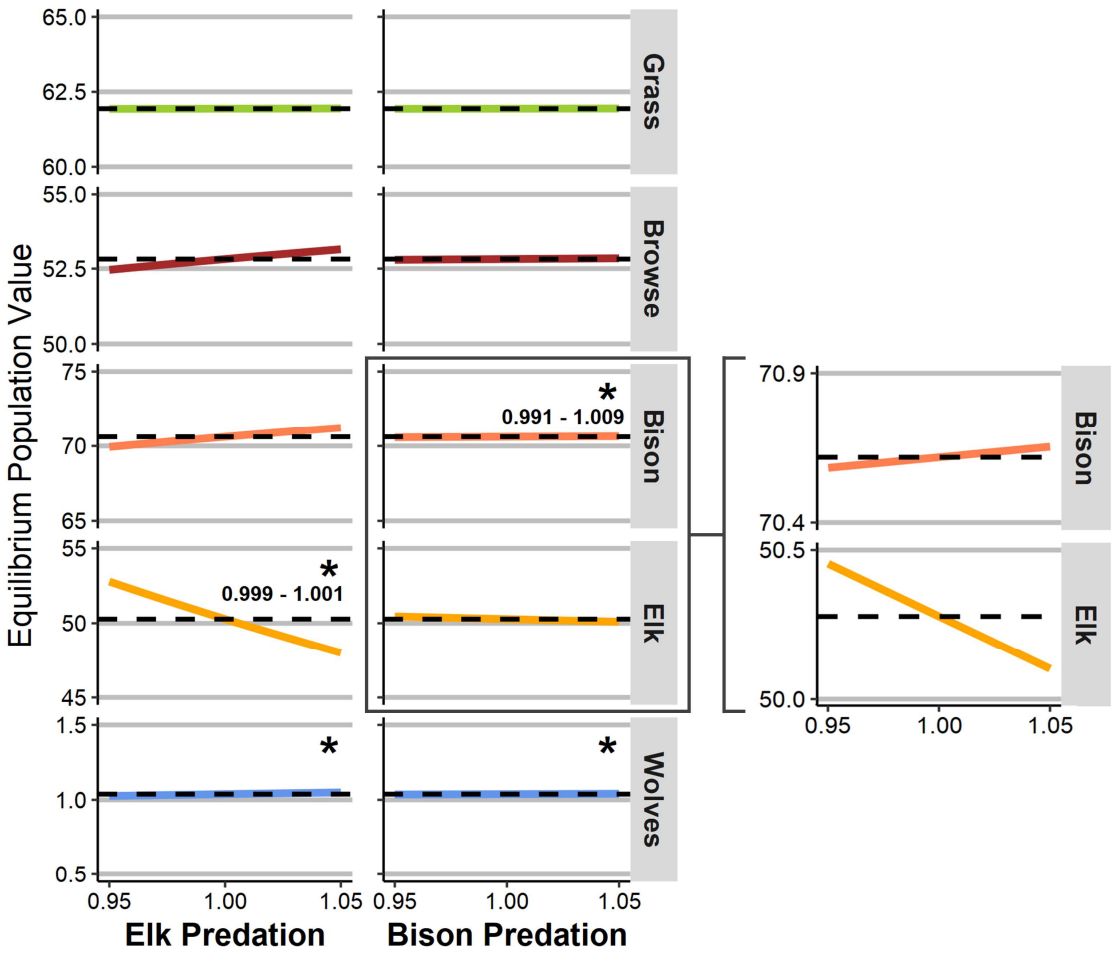


Figure 3: Equilibrium population values under adjustment of the strengths of wolf-elk and wolf-bison predation interactions (survival terms). Interaction terms in growth equations of both focal species in each interaction were simultaneously adjusted. Asterisks indicate species with model terms adjusted. X-axes illustrate the adjustment range applied to interaction terms in predator equations. Numerical annotations represent the elasticity-weighted range of adjustments made to interaction terms in prey equations. Greater adjustment values represent a strengthening of the interaction. Dashed lines indicate species equilibrium populations for the unadjusted model. Subplot presents finer y-axis interval for visibility of elk and bison population trends.

Herbivory interactions

Elk and browse equilibrium populations did not notably vary with the strength of elk-grass herbivory (figure 4), whilst greater elk-grass herbivory led to a marked increase in the wolf population ($\frac{\partial N_W}{\partial(\beta_{GE},\beta_{EG})} = 19.3$). The elk population appeared able to withstand greater predator abundance without experiencing a population decline when their grazing

efficiency was improved. The effect of enhanced grazing in elk was therefore transferred upwards to the wolves, implying that the constraint of elk on wolves depends on the ability of elk to assimilate resources for population recovery. Bison declined ($\frac{\partial N_B}{\partial(\beta_{GE},\beta_{EG})} = -24.4$) under greater predation pressure from the increasingly numerous wolves and reduced competitive ability versus elk in this scenario (fig. 4). Additionally, grass experienced grazing release under lower bison numbers ($\frac{\partial N_G}{\partial(\beta_{GE},\beta_{EG})} = 10.3$). Although less pronounced, a similar pattern occurred when elk-browse herbivory was manipulated, although browse resource level declined under to greater browsing pressure ($\frac{\partial N_A}{\partial(\beta_{AE},\beta_{EA})} = -7.2$). Improved assimilation of browse by elk corresponded to growth in the wolf population ($\frac{\partial N_W}{\partial(\beta_{AE},\beta_{EA})} = 1.6$), but no substantial growth in the elk population.

Manipulating bison-grass herbivory led to profound changes in community organisation. Greater bison grazing efficiency led to a marked increase in bison ($\frac{\partial N_B}{\partial(\beta_{GB},\beta_{BG})} = 163.2$), and a decrease in grass resource level ($\frac{\partial N_G}{\partial(\beta_{GB},\beta_{BG})} = -72.4$). This coincided with a slight decline in elk ($\frac{\partial N_E}{\partial(\beta_{GB},\beta_{BG})} = -8.6$) and a concurrent release of browse ($\frac{\partial N_A}{\partial(\beta_{GB},\beta_{BG})} = 1.2$). The wolf population declined steeply ($\frac{\partial N_W}{\partial(\beta_{GB},\beta_{BG})} = -20.1$) under increasing bison herbivory as the prey species ratio shifted in favour of bison, their less preferred prey species.

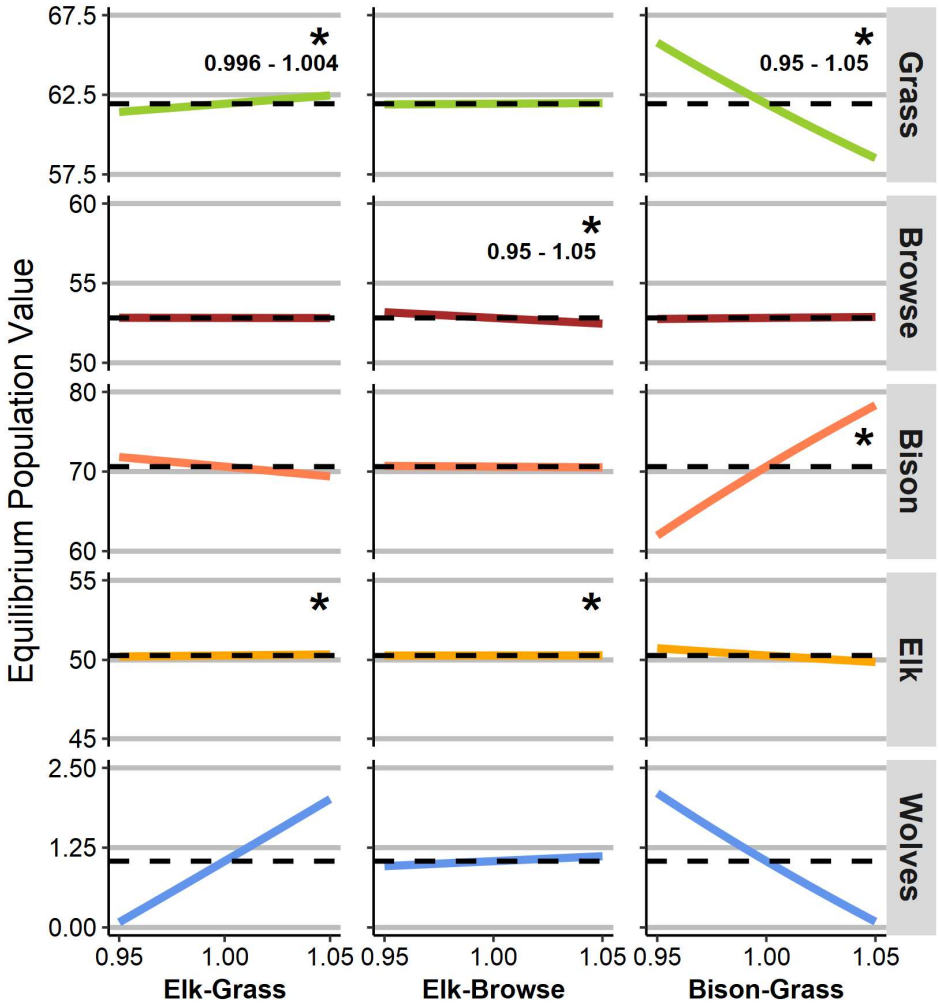


Figure 4: Equilibrium population values under adjustment of the strengths of elk-grass, elk-browse, and bison-grass herbivory interactions (animal survival terms). Interaction terms in growth equations for both animal species and vegetation categories in each interaction were simultaneously adjusted. Asterisks indicate species with model terms adjusted. X-axes illustrate the range of adjustments applied to interaction terms in herbivore equations. Numerical annotations represent the elasticity-weighted range of adjustments made to interaction terms in vegetation equations. Greater adjustment values represent a strengthening of the interaction. Dashed lines indicate species equilibrium populations for the unadjusted model.

5.4 Discussion

Our analysis of a simulated Yellowstone ecosystem predicted that indirect effects are widespread and dominant. Whilst we did not model all the complexities nor species of the system, we developed our model using the available empirical information concerning life histories and direct species interactions of our model populations. The resulting system dynamics capture the processes of the real-world system with reasonable accuracy. Although it is doubtless that the real-world community dynamics are driven by more complex processes occurring among more elements than those of our model, we believe our model was not broadly erroneous in terms of the dynamics it predicts. Our model reveals the dynamics of Yellowstone's key species, the importance of indirect effects occurring among them, and generalisable insights into community dynamics in simulated communities.

Model community dynamics and northern Yellowstone

The decline of elk under increasing predation and the subsequent release of browse reflects elk population decline and the gradual increase in the availability of woody plants reported in Yellowstone after wolf reintroduction (Ripple and Beschta, 2012; Peterson *et al.*, 2020). While the link between Yellowstone's wolf restoration and the recovery of aspen remains uncertain (Kimble *et al.*, 2011; Winnie, 2012; Kauffman, Brodie and Jules, 2013), and the strength of predator-driven changes in browse growth may have been substantially overestimated (Brice, Larsen and MacNulty, 2022), our results unambiguously depict an ongoing, but relatively slow, trophic cascade. In our model system, intensified wolf-elk predation drove cascading indirect effects that led to a decreasing abundance of elk relative to bison, and a gradual increase in the availability of browse vegetation.

Early work following the reintroduction of wolves anticipated a strong effect of behavioural change in elk populations (Laundré, Hernández and Altendorf, 2001; Hernández and Laundré, 2005) via the re-establishment of a 'landscape of fear' (Bleicher,

2017). However, it has been argued that wolves predominantly influence elk population dynamics via direct consumptive effects (Eberhardt *et al.*, 2003; Kauffman, Brodie and Jules, 2010; Middleton *et al.*, 2013; see also Boyce, 2018) and that wolves do not significantly influence elk reproduction by inducing chronic stress (Creel, Winnie and Christianson, 2009). Our focus on the impact of resource availability and predation on the survival of the animal species aligned with evidence that the dynamics of Yellowstone's wolf-elk interaction is primarily driven by direct predation. This—combined with the potential for predator-induced changes in the reproductive physiology of prey species in other systems—suggests that partitioning population dynamics into the survival and recruitment of model species can be a useful tool to explore the impacts of multiple components of predator-prey interactions, while also providing greater biological validity and a means to independently parameterise each component of population change.

In our model, the competitive release of bison under intensifying wolf-elk predation mirrors the upward population trend in Yellowstone's bison after wolf reintroduction (see Tallian *et al.*, 2017). Whilst we did not seek to model the full complexity of the relationship between herbivory and vegetation productivity, improving the efficiency of bison herbivory—and the associated increase in the ratio of bison to elk—exerted a profound impact on grass in our model. Indeed, the relative abundance of these species is reportedly a key driver of grazing intensity and primary productivity in Yellowstone (Frank, Wallen and White, 2016), though the long-term vegetation impacts of the growing bison population require further monitoring.

Our model captures patterns in community dynamics that have been described in northern Yellowstone, suggesting that our parameterisation was approximately appropriate for the purposes of the model. The recent shift to a bison dominant ungulate community and reduced elk abundance has been linked to a reduced proportion of elk in wolf diets, increased bison predation and bison scavenging (Metz *et al.*, 2016). Our results indicated that the model wolves were sensitive to the proportion of their preferred prey in

the ungulate populations. It remains to be seen whether—and at what state—Yellowstone's ungulate populations will stabilise. In addition to restored wolf predation, the dynamics of the ungulate community are likely impacted by the annual cull of Yellowstone bison. The cull removes a substantial number of bison annually, potentially influencing the age structure, sex ratio, productivity and size of the bison population (White *et al.*, 2011). Whilst we did not deem the form of our model to be appropriate to assess the impact of bison removal across timesteps, our model did indicate that the changes in the dynamics of primary consumers that share resources and predators—as in Yellowstone—can lead to pronounced changes in community organisation. We believe that similar dynamic models, perhaps using age and sex structured populations, offer a potential route to anticipate the long-term impacts of ungulate management by culling.

The sensitivity of bison to changes in the grass parameters suggests that our simulated bison, as in Yellowstone, were generally regulated by bottom-up processes. This contrasted the stronger top-down regulation of elk. That bison appeared to be competitively released when the elk population experienced stronger predation suggests that wolves have the potential to play a considerable intermediary role in the dynamics of elk-bison competition. It may therefore be useful to evaluate multiple simultaneous paths of regulation occurring within Yellowstone and other communities, in addition to judging the dominance of top-down versus bottom-up processes. Our dynamical model illustrates the potential complexity of regulatory processes in communities and that community simulation models can be a useful tool to explore these processes.

The dynamics of multispecies models

In addition to broadly simulating the community dynamics of northern Yellowstone, our model also offered general insight into the influence of direct species interactions on population dynamics in ecological communities. Our modelling approach revealed that widespread, substantial indirect effects (DMIIs) can surface in a simulated community of directly interacting species. Though there are limited examples (e.g. Heimpel, Neuhauser

and Hoogendoorn, 2003), testing for the emergence of indirect effects from direct interactions remains rare in model communities. Adjusting direct interactions proved an effective method to explore the dynamics of the community. Pairwise interactions very commonly impacted outcomes for non-focal species in our model—a central assumption of trophic cascade theory (Knight *et al.*, 2005). The dynamic nature of this model meant that changes in a species' resource assimilation could readily manifest change across trophic levels and throughout the model community.

When the corresponding impact on the resource was scaled appropriately, manipulating the efficiency by which a species consumed a resource did not necessarily engender substantial change in the population of the focal species. Species with greater efficiency in assimilating a limiting resource are predicted to be better competitors (Tilman, 1980, 1990). When we improved the efficiency of wolf predation of elk for example, we effectively lowered the prey abundance required for wolves to sustain their population, termed R* (Tilman, 1980). In turn, the elk population was more strongly constrained by predation. From this perspective, increases in the efficiency of resource acquisition enabled wolves to persist at lower densities of their preferred prey, whilst their own population remained stable. A related pattern occurred when a greater efficiency of elk herbivory increased the ability of the elk population to withstand predation from a larger wolf population. In the context of the model community therefore, variation in the fitness of a species (here in terms of resource assimilation efficiency) did not necessarily manifest change in that species. Our results highlight that measuring the success of a species may require the observation of processes beyond those occurring its own populations. The dynamics of our model community suggest that assessing population processes occurring in multiple key species across communities may be necessary to understand the influence of a species on community dynamics.

Species which do not appear to compete strongly can exhibit strong responses when the other is no longer present (Tuck, 2018). Interestingly, elk and bison were thought to have not competed strongly during the period of wolf absence (Singer & Norland 1994). In our model, the elk and bison populations behaved antagonistically. Our results indicated that the emergent competition operating between the ungulates, including apparent competition, coincided with change in the predator population and vegetation pools. Our results demonstrate that substantial competition between indirectly linked species can arise by parameterising for the interactions between species and their shared resources and predators, and that this competition can notably impact model community dynamics.

Our model excludes several species present in the northern Yellowstone community. Our model does not include populations of less-preferred, rarer wolf prey species such as pronghorn antelope (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), on the assumption that the availability of elk exerts the greatest influence over wolf dynamics of these prey species due to their strong preference for elk. For model simplicity, we also exclude other known predators of elk including bears (*Ursus arctos horribilis* and *Ursus americanus*), mountain lions (*Puma concolor*), and humans; species that also influence the dynamics of the Yellowstone elk population (Vucetich, Smith and Stahler, 2005; Barber-Meyer, Mech and White, 2008; Ruth, Buotte and Hornocker, 2019). Though we only parameterise wolves for the purpose of simplicity, our model may be thought of as capturing the general effects of Yellowstone's multiple predators. The compound predation impact of these species remains an outstanding question (Stahler, Wilmers, *et al.*, 2020). Whilst it would be possible to build community models using a similar approach for a greater number of species or anthropogenic factors, parameterisation may be limited by the availability of the required empirical data. Purposefully limiting community models to key species, however, is advantageous by limiting unnecessary or potentially confounding complexity.

Our results demonstrate that nuanced indirect interaction dynamics can arise in model communities composed from relatively simple direct interactions only, and that these indirect effects can substantially influence community dynamics. Additionally, our model system broadly characterised the purported trophic cascade of Yellowstone National Park, indicating that relatively simple model communities can produce a substantial degree of complexity. Modelling a real-world community by basing the growth of each population on species specific life histories, and by informing the strengths of direct species interactions with empirical consumption rates, produced a simulated community with similar dynamics to those observed in the wild. Our results suggest that the browse experiences release and exhibits recovery under restored wolf predation, albeit slowly. Since the effects of variable interaction strengths readily transferred across trophic levels in dynamical systems, we advise assessing population responses occurring throughout simulated food webs.

Chapter VI

Discussion

Chapter VI: Discussion

In this thesis, I investigated the relationships between individual, social, and population level processes, and patterns of movement, demography, and community structure through time. My results illustrate the importance of individual and group attributes to wolf movement and demography and predict the role of wolves in shaping the dynamics of their community.

Social living, demography and movement in wolves

In Chapter 2, I performed an analysis of individual movement rates across life stages and time of year. Despite identifying declining survival with age (Chapter 3), our analysis did not detect a signal of senescence via measures of movement (Chapter 2). Whilst we were unable to attribute social status to wolves in our sample, older wolves are more likely to hold dominant breeding positions in the pack, and so may move more than subordinates as part of a greater investment into pup provisioning. The utility of movement as a measure of functional senescence may therefore be clouded by social status and group effects in social predator species. Whilst my results did reveal interesting patterns of movement across ages and within years, it is possible that the unique social ecology of wolves limits the detection of senescence in movement. I suggest that a similar analysis for movement data of wide-ranging solitary species may be instructive as to the detection of functional senescence in free living animals. Alternatively, an analysis of movement rates in prey species may test for senescence in movement preceding death via predator.

My results consistently underscore the significance of social living to the ecology of wolves (Mech and Botani, 2003; MacNulty, Stahler, Coulson, *et al.*, 2020). Pack size was important across all measures of demography (Chapter 3), with bigger packs generally enjoying demographic advantages. However, it seems that the fitness consequences of social living at the level of individuals are altogether more complex.

In Chapter 4, I used the results from my analysis of environmental and social drivers of individual and group demography to parameterise an age and group structured simulation model of Yellowstone's northern range wolf population. I supplemented demographic dynamics with a dispersal process weighted by pack size to test for the potential regulatory effect of subordinate dispersal. I found that the relationship between an individual and its social group can be key to the dynamics of group-structured populations. This is perhaps unsurprising since all aspects of wolf ecology must be viewed through the lens of social living, from hunting, territoriality, auditory communication, to their demography (Mech and Botani, 2003; Stahler, Smith, *et al.*, 2020). Our results point to a strong possibility that an inequality in the fitness value of pack size between dominants and subordinates can constrain group (and population) size via subordinate movement. This notion parallels observations that African lion *Panthera leo* social groups fracture into subgroups under conditions of increased competition (Mbizah *et al.*, 2020). Population-level outcomes were strongly influenced by the rate of intergroup movements, and specifically, the rate of survival of dispersing wolves. A key aim for the future of Yellowstone wolf research is to describe how environmental conditions and pack composition influence dispersal (Stahler, Smith, *et al.*, 2020). Overall, our results justify this aim by demonstrating that dispersal can strongly affect the dynamics of group structured populations.

Future work may look to identify traits common to dispersing individuals. Indeed, recent work has linked parasite infection to higher dispersal in wolves via increases in risky behaviour (Meyer *et al.*, 2022). In naked mole rats—another socially reproductive mammal—dispersers represent a physiologically and anatomically distinct morph to non-dispersers, equipping them with traits that improve dispersal success (O'Riain, Jarvis and Faulkes, 1996). Analogously, one might predict that subordinate wolves of larger size or of better body condition are more likely to disperse if these factors mitigate the risks faced by dispersing wolves.

Whilst the movement of individuals to and from populations is central to population dynamics (Morales *et al.*, 2010), it is difficult to quantify how movements to and from social groups relate to individual demography since movement and reproductive data are rarely available in combination (Harrison *et al.*, 2011). My model was limited by an inability to explicitly parameterise for the fitness trade off faced by subordinates between the benefits of remaining in a pack as a non-breeder and risking dispersal. Future work should therefore attempt to understand dispersal in terms of two key components. Firstly, the proximal causes of dispersal—i.e., how do social and environmental conditions relate to subordinate dispersal rates; and secondly, the consequent fitness value of dispersal—i.e., the survival and reproductive fates of dispersing subordinates. A combined understanding of these mechanisms should provide insight into dispersal as an adaptive behaviour and further decompose the effect of dispersal on group structure and population dynamics. Applying these questions to other study species, may allow insight into whether the dynamics described above are generalised across socially reproductive species.

Implications of predation dynamics

Across my analyses, there was a tendency for the best performing models to exclude terms for the abundance of elk—the preferred prey of Yellowstone wolves. Generally, wolf populations are thought to be limited by prey density (Packard and Mech, 1980; Peterson and Page, 1988; Fuller, Mech and Cochrane, 2003), but we do not yet understand how prey availability relates to vital demographic rates in Yellowstone wolves (Smith, Cassidy, *et al.*, 2020). Given that northern Yellowstone's wolf population has consistently comprised of around 40 wolves in 4 to 5 packs for the past decade, it seems that this area cannot support higher wolf densities under normal conditions. This seems consistent with the population being limited by the extent of land containing sufficient prey densities to support wolf packs (Fuller, Mech and Cochrane, 2003). Given that I identified numerous other drivers of demographic rates (Chapter 3)—particularly with respect to social

processes—I suspect that the relationship between prey availability and wolf demography is more complex than could be captured by the form of my models.

There is some evidence for weak spatiotemporal avoidance of wolves by elk (Cusack *et al.*, 2020), and for the selection of areas according to combined risk from wolves and cougars (Kohl *et al.*, 2019). The elk population of northern Yellowstone is also partially migratory—a minority of the elk population leave the park during the summer months (White *et al.*, 2010). It is likely that these sources of variation in the distribution and local abundance of elk also influence predation rates and therefore wolf demography to some degree. In any case, it seems feasible that the spatiotemporal complexity of wolf-elk predation explains why our best performing statistical models did not include terms for the elk population. Indeed, the relationships between the quality of wolf pack territories, prey acquisition and demography are poorly understood (Stahler, Smith, *et al.* 2020). My results were therefore limited by the difficulty of capturing the demographic effects of complex predation dynamics at the relatively broad scale of the analysis.

Ecological perturbation, community organisation and the role of top predators

Human activity is a frequent and widespread source of ecological perturbation, whether via the exploitation of natural populations, the translocation of invasive species, or via global climate change (Corlett, 2015). Perturbation can alter the ecological and evolutionary trajectories of communities (Coulson, 2021a). The reintroduction of wolves may be considered a deliberate ecological perturbation to restore a community and potentially recover the health of the ecosystem. The removal or restoration of a predator is generally followed by a period of transience (Hastings, 2004), whereby the abundance and organisation of species within a community undergo a period of change, leading to a new stable or quasi-stable state of equilibrium (Coulson, 2021a). These effects may constitute a trophic cascade, where the loss or restoration of a species has effects that radiate throughout the food-web (Pace *et al.*, 1999). However, disentangling the

complexity of direct and indirect effects across food webs, in addition to feedbacks with the physical environment, means that identifying cascading effects is a considerable challenge.

In natural experiments, a lack of duplicates and controls limit the attribution of cause for observed events. A practical and useful way to predict the origin of empirically observed outcomes—and even project into the future of a system—is to produce structured demographic models that characterise the system of interest (Coulson, 2021a). In Chapter 5, I constructed a demographic model of wolves, their primary ungulate prey species, and two categories of vegetation resource. My simulation model results suggest that predation can induce cascading indirect affects across the food web, contributing to community-wide reorganisation. My results also illustrate that substantial complexity can arise from relatively straightforward direct interactions between only a few species. My approach simulated trophic interactions weighted by empirical predation and herbivory rates and decomposed species-specific demography into survival and reproduction according to their respective life histories. Whilst this novel approach to modelling communities by direct effects was limited to direct trophic interactions only, the retrieved dynamics appeared to approximate the study system well.

In Chapter 5, a central finding concerned the gradual recovery of browse under increasing wolf-elk predation. The purported trophic cascade in Yellowstone is typically attributed to this restored interaction (Beschta and Ripple, 2019; Peterson *et al.*, 2020). Whilst our results present a mechanistic explanation for the gradual recovery of slow-growing vegetation via restored predation, the recovery of browse is incomplete and spatially inconsistent (Marshall, Thompson Hobbs and Cooper, 2013; Peterson *et al.*, 2020). Overall, our results are consistent with—and provide a predictive framework for—arguments that the recovery of browse via numerical rather than behavioural changes in elk (Kauffman, Brodie and Jules, 2010; Painter *et al.*, 2015; Boyce, 2018).

Besides these cascading effects, of additional interest was that the fitness of a species can be described by its ability to persist at lower prey or resource densities. This effect emerged when the strength of wolf-elk predation was increased, leading to a decline in elk but no substantial change in wolf abundance. In essence, this adjustment increased wolf fitness by improving their ability to kill elk. We therefore suggest that when examining the effect of a focal species on the dynamics of a model community, ecologists should consider change in focal and non-focal species simultaneously.

I deliberately limited the model community to those species thought most important to the purported trophic cascade (i.e., wolves and their preferred ungulate prey species). Though model simplicity is practically advantageous, other processes surely contribute to community dynamics. Wolf predation varies within years according to seasonal variation in prey vulnerability (Metz *et al.*, 2012a). Also, wolf predation dynamics vary over longer time scales. For example, their consumption of bison increased as bison became more abundant (though primarily via scavenging; Metz *et al.*, 2020). Yellowstone has multiple large predators that also kill ungulates (including black and grizzly bear, and cougar) (NPS, 2019). Ungulate predation in Yellowstone is therefore impacted by variation in wolf predation and the net effects of multiple competitive predators (Stahler, Wilmers, *et al.*, 2020). As I note in Chapter 5, one may consider the effects of wolf predation predicted by the simulation model to represent the effects the wider Yellowstone predator guild. However, further work is needed to understand the relative impact of multiple predator species, hunting and climate on the dynamics of the elk population (Stahler, Wilmers, *et al.*, 2020).

Yellowstone is a highly seasonal environment, with harsh snowbound winters and warm summers. In Chapter 2, I showed that wolf movement is also seasonal, which I interpret as arising from seasonal variation in ground conditions and prey availability. These patterns reflect seasonal variation in predation dynamics, since wolf diets vary in terms of the demographic and species composition of prey (Metz *et al.*, 2012a). However,

our analysis was limited by the inability to relate movement to the ground conditions experienced by wolves across movement trajectories, and instead used month as a proxy for seasonal variation in conditions. Climatic conditions in Yellowstone have changed over recent decades, with reduced snowfall, warmer temperatures and shorter winters (Wilmers and Getz, 2005). Future work should consider how climate change will impact predator-prey interactions by differentially impacting the movement of predator and prey species, and how these effects may alter the population dynamics examined in this thesis.

Conclusions

Population dynamics in natural systems are vastly complex. Ecologists must balance this reality with the practicality and elegance of simpler models. The return of wolves to Yellowstone has come to represent a textbook example of a natural experiment. Combining the analysis of empirical data from natural systems with mechanistic models to examine their dynamics is a viable and useful means to understand patterns that we observe in the wild. In this thesis, I used this approach to describe major drivers of demography and population dynamics in a restored community. However, like many of our ecosystems, Yellowstone faces substantial changes to our global climate, and is not fully insulated from human interference. The ongoing challenge for Yellowstone science—and for all conservation ecology—is to predict, from out of all their complexity, how our planet's ecosystems will react to the pressures of the future.

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